Reconstructing Past Environments

A study to the ecological changes in the Middle Pleistocene site Schöningen 13 II

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Content

Abstract

This thesis discusses the environmental changes in flora and fauna from the Middle Pleistocene site Schöningen 13 II, Germany. Most of the environmental components have been examined separately and yielded so far their own interpretations of the record. In this thesis, these data are analysed as an entity to gain insight into the structure of the environmental changes at this site. The theoretical framework of this thesis is relevant to an understanding of the reconstruction of palaeoecosystems in general, by focussing on ecology of contemporary species as well as taphonomy. The data in this thesis consists of the ecological data from Schö 13 II as well as faunal data from Middle Pleistocene archaeological sites and data from present day national parks in Europe. This data is used to get insight in species compositions in various types of environments.

The environment in Schöningen changed gradually in the four levels, Schö 13 II-1 to 13 II-4 from interglacial optimum to stadial phase with an onset to a glacial phase. The floral data gave detailed indications of fluctuations in the environment, whereas the faunal data showed a more gradual change in the environment. The elements in Schö 13 II-1 are indicative for an interglacial phase, 13 II-2 contains elements of both interglacial and (inter)stadial phases and levels 13 II-3 and 13 II-4 are indicative for stadial contexts. Characteristic for the patterns in species diversity is that it is variable throughout the levels. Schö 13 II-1 and 13 II-3 both show a relatively low diversity, whereas the diversity in 13 II-2 and 13 II-4 is higher, but still not exceptionally high if compared to other Middle Pleistocene sites. These differences in diversity can be explained by potential deformations by taphonomical processes. The non-analoguous patterns in large mammal compositions of the site can be explained in terms of species behaviour and potentially taphonomy.

Samenvatting

In deze scriptie zijn de klimatologische veranderingen in de flora en fauna van de Midden Pleistocene site Schöningen 13 II, Duitsland, beschreven. De meeste data is reeds geanaliseerd met elk hun eigen interpretaties over de ecologische veranderingen in het archeologisch bestand van 13 II. In deze scriptie zijn de data op nieuw geanaliseerd om inzicht te krijgen in de ecologische veranderingen in deze site. Het theoretische kader van deze scriptie richt zich op de reconstructie van paleoecosystemen in het algemeen, met een focus op hedendaagse ecologie en tafonomie. Extra data die voor deze scriptie is gebruikt bestaat uit de fauna samenstellingen van Midden Pleistocene archeologische sites en hedendaagse nationale parken in Europa. Deze data is gebruikt om inzicht te krijgen in soortsamenstellingen in verschillende typen omgeving.

De natuurlijke omgeving in Schöningen 13 II-1 tot 13 II-4 is geleidelijk veranderd van interglaciaal optimum tot stadiaal, als tussenfase naar een volgend glaciaal. De palynologische data geeft een gedetaileerd beeld van de fluctuaties in de omgeving, terwijl de fauna een meer geleidelijke ontwikkeling toont, zonder gedetaileerde fluctuaties. De flora en fauna in Schö 13 II-1 is indicatief voor een interglaciale fase, Schö 13 II-2 bevat elementen die indicatief zijn voor zowel een interglaciale fase als (inter)stadiale fases en de lagen 13 II-3 en 13 II-4 zijn indicatief voor een stadiale fase. Karakteristiek voor de soortdiversiteit in Schö 13 II is de variabiliteit die niet direct is gecorreleerd aan climatologische onstandigheden, maar deze diversiteit kan verklaard worden door tafonomische processen. De samenstelling van grote zoogdieren in Schö 13 II, onder andere de afwezigheid van grote roofdieren in enkele lagen, kan worden verklaard door zowel ecologie en gedrag als tafonomie.

1. Introduction

The Middle Pleistocene site of Schöningen 13 II, Germany, is well known for its wooden spears. These finds were crucial in the hunter-scavenger debate; for a long time, Middle Pleistocene (Lower Palaeolithic) hominins were seen as scavengers, passively interacting with the surrounding environment. The spears placed Middle Pleistocene hominins in the position of hunter rather than scavenger. The Schöningen spears as well as the generally good preservation of bone material made Schöningen 13 II a key site in both European and worldwide Palaeolithic archaeology.

In order to get a better understanding of hominin behaviour in the Middle Pleistocene it is important to analyse environmental aspects in addition to the general analysis of the material culture and subsistence patterns. By analysing a multi-proxy record at the sites of Schöningen, possible changes in ecology may give insights into the way in which hominins interacted with the environment. Archaeological indicators of human presence, such as flint tools and hearths together with cut-marked animal bones only provide information about one end of the spectrum. This occasionally gives a one-sided view of hominin behaviour, in which certain changes in the behavioural pattern might not be explained. Changes in the behavioural pattern can for example be caused by fluctuations in the availability of resources, caused by environmental changes. An ecological view of the sites, concerning the change in the environment, can give supplementary information to archaeological research. The discipline applied in this study can give insights into environmental changes through time, as well as in the physical environment in which hominins acted.

Mammal remains in archaeological sites are often analysed in order to reconstruct the palaeodiet. Apart from providing evidence about subsistence, mammal remains and other faunal elements can also be used in environmental and climatic reconstructions. If the archaeological bone assemblage is used alongside the palaeontological assemblage it is important to pay attention to possible accumulation by hominins and other taphonomical aspects altering the ecological compositions.

The Schöningen excavations have been carried out since 1982. Research has been conducted on the different find categories, but there are still unanswered questions and potential problems related to the stratigraphy and the correlation of channel deposits from the sites. Subsequent research has been carried out on the various sites in Schöningen. Up to now different classes of animals and the floral component have been examined. Each category has thus been examined and conclusions have been drawn based on the different categories of data, but all the data has not yet been put together, to compare the different outcomes and to see how the data correlates. By far the most research has been done in the field of zooarchaeology, the large mammal fauna in particular. Fields of interest were the evolution of various species/genera, species compositions and environmental reconstructions.

The data for this thesis will be faunal data, including mammals, birds, fish, reptiles and amphibians, and molluscs, as well as palynological data. Plant macrofossils from Schö 13 II will be discussed briefly. This thesis will combine the environmental data. A crucial element of this research is to analyse which methods can be applied to environmental reconstruction; the value of modern analogues and the discrepancies in the fossil record of the different faunal classes.

In this thesis, I will discuss the environmental changes in the archaeological record in the levels 13 II-1 to 13 II-4. The goal is to carry out an environmental reconstruction that is as accurate as possible, based on the data that is available from this excavation, including flora and fauna. The environmental information that can be deduced from the flora and fauna is not restricted to general interpretations on climatic change, but can be more specific, if the correct proxies and analyses are applied. In order to make environmental interpretations of the fossil record, I shall analyse the environmental preferences of the species found in Schöningen 13 II, and combine the information about these preferences per level to get insights into the accuracy of the different elements.

This work will not only serve as an analysis of the data, resulting in the inferred palaeoenvironment, but will also address methodological and other considerations in the analysis of fossil records. It is, for example, hard to examine whether the absence of species reflects their absence from the palaeoecosystem, or whether the absence is a result of various taphonomical or ecological factors. I hope to tackle part of this problem by analysing species compositions and predator-prey patterns in both modern and fossil assemblages. The case studies based on modern analogues are used to get an insight in the co-occurrence of several predator and prey species in various environments, from barren Lapland to southern European valleys. The fossil assemblages analysed for this thesis are from roughly the same period as Schö 13 II; the Middle Pleistocene. One exception to this age is the German site Untermaßfeld, which dates to the later Early Pleistocene. This site is included, because it yields a rich large carnivore fauna that has no parallels in other fossil assemblages. The exceptionally high amount of (large) carnivores in Untermaßfeld is in contrast to the low amount of (large) carnivores at Schö 13 II.

