Importance of climate, forest fires and human population size in the Holocene boreal forest composition change in northern Europe

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The relative importance of climate, forest fires and human population size on long-term boreal forest composition were statistically investigated at regional and local scales in Fennoscandia. We employ pollen data from lakes, reflecting regional vegetation, and small forest hollows, reflecting local vegetation, from Russia, Finland and Sweden to reconstruct the long-term forest composition. As potential drivers of the Holocene forest dynamics we consider climate, generated from a climate model and oxygen isotope data, past forest fires generated from sedimentary charcoal data and human population size derived from radiocarbon dated archaeological findings. We apply the statistical method of variation partitioning to assess the relative importance of these environmental variables on long-term boreal forest composition. The results show that climate is the main driver of the changes in Holocene boreal forest composition at the regional scale. However, at the local scale the role of climate is relatively small. In general, the importance of forest fires is low both at regional and local scales. The fact that both climate and forest fires explain relatively small proportions of variation in long-term boreal vegetation in small forest hollow records demonstrates the complexity of factors affecting stand-scale forest dynamics. The relative importance of human population size was low in both the prehistorical and the historical time periods. However, this is the first time that this type of data has been used to statistically assess the importance of human population size on boreal vegetation and the spatial representativeness of the data may cause bias to the analysis.

Boreal forests represent one-third of the global forest cover and form a major global carbon sink, containing 32% of the world’s terrestrial biomass carbon stock (Pan et al. 2011). Presently, the boreal ecosystem is under pressure as changing climate, intensive human exploitation, and natural and human-induced disturbances are changing forest dynamics. Northern latitudes have experienced the greatest warming during the last century and are predicted to be vulnerable to the projected accelerating warming throughout the 21st century (Christensen et al. 2013). The effects of the projected climate change on boreal forests have recently been investigated in several model simulations (e.g. Koca et al. 2006; Thuiller et al. 2008; Shuman & Shugart 2009; Hickler et al. 2012), and the potential northward range shift of temperate and boreal species in a warming climate is well recognized. Evergreen boreal trees are likely to be replaced by deciduous temperate trees, changing the composition of forest and causing a northward shift in the southern boundary of the boreal zone (Bonan 2008; Fischell et al. 2014). In addition to simulations of the future, the role of climate can be explored by studying past regional-scale vegetation changes. Range shifts in tree taxa such as holly (Ilex aquifolium) (Iversen 1944), hazel (Corylus) (Giesecke et al. 2011; Seppä et al. 2015) and alder (Alnus) (Giesecke et al. 2011), for example, have been related to past climate changes. Most of these studies have concentrated on species range dynamics and regional vegetation changes. However, the potential drivers of local-scale changes in past vegetation are less understood. Recent studies have highlighted that the effects of climate on vegetation composition on subregional and local scales are mediated by local processes, such as forest fires, wind throw, topography, soil characteristics, interspecific competition and successional state (Chapin et al. 2004; Kröel-Dulay et al. 2015). Therefore it is crucial to improve understanding of the significance of the spatial scale when considering possible future changes in boreal vegetation dynamics triggered by projected climate change.

Anthropogenic influence has been another important factor in shaping the Holocene vegetation in Europe. Archaeological and palynological evidence shows that
early hunter-gatherer societies had (local) impacts on the surrounding environment through burning, over-hunting or favouring particular plants for food (Birks et al. 2014; Warren et al. 2014; Franklin et al. 2015). During the Holocene, remote northern and eastern areas in Fennoscandia have been less populated and therefore under lower human impact than southern Fennoscandia (Bergman et al. 2004). However, the palynological and archaeological evidence from northern Fennoscandia indicates that the effect of hunter-gatherers on vegetation is locally detectable even here (Bergman et al. 2004; Hörnberg et al. 2005; Kuoppamaa et al. 2009). Fire is one of the most important factors in natural boreal ecosystems, promoting regeneration and maintaining the mosaic age structure and patchy composition typical of boreal forest. The human activity during the Holocene has affected the natural fire regime in much of the boreal forest area (Wallenius et al. 2011). Slash-and-burn cultivation practices with shorter fire return intervals and agricultural deforestation caused change towards monocultural forest structure (Huttunen 1980; Taavitsainen 1987; Angelstam 1998; Pitkänen & Huttunen 1999; Granström & Niklasson 2008). After the cessation of slash-and-burn cultivation the main form of human influence in boreal forests has been forest logging and related forms of forest management, which led to efficient fire suppression, especially in Finland and Sweden, preventing natural disturbance regimes in boreal forests (Wallenius et al. 2011; Halme et al. 2013).

