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Chapter 14
Using pollen data and models to asses landscape structure and the role of grazers in pre-agricultural Denmark

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Abstract

Pollen records can provide information on past landscape structure, but the interpretation is not straightforward, as plants differ in their pollen production and -dispersal properties. Especially open areas are generally under-represented in pollen diagrams. However, in recent years new models have been developed, which take these factors into account and allow us to correct for them, for example by simulating pollen sedimentation in hypothetical landscapes.

In this study, simulated landscapes were created based on landscapes without and with different levels of grazing impact. Pollen deposition in these landscapes was simulated using a model of pollen representation, dispersal and deposition, and the resulting pollen spectra were statistically compared to existing pollen records from Denmark from the Atlantic period (ca. 6800-3900 BC).

The analysis showed that many of the pollen diagrams from eastern Denmark were most similar to the scenarios based on a rather closed forest landscape with some wetland areas, whereas for many diagrams in western Denmark, the pollen diagrams are compatible with a landscape which was more open. This openness was possibly due to a larger impact from grazing animals, which had a higher diversity in western than in eastern Denmark, but other factors, especially soil types and the frequency of fire disturbance, may also have played a role, as these also differ between eastern and western Denmark. Certain aspects of the pollen signal, for example the large proportion of Hazel, were not well explained by any scenarios, and require further study.

Introduction

Preserving or recreating natural habitats and landscape types can be considered among the most important goals of good nature management. Other such goals may include promoting the highest possible biodiversity or protecting specific organisms, such as rare or endangered species. These different goals may not always be compatible when it comes to management decisions.

But which landscapes and habitats are actually natural? There hardly exists an area in Europe today which can be considered completely free from human impact. Therefore, much of our knowledge about the present natural landscape is obtained from studies of relict areas with limited human impact. Such areas are often small, and this limits our interpretation possibilities of natural processes at a larger spatial scale. Another approach is to use palaeoecological data to reconstruct what the landscape looked like in the past, and which processes affected and shaped it.

Studies of pollen grains preserved in lake and bog sediments are an important source of data on the past landscape. Pollen records can provide information on past landscape structure and vegetation composition, which can potentially provide information of the role of grazing animals in different periods. However, the interpretation of the pollen data is complicated by differences in pollen production between plant species; by differences in pollen dispersal between plant species and between different types of pollen sites; and by mixing of local and regional scale pollen signals within the record.

Thus, pollen percentages cannot be regarded as a simple measure of vegetation composition. For example, landscape openness is often underestimated, because many tree species produce more pollen than most herb species (Broström et al., 2008) and their pollen is dispersed more effectively. However, in recent years, new models have been developed, which have improved our possibility to quantitatively interpret fossil pollen data. By using models of pollen dispersal and deposition (Prentice, 1985; Sugita, 1993, 1994) combined with estimates of the relative pollen productivity of different species (e.g. Broström et al., 2008) it is now possible to calculate the expected pollen spectra in different simulated landscapes using the programmes MOSAIC and HUMPOL (Bunting and Middleton, 2005). These models can be applied to interpret the composition of pollen spectra from different sites. One method is the so called Multiple Scenario Approach (Bunting and Middleton, 2009) where hypotheses about the structure and composition of past landscapes are transformed into a number of simulated landscapes. Using HUMPOL, pollen loading to different sites in these landscapes is calculated, and these simulated pollen spectra are then compared to observed fossil pollen spectra using analogue matching techniques.

This is the approach taken in the current study, which focuses on the Danish landscape during the Atlantic period, ca. 6800-3900 BC. This is the latest period of the Mesolithic i.e. before agriculture was introduced to Denmark.