The fossil record can be used to interpret environmental and climatic change. By analysing the fossil record of Schö 13 II, correlated to the Reinsdorf Interglacial, we can get insight into the environmental changes that are characteristic for this interglacial phase. This is of interest because there are still many questions regarding the chronology and environmental characteristics of Middle Pleistocene (post-Holsteinian) interglacials. This work can give insight into the structure of interglacial successions in a regional framework.

1.1. Aims

The aim of this thesis is to analyse the environmental changes in the archaeological record of Schöningen 13 II, by comparing the floral and faunal compositions from level 13 II-1 to 13 II-4. Each category, flora and fauna, will be discussed separately to get an understanding of the changes in the palaeoenvironment and the difficulties related to reconstructing environments based on floral and faunal proxies. It can be assumed that the various proxies will not always provide the same environmental outcomes as the other data. It is the combination of all proxies that make environmental reconstructions possible.

To be able to make accurate assumptions in environmental reconstructions, it is crucial to understand the nature of ecosystems and the influence of taphonomy on the composition of the fossil record. The theoretical part of this thesis will focus on the reconstruction of palaeoecosystems. For my research, I will analyse various theories and methods related to environmental reconstruction in terms of usability and applicability, to test several hypotheses on the structure of the fossil record.

A study of the potential taphonomic processes at the site is crucial for the understanding of the state of the fossil record; it is important to realise that the fossil record is no direct reflection of the past ecosystem. A range of taphonomic processes is responsible for the record as we encounter it, therefore we must analyse the potential sources of taphonomy. Also, an understanding of ecological systems is important for the study of the fossil record, as this may explain certain patterns of presence and absence of species, which are not caused by taphonomical processes. In particular animal and hominin behaviour may result in the absence of species in the fossil record, while the species could have been present in the past. In this respect, a category of high interest is the carnivore fauna, because this group may have had a role in both large mammal distribution and the accumulation and distribution of faunal remains.

The aim of the environmental analysis based on flora and fauna is not solely meant to be a straightforward analysis of the changes in the fossil record, and the related interpretations of environmental change and climatic changes. I present here the data that is known from the levels Schö 13 II-1 to 13 II-4, and I will analyse this data using several methods, in order to extract as much information as possible, not only from the presence of species, but also from their absence. It is widely known that absence in the fossil record does not equal absence of the species in the past, thus we must not neglect the absent part of the assemblage. Whereas the main question focuses on the change of the environment represented in the fossil record from level 1 to level 4, the sub-questions are added to seek answers to the patterning of the fossil record, and the understanding of the fossil record. This thesis may shed new light on the reconstruction of palaeoecosystems by creating more awareness of the need to take the taphonomical and ecological influences into account, and to avoid linking fauna and flora to environmental aspects, without observing the potential taphonomical factors and ecological influences. By comparing the individual layers, and eventually the entire framework of this specific site, the ecological and climatic succession can be mapped. In this thesis, it will be shown whether the data, the differing taxa of flora and fauna, are in accordance or generate different outcomes.

1.2. Research questions

The main question in this thesis is: how does the ecological composition of flora and fauna change over time between Schö 13 II-1 and 13 II-4? To answer this question and to get a better insight into the reconstruction of past environments, I include several sub-questions that address the state of the ecological record.

- Does the environment based on flora show similar patterns in ecological change to the data derived from the faunal proxies?
- How can we explain the species diversity patterns in Schö 13 II-1 to 13 II-4?
    - What are possible forcing factors behind the change in ecological composition over time?
- How can Schö 13 II be placed in time in relation to the climatic fluctuations of the Middle Pleistocene, based on the environmental data?
- Is the ecological composition (of flora and fauna species) comparable to present-day distributions and compositions?
- What environmental proxies are most reliable in this context?

1.3. Archaeological relevance

This study is of archaeological relevance, because it addresses problems related to environmental reconstruction based on the floral and faunal data. This thesis will show the differences in environmental information that is retrieved from the various faunal groups and whether this can be directly linked to the changes in the flora. As I will show later on in this thesis, species compositions based on single groups can provide misleading information, if these are not compared to other proxies. Also the level of detail in environmental information may vary per species or per group.

Part of this thesis will show that the environmental data retrieved from the archaeological record is heavily subjected to bias, brought about both by taphonomical processes and by archaeological sampling. This will be proven by using modern analogues and data from archaeological sites. What we will for example see here is that the absence of carnivores in the fossil record does not necessarily reflect a true absence in the past ecosystem, but that it rather reflects the species' behaviour and/or taphonomical effects. The aim of this thesis is to raise awareness about the gaps in the fossil record that may lead to incorrect interpretations of the past environment.

It is well known that the European Pleistocene record is highly non-analoguous with the Holocene records. Direct comparisons with modern faunal distributions is difficult, but it is not the species account itself that will be used as direct link to the past environment, but the relative composition between predators and prey species. Modern relationships between carnivores and herbivores can be used as a proxy for the absent carnivore data in the fossil record, where the herbivore community is abundant.

In many cases, climate change is the main focus of ecological research, while faunal and floral community change, which is indirectly or directly related to climate change, can have a higher impact on the shorter term. One of the aims of this research is to aim a better understanding of the relation between changes in the environment and the presence and activities of hominins. Hominins rely heavily on the natural world. Changes in the faunal community and vegetation would have altered the range of food resources available, their abundance, distribution and accessibility as well as that of other resources. These changes could have had influence on the behavioural patterns of Middle Pleistocene hominins. Research on the ecological changes is thus of considerable importance. Changes in the environment could for example mean that hominins should adapt to other strategies in order to survive the changes. On a more ecological scale, this research could give a more detailed insight in the chronology and ecological successions in the Reinsdorf Interglacial.

From the wooden spears and other artefacts, it is known that hominins were present at the site. The surrounding environment plays a significant role in the functioning of hominins, because of the presence and abundance of resources and the potential competition with other predators. Hominins subsequently change the compositions in the environment by hunting and scavenging, and accumulating the preyed species in a specific area. This hominid interaction, in combination with the site formation and taphonomical processes causes the distribution pattern we find as archaeologists.

In a wider frame, research on the ecological component of archaeological excavations tends to be underestimated. Most focus will be applied to the contexts that are in direct relation to human presence or human influence, while the ecological background can provide supplementary, crucial information on hominin presence. A detailed reconstruction of hominin environments is important for understanding hominin behaviour. The importance of a detailed reconstructed environment for the understanding of hominin behaviour is for example discussed in Gamble (1986). In this article the environmental characteristics and implications of the separate phases of marine isotope stage 5e-5a (Eemian and Weichselian) are discussed. The productivity of the environment changes with changes in the type of vegetation; each type of environment is linked with its own productivity and requires a specific exploitation strategy (Gamble 1986, 100). Full interglacial forests, for example, are less productive than early interglacial (open) shrub- and grasslands, in terms of costs and benefits (Gamble 1986, 100-101). Because of these constraints and changes in vegetation cover over the course of glacial-interglacial cycles, fauna also comprised an important part of the diet. Over the course of an (inter)glacial, there is some, but no drastic, change in the availability of faunal resources (Gamble 1986). The availability of energy was not limiting the structure of resources, but the organisation of the environments to which Palaeolithic groups had to adapt no doubt imposed constraints (Gamble 1986, 114-115).