Studies concerning the association between anthropogenic activity and changes in long-term vegetation have concentrated mainly on studying how the pollen records reflect the possible cultivation practices or other indications of human activity. The question as to whether there is a connection between the changes in Holocene human population size and boreal vegetation has not been statistically investigated, mostly due to the lack of quantitative data on the changes in prehistoric human population size. However, during recent years a new approach of using the temporal frequency distribution of archaeological radiocarbon dates to quantify changes in human population size during the Holocene has been adopted (Gamble et al. 2005; Shennan & Edinborough 2007; Shennan et al. 2013). In Finland Oinonen et al. (2010) and Tallavaara et al. (2010) utilized this approach and applied the summed probability distribution of radiocarbon-dated archaeological findings as a proxy for human population size during the Holocene. This new proxy provides a method for using human population size as an independent explanatory variable, together with natural drivers such as climate and forest fires, when investigating the potential drivers of long-term boreal forest vegetation dynamics.

A previous study from Russian Karelia (Kuosmanen et al. 2015) showed the potential of using pollen and charcoal records from small forest hollow and lake sites to investigate the relative importance of climate for regional and local Holocene vegetation patterns. Here, we further investigate this with a synthesis of pollen and charcoal data from lakes, reflecting regional vegetation, and from small forest hollows, reflecting local vegetation, in a west–east transect from Sweden across Finland to western Russian boreal forest. We assess the relative importance of Holocene climate, forest fires and human population size (based on a human population size proxy from Finland) as explanatory factors affecting the long-term boreal forest composition. More specifically, our objectives are: (i) to assess the amount of variation in long-term boreal forest composition explained by climate and further test the hypothesis that climate would be expected to explain more of the variation in long-term boreal forest composition at regional scale (lake records) than at local scale (small hollow records); (ii) to test if the relative importance of forest fires is higher in the variation in long-term boreal forest composition at local scale than at regional scale, and (iii) to explore and discuss whether it is possible to use the available human population size data as an explanatory factor, given that these data are highly approximate and obtained from regional archaeological data and do not thus necessarily correspond with the site locations where the pollen records are collected. In this light we investigate the relative importance of human population size on the variation in long-term boreal forest composition during prehistoric (9000–1000 cal. a BP) and historical (1000–0 cal. a BP) time periods in Finland.

Material and methods

Study area

The study area is located in Fennoscandia between 59 and 63°N, spanning a west–east transect from Sweden (14°37'E) to Finland and Russia (37°46'E) in the southern part of the boreal forest zone (Fig. 1). The vegetation is characterized by mixed boreal coniferous and deciduous tree species, such as Norway spruce (Picea abies), Scots pine (Pinus sylvestris), silver birch (Betula pendula), downy birch (Betula pubescens), aspen (Populus tremula), grey alder (Alnus incana) and black alder (Alnus glutinosa). At easternmost sites, Siberian larch (Larix sibirica) is present as a mixed species in spruce and pine dominated forests. The study area is located in the boreal climate zone and the climate conditions gradually shift towards higher continentality in the east.

Site selection

Pollen and charcoal data from 17 sites (eight small hollows and nine lakes) were selected. Of the selected sites
14 are analysed here by the authors, data for one site (Arapisto) were received from the original researcher and data for two of the sites (Holtjärnen and Lilla Gloppsjön) were obtained from the European Pollen Database (EPD 2015). The small hollow sites are located in forested areas with no evident human impact in the vicinity of the sites. The small hollows are <0.1 ha in size and the pollen and charcoal data from these sites therefore predominantly reflect local vegetation and local fires (Jacobson & Bradshaw 1981; Sugita 1994). The size of the lakes varies from 1 to 90 ha with an average of 30 ha. Pollen and charcoal data from the larger lakes reflect regional vegetation, whereas the smaller lakes (Holtjärnen and Arapisto) reflect more local vegetation (Sugita 1994, 2006). In general, the sediment cores from study sites cover the last 9000 years (9000 cal. a), except for the Fiby Forest Hollow where the record extends to 4200 cal. a BP, Rentukka Hollow to 4000 cal. a BP, Vesijako Hollow to 5000 cal. a BP and Mosquito Hollow to 6800 cal. a BP. Detailed site information is provided in Table S1.