Traditionally, the pre-agricultural Danish landscape has been interpreted as mainly closed deciduous forest with rather sparse herb vegetation, where the recruitment of trees occurs in small gaps created by old trees dying or by storm felled trees. This interpretation was described by among others Iversen (1973), and is based partly on pollen evidence, but without the application of pollen dispersal and representation models. It is also supported by the observation that most European landscapes today quickly become tree covered in the absence of human impact. The climax forest hypothesis has until recently been widely accepted by ecologists and nature managers. More recently however, this interpretation of the pre-agricultural landscape has been questioned by several researchers. Especially the book by Franz Vera (2000): ”Grazing ecology and forest history” has received a lot of attention. Here, large wild grazing animals, such as aurochs, wild horse and red deer, are considered to play a leading role in the natural dynamics of the landscape. According to this hypothesis, the natural landscapes of Northwest Europe were a mosaic of forest groves, open park like areas and dense shrubs. In the groves, practically no recruitment of young trees is expected, due to shade and grazing pressure. The grove persists until the trees age and gradually collapse, after which the area becomes open, with single old tress and grassland or heathland type vegetation, depending on soil types. The vegetation is kept open for a certain time by the grazing animals, but gradually shrubs of mainly thorny bushes becomes established. Inside these, young trees can grow up, sheltered from the animals, and when the tree are large enough to shade out the shrubs, a new grove is formed.

Finds of bones show that aurochs, red deer, moose and wild boar were present in Denmark at the beginning of the Atlantic period, but they do not show how abundant the animals were (Aaris-Sørensen, 1998). During the first half of the Atlantic, aurochs and moose became extinct on the eastern Danish island of Zealand, while they still remained in Jutland and on the island Funen. In the later part of the period, wild horse reappeared in these western parts of Denmark, after being extinct in the early Holocene (Aaris-Sørensen, 1998).

Material and methods

Pollen productivity estimates exist for most tree genera and the most important herb types from Southern Sweden (Sugita et al., 1999; Broström et al., 2004), which can be applied in the Danish landscape to simulate pollen loading to lakes and bogs from hypothetical landscapes. This approach has been validated for small lakes in Denmark (Nielsen, 2004).

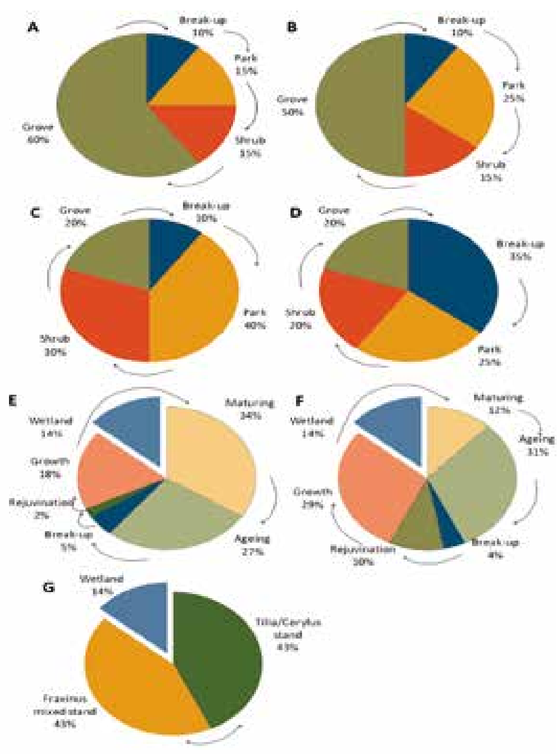
Existing pollen data from the Atlantic period (ca. 6800-3900 BC), the last period before the introduction of Agriculture in Denmark, were collected for comparison with the pollen simulations. Data from 17 sites, including large raised bogs, mediums sized lakes and small forest hollows were collected partly in the form of raw data from the pollen analysts, partly from publications (Nielsen, 2009).

Simulation set up

To investigate the potential role of large grazing animals, a series of simulated landscapes were created with different levels of grazing impact. The vegetation structure and compositions of these were based on the landscapes modeled by Kirby (2004), who presented a possible

Figure 14.1

Schematic illustration of the dynamic between different patch types assumed in each simulation, and the proportions of different patch types



The species composition of the patch sizes is described in Table 13.2.

quantitative interpretation of a landscape following the Vera (2000) hypothesis, based on the expected duration and spatial extent of the different elements of the landscape mosaic. Another set of simulated landscapes were based on present day vegetation structure in two natural forests in Denmark without grazing, i.e. Suserup forest in eastern Denmark (Christensen et al., 2007) and Draved forest in western Denmark (Andersen, 1970). The vegetation patch types and their proportions in the different landscapes are illustrated in Figure 14.1, and the basic simulation setup is described in Table 14.1.