1.4. Data

The data used for this study comprises mammals, amphibians, reptiles and fish. An analysis of mollusc data will also be included in this thesis, but as the data of this group does not provide detailed information on the exact level of provenance of all mollusc species, I shall only include the general environmental implications of this group in the analysis of environmental changes in the site. Also the avifauna is discussed, but because of the incompatibility of bird species ratios in modern analogues with the remains in the fossil record, this group is left out of the statistical discussions. The analysis of the archaeological and palaeontological remains from Schö 13 II is subjected to a variety of potential research problems. The first is that the archaeological material has been analysed by different resources. As each person has its own determination methods, it is possible that there are differences in the consistency of species determination. Related to this problem, it could occur that the identifications are not detailed; few species level identifications, and relatively much genus or family level identifications. Also, because of the significance of the wooden spears found in 13 II-4, it is possible that the research intensity in 13 II was higher in level 4 than in the other levels, resulting in a potential lower number of samples, and thus a related lower species diversity.

To get an overview I will discuss the environmental preferences of the species found in the Schöningen 13 II sediments. The principle aim is to analyse the species that are found in the archaeological assemblage, and to compare these assemblages to general species patterns in modern analogues and fossil assemblages. If these records prove to be non-analoguous, even for the Middle Pleistocene standards, I shall try to interpret how the assemblage does not fit the assumed patter, for example in discrepancies between the flora and fauna, but also in discrepancies between the faunal assemblages itself.
Additionally, there is also a case study concerning several archaeological sites. By studying species compositions from both past and present ecosystems, we can get insights in the similarities and differences of Pleistocene and Holocene species relations.

It is important to look at the data in another way than solely labelling species in terms of environmental characteristics, and linking these together per level. What becomes clear when comparing the floral record with the faunal assemblages, is that the stratigraphic sequences in which the fauna is excavated are not in line with the major climatic fluctuations that can be derived from the pollen diagram.

1.5. Outline

In this thesis, a theoretical framework concerning environmental change in the Middle Pleistocene shall be discussed. The Middle Pleistocene climatic history is important in this framework, because of the limited information on the state of post-Holsteinian interglacials. In the light of Middle Pleistocene climatic change, this thesis will discuss the geological situation and sedimentary context of Schöningen 13 II. In chapter three the theoretical base of environmental reconstruction will be discussed, including the purpose of including modern and fossil analogue assemblages and ecological and behavioural limitations to presence of species in the fossil record. Chapter four will discuss the taphonomical processes responsible for creating the fossil record as we encounter it. Chapter five discusses the methods applied to this study. In the sixth chapter, the floral and faunal data from Schö 13 II-1 to 13 II-4 are discussed. Chapter seven concerns the analysis of the faunal remains by applying methods that are unconventional in zooarchaeological research. Chapter eight is a summarising chapter of the environmental development from Schö 13 II-1, an interglacial optimum, tot Schö 13 II-4, a stadial phase.

2. Middle Pleistocene climatic history

The climate in the Pleistocene shows a general cooling trend (fig. 1), with an increased amplitude between cold phases and warm phases. The Middle Pleistocene, dating from 780-120 ka (Cohen and Gibbard 2011), is characterised by a high intensity of climatic fluctuations. The climatic changes in the Middle Pleistocene are a result of change in the Earth's orbit and cyclicity. Precession and obliquity show cycles of 23 kyr and 41 kyr, whereas eccentricity is characterised by a dominating 100 kyr cycle (Berendsen 2005, 8-10).

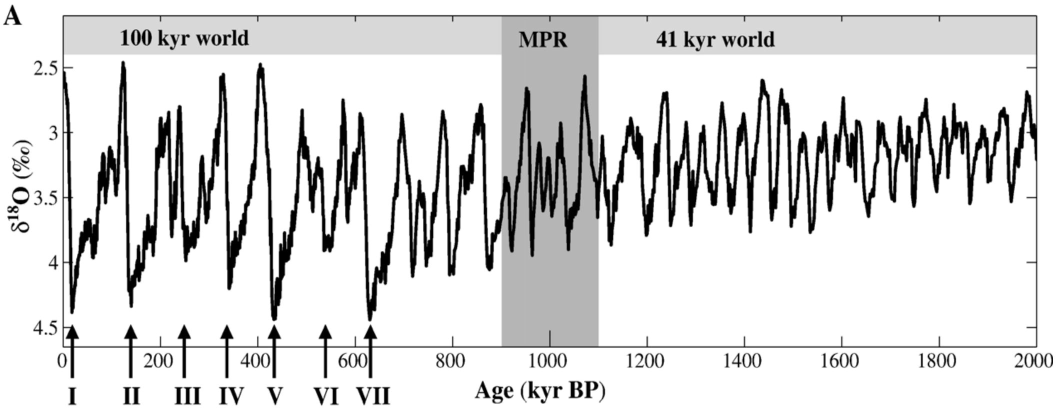

Figure 1 Fluctuations in δ^{18}O ratios in the Lower, Middle and Upper Pleistocene. The transitional phase between the dominance of 41 kyr cycles and 100 kyr cycles is described in this figure as the 'Middle Pleistocene revolution' (MPR). The Roman numerals indicate the Terminations, events of abrupt climatic warming. The most significant transformations are I, II and V, respectively the terminations of the Weichselian, Saalian and Elsterian (Shackleton 2000)

Fig. 1 indicates that the frequency and amplitude of climatic fluctuations have changed over the course of time, from a domination of 41 kyr and 23 kyr cycles to a domination of 100 kyr cycles (Berendsen 2005, 11). The climatic signal of the Middle Pleistocene is significantly different from the Pliocene and Early Pleistocene because of the higher amplitude in climatic change, causing a more significant difference in climates of interglacial and glacial optima. The climatic fluctuations in the Middle and Late Pleistocene have led to many changes in the geological and biological record, by creating a dynamic environment with fluctuations in sea level, and related climatic influences, as well as the advance and retreat of ice sheets in Northwestern and Central Europe.

The lowest part of the Middle Pleistocene corresponds to the Cromerian Complex. This stage of glacial-interglacial intervals is followed by the Elsterian glaciation. Succeeding the Elsterian, is the Holsteinian interglacial and the Saalian Complex. The last cold phase of the Saalian Complex, the Warthe glaciation marks the end of the Middle Pleistocene.

The $\delta^{18}O$ fluctuations and correlations with marine oxygen isotope stages are depicted with more detail in fig. 2.