Pollen data

The Holocene forest composition is reconstructed from sedimentary fossil pollen data from the 17 study sites. All pollen samples were prepared using standard procedures. The most common pollen and spore taxa (Pinus, Alnus, Betula, Populus, Corylus avellana, Ulmus, Quercus, Tilia, Fraxinus, Juniperus, Salix, Rhamnus frangula, Calluna, Ericaceae undiff., Cyperaceae undiff., Poaceae, Ranunculaceae undiff., Equisetum, Pteridium aquilinum, Lycopodium annotinum, Pteridium aquilinum, ...).
Polypodiaceae), which account for over 95% of all the taxa in all records used in the statistical analyses. For the statistical analyses the data were averaged over 200-year intervals. If more than one pollen sample was included in one bin, an average percentage value was calculated for each pollen type. Pollen records from each study site are presented in pollen diagrams with selected taxa in Figs S1–S17.

Climate parameters

Climate data include three parameters: mean summer (summ_T) and winter (wint_T) temperatures and oxygen isotope (δ18O_SAAR) data reflecting hydroclimatic conditions. Temperature data were derived from the LOVECLIM-climate model providing regional climate data at monthly resolution (Renssen et al. 2009; Goosse et al. 2010). The spatial resolution of one grid cell of the model is 5.6 × 5.6° and a total of seven grid cells were used to provide the regional temperature data for the selected sites. Mean summer (June–August) and winter (December–February) temperatures were calculated for each grid cell (Fig. 2A). The values are expressed as differences from the pre-industrial (250–550 cal. a BP) mean. The oxygen isotope (δ18O) record from Lake Saarikko in southern Finland (Heikkilä et al. 2010) was included in the climate variable to provide a palaeoclimatic parameter that is independent of the modelled output. The values reflect the oxygen isotope composition of past lake water (δ18O) and are based on lake sediment cellulose. The records reflects changes in summertime effective humidity (Heikkilä et al. 2010). All climate parameters were averaged over 200-year intervals for the statistical analyses.

Charcoal data

Charcoal data reflecting past forest fires were available from seven small hollows and four lakes (Fig. 2B). In all records the charcoal concentrations (particles cm–3) were used for the analysis. Microscopic charcoal data were available from three small hollows (Larix Hollow, Olga Hollow and Mosquito Hollow) from Russia and from four lake records (Nautajärvi, Huhtasjärvi, Orijärvi and Kirkkolampi) in Finland. Macroscopic charcoal data were available from three small hollows (Sudenpesa Hollow, Vesijako Hollow and Rentukka Hollow) in Finland, one small hollow (Fiby Forest Hollow) in Sweden and one small hollow (Kukka Hollow) in Russia. The charcoal data were not analysed for the whole core length in lakes Nautajärvi and Kirkkolampi. In Nautajärvi, analysed charcoal data extended from 3200 cal. a BP to the present and in Kirkkolampi from 4200 cal. a BP to the present. All charcoal data were averaged over 200-year intervals for the statistical analyses. If more than one charcoal sample was included in one bin, an average concentration value was calculated. Site-specific descriptions of the charcoal data are presented in Table S1.

Human population size

Data for human population size were available only for Finland and therefore the relative importance of human population size on long-term boreal forest composition was analysed only for the lake sites located in Finland. The variation explained by human population size was not analysed with small hollow pollen data, as the local forest composition reflected by the small hollow data is not compatible with the regional human population size data. In the analyses, two separate data sets were used for the human population size. For prehistorical time period (9000–1000 cal. a BP) the human population size was derived from the archaeological data set of Tallavaara et al. (2010), within which the summed probability distribution of archaeological radiocarbon dates is used as a proxy for past population size. This data set does not provide absolute human population values, but is assumed to reflect relative trends in the Holocene human population (Tallavaara et al. 2010). The data set is divided into three sub-regions (southern, central and northern Finland) and for the analyses we used data from the southern and central sub-regions (Fig. 2C). Instead of the summed probability distribution used in Tallavaara et al. (2010), the human population size trend is reconstructed from the frequencies of calibrated median ages of radiocarbon-dated archaeological findings in 200-year bins. As the archaeological proxy record for human population size extends only for the time period before 1000 cal. a BP, we used the absolute size of the population in Finland to assess the effect of population size on long-term boreal forest composition during the historical time period in Finland (1000–0 cal. a BP). The absolute population data were derived in 100-year intervals for the whole of Finland from the literature (Huurre 1998; Virrankoski 2001; Meinder & Autio 2006; Tilastokeskus 2015; Fig. 2D).
**Statistical analyses**