Each of the simulated landscapes consisted of different vegetation patch types, and to each patch type a species composition was assigned. For the landscapes with grazing (landscapes A-D), the species composition was based on the descriptions of the landscape scenarios by Kirby (2004). For the closed forest scenarios (Landscapes E-G), the composition of the modern forests (Christensen et al., 2007; Andersen, 1970) had to be adjusted due to the fact that *Fagus*, which is a dominant species in the Danish forests today, had not yet immigrated in the Atlantic period. Thus the species composition was based on a combination of the modern forest data and the descriptions of the Atlantic forest by Iversen (1973). Several different species compositions were tested (Nielsen, 2009) (Table 14.2), but the one presented here resulted in the best resemblance between modeled and observed pollen assemblages. It follows Iversen (1973) in assuming that *Quercus* occurred on the wetter soils, but did not play an important role in the upland forest.

Pollen deposition at randomly placed sampling sites in these virtual landscapes was simulated using HUMPOL, based on the Prentice (1985) model of pollen dispersal and deposition and on pollen productivity estimates from

Table 14.1

Simulation setup (Nielsen, 2009)

Landscape	Landscape structure	Landscape size	No. of landscapes	No. of sampling points
A: Low grazing pressure	Kirby 2004 scenario 3b	50 × 50 km	2	2 × 9 = 18
B: Medium grazing pressure	Kirby 2004 scenario 1	50 × 50 km	2	2 × 9 = 18
C: High grazing pressure	Kirby 2004 scenario 3a	50 × 50 km	2	2 × 9 = 18
D: "Savannah like"	Kirby 2004 scenario 5	50 × 50 km	2	2 × 9 = 18
E: No grazing 1	Suserup forest 1992	5 × 5 km	5	5 × 4 = 20
F: No grazing 2	Suserup forest 2002 (after storm)	5 × 5 km	5	5 × 4 = 20
G: Wetland forest	Simplified Draved forest	50 × 50 km	2	2 × 9 = 18

Table 14.2

Patch types and species composition used in the simulated landscapes (Nielsen, 2009)

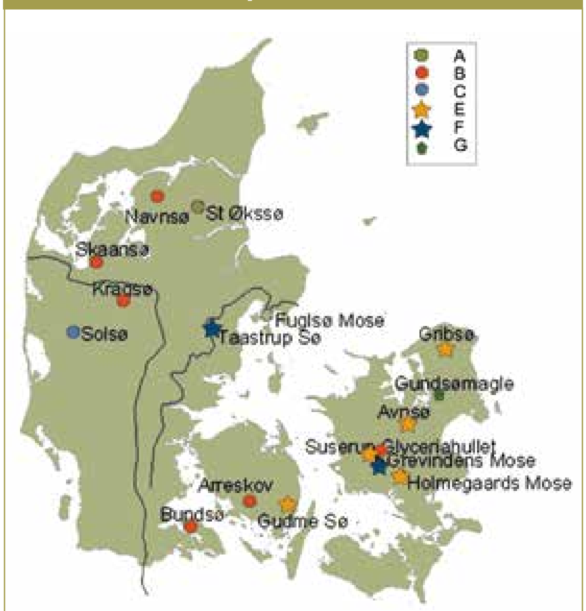
Patch type	Fraxinus	Quercus	Tilia	Ulmus	Alnus	Betula	Corylus	Poaceae	Cyperaceae	Salix	Calluna
Landscapes A-D											
Shrub	4	4	4	4	2	8	70	10	6	13	3
Grove	20	10	20	20	10	6	20	3	2	2.5	2
Break-up	5	13	10	10	2	20	0	15	5	0	5
Park	0	3	2	0	0	4	4	50	20	1	10
Landscapes E-F											
Maturing	15	0	40	35	0	0	10	0	0	0	0
Ageing	10	0	45	40	0	0	5	0	0	0	0
Break-up	15	0	30	25	0	5	10	10	5	0	0
Rejuvination	41	0	11	11	0	10	10	10	5	0	2
Growth	35	0	30	25	0	0	10	0	0	0	0
Wetland	26	12	0	7	35	6	6	10	10	10	2
Landscape G											
Tilia/Corylus stand	0	12.04	22.06	5.79	10.83	7.18	40	10	10	0	1
Fraxinus mixed stand	14.45	15.65	6.79	4.86	11.12	13.79	0	15	15	0	1
Wetland	26	12	0	7	35	6	6	10	10	10	2