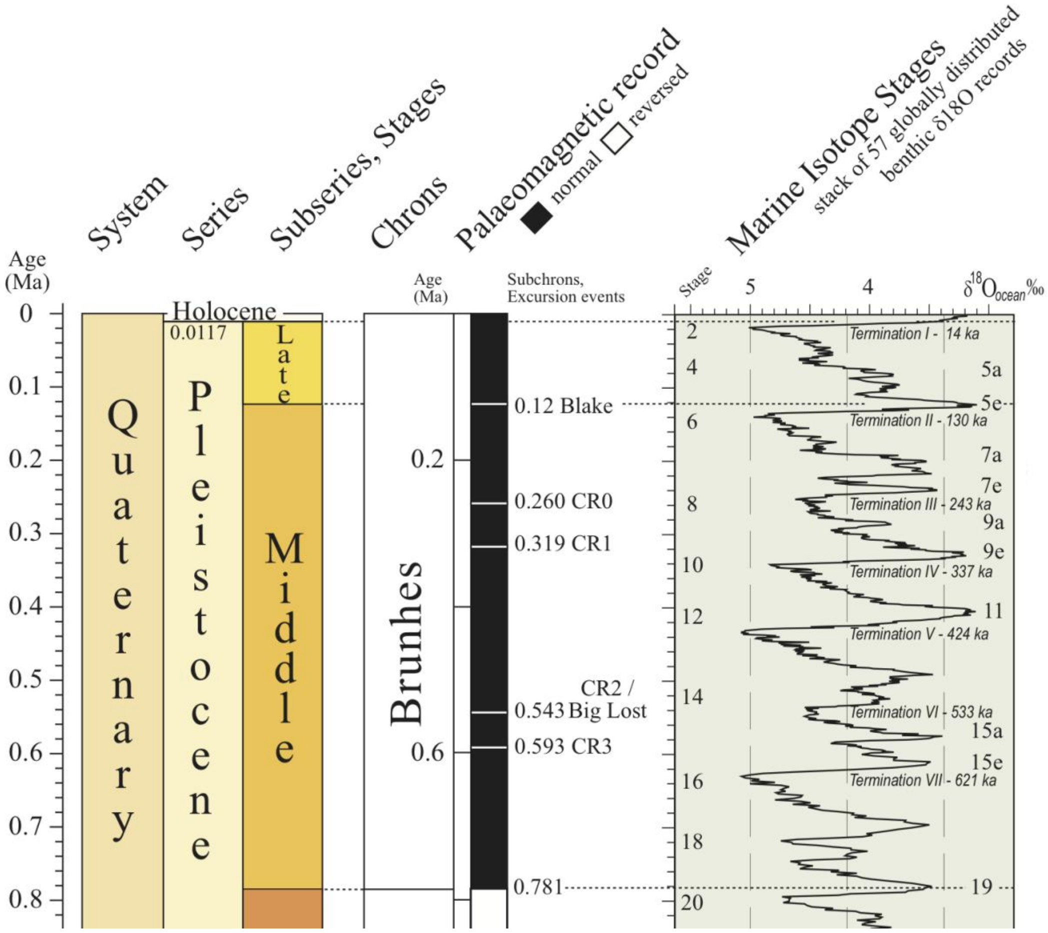

Figure 2 Climatic oscillations in the Middle and Late Pleistocene (http://www-qpg.geog.cam.ac.uk)

The high intensity of climatic fluctuations has significant influence on the fauna and vegetation compositions. The dynamic climate cycles resulted in the evolution and extinction of many species. The fauna turnovers in the Middle Pleistocene are not as high as around 1.8 ma (the former Pliocene-Pleistocene boundary), but nevertheless, this period is characterised by a high level of fauna shifts in the glacial-interglacial intervals, indicating both extinctions and migrations of temperate and cold-adapted fauna (Von Koenigswald 2007).

The major glaciations in the later Middle Pleistocene in Central Europe are the Elsterian glaciation and Saalian glaciation. These glaciations are preceded by the Cromerian Complex, consisting of a series of glacial and interglacial phases. The maximum extent of the Elsterian and Saalian glaciations have a similar distribution in northeast Germany (Läng *et al*. 2012, 3). The Elsterian and Drenthe (Older Saalian) ice sheets have transgressed the Schöningen area, whereas the Warthe (Younger Saalian) and Weichselian ice advance have not reached the Schöningen (Läng *et al*. 2012, 3).

In the Middle Pleistocene there is much variation in the regional climatic stratigraphies. Each interglacial has a characteristic, unique environmental succession. An analysis of the Schöningen 13 II sequence can give insight the nature of climatic fluctuations in post-Holsteinian contexts in Central Europe. There is still an ongoing debate about the correlation of the regional records for post-Holsteinian contexts. Also, the relationship between global climate records (fig. 1 and fig. 2) and regional terrestrial environments is unclear, because of the difference in preservation and the general absence of complete terrestrial stratigraphic and palynological sequences (Von Koenigswald 2007, 449). This work will help to reconstruct the environment of one of the interglacials represented at Schöningen, the Reinsdorf Interglacial correlated with the site Schö 13 II, and will help in understanding environmental change in this region. It will also help in understanding the relationship between interglacials at Middle Pleistocene records in different regions in Northern Europe.

2.1. Middle Pleistocene interglacials

The number of interglacials between the Elsterian and Saalian ice advance is debated. Mania and Thomae (2006) distinguish four independent interglacial phases within the Holsteinian Complex and two interglacials in the Saalian Complex (Von Koenigswald 2007, 448). Litt *et al*. (2005) accepted one or two interglacial phases after the Holsteinian and before the Drenthe glaciation (old Saalian ice advance), rejecting interglacial phases between the Drenthe and Warthe glaciations. Besides the Holsteinian, only one or two additional interglacial phases antedating the Holsteinian are accepted (Von Koenigswald 2007, 449). Urban (2007) discusses that there is evidence for three interglacials and at least 10 interstadials between the end of the Elsterian and the start of the Drenthe glaciation. There appears to be no evidence for a distimct interglacial phase from between the two major Saalian glaciations. The tills are separated by meltwater deposits, rather than organic deposits that would be expected to be found if warmer phases have occurred (Läng *et al*. 2012, 3).

The succession of warm stages in the Schöningen sites is discussed as debatable, because the deposits do not all occur in the same outcrop, in perfect superposition. Nevertheless, Urban (2007) states that there is sufficient evidence, in terms of superposition of stratigraphic units and overlap between various sedimental units, to assume the presence of more than one interglacial phase between the Elsterian and Drenthe ice advance. The post-Elsterian, pre-Drenthe interglacials accepted by Urban (1995; 2007; Urban *et al.* 2011) are the Holsteinian Interglacial, Reinsdorf Interglacial and Schöningen Interglacial. In contrary, Litt et al. (2007) interpreted the Reinsdorf Interglacial as a part of the Holsteinian interglacial (Läng *et al*. 2012, 3). Tab. 1 describes the differences between the

Holsteinian and Reinsdorf Interglacial, showing a differentiation in age, MIS correlation, related stratigraphic complex and floral elements that are characteristic for these interglacials.