To investigate the relative importance of climate, forest fires and human population size on variation in the Holocene boreal forest composition we used variation partitioning, which is a method that can be used to statistically analyse the individual effect of a single explanatory variable, joint effect of two or more variables, and the undeterminable variation in the total variation of a given response variable (Borcard et al. 1992; Reitalu et al. 2013). In the analyses, the long-term boreal forest composition, as reflected in the pollen data, was used as the response matrix and climate (summ_T, wint_T and δ^{18}O_SAAR), forest fires (charcoal) and human population size were applied as explanatory variables. Site was also included as an explanatory variable to detect the variation explained by site-specific characteristics. To assess the association between long-term boreal forest composition and the environmental variables, redundancy analysis (RDA; Legendre & Legendre 1998) was employed. For all statistical analyses the pollen data were Hellinger-transformed in order to analyse community data using an ordination method based on Euclidean distance (Legendre & Gallagher 2001). Charcoal data were log-transformed for analyses as the data were log-normally distributed.

To assess the relative importance of climate, variation partitioning was at first performed individually for each lake and small hollow. The long-term boreal forest composition was used as the response matrix and climate parameters (summ_T, wint_T, δ^{18}O_SAAR) were used as explanatory variables. To explore the synthesis of the regional (lakes) and local (small hollows) effects of climate on the long-term boreal forest composition the analysis was performed for all data from lake sites (nine lakes) pooled together and for all data from small hollow sites pooled together (eight small hollows). In the analyses, the long-term boreal forest composition was used as the response matrix and climate parameters (summ_T, wint_T, δ^{18}O_SAAR) and site variable as explanatory variables.

To assess the relative importance of forest fires, variation partitioning was performed individually for the sites with charcoal records (four lakes and seven small hollows). In the analyses long-term boreal forest composition, reflected by pollen data, was used as a response matrix, and climate (summ_T, wint_T, δ^{18}O_SAAR) and charcoal data as explanatory variables. To explore the synthesis of the regional (lakes) and local (small hollows) effects of forest fires on variation in long-term boreal forest composition, the analysis was performed for lake sites with the charcoal records (four lakes) pooled together and for small hollow sites with charcoal (eight small hollows) records pooled together. In the analyses, the long-term boreal forest composition was used as a response matrix and forest fires and site variable as explanatory variables.

RDA was carried out for all lake and small hollow sites with charcoal records. Long-term boreal forest composition derived from pollen data was used as the response matrix and the climate parameters (summ_T, wint_T and δ^{18}O_SAAR) and forest fires (charcoal) as constraining variables. The significance of the marginal effects of a single constraining variable was assessed by the ANOVA permutation test with 999 randomizations.

To assess the relative importance of human population size during prehistorical and historical times in Finland, variation partitioning was performed for six lake sites located in Finland. First, the analyses were performed individually for all six lakes for the prehistorical time period of 9000–1000 cal. a BP. The long-term boreal forest composition data were used as a response matrix and human population size (median radiocarbon ages of archaeological samples) and climate parameters (summ_T, wint_T, δ^{18}O_SAAR) as explanatory variables. For the synthesis of all lakes, data from the six lakes were pooled together. The long-term boreal forest composition was used as the response matrix and the human population size (median radiocarbon ages of archaeological samples), climate parameters (summ_T, wint_T, δ^{18}O_SAAR) and site variable were used as explanatory variables.

Second, the analyses were carried out for the historical time period of 1000–0 cal. a BP. Pollen data from four lakes in Finland were included in the analysis. It was not possible to analyse the explained variation during the last 1000 years from lakes Arapisto and Huhdasjärvi as in the latter the sedimentary record does not extend to the present and in Lake Arapisto the period of the last 1000 years did not provide a sufficient number of samples for statistical analyses. For these analyses all data, including climate parameters and pollen data, were averaged over 100-year intervals, as the absolute human population data were in 100-year intervals for the last 1000 years. The variation explained by human population size was analysed individually from four lakes. The long-term boreal forest composition derived from pollen data was used as the response matrix and the human population size (absolute number of population) and climate parameters (summ_T, wint_T, δ^{18}O_SAAR) were used as explanatory variables. For the synthesis of all sites, pollen data from the four lakes were pooled together and used as the response matrix and the human population size (absolute data), climate parameters (summ_T, wint_T, δ^{18}O_SAAR) and site variable were used as explanatory variables.
Results

