Long-term drivers of forest composition in a boreonemoral region: the relative importance of climate and human impact

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ABSTRACT

Aim To assess statistically the relative importance of climate and human impact on forest composition in the late Holocene.

Location Estonia, boreonemoral Europe.

Methods Data on forest composition (10 most abundant tree and shrub taxa) for the late Holocene (5100–50 calibrated years before 1950) were derived from 18 pollen records and then transformed into land-cover estimates using the REVEALS vegetation reconstruction model. Human impact was quantified with palaeoecological estimates of openness, frequencies of hemerophilous pollen types (taxa growing in habitats influenced by human activities) and microscopic charcoal particles. Climate data generated with the ECBilt-CLIO-VECODE climate model provided summer and winter temperature data. The modelled data were supported by sedimentary stable oxygen isotope (δ18O) records. Redundancy analysis (RDA), variation partitioning and linear mixed effects (LME) models were applied for statistical analyses.

Results Both climate and human impact were statistically significant predictors of forest compositional change during the late Holocene. While climate exerted a dominant influence on forest composition in the beginning of the study period, human impact was the strongest driver of forest composition change in the middle of the study period, c. 4000–2000 years ago, when permanent agriculture became established and expanded. The late Holocene cooling negatively affected populations of nemoral deciduous taxa (Tilia, Corylus, Ulmus, Quercus, Alnus and Fraxinus), allowing boreal taxa (Betula, Salix, Picea and Pinus) to succeed. Whereas human impact has favoured populations of early-successional taxa that colonize abandoned agricultural fields (Betula, Salix, Alnus) or that can grow on less fertile soils (Pinus), it has limited taxa such as Picea that tend to grow on more mesic and fertile soils.

Main conclusions Combining palaeoecological and palaeoclimatological data from multiple sources facilitates quantitative characterization of factors driving forest composition dynamics on millennial time-scales. Our results suggest that in addition to the climatic influence on forest composition, the relative abundance of individual forest taxa has been significantly influenced by human impact over the last four millennia.

Keywords Anthropogenic impact, community history, Estonia, forest composition, forest ecology, meta-analysis, millennial time-scale, palaeoecology, pollen data, variation partitioning.
INTRODUCTION

Forest composition changes in Europe during the Holocene are attributable to changing climate (Birks, 1986; Huntley, 1990), climate-associated migration processes with possible time-lags (Huntley & Birks, 1983; Svenning & Skov, 2005), species competition and replacement (Bennett & Lamb, 1988; Seppä et al., 2009), and long-term soil development (Birks, 1986). In addition, human activities have influenced European forest composition, especially during the late Holocene (Iversen, 1973; Behre, 1988; Bradshaw & Hannon, 1992; Keller et al., 2002; Magny et al., 2002). The impact of growing human population and agriculture on boreonemoral forests is clearly demonstrated by an increase of crop-fields and other open habitats (Poska et al., 2004; Mitchell, 2005; Overland & Hjelle, 2009; Fyfe et al., 2010). However, the possible long-term influence of human impact on species composition in the remaining tree-covered areas is less clear, and the relative importance of human impact and climatic factors in determining the late Holocene forest composition is largely unknown. One way to assess the relative importance of climatic and anthropogenic factors on long-term community dynamics is to use dynamic vegetation models in combination with pollen records (Keller et al., 2002; Lischke et al., 2002; Bradshaw, 2008; Miller et al., 2008). This modelling approach requires considerable knowledge about the bioclimatic optima and tolerances, dispersal capacities and disturbance responses of the species. Pollen records are then used to assess simulation outcomes. This approach has been effective in evaluating model performance in relation to past and future climate changes; however, the incorporation of human impacts into dynamic vegetation modelling has hitherto been limited (but see Keller et al., 2002).