	Holsteinian Interglacial	Reinsdorf Interglacial
Age	410-370 ka (Berendsen 2004) 310-330 ka (Geyh and Müller 2005)	300 ka (Urban *et al*. 2011)
Correlation	MIS 11 (Cohen and Gibbard 2011*; Ashton *et al.* 2008; Van Gijssel 2006; Nitychoruk *et al.* 2005; Berendsen 2004; Grün and Schwarcz 2000) MIS 11/9 (Urban 2007) MIS 9 (Litt *et al.* 2007; Läng *et al.* 2012; Geyh and Müller 2007)	MIS 9 (Urban 2006; Urban *et al.* 2011; Läng *et al*. 2012; Jöris and Baales 2003) MIS 9/7 (Urban 2007)
Related Complex	Holsteinian	Holsteinian (Litt *et al.* 2007) Saalian (Urban 2007)
Characteristic floral elements	*Carpinus, Fagus, Pterocarya, Abies, Azolla filiculoides* (Urban 2007, 68)	*Quercus, Fraxinus, Tilia, Corylus, Alnus, Carpinus, Picea, Abies* (Urban 2007, 71)

Table 1 Differences between the Holsteinian Interglacial and Reinsdorf Interglacial in Central Europe. *MIS correlation based on a global record (Cohen and Gibbard)

2.2. Schöningen

Schöningen is an open-cast lignite mine situated roughly between Hannover and Magdeburg, at the former border of East and West Germany (fig. 3). Systematic archaeological research has been carried out since 1982 on several locations in the quarry (Thieme 2007). In the mine a number of sites has been excavated, correlated with the channels (fig. 5; fig. 6). The site Schöningen 13 II is still actively excavated (Urban *et al.* 2011). The excavations in Schöningen have uncovered many different sequences of Pleistocene and Holocene age. The large scale project of retrieving brown coal from the sediments revealed many archaeological and palaeontological remains. Archaeological remains found on the sites are spears, flint flakes and artefacts, fire places and impacted faunal material.

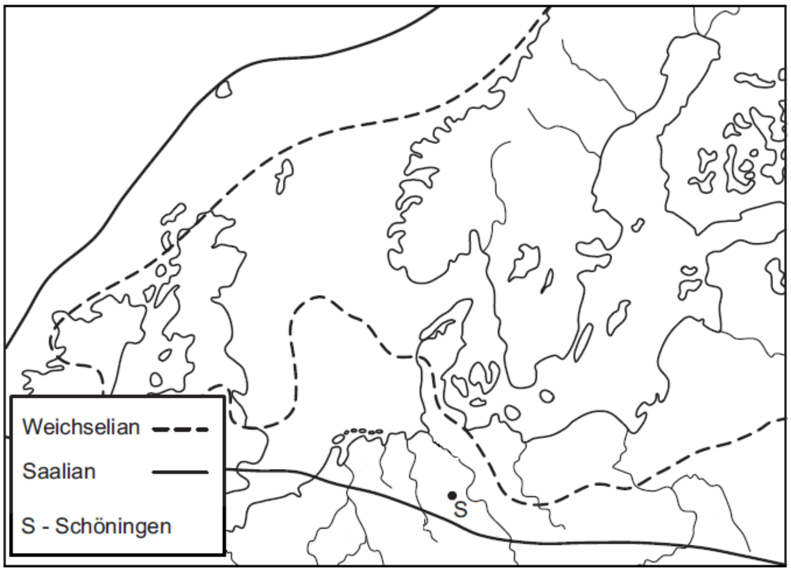

Figure 3 Location of Schöningen and the maximum extent of the Weichselian and Saalian ice advances (after Urban *et al.* 2011)

Geographically, Schöningen is situated at the northern border of the *Mittelgebirge* and the spurs of the Harz mountains in a transitional area towards the north German *Tiefland* (fig. 3, Thieme 2007, 18). The quarry is located in the outer margin of the south-west orientated rim syncline of the Beiersrode-Helmstedt-Staßfurt salt structure (fig. 4, Läng *et al*. 2012, 3; Van Gijssel 2006, 84). This salt dome structure, extending over a length of 70 km, was crucial for the formation of the depressions at the Schöningen sites in which the sediments were deposited, as the salt dome influenced the formation and location of the local stratigraphy (Läng *et al*. 2012, 3; Mania 2007, 40).

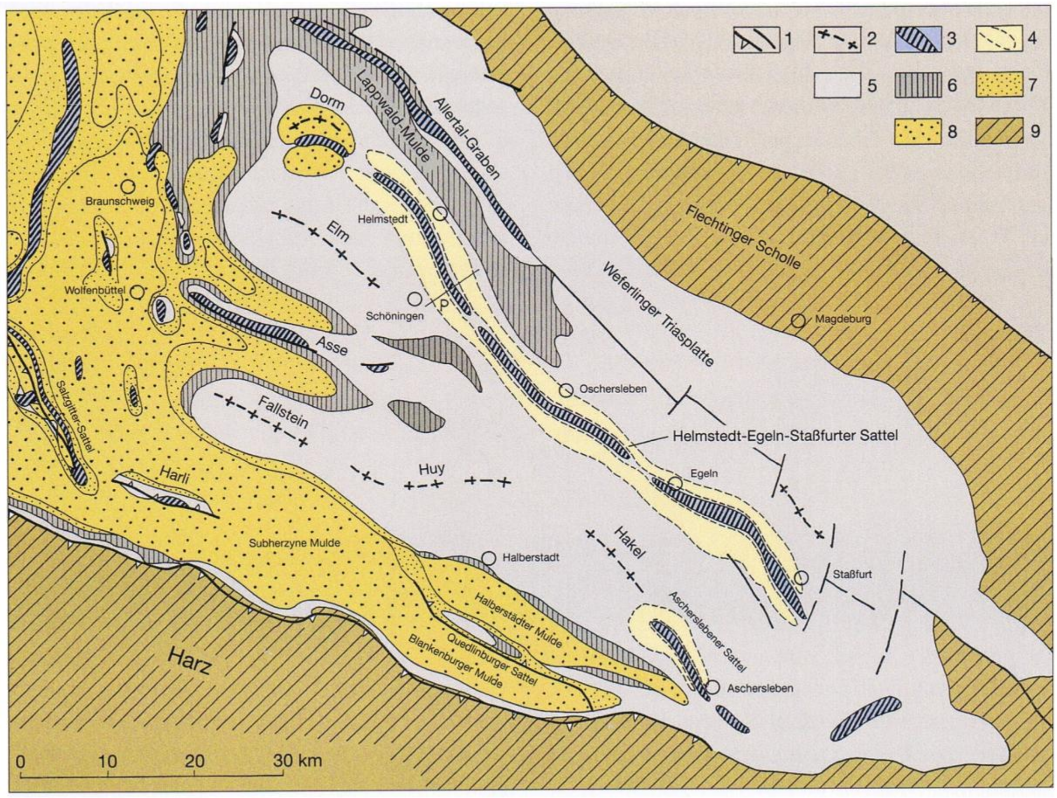

Figure 4 Geological map of the salt dome in the Schöningen-Helmstedt area. 1. tectonic disturbances, 2. Anticlinical axis, 3. Salt intrusion, 4. secondary salt intrusion/salt pillow, 5. Trias, 6. Jura, 7. Lower Cretaceous, 8. Upper Cretaceous, 9. profile in 'Helmstedter Sattel'/ basement (Mania 2007, 39)

The base of the rim-syncline is formed by Mesozoic mud- and limestone (Läng *et al*. 2012, 3). The main fill of the rim-syncline consists of a 360 m thick succession of Palaeogene lignite strata interlaced with laminated fine sand, silt and clay of marine origin (Läng *et al*. 2012, 3; Van Gijssel 2006, 84). The Pleistocene sequence unconformably follows the Tertiary strata, indicating that the Pleistocene deposits have eroded. The maximum thickness of the Pleistocene sediments reaches 40 m (Läng *et al.* 2012, 13) to 45 m (Van Gijssel 2006, 84-85). The oldest Pleistocene sediments at the Schöningen sites date from the Elsterian. The basal sedimentary succession consists of Elsterian meltwater deposits and till (Läng *et al*. 2012, 3).