Variation explained by climate and forest fires

The relative importance of climate on long-term boreal forest composition varied from 58.6% in Lake Pichozero to 68.7% in Lake Laihalampi (Fig. 3), when the analyses were performed for individual lake sites. The relative importance of climate in individual small hollows varied from 0.5% in Rentukka Hollow to 56.4% in Fiby Forest Hollow (Fig. 3). Climate explained 25.4% of the variation when all lakes were included in the analysis. In comparison, climate explained only 9.1% of the variation when all small hollows were included. Variation explained by site variable was notably higher in small hollows (49.6%) than in lakes (27.8%) (Fig. 3). In general, climate explained more variation in long-term boreal forest composition for regional (lakes) than local scale (small hollows) forest composition changes.

The variation partitioning results for lakes and small hollows with charcoal records showed that in pollen data from the lakes, the individual effect of forest fires is highest in Lake Nautajärvi (6.8%) and lowest in Lake Orijärvi (0.1%) (Fig. 4). In small hollows, the individual effect of forest fires is highest in Larix Hollow (6.9%) and lowest in Rentukka Hollow (<0%). When data from all lakes were pooled together, forest fires explained only 0.5% of the variation in long-term boreal forest composition (Fig. 4). The results from small hollows pooled together show that forest fires explain individually 1.1% of the variation and that 10.8% of the variation is explained jointly by forest fires and site.

The RDA results indicate that in both lake and small hollow data, Picea is associated with mean winter temperature (Fig. 5). In pollen data from lakes, temperate deciduous tree taxa (Fraxinus, Corylus, Tilia and Ulmus) are associated with mean summer temperature (Fig. 5A). The RDA results further show that ferns and grasses are related to the forest fires in small hollows (Fig. 5B). For both lake and small hollow pollen data, long-term boreal forest composition is significantly associated ($p < 0.05$) with all climate parameters (summ_T, wint_T, $\delta^{18}$O_SAAR) and with forest fires ($p < 0.05$).
Variation explained by human population size in Finland

During the prehistorical time period (9000–1000 cal. a BP) the relative importance of human population size is rather low, varying from 0.4% in Lake Arapisto to 7.1% in Laihalampi (Fig. 6). When pollen data from all six lakes were pooled together, climate explained the highest percentage (24.3%) of the variation in long-term boreal forest composition, whereas the variation explained by human population size was rather low (1.6%) (Fig. 6). The variation explained jointly by climate and human population size was relatively high (15.1%). Site variable explained 25.3% of the variation.

During the historical time period (1000–0 cal. a BP) the relative importance of human population size on variation in long-term boreal forest composition is generally higher than during the prehistorical time period. Variation explained by human population size in individual lakes is 10.1% in Nautajärvi, 19.5% in Laihalampi, 13.2% in Orijärvi and 1.4% in Kirkkolampi (Fig. 6). When pollen data from four lakes were pooled together, the relative importance of human population size was slightly higher (2.0%) than during the prehistorical time period. The variation explained by climate is only 3.9%, whereas site variable explains almost half of the variation (49.6%).

Discussion

Climate drives the regional-scale vegetation changes

The most obvious result of our study is that climate has clearly driven the regional long-term boreal forest composition change. Our results are in line with the previous results of Kuosmanen et al. (2015) from Russian Karelia based on a similar statistical approach. In general, climate, especially mean summer and winter temperatures, is considered the main limiting factor that defines the northern range boundaries of the distribution of boreal tree species (Woodward et al. 2004). However, the picture is different when we look at boreal forest dynamics at a local scale. In stand-scale dynamics of boreal forest, intrinsic, site-specific factors mostly overrule the importance of regional climate. It
is important to note that none of the explanatory factors considered in our study explained nearly as much variation in the small hollow data as climate did for the lake data. Thus, in local forest composition change the environmental control over long-term vegetation history is more complex and includes factors that were not included in this study. In addition to climate and forest fires, soil characteristics, topography, slope, microclimate, local hydrological conditions and disturbances such wind throws and insect outbreaks can alter the site conditions and hence have an impact on the vegetation. Furthermore, biotic interactions are important ecological drivers of local vegetation dynamics (Mitchell et al. 2006; Post 2013), but are difficult to account for in variation partitioning analysis in palaeoecological studies.