Here, we provide a novel approach for evaluating the relative importance of climate change and human impact on forest dynamics based on fossil pollen. We utilized recent advances in pollen-based vegetation reconstruction and in palaeoclimatic modelling to test statistically the significance of climatic and anthropogenic factors on long-term vegetation dynamics in Estonia. Estonia is situated in the boreonemoral zone of northern Europe and is well suited for this study because of an exceptionally dense network of pollen sites and a long history of human impact. Furthermore, independent palaeoclimatological proxy records are available from regions adjacent to Estonia. We focused on the late Holocene (5150–50 cal. yr BP, calibrated years before 1950) because it was the period of expanding anthropogenic land use in Estonia (Poska & Saarse, 2002; Poska et al., 2004) and the pollen records show that all the major tree taxa currently growing in Estonia were present in the region over the entire study period (Saarse et al., 1999; Saarse & Veski, 2001).

Sedimentary pollen records provide insight into past vegetation dynamics, but interpreting these data in terms of vegetation composition is not straightforward. Notably, the representation of surrounding vegetation in the pollen samples depends on numerous factors such as intertaxonomic differences in pollen productivity and dispersal, the patchiness of the surrounding vegetation and the size of the sedimentary basin. However, recent theoretical and modelling advances in pollen analysis (Sugita, 2007a,b) have improved reconstructions of regional and local vegetation composition (Hellman et al., 2008; Nielsen & Øgaard, 2010; Sugita et al., 2010). We used the REVEALS (regional estimates of vegetation abundance from large sites) model (Sugita, 2007a) to reconstruct regional vegetation composition at 18 sites in Estonia during the 5100-year study period. The REVEALS-reconstructed tree and shrub composition was compared with simulated and reconstructed records of climate and human impact. The simulated temperatures were based on the palaeoclimatic model ECBilt-CLIO-VECODE (Renssen et al., 2009). As complementary palaeoclimatic data independent of vegetation dynamics, we used stable oxygen isotope records from lacustrine sediments in neighbouring regions (Hammarlund et al., 2003; Heikkilä et al., 2010).

The quantity of past archaeological finds has been used to indicate the intensity of past human impact on the natural environment (Magny et al., 2002; Pärtel et al., 2007; Tallavaara & Seppä, 2011). However, such data are seldom available for larger regions and at sufficiently high temporal resolution. In Estonia, numerous case studies show a correspondence between agricultural establishment phases of human populations as revealed by archaeological finds and increases in landscape openness as inferred from pollen data, particularly from the occurrence of hemerophilous (growing in habitats influenced by human activities) and cultivated plant taxa (e.g. Poska & Saarse, 1999; Poska et al., 2004). The abundance of charcoal particles in lake sediments is also a good indicator of human activities in northern Europe (Behre, 1981; Bradshaw & Hannon, 1992; Koff et al., 1998). Thus, we used landscape openness, percentage cover of hemerophilous and cultivated taxa, and charcoal concentration as indicators of human impact.

This study addresses the following questions through statistical analyses of the combined long-term records of forest composition, climate and human impact.
1. Are climate and human impact statistically significant predictors of late Holocene forest composition change?
2. To what extent was the forest composition change during the late Holocene influenced by climate, human impact, and their combined effect?
3. What are the responses of individual tree and shrub taxa to climate and human impact?

MATERIALS AND METHODS

Study area

Estonia (58–60° N, 22–28° E) is situated in the boreonemoral forest zone (Fig. 1). The vegetation is characterized by a mixture of boreal coniferous and deciduous tree species (Picea abies, Pinus sylvestris, Betula pendula and Betula pubescens), with nemoral deciduous species (e.g. Corylus avellana,
Tilia cordata, Ulmus glabra and Quercus robur) being also widespread but much less frequent. Climatically, Estonia lies in the northern part of the temperate climate zone and at the transition between moderately continental (to the east) and slightly more maritime climate (to the west). At present (mean values of 1971–2000), mean temperature is 16.7 °C in July and −4.7 °C in February, and annual precipitation is 650 mm (EMHI, 2011). Based on sedimentary pollen records, the warmest period in the Holocene was c. 8000–4400 years ago, when mean annual temperature was c. 2–3 °C warmer and effective moisture was lower than today (Seppä & Poska, 2004).