2.2.1. The Schöningen channels

A total of six channels are present in the record of Schöningen (fig. 5; Mania 2007). The channels were formed during the Elsterian ice advance. The origin of the channels is debated. Whereas Elsner (1987) proposed that the channels were a result of the melting of dead-ice in shallow kettle-holes (Läng *et al*. 2012, 3), Mania assigns the origin of the channels to a combination of fluvial action and salt solutions in the superficial sediments (Läng *et al*. 2012, 3; Mania 2007). According to Läng *et al.* (2012) the Middle Pleistocene succession of Schöningen is interpreted as infill of a 300 to 400 m wide subglacial tunnel valley that was incised during the Elsterian glaciation. The climatic cycles are represented by sand and gravel deposits at the erosional base, followed by fine sand and silts, overlain by lake muds and silts that are alternated with peat layers (Van Gijssel 2006, 86). The fine sand and silt units are of allochtonous origin, comprising subaerial aeolian sediments, deposited in periglacial environments. The aeolian sediments are generally reworked by solifluction and slope wash (Van Gijssel 2006, 86). The lake and mire sequences in the deposits are indicative of changing open-water hydrological conditions during warm phases (Van Gijssel 2006, 86).

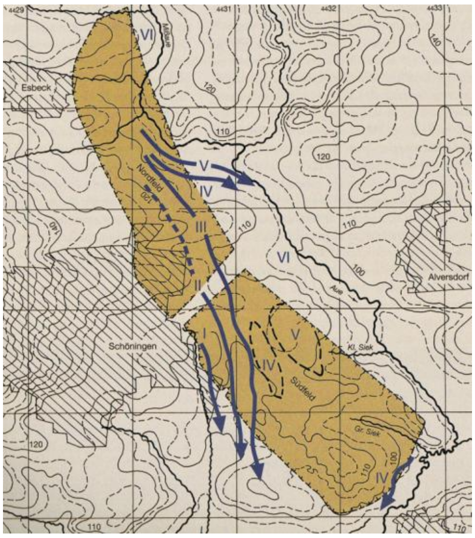

Figure 5 Relief map of the Schöningen brown coal quarry (open-cast lignite mine) depicting the channels (Mania 2007, 49)

Figure 6 Distribution of the Schöningen sites in the open-cast lignite mine (Mania 2007, 23)

The fill of these channels is related to fluctuations in climate. It is assumed that every channel represents a glacial-interglacial cycle, whereas the individual channels are separated by cold phases (Mania 2007, 47). It is assumed that there is evidence for four interglacials between the Elsterian ice advance and the Holocene[1]. The interglacials identified

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[1] Although there are six channels found in the lignite mine of Schöningen, it is assumed that four interglacial cycles could be distinguished in the channels I (Holsteinian Interglacial), II (Reinsdorf

in Schöningen are, from oldest to youngest, the Holsteinian, Reinsdorf, Schöningen and Eemian (Urban 2007, 147). The first three interglacial cycles are deposited before the Drenthe (Early Saalian) ice advance. Channel I is associated with the Holsteinian Interglacial, channel II with the Reinsdorf Interglacial, channel III with the Schöningen Interglacial and channel V with the Eemian Interglacial.

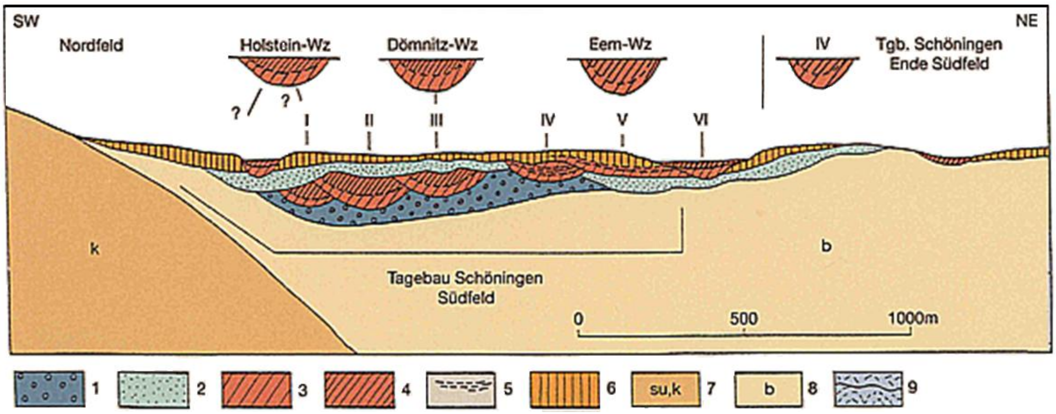


Figure 7 Schematic depiction of the Schöningen channels, channel I: Holsteinian, Channel II: Reinsdorf, channel III: Schöningen, channel IV: pre-Drenthe pedocomplex in alluvial loess, channel V: Eemian, channel VI: Holocene (Urban 2007, 432). 1. Elsterian glacial sequence, 2. Saalian glacial sequence, 3. Subaerial sequence, 4. Lake and mire sequence, soil complexes, 6. Subaerial (loess) sequence, 7. Palaeolithic horizon, 8. Tertiary, 9. Cap rock (Mania 2007, 45)

Channels I, II and III are interpreted by Thieme and Mainia (1993) as laterally superimposed ‘climatocyclic’ depositional sequences that were deposited preceding the Saalian glaciation (Van Gijssel 2006, 86). The relative position of the channels is depicted in fig. 7, showing an eastward shifting position of the channels towards the salt dome (Van Gijssel 2006, 86).

The general climatic fluctuation in the cycle of Schöningen II is described by Mania (2007, 52-57; fig. 8). This climatic cycle is regarded to as the Reinsdorf Interglacial, an interglacial phase distinct from the Holsteinian Interglacial. The climatic cycle representing Schöningen II is characterized by six levels[2]. For this thesis only the first four levels of Schöningen 13 II have been examined, because the data was more abundant for these levels than for levels Schö 13 II-5 and 13 II-6.

Interglacial, III (Schöningen Interglacial) and V (Eemian Interglacial). No distinct interglacials phases are assigned to the channels IV and VI.

[2] The number of individual levels in Schö 13 II is interpreted differently. Whereas Böhme (2007) and Urban (2007) distinguish five levels, Mania (2007) distinguishes six levels in the malacological research. In this thesis only the first four levels are discussed, because the majority of the mammalian faunal material originated from Schö 13 II-1 to Schö 13 II-4.