Radiocarbon dating of basal peat in peatland forests in Fennoscandia has shown that there may have been substantial changes in groundwater level and associated increases in paludification (Edvardsson et al. 2012). In our previous study in NW Russia (Kuosma- nen et al. 2015), we tried to account for the changes in growing site wetness by including the degree of peat humification as an explanatory variable in variation partitioning. Growing site wetness explained relatively little of the variation in long-term vegetation, but this may have been due to a too small data set. Based on the evidence that there have been major changes in the groundwater level and peatland initiation trends in Fennoscandia (Almqquist-Jacobson 1994; Hammarlund et al. 2003; Vääränta et al. 2007; Weckström et al. 2010), it seems evident that in further studies, changes in growing site wetness is a factor that needs to be added as an explanatory variable to increase the feasibility of variation partitioning analyses of long-term boreal forest dynamics.

Implications of the results

The results of the Fennoscandian data set are important because they confirm two assumptions often intuitively presented in palaeoecology. First, they demonstrate that species distribution models that are based on regional climate data to reconstruct and predict past and future species distribution data are relevant only for regional-scale vegetation patterns. Dynamic vegetation models may be more reliable for reflecting more local vegetation features, as these models can, to some extent, account for factors that are important for local vegetation, such as species interactions and disturbances (Smith et al. 2001; Miller et al. 2008). However, it is likely that local vegetation features, as reflected in our small hollow data, are influenced by a complex set of factors and hence are too individual to be accurately modelled by any currently available modelling approach.

The other assumption concerns the use of pollen data in palaeoclimate reconstructions. Pollen-based temperature reconstructions from pollen data from lake records have been used to reconstruct past temperatures (e.g. Seppä & Birks 2001; Heikkinen & Seppä 2003). The high explanatory value of climate explaining the variation in pollen data from lakes shows that these sites are suitable for such reconstructions, whereas the low explanatory values of climate explaining the variation in pollen data in small hollow records suggest that pollen records from small hollows or small lakes are not suitable for reconstructing past climate.
as was also observed by Clear et al. (2015). The same is true in the pollen-climate calibration models on which the pollen-based climate reconstructions are based. In such calibration models it is assumed that pollen composition is related to the regional climate (Seppälä et al. 2004). However, this is not the case if the pollen data are obtained from small hollows, soil samples or other sedimentary sites that reflect local and not regional vegetation.

The role of forest fires in long-term vegetation dynamics

The variation explained by forest fires was very low both at regional and local scales. This was unexpected because it has traditionally been thought that fire is one of the key disturbance factors in boreal forests in Fennoscandia. The role of forest fire has been demonstrated in a number of studies (e.g. Zackrisson 1977; Hörmberg et al. 1995; Kuuluvainen & Aakala 2011; Drobyshev et al. 2014) and as forest fires can be very local and abrupt events, they can be expected to be especially important in the local stand-scale vegetation over short intervals. There are a number of reasons that can explain the low proportion of variation explained by forest fires in our data. Josefsson et al. (2010) suggested that the importance of fire as a key factor in the ecology of boreal forest may be overshadowed by other factors such as the disturbance intervals are equal or longer than the life span of the dominating tree species. Rogers et al. (2015) pointed out that fire regimes differ between North American and European boreal forests. They showed that in North American boreal forests, dominated by species that favour frequent fires, such as Black spruce (Picea mariana) and Jack pine (Pinus banksiana), fires have more severe impacts than in Europe, where the tree species that can resist fires, such as Scots pine and Siberian larch, are not harmed by fires and in forest stands dominated by tree species that are intolerant of fires, such as Norway spruce, fire frequency is low. Spruce and pine are the dominant tree taxa in our sites, and in spruce-dominated sites the fire histories show long fire intervals, whereas in pine-dominated sites fires are frequent but do not necessarily cause fatal damage to the trees. Therefore from a long-term perspective the variation explained by fires may remain low.