The earliest records of Stone Age human activities date to 11,000–10,000 cal. yr BP. The early anthropogenic impact on vegetation was probably limited and only small areas of forest were cleared in the immediate surroundings of the settlements (Veski et al., 2005). The earliest evidence of cultivation in different parts of Estonia dates back to the Neolithic (6900–3800 cal. yr BP) (Poska et al., 2004). Agriculture became a major source of subsistence during the Bronze Age (3800–2500 cal. yr BP) (Lang, 2007). The study period (5150–50 cal. yr BP) covers most of the period of agricultural development in Estonia except for the last 100 years when rapid political and socio-economic changes caused major land-cover shifts.

Site selection

Pollen records from small lakes and bogs reflect the local vegetation within c. 10–100 km² and those from large sites reflect the regional vegetation within c. 10,000–100,000 km² (Sugita, 1993). We focused on regional-scale changes in forest composition and selected pollen records from sites 250–2800 m in radius (Fig. 1, and Appendix S1 in Supporting Information). In two regions where there were no data available from large sites – Viitna (site no. 18) and southern Estonia (site no. 17) (Fig. 1) – data from small sites were pooled by summing up the pollen counts from respective time periods (Sugita, 2007a). In the case of site 5 (Kiilaspere/Velise, Fig. 1), two closely situated pollen records that cover different time periods were combined and treated as one site.

**Chronologies**

Based on the conventional and accelerator mass spectrometry (AMS) radiocarbon dates, the chronologies of the selected sequences were calculated using a standardized methodology based on the weighted averages of the ranges of the calibrated radiocarbon dates using the IntCal09 calibration data set (Reimer et al., 2009) and the OxCal 4.1 program (Bronk Ramsey, 2009). To combine radiocarbon ages and lithological data, sedimentary deposition models (Bronk Ramsey, 2008) were used. The 5100-year study period was divided into seventeen 300-year time windows, which were used as study units. All data were averaged within each of the 300-year time windows.

**REVEALS modelling**

We ‘translated’ pollen count data to abundances (% cover) of the corresponding plant taxa in the surroundings of the study sites using the REVEALS model (Sugita, 2007a). The details of the model are provided in Appendix S2. Similar to earlier studies that have used the REVEALS model (e.g. Hellman et al., 2008; Nielsen & Odgaard, 2010; Sugita et al., 2010), the assumed extent of reconstructed vegetation was approximately 100 km × 100 km for each site. In total, the REVEALS reconstruction included 22 taxa (trees, shrubs and herbs) that were abundant in our pollen records (Appendix S2).

**Forest composition**

Forest composition was characterized by the REVEALS abundance estimates of the 10 most common shrub and tree taxa:
one shrub (*Corylus*), eight trees (*Alnus, Betula, Fraxinus, Pinus, Picea, Quercus, Tilia and Ulmus*), and one taxon including both shrubs and trees (*Salix*). This taxonomic simplification was necessary because pollen identification is mostly at the genus level (Appendix S2). The REVEALS-estimated percentages of the 10 taxa were recalculated to sum to 100% to quantify the taxonomic composition of the forested area instead of the entire landscape.

**Indicators of human impact**

To estimate the openness (OPEN), we used the sum of REVEALS estimates of the pollen taxa that indicate non-forested conditions (*Artemisia, Filippendula, Plantago lanceolata, Plantago major/media, Poaceae, Cyperaceae, Rumex acetosa/acetosella, Juniperus and Cerealia*). Because OPEN was strongly dependent on Poaceae and Cyperaceae that are also present in natural habitats, we used an additional variable (HEMER) to reflect the occurrence of taxa that are more closely related to human impact. HEMER was calculated as the sum of REVEALS estimates of hemerophilous (*Artemisia, Plantago major/media, Plantago lanceolata, Rumex acetosa/acetosella*) and cultivated taxa (Cerealia).