south Sweden (Sugita et al., 1999; Broström et al., 2004) and the resulting pollen spectra were compared using Squared Chord Distance (SQD) to the actual collected fossil pollen records.

Results

The analysis showed that many of the pollen diagrams from eastern Denmark were most similar to the scenarios based on closed forest landscape with some wetland areas (scenarios E and F) (see Figure 14.2). This indicates that the pollen assemblages from these sites are most compatible with those expected, according to the pollen dispersal model, in closed forest landscapes with small gaps. A restricted occurrence of more light demanding plants (Poaceae, Cyperaceae and *Calluna* in the analysis) to the gaps and to wetland areas seems to be enough to explain the proportions of these pollen types observed in the eastern pollen diagrams. Also the occurrence of *Quercus* can be explained by occurrence on wetter ground, and does not in itself require larger open areas. Most eastern sites have the majority of the closest analogues in landscape structure E, corresponding to Suserup forest before the big storm in 1999 (Christensen et al., 2007), while Taastrup Sø and Grevindens Mose have most analogues in landscape F, corresponding to the structure after the storm, with higher proportions of rejuvenation and growth (see Figure 14.1), and thus somewhat more Poaceae and Betula in the simulated vegetation. However, the analysis indicated that the difference in the expected pollen assemblages in these two landscapes was rather small.

Map of Denmark showing the results of the analysis — **Figure 14.2**



The symbols indicate which simulated landscape group the majority of the 5 closest analogues for each site belong to. None of the closest analogues were found in landscape D.

Although the best analogues for these eastern sites were to be found in the landscapes based on Suserup forest, there were some differences between the simulated and observed pollen assemblages, resulting in relatively high SQD values. Especially the observed proportions of *Corylus* pollen was higher than could be explained by the simulated landscape composition.

For many diagrams in western Denmark, the analysis indicates that landscape was more similar to landscapes A-D (see Figure 14.2). The landscape here appears to have been more open, as the proportions of Poaceae, Cyperaceae and Calluna pollen are higher than would be expected from a landscape like those at Suserup and Draved forests, and correspond more to those expected from the grazing scenarios. For the sites in Jutland, the SQD values a generally lower than for the sites on the Danish islands, indicating a better fit between modelled and observed pollen proportions, but even here observed *Corylus* pollen proportions are higher than the simulated values, despite the fact that *Corylus* makes up a large proportion of the vegetation in the shrub phase in the grazing scenarios. For Bundsø on the small island Als, and Arreskov Sø on Funen, the SQD values are somewhat higher.

Only for one site, Gundsømagle Sø (Rasmussen et al., 1998), did the pollen assemblages most resemble those from scenario G, based on Draved forest, although some good analogues were also found among the Kirby scenarios. Gundsømagle Sø is surrounded by high proportions of wetland, which may explain the resemblance to Draved forest, which is also characterized by a high groundwater table (Møller and Bradshaw, 2001).

The three small forest hollows among the pollen sites analyzed, Grevindens Mose and Glyceria hollow (Andersen, 1985) and Suserup hollow (Hannon et al., 2000) are located within a few kilometers from each other on central Zealand. Pollen from such sites represents the local vegetation vegetation with ca. 20-50 m around the site. Interestingly, their pollen assemblages are very different, and their closest analogues among the simulated landscapes fall in different landscape groups, landscapes E, F and C respectively. This indicates a large heterogeneity in the landscape at a small spatial scale during the Atlantic period, larger than that captured by the patchiness of each of the single simulation scenarios.