As the RDA results indicate a significant role of forest fires in long-term stand-scale dynamics (Fig. 5B), it
is possible that the data and technique used here are biased in the analysis of the relative importance of forest fires on variation in long-term boreal forest composition. It may be that the variation partitioning method shows the connection between climate and regional vegetation accurately, whereas in the case of forest fires the variation partitioning method does not account for the fact that the forest composition changes caused by forest fires may not be immediate. Post-fire plant succession can take place over tens or even over hundreds of years after the fire (Kuuluvainen 2002; Angelstam & Kuuluvainen 2004; Shorohova et al. 2009) and the peak in charcoal record does not necessarily correspond with the change in pollen record. Such a time-lag in the vegetation response can possibly be accounted for in the future using more flexible variation partitioning techniques based on, for example, Bayesian approaches (Toivonen et al. 2001; Holmström & Erästå 2002).

Another possible source of bias is the reliability with which forest fires are recorded in lake and small hollow sediments. In lake sediments the charcoal record may show so-called ‘false positive’ estimates of the fire frequency. This may result from the time-lag between the occurrence of the fire and the time period over which charcoal particles keep accumulating in the lake after the fire. Another possible reason is that charcoal deposited in lakes may have been transported by wind and streams from distant fires (Higuera et al. 2005). In small hollows charcoal layers may provide too conservative estimates about the fire frequency and detecting the fire in sedimentary records depends on the fine-scale spatial patterns of the fire (Pitkänen et al. 2003; Higuera et al. 2005). Fires may not advance over the whole surface of the peat depression and when only one point is sampled it is probable that some fires remain undetected (Pitkänen et al. 2003) and hence the sedimentary charcoal record may underestimate the fire frequency. The reliability of the fire frequencies reflected in sedimentary charcoal has also been evaluated against fire scar data. According to Higuera et al. (2005), severe high-intensity fires are quite accurately recorded in small hollows, but more moderate- and low-severity fires may remain undetected. In addition, Whitlock et al. (2004) reported from the northwestern USA and Pitkänen et al. (1999) in their study from eastern Finland, that in general charcoal records in lake sediments reflect local fires, but the individual fires indicated by fire scars may be undetected.

**Role of human population size in boreal vegetation in Finland**

Although human population size individually explains a relatively small amount of the variation in boreal forest composition, during the prehistorical time period in general, the joint effect of climate and human population size is higher. This may be attributable to the notch peak in human population size at 7000–5500 cal. a BP (Oinonen et al. 2010; Tallavaara et al. 2010), corresponding with the Holocene thermal maximum (HTM). Tallavaara & Seppä (2011) related the HTM population peak to higher ecosystem productivity owing to the higher temperatures. Based on our results it is difficult to judge whether the human population size influenced vegetation composition or if the climate-driven changes in forest composition enabled the change in human population size. There is a variety of views about the role of hunter-gatherers in Holocene vegetation changes. Whereas our results suggest a relatively small role in general, Josefsson et al. (2009) argued that the role of human impact on the northern boreal forests is more significant than previously thought. They suggested that some forested areas in northern Sweden considered to be pristine were in fact affected by the Mesolithic communities. The hunter-gatherers might have also influenced the distribution of some economically important tree taxa. For example, during the HTM, hazel was growing north of its present distribution limits in Finland (Seppä et al. 2015) and is known to have provided a source of nutrition to hunter-gatherer communities (Luoto 1991). Holst (2010) suggested the importance of hazel (Corylus) for the subsistence of the Mesolithic communities in northern Germany, which may have affected the natural hazel populations through harvesting. However, in general there is very little evidence of human influence in northern boreal forests during the early and middle Holocene in palynological records. During the historical time period the overall relative importance of human population size on boreal forest composition was unexpectedly low (Fig. 6). However, in individual lakes variation in boreal forest composition explained by the human population size is evident (Fig. 6), which is congruent with the fact that by the beginning of the historical time period at AD 1000 in Finland, the expansion of agricultural land use and the growing human population caused pressure on the boreal forests.