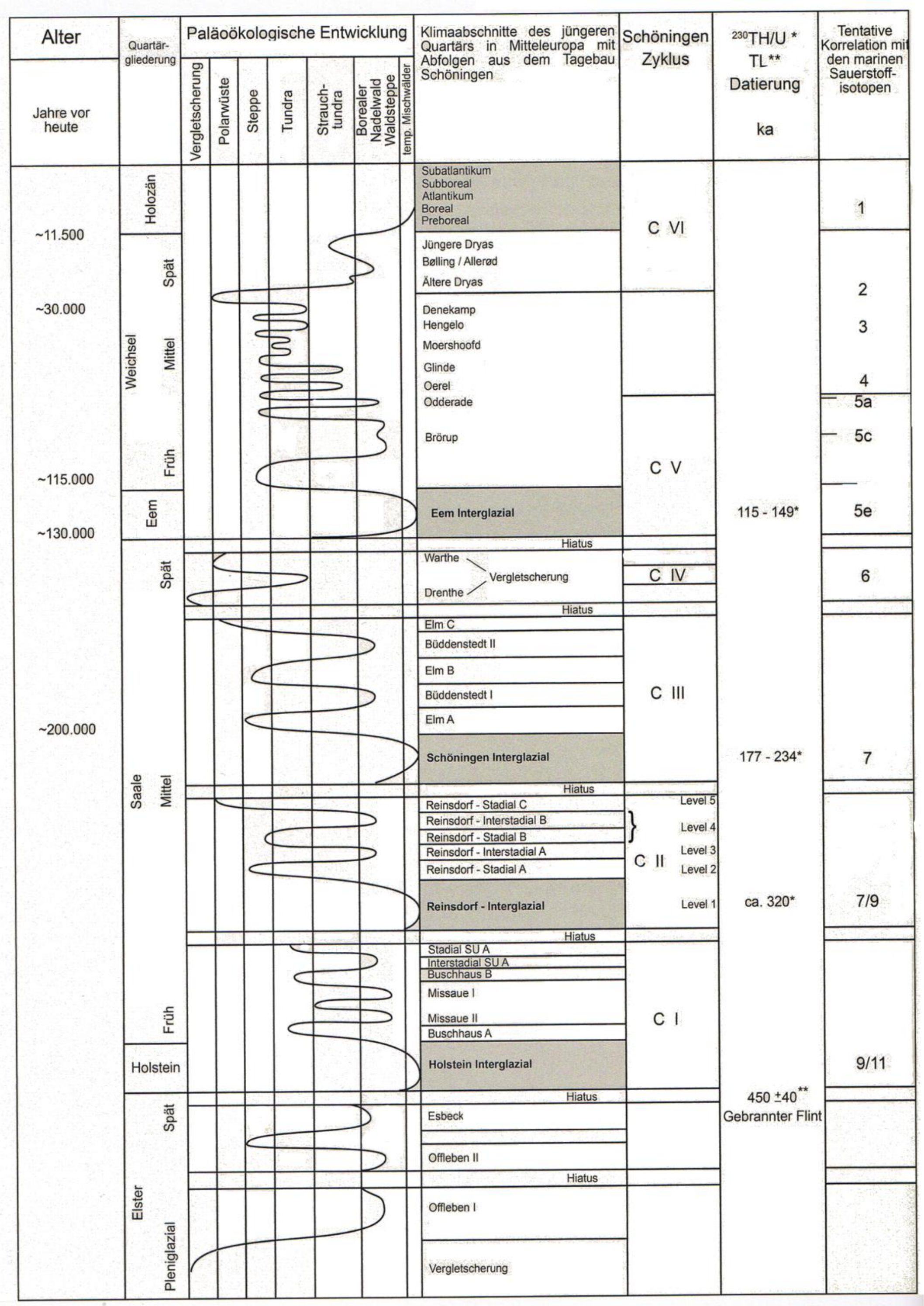


Figure 8 Environmental fluctuations from the middle Middle Pleistocene (Elsterian ice advance) to the Holocene describing the climatic subdivisions, Schöningen channels and relative age and marine oxygen isotope correlations. Of interest for this thesis is the Reinsdorf sequence, dated in this scheme to 320 ka, correlated with MIS 7/9 (Urban 2007, 72)

2.2.2. Stratigraphy

The stratigraphy of Schö 13 II shows a succession of different sediments, deposited in the course of the Reinsdorf interglacial. The stratigraphic sequences (fig. 7 and fig. 9) show that the deposits of the Reinsdorf Interglacial follow Elsterian glacial deposits, indicating a hiatus. The deposits from the Reinsdorf sequence are overlain by by sediments from a stadial phase. The sediments do not show a complete succession from the end of the Elsterian glaciation to the start of the Saalian glaciation, with the three interglacial phases in between.

2.2.3. Sedimentology

The sediments from the lower part of the section, associated with level 13 II-1, consists of silt and clay. This part of the sediment is characterized by a low amount of organic carbon, a neutral pH and a relatively low salt content (Urban *et al*. 2011, 132). The carbon content increases to 20% in the gyttja layers, whereas the subsequent layers of fen peat are carbonate free and are characterized by acid pH values (Urban *et al*. 2011, 132). The sedimentological composition changes in level 13 II-2, with an increase of fine sand in the marly and silty mud. The middle part of the 13 II-2 profile is carbonate-rich, while the level of organic carbon in this part of the profile is low. The pH varies from neutral in the middle part of the profile to acidic in the fen peat layer in the higher parts of this level (Urban *et al*. 2011, 132). The overlying layers associated with 13 II-3 and 13 II-4 consists alternatingly of marly, organic muds and gyttja, with varying levels of pH, acidic in level 13 II-3 and more neutral in 13 II-4.

The boundaries between the sediments of level 1 to 4 are gradual, while the boundary between level 4 and level 5 is characterized by periglacial elements from layer 5, ice wedges and signs of solifluction, that have penetrated the underlying sediments (fig. 9). These sedimentlogical actions could have affected the fossil record that was deposited in level 4, by either movement of remains or erosion. In the fourth level, evidence was found in the sedimentological record for a change towards a long term climatic phase with an arctic-subarctic character. The nature of the previous two levels is then seen as an unstable climate, fluctuating between stadials and interstadials (Urban *et al*. 2011, 132).