Charcoal particle counts from pollen samples spiked with *Lycopodium* marker grains were available from seven lakes in Estonia (Appendix S1). In each sample, charcoal concentration was calculated as: (added *Lycopodium* × counted charcoal)/(counted *Lycopodium* × sample volume), giving the number of charcoal particles per cm² of sediment. The average charcoal concentration for each of the 300-year time windows gave an estimate of CHARC.

**Climate**

For the temperature changes over the study period, we used the results from a transient simulation experiment with the EC-Bilt-CLIO-VECODE climate model, forced by annually changing values of orbital parameters, atmospheric CO₂ and CH₄ concentrations, ice sheet surface albedo, topography and melt flux. An overview of this simulation (named OGMELTICE) has been published by Renssen et al. (2009). The model reconstructions cover the whole world at 5.6° × 5.6° spatial resolution and monthly temporal resolution. The average summer (May–August) and winter (December–February) temperatures (SUMM_T and WINT_T, respectively) for Estonia (two grid-cells) were used for the 300-year time windows. Temperatures were expressed as the differences from the pre-industrial mean simulated in the climate model (250–550 cal. yr BP).

In addition to the simulated temperatures, we used stable oxygen isotope (δ¹⁸O) records from two sites near Estonia: a lacustrine carbonate record from Lake Igelsjön (δ¹⁸O_IJ Gel) in southern Sweden (Hammarlund et al., 2003; Jessen et al., 2005) and an aquatic cellulose record from Lake Saarikko (δ¹⁸O_SAAR) in southern Finland (Heikkinen et al., 2010). At these two sites, δ¹⁸O reflects mainly centennial-scale changes in effective moisture. In general, high δ¹⁸O values reflect drier and warmer climate, and low δ¹⁸O values reflect colder and moister climate (Hammarlund et al., 2003; Heikkinen et al., 2010).

The present-day climate in Estonia is relatively maritime in the coastal areas and more continental further inland. We assume that this gradient has been consistent over the late Holocene. To account for that gradient, we calculated a coefficient of continentality for each pollen site based on the present-day winter and summer temperatures. The mean temperature of the coldest quarter of the year and the mean temperature of the warmest quarter of the year for the pollen sites were extracted from the WorldClim global climate database (BIOCLIM database at 2.5-arc-minute resolution, http://www.worldclim.com/; Hijmans et al., 2005). The difference between the temperature of the warmest and coldest quarters gave an estimate of continentality (CONT) (Tuhkanen, 1980).

**Statistical analyses**

For all the statistical analyses we used the 300-year time windows as study units. Some pollen records did not cover the entire 5100-year study period (Appendix S1) and altogether the data set used for statistical analyses consisted of 277 study units (n = 277).

To evaluate general trends in the associations among forest composition, human impact and climate, we used redundancy analysis (RDA). We assigned forest composition data as the response matrix and climate and human impact data as constraining variables. The forest composition data were square-root transformed prior to the RDA to ensure a more even distribution of data in the ordination space. Significances of the marginal effects of single constraining variables were evaluated using Monte Carlo permutation tests (999 randomizations) and non-significant (P < 0.05) constraining variables were removed by a backward selection procedure. To illustrate the community change through time at individual sites, we superimposed the time-trajectories of the sites on the RDA plot.

Variation partitioning (Borcard et al., 1992) was used to provide insight into the relative impacts of the three groups of variables – ‘human impact’ (OPEN, HEMER, CHARC), ‘climate’ (WINT_T, SUMM_T, δ¹⁸O_IJ Gel, δ¹⁸O_SAAR, CONT) and SITE. To understand how the relative roles of climate and human impact change over time, we repeated the variation partitioning analysis in subsets of the data defined by a moving period of 1200 years (four 300-year study units). This resulted in 14 analyses of overlapping data sets. The significances of the individual effects of the partitions were estimated with Monte Carlo permutation tests (999 randomizations) in each of the analyses.