**Assessment of the human population size data**

An advantage of our analysis is the independence of the human population size proxy from the pollen data, which is used to reconstruct the long-term forest composition. It offers a unique opportunity to study the relative importance of the human population size on Holocene vegetation in Finland. However, as this is the first time that the importance of human population size for long-term vegetation changes has been statistically assessed, the results must be considered with caution. Although the method of reconstructing human population size from radiocarbon-dated archaeological findings has been widely used (e.g. Holdaway &
Porch 1995; Shennan & Edinborough 2007; Peros et al. 2010; Tallavaara et al. 2010; Shennan et al. 2013; Tallavaara et al. 2015), it is not unproblematic. Time-dependent loss of archaeological material may lead to under-representativeness of older sites relative to younger sites in temporal frequency distributions (Surovell & Brantingham 2007; Surovell et al. 2009; Williams 2012). Furthermore, calibration of radiocarbon dates creates noise, which may hamper the detection of true short-term demographic variation (Shennan et al. 2013). Most importantly, the prehistoric population estimate is an average value for southern and central Finland, and the historical population estimate is for whole of Finland. Therefore, it is likely that these average values do not reliably reflect the changes in human population trends around the individual lakes from where the pollen data, reflecting the regional forest composition, in this study were derived.

Previously, Reitalu et al. (2013) studied the relative importance of human impact on boreonemoral vegetation in Estonia using sedimentary pollen and charcoal records to reconstruct human influence. Based on their study, during the last 5000 cal. a BP, human impact explained 3.8% of the variation in vegetation and during the last 1000 years 10% of the variation. These results are higher than those obtained in our study. However, the higher human impact is somewhat expected, as permanent agriculture was established in Estonia about 1000 years earlier than in Finland (Poska et al. 2004). Furthermore, there are clear differences between their analysis and the one used in this study and hence the results should not be directly compared. Reitalu et al. (2013) reconstructed the human impact variable from sedimentary fossil pollen and charcoal data, thus incorporating forest fires into the human impact variable. The advantage of using sedimentary fossil records to reconstruct the human impact variable is the more local signal of human activity than in our data. However, reconstructing the human impact variable from the same pollen records from which the forest composition reconstruction is derived creates a danger of circularity.

Conclusions

The relative importance of climate, forest fires and human population size on variation in long-term boreal forest composition was studied from lake and small hollow pollen data in Sweden, Finland and Russia. The most obvious result is that climate is the main driver of long-term boreal forest composition. However, at the local scale both climate and forest fires explain relatively little of the variation in long-term boreal forest composition, indicating that stand-scale boreal forest dynamics are driven by a complex set of processes and that several local factors have an effect on long-term changes in forest composition. These results imply that species distribution models that are based on regional climate data are relevant only when reconstructing regional vegetation patterns. The surprisingly low amount of variation explained by forest fires at the local scale might be due to the bias caused by the nature of the analyses, which do not consider the time-lag between the resultant peak in the sedimentary charcoal record and the change in forest composition. Therefore, in future studies alternative possibilities would be the use of other statistical methods such as a Bayesian approach instead of variation partitioning or the analysis should be conducted using shorter time intervals for more accurate results.

The human population size, derived from radiocarbon-dated archeological findings, was used as one potential driver of Holocene boreal forest composition. This was the first time that this type of data has been statistically applied to explain the long-term changes in boreal forest composition. The analyses were divided into the prehistorical (9000–1000 cal. a BP) and historical (1000 cal. a BP to present) time periods. In general, the variation explained by human population size was relatively low in both time periods. However, our conclusion is not that human influence on vegetation would have been insignificant during the Holocene. Rather, the low explained variation may be due to mismatches between the regional representativeness of the pollen data and the human population records used for explaining the changes in regional vegetation reflected in pollen data from lake records.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at http://www.boreas.dk.

Fig. S1. Pollen diagram for Lake Lilla Glopsjön.
Fig. S2. Pollen diagram for Lake Holtjärnen.
Fig. S3. Pollen diagram for Lake Arapisto.
Fig. S4. Pollen diagram for Lake Nautajärvi.
Fig. S5. Pollen diagram for Lake Laihalampi.
Fig. S6. Pollen diagram for Lake Huhdasjärvi.
Fig. S7. Pollen diagram for Lake Orijärvi.
Fig. S8. Pollen diagram for Lake Kärkkolampi.
Fig. S9. Pollen diagram for Lake Pichozero.
Fig. S10. Pollen diagram for Fiby Forest Hollow.
Fig. S11. Pollen diagram for Sudenpesä Hollow.
Fig. S12. Pollen diagram for Vesijako Hollow.
Fig. S13. Pollen diagram for Rentukka Hollow.
Fig. S14. Pollen diagram for Kukka Hollow.
Fig. S15. Pollen diagram for Olga Hollow.
Fig. S16. Pollen diagram for Larix Hollow.
Fig. S17. Pollen diagram for Mosquito Hollow.

Table S1. Description of all sites included to the analyses.