Discussion

At first glance, the results of the simulation and analogue matching study lends some support to the Vera hypothesis, that grazing animals were important in determining the vegetation structure before the introduction of agriculture. Applying the models of pollen dispersal and deposition generally reveals that the landscape was not as densely tree covered as may be assumed from the uncorrected tree pollen percentages. At most of the sites in western Denmark, the pollen assemblages fit better with the

Kirby scenarios, while those in eastern Denmark indicate a more closed forest with smaller gaps. We know that the diversity of grazers in the Atlantic period was higher in western Denmark, while aurochs, wild horse and Moose went extinct on Zealand (Aaris-Sørensen, 1998). Therefore, a more closed vegetation structure here could be expected.

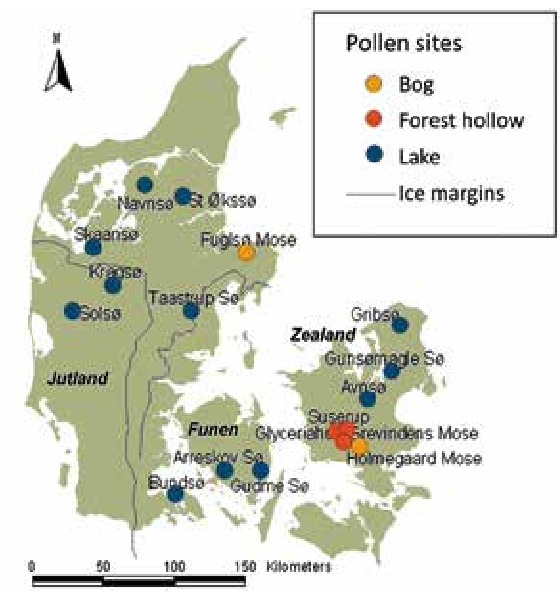
However, while the pollen composition and the degree of openness which is indicated by the pollen data from western Denmark could fit with grazed landscapes as those suggested by Kirby (2004), this analysis does not exclude that other factors, especially soil type, wind and fire, may have been the determining factors for landscape openness. Soil types differ between eastern and western Denmark. The southwestern part of Jutland was not glaciated during the Weichelian at all, and much of eastern Jutland was deglaciated rather early, while the young Baltic ice sheet only reached a short distance west of the present eastern coast of Jutland (Lagerlund and Houmark-Nielsen, 1993) (see Figure 14.3). For this reason, soils in the west are sandier and more nutrient poor than those in the east, which are richer in clay and more calcareous.

The sandy soils in the west may have in themselves have led to a naturally more open landscape structure (Odgaard, 1994), as secondary succession after a disturbance will be slower when the plants have fewer nutrients available (Kalis et al., 2003). Sandy soils are also more well drained, providing drier conditions at the soil surface during the summer, despite the fact that precipitation is somewhat higher in western than in eastern Denmark, and these drier conditions have probably resulted in more frequent natural fires. This is supported by records of relatively high amounts of subfossil charcoal from western Jutland throughout the Holocene, and the occurrence of fires may have been a very important factor in maintaining a more open landscape with higher proportions of light demanding plant species, including dwarf shrubs (especially Calluna) and grasses (Odgaard, 1994). Thus, the differences in soil conditions may be able to explain the east-west gradient in the pollen modeling results, without including the difference in the occurrence of large grazing animal species as a determining factor.

That soil type may be the more important cause for determining landscape openness is supported by the fact that Taastrup Sø, east of the east Jutland ice margin, has a similar pollen spectrum as the sites on Zealand, although the same animal species would have occurred here as in other parts of Jutland, and that the most open landscape is found around Solsø in the far west. However, there are also sites east of this line which have their closest analogues among the grazing type simulations, i.e. Fuglsø Mose and Bundsø (Aaby, 1986), Arreskov Sø (Nielsen, unpublished) and Glyceriahullet (Andersen, 1985).

Large amounts of wetland areas can also contribute to landscape openness. The 14% wetland used in the forest scenarios is based on the situation in Denmark around AD 1800, i.e. before modern drainage of the agricultural land and forests, but it is possible that the proportion was even higher in the Atlantic period. This might explain the larger openness than expected from the forest scenarios, but does not account for the difference between east and west.