To explore the individual responses of different forest taxa to the factors reflecting human impact and climate, we used linear mixed effects (LME) models with each of the 10 taxa (Fig. 2a) as response variables. LME models allow one to
estimate the effects of fixed explanatory variables (OPEN, HEMER, CHARC, SUMM_T, WINT_T, $\delta^{18}$O_SAAR, $\delta^{18}$O_IGEL) and to account for variation due to random effects, such as among-site variability and temporal autocorrelation (Zuur et al., 2009). The abundances of forest taxa were square-root transformed prior to the analysis and the explanatory variables were standardized to zero mean and unit variance. In the random part of the models, we included SITE to account for the fact that samples from one site tended to be similar and temporal autocorrelation structure with autoregressive moving average (corARMA) model where the number of autoregressive parameters and the number of moving average parameters were both set to one. We used a stepwise backward selection procedure with the likelihood ratio test (Zuur et al., 2009) where, at each step, the variable (or quadratic term) giving the highest $P$-value was left out until only significant ($P < 0.05$) terms remained. To evaluate the goodness of fit of the LME model, we calculated squared correlation coefficient ($r^2$) between the response variable and the model-estimated values.

The results of the variation partitioning analysis showed that the variable groups ‘climate’ (SUMM_T, WINT_T, $\delta^{18}$O_SAAR, $\delta^{18}$O_IGEL, CONT) and ‘human impact’ (CHARC, OPEN, HEMER) together with SITE, explained 69.0% of the variation in the forest composition across the whole 5100-year study period (Fig. 4a). The decomposition of the variation showed that the largest fraction of the variability was accounted for by SITE (27.7%), followed by the shared effect of ‘climate’ and ‘human impact’ (21.3%). The individual effect of ‘climate’ on forest composition was 10.2% and the individual effect of ‘human impact’ was 3.8%.

Variation partitioning within the 1200-year time periods indicated a rapid increase in the relative importance of the
human impact from around 0% in the first time period (5150–3950 cal. yr BP) to 14% in the fifth time period (3950–2750 cal. yr BP) (Fig. 4b), after which the importance of human impact slowly decreased. Climate explained 17–20% of the variation in forest composition during the first two time periods and < 10% during the rest of the study (Fig. 4b).

Separate LME models for each taxon produced roughly the same results as the RDA. Nemoral deciduous taxa (*Corylus*, *Tilia*, *Fraxinus*, *Quercus* and *Ulmus*) were positively associated with summer temperature and $\delta^{18}O$ (Table 1). *Alnus*, *Quercus* and *Ulmus* were also positively associated with landscape openness. *Betula*, *Pinus* and *Salix* were strongly posi-
tively associated with human impact, as shown by the positive association with the proportion of hemerophiles, with *Betula* and *Pinus* also negatively associated with summer temperature. The only taxon that was negatively associated with human impact was *Picea*.

**DISCUSSION**

We demonstrated that over the 5100-year study period in the late Holocene, climate explained about four times more variation in forest composition in boreonemoral Estonia than human impact. Many earlier palaeoecological studies have qualitatively shown that the importance of human impact on overall vegetation composition in Europe has increased over the last few millennia with the expansion of agriculture and forest management (e.g. Behre, 1988; Lindbladh *et al.*, 2000; Poska *et al.*, 2004; Feurdean *et al.*, 2010). In accordance with dynamic modelling studies (Easterling *et al.*, 2001; Keller *et al.*, 2002), our analysis showed that human activities have not only caused increased landscape openness, but have also affected the species composition in the remaining forests. The results of the variation partitioning analysis within shorter time periods revealed that human impact became a dominating driver of forest compositional change at 3950–1850 cal. yr BP, which is the period of establishment and expansion of permanent agriculture in Estonia (Poska *et al.*, 2004). Our results thus suggest that the first opening of the landscape had effects on forest composition exceeding the effects of increasing non-forested agricultural land area over the last 2000 years of the study period.