Figure 14.3 **Map of Denmark showing the pollen sites included in the comparison, indicating site type**



The maximum ice extent of the Late Weichselian and of the young Baltic east Jutland stage is also shown.

The occurrence pollen types from plant species which are more often associated with grazed than ungrazed landscapes today (Nielsen, 2009) indicate that grazing animals probably did influence the vegetation in some places, at least at a local scale. This may also explain the large heterogeneity between the small eastern Danish forest hollows. But the extent of their impact at a landscape scale cannot be determined based on these finds of indicator species, which only occur in quite low numbers. In order to disentangle the effect of grazers and soil on landscape openness and plant species composition it would be useful to include pollen data from neighboring countries, to study variations in the two factors independently.

However, to determine the causality behind the composition and structure of the landscape, it will be necessary to combine pollen studies with other palaeoecological proxies. Plant macrofossils can often be identified to species, and can therefore provide more information on the occurrence of indicator species than pollen. Remains of beetles can also be identified, and as many species are specific to either open of closed forest conditions, and certain species are tied to animal dung, they are important indicators for the role of grazing (Whitehouse and Smith, 2010). Other insects and mollusks can also be indicators of landscape openness. Of course, a better knowledge of the occurrence and abundance of grazing animal from bone finds would be very valuable, but such studies are restricted to sites where bone can be preserved.

Certain aspects of the pollen signal, especially the large proportion of *Corylus* (Hazel) pollen, were not well explained by any of the scenarios. The abundance of *Corylus* is one of the arguments used in favour of the Vera hypothesis, as this species does not regenerate well in closed canopy conditions (Vera, 2000). However, even in the grazing based scenarios, the expected pollen proportions of *Corylus* are lower than those observed. This shows that we probably do not yet understand the ecology, and possibly the pollen productivity of *Corylus* in the Atlantic landscape very well. On the other hand, the observed occurrence of *Quercus* pollen in the Danish pollen diagrams, another of the key species for the Vera (2000) hypothesis, can be explained by relatively low numbers of *Quercus* trees growing on wetter soils, where there would have been better light conditions even without grazing animals, as the shade trees, particularly *Tilia* do not thrive there (Iversen, 1973).

Conclusions

Comparing the Atlantic pollen assemblages from Danish sites with simulated pollen signals from model landscapes with and without grazing shows that the pollen finds in most of western Denmark is compatible with the grazing landscapes, while those in the east indicate more closed forest. However, the analysis does reveal the cause of the difference in landscape openness, which could be assigned to differences in soil types, related variations in fire frequency, or to differences in the occurrence of large grazers.

While models of pollen dispersal and deposition are a powerful tool to study past landscape composition and openness in quantitative terms, and thus improve the interpretation possibilities of pollen data, it may be necessary to also include other proxies than pollen, such as plant macrofossils and insect remains, as well as more studies on the occurrence of large mammals, to shed more light on the question of the role of grazing animals in the natural landscape.

References

Aaby, B., 1986. *Trees as anthropogenic indicators in regional pollen diagrams from eastern Denmark.* In K. E. Behre (Ed) Anthropogenic Indicators in Pollen Diagrams. A.A.Balkema, Rotterdam.

Aaris-Sørensen, K., 1998. *Danmarks Forhistoriske Dyreverden*. Gyldendal, København.

Andersen, S.T., 1970. *The Relative Pollen Productivity and Pollen Representation of North European Trees, and Correction Factors for Tree Pollen Spectra.* Danmarks Geologiske Undersøgelser, Copenhagen.

Andersen, S.T., 1985. Natur- og kulturlandskaber i Næsbyholm Storskov siden istiden. Fortidsminder. *Antikvariske Studier*, 7: 85-107.

Broström, A., Sugita, S. and Gaillard, M.-J., 2004. Pollen productivity estimates for the reconstruction of past vegetation cover in the cultural landscape of southern Sweden. *Holocene*, 14: 368-381.