In addition to the statistically significant individual effects of climate and human impact, there is a large shared effect of these two groups of variables on forest composition. The shared effect can be attributed to climate influencing agricultural and other human activities. In northern Europe, warmer periods are believed to promote the expansion of agriculture (Berglund, 2003). In our data set, however, all three indicators of human impact increase when temperature decreases (Fig. 2b), indicating that agricultural expansion occurred irrespective of climatic trends (cf. Sillasoo *et al.*, 2009). The shared effect in our analysis suggests that, coincidentally, climate change and human impact have simultaneously affected forest composition: the same tree taxa that benefited from human disturbances (*Betula, Pinus* and *Salix*) were able to better withstand the late Holocene cooling than the nemoral deciduous taxa (Seppä *et al.*, 2009). Similar parallel ecological trajectories between human influence and climate have been observed in the Mediterranean region (Jalut *et al.*, 2009).

The RDA results (Fig. 3, Appendix S3) showed that the forest composition was relatively homogeneous at the beginning of the study period, being mainly characterized by nemoral deciduous taxa, such as *Tilia, Ulmus, Corylus, Fraxinus* and *Quercus*. Around 4000 cal. yr BP, however, geographical differences in the vegetation started to evolve. Coastal sites in northern and western Estonia became dominated by *Pinus, Betula* and *Salix*, whereas sites in southern and eastern Estonia became first characterized by *Picea* and thereafter by *Pinus, Betula* and *Salix* at about half of the sites (Fig. 3b, Appendix S3). One possible explanation for this geographical pattern may be related to the differences in soil properties. The coastal areas of Estonia have calcareous bedrock and the soils are shallow and less suitable for the growth of *Picea* than the deeper soils on top of sandstone and clay in southern Estonia (Laasimer, 1965). *Picea* is also the latest of the
major tree species to immigrate to Estonia and began to spread from the most continental part in the south-east around 8000 cal. yr BP (Saarse et al., 1999). It is possible that *Picea* never really became dominant in the coastal areas because the relatively maritime climate favoured the nemoral deciduous species and postponed the dominance of *Picea* until the fertile areas suitable for the growth of *Picea* had already become arable fields. In southern and eastern Estonia, on the other hand, *Picea* had already become dominant before the expansion of arable fields occurred. The sites where *Picea* dominated throughout the end of the study period (Saviku, Konsu, Ernistu and Parika; Appendix S3) are the sites with the lowest human impact in the surroundings until the present day. It is likely that without human impact, *Picea* would be more dominant in Estonia and elsewhere in the boreonemoral zone.

The taxon-wise analyses of the 10 major tree and shrub taxa showed that the nemoral deciduous taxa (*Tilia*, *Corylus*, *Fraxinus*, *Quercus* and *Ulmus*) were positively associated with warmer (and drier) climate, as indicated by the significant positive associations with SUMM_T and $\delta^{18}$O_SAAR. The decline of nemoral deciduous taxa during the late Holocene has often been associated with increasing human impact in central Europe (e.g. Behre, 1988; Brashaw & Hannon, 1992; Lindbladh et al., 2000; Cowling et al., 2001), but in Estonia these taxa occur close to their climatic distribution limits (Hultén & Fries, 1986), and the influence of cooling is likely to overshadow the influence of human impact. Seppä et al. (2009) suggested that the interspecific competition associated with the mid-Holocene expansion of *Picea* played a major role in forest ecosystem change in Fennoscandia. *Picea* is a shade-tolerant and competitively superior taxon, and its rapid population rises may have suppressed nemoral deciduous taxa, especially *Tilia* and *Corylus*. We did not explicitly test the associations between *Picea* and deciduous taxa in our data but it is notable that the initial decline of *Tilia* and *Corylus* coincided with an increase of *Picea* around 4500 cal. yr BP (Fig. 2).