Broström, A., Nielsen, A.B., Gaillard, M-J., Hjelle, K., Mazier, F., Binney, H., Bunting, J., Fyfe, R., Meltsov, V., Poska, A., Räsänen, S., Soepboer, W., Stedingk, H. von, Suutari, H. and Sugita, S., 2008. Pollen productivity estimates of key European plant taxa for quantitative reconstruction of past vegetation: a review. *Vegetation History and Archaeobotany*, 17: 416-478.

Bunting, M.J. and Middleton, R., 2005. Modelling pollen dispersal and deposition using HUMPOL software, including simulating windroses and irregular lakes. *Review of Palaeobotany and Palynology*, 134: 185-196.

Bunting, M.J. and Middleton, R., 2009. Equifinality and uncertainty in the interpretation of pollen data: the Multiple Scenario Approach to reconstruction of past vegetation mosaics. *The Holocene*, 19: 799-803.

Christensen, M., Emborg, J. and Nielsen, A.B., 2007. The forest cycle of Suserup Skov – revisited and revised. *Ecological Bulletins*, 52: 33-42.

Hannon, G. E., Bradshaw, R. and Emborg, J., 2000. 6000 years of forest dynamics in Suserup Skov, a seminatural Danish woodland. *Global Ecology and Biogeography*, 9: 101-114.

Iversen, J., 1973. The development of Denmark's nature since the last glacial. Danmarks. *Geologiske Undersøgelse V.række,* 7(C): 1-126.

Kalis, A.J., Merkt, J. and Wunderlich, J., 2003. Environmental changes during the Holocene climatic optimum in central Europe - human impact and natural causes. *Quaternary Science Reviews,* 22: 33-79.

Kirby, K.J., 2004. A model of a natural wooded landscape in Britain as influenced by large herbivore activity. *Forestry*, 77: 405-420.

Lagerlund, E. and Houmark-Nielsen, M., 1993. Timing and pattern of the last deglaciation in the Kattegat region, southwest Scandinavia. *Boreas*, 22: 337-347.

Møller, P.F. and Bradshaw, R.H.W., 2001. Draved skov – et dansk forskningsprojekt gennem mere end 50 år. *Geologi- Nyt fra GEUS*, 4: 1-16.

Nielsen, A.B., 2004. Modelling pollen sedimentation in Danish lakes around AD 1800 - an attempt to validate the POLLSCAPE model. *Journal of Biogeography*, 31: 1693-1709.

Nielsen, A.B., 2009. *Urskovsklandskabets åbenhed og sammensætning og græsningens betydning i Atlantisk tid belyst ved palæobotaniske metoder.* GEUS report 2009/23, Geological survey of Denmark and Greenland, Copenhagen.

Odgaard, B.V., 1994. *The Holocene vegetation history of northern West Jutland, Denmark*. Opera Botanica, 123.

Prentice, I.C., 1985. Pollen Representation, Source Area, and Basin Size: Toward a Unified Theory of Pollen Analysis. *Quaternary Research*, 23: 76-86.

Rasmussen, P., Hansen, H.J. and Nielsen, L.B., 1998.

Kulturlandskabet i et langtidsperspektiv. To sjællandske områder gennem de sidste 6000 år. *Nationalmuseets Arbejdsmark,* 1998: 101-113.

Sugita, S., 1993. A Model of Pollen Source Area for an Entire Lake Surface. *Quaternary Research,* 3(2): 239-244.

Sugita, S., 1994. Pollen representation of vegetation in Quaternary sediments: Theory and method in patchy vegetation. *Journal of Ecology,* 82: 881-897.

Sugita, S., Gaillard, M.-J. and Broström, A., 1999. Landscape openness and pollen records: A simulation approach. *The Holocene,* 9(4): 409-421.

Vera, F.W.M., 2000. *Grazing Ecology and Forest History*. CABI Publishing, Wallingford.

Whitehouse, N.J. and Smith, D., 2010. How fragmented was the British Holocene wildwood? Perspectives on the “Vera” grazing debate from the fossil beetle record. *Quaternary Science Reviews,* 29: 539-553.