In addition to the strong associations with climate variables, three nemoral deciduous taxa (*Quercus*, *Ulmus* and *Alnus*) were positively associated with landscape openness (Table 1). The positive association of *Quercus* with openness may be the result of its demand of light (Diekmann, 1996). *Quercus* was also preferred by human management in the wooded meadows and wood pastures, which were half-open seminatural habitat types common in Estonia (covering up to 19% of the land area) and elsewhere in northern Europe for thousands of years (Iversen, 1973; Kukk & Kull, 1997; Fyfe et al., 2010). The declines of *Ulmus* and *Alnus* have previously been associated with increasing human impact in Estonia (Poska et al., 2004; Saarse et al., 2010). Our present analysis, using multiple linear models, however, revealed that when the climate variables were accounted for, both *Ulmus* and *Alnus* were more common in areas with high levels of openness. The species of both taxa (especially *A. glutinosa*, *A. incana* and *U. laevis*) are known to be associated with forest edges, river banks and lake shores in the present-day landscape (Kukk, 2004), which may explain their relative commonness in more open areas. *A. glutinosa* and *A. incana* are both early-successional species that are common invaders of abandoned arable fields and pastures.

Contrary to the findings for the nemoral deciduous taxa (*Ulmus*, *Tilia*, *Corylus*, *Quercus* and *Fraxinus*), the boreal taxa (*Picea*, *Pinus* and *Betula*) were significantly negatively associated with SUMM_T and $\delta^{18}$O_SAAR, showing that the cooler and wetter climate has favoured these taxa. Human impact was also significantly associated with all boreal taxa, positively with *Pinus*, *Salix* and *Betula*, and negatively with *Picea*. Agriculture has focused primarily on fertile and mesic soils (Poska et al., 2004), causing the decline of *Picea*, and nutrient-poor and wet soils have remained forested, explaining the increasing relative abundances of *Pinus*, *Betula* and *Salix*. *Betula*, *Salix* and *Picea* are also usual invaders of abandoned arable fields, further increasing the relative importance of these taxa in the agricultural landscape.

**CONCLUSIONS**

Although the effects of climate and human impact cannot be fully decoupled, our results show that both climate and human impact are statistically significant predictors of long-term forest compositional change during the late Holocene. While climatic influence on forest composition is dominant in the beginning of the study period, the importance of human impact becomes a dominating driver behind forest compositional change in the middle of the study period (c. 4000–2000 years ago), which is the period of establishment and expansion of permanent agriculture. Late Holocene cooling negatively affected the populations of nemoral deciduous taxa (*Tilia*, *Corylus*, *Ulmus*, *Quercus*, *Alnus* and *Fraxinus*) and favoured the expansion of boreal taxa (*Betula*, *Salix*, *Picea* and *Pinus*). Human impact in Estonia favoured early-successional fast-growing taxa that can colonize abandoned fields (*Betula*, *Salix* and *Alnus*) or grow on less fertile soils (*Pinus*). Increased landscape openness and possibly selective logging have favoured light-demanding taxa such as *Quercus*.

Our study demonstrates that meta-analysis of palaeoecological and palaeoclimatic data has the potential to provide an alternative and comparative approach to dynamic vegetation modelling in characterizing long-term ecological processes. Compiling a large data set of pollen records helps to overcome inter-site variation in pollen data and enables the evaluation of general regional trends in vegetation types and species composition. Combining palaeoecological and palaeoclimatic data with statistical analyses allows us to reveal associations that are unobservable in purely descriptive pollen studies. The increasing availability of high-quality pollen records (Fyfe et al., 2009) makes it possible to expand our synthetic approach to larger data sets and other forest ecosystems to assess the generality of the trends demonstrated in Estonia.
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Forest composition, climate and human impact

BIOSKETCH

Triin Reitalu is a plant ecologist interested in historical processes that influence the present-day vegetation patterns, with a special interest in the role of human impact in the formation of diversity patterns. Currently, she is a post-doctoral researcher at the Institute of Geology, Tallinn University of Technology in the group of Siim Veski, exploring various ecological hypotheses using palaeoecological and palaeoclimatological records.

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