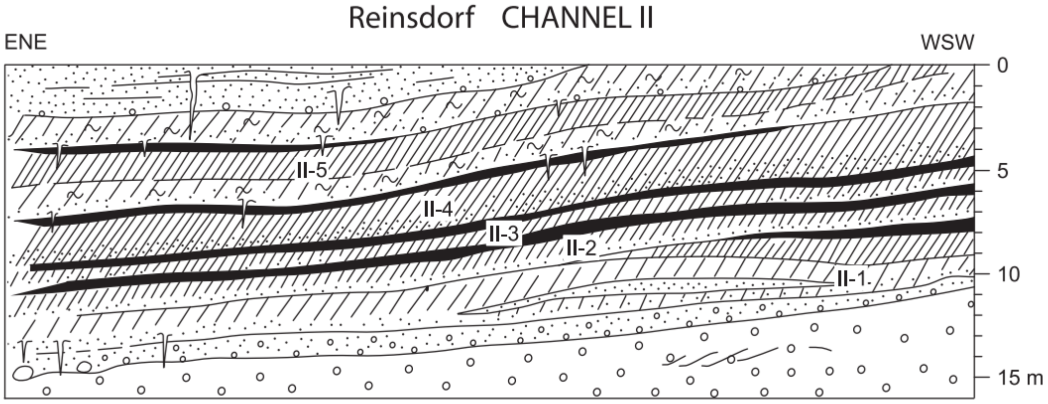


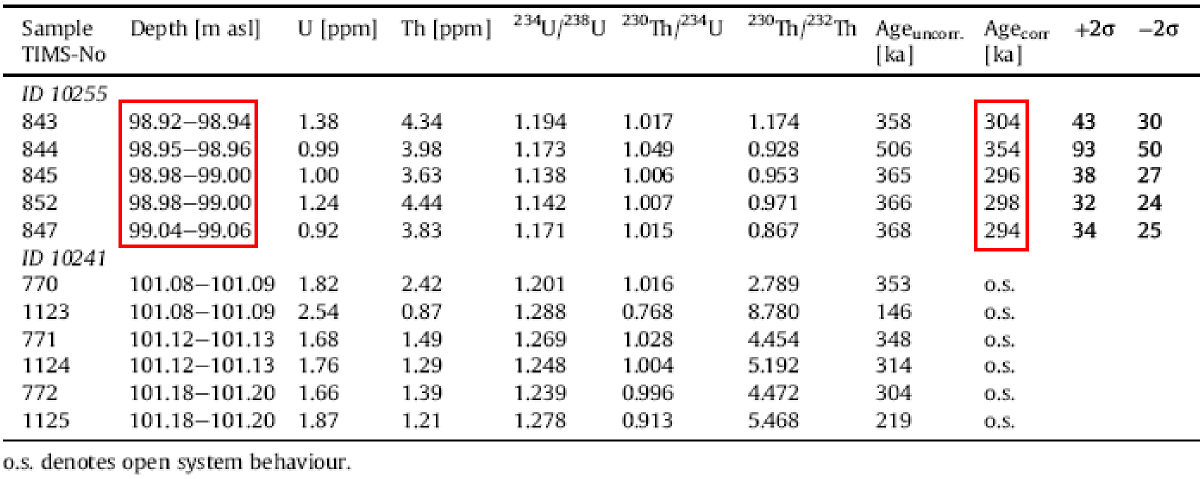
Figure 9 Sedimentological sequence of the Reinsdorf interglacial in Channel II. The channel shows a succession of glacial, interglacial and stadial deposits, covered by Saalian deposits (Urban *et al*. 2011, 130)

Frost cracks are formed in times of permanent permafrost, indicating that level 13 II-5 was characterised by cool conditions. The most favourable environments for the formation of ice wedges are poorly-drained tundra lowlands underlain by continuous permafrost (French 2007, 176). The gradual formation of ice wedges requires periods of both frost and thaw to be able to expand. In the formation process, the surrounding soil is subject to deformation and dislocation of sediments (French 2007, 176). These anomalies can cause an alteration of the fossil record. This potential taphonomic influence could be linked to patterns of distortion found in the fossil record. The black layers in the figure indicate the presence of peat layers. Peat is indicative of the presence of permanent water, and is generally associated with a wetland environment (Holliday 1992, 194; Hillel *et al.* 2004).

2.2.4. Dating

The age of Schöningen 13 II is still under debate. In *Die Schöningen Speere* (Thieme 2007), the relative age of 13 II-4 was set at 250-350 ka, based on TL (thermoluminescence) dates from the underlying and superimposed sediments (Richter 2007, 64). Other dating methods used were OSL (optically stimulated luminescence) to date sediments and ESR (Electron spin resonance) to date teeth (Richter 2007, 64). More recent dates of Schöningen 13 II reveal an averaged, corrected, age of 300 ± 40 ka for the lower part of Schöningen 13 II-2 (Urban *et al.* 2011, 135). Läng *et al*. (2012, 3) use the date by Urban *et al*. (2011) and the age determinations of 294 ± 10 to 297 ± 12 ka by Sierralta *et al*. (in press) as support for the interpretation that the Reinsdorf succession reflects a Holsteinian age, correlated with MIS 9 (Läng *et al*. 2012, 3). Van Gijssel (2006) discusses a ^{230}Th/^{234}U age of the travertine deposits in the Reinsdorf sequence (not specified on level) of 320-350 ka and an ESR date of 282-414 ka, correlating to MIS 9 (Schwarcz *et al.* 1988; Van Gijssel 2006, 89)

The higher parts of Schöningen 13 II-2 reveal an uncorrected $^{230}Th/^{234}U$ age of between 146 ka and 353 ka (fig. 10). Given the fact that the corrected dates of the lower levels of 13 II-2 are averaged around 300 ka, the spear horizon 13 II-4 is supposedly younger than the frequently assumed 300-400 ka (Urban *et al.* 2011, 135). The relative age of the sites located in the six channels correspond to succeeding climatic phases. The signal in the pollen diagram makes it that these age ranges can be associated with the climatic fluctuations based on marine oxygen isotopes.



Sample TIMS-No	Depth [m asl]	U [ppm]	Th [ppm]	$^{234}U/^{238}U$	$^{230}Th/^{234}U$	$^{230}Th/^{232}Th$	$Age_{uncorr.}$ [ka]	Age_{corr} [ka]	$+2\sigma$	-2σ
ID 10255										
843	98.92–98.94	1.38	4.34	1.194	1.017	1.174	358	304	**43**	**30**
844	98.95–98.96	0.99	3.98	1.173	1.049	0.928	506	354	**93**	**50**
845	98.98–99.00	1.00	3.63	1.138	1.006	0.953	365	296	**38**	**27**
852	98.98–99.00	1.24	4.44	1.142	1.007	0.971	366	298	**32**	**24**
847	99.04–99.06	0.92	3.83	1.171	1.015	0.867	368	294	**34**	**25**
ID 10241										
770	101.08–101.09	1.82	2.42	1.201	1.016	2.789	353	o.s.		
1123	101.08–101.09	2.54	0.87	1.288	0.768	8.780	146	o.s.		
771	101.12–101.13	1.68	1.49	1.269	1.028	4.454	348	o.s.		
1124	101.12–101.13	1.76	1.29	1.248	1.004	5.192	314	o.s.		
772	101.18–101.20	1.66	1.39	1.239	0.996	4.472	304	o.s.		
1125	101.18–101.20	1.87	1.21	1.278	0.913	5.468	219	o.s.		

o.s. denotes open system behaviour.

Figure 10 Corrected dates of Schö 13 II-2 linked to depth in m above sealevel (After Urban *et al.* 2011, 135)

3. Reconstructing ecosystems

In this chapter, I shall address the functioning of ecosystems and the importance of understanding the patterns for the reconstruction of ecosystems, and focussing on the aspects of ecosystem functioning that are relevant for the interpretation of the fossil record. Ideally, the fossil record would reflect the past environment in its original species content and ratios. There are, however, many factors that influence the eventual sample. The environment we want to interpret is a combination of the flora and fauna species that are present at the site, but also includes the environmental proxies of temperature indications, humidity and the nature of present waterbodies. Ecosystems of the past can be reconstructed based on the data recovered from the fossil record, and additional data on the functioning of present day ecosystems. The latter is important to analyse, because the fossil data on its own is not sufficient to retrieve environmental information. This thesis deals with fossil data from various faunal categories and flora. The theoretical background of ecosystem functioning is especially of interest for the mammal fauna. The majority of the large mammal fauna is not indicative of specific environments or biomes, but the relation in the food webs, predator-prey relationships, can reveal information on potential large mammal faunal compositions.

The reconstruction of palaeoenvironments based on the floral and faunal data from archaeological sites may seem a straightforward act, but the composition of the fossil record is not a solid reflection of the past assemblage. It may occur that some of the crucial elements of the ecosystem are missing in the fossil record, due to various potential pre- and post-depositional actions. The data we find at archaeological sites cannot be used as a direct proxy for environmental conditions, but it is important to analyse the state of the record to get insight into which elements are missing, underrepresented, overrepresented or allochthonous. Even after sampling, new biases are created; not every remain may be identifiable to species or genus level. In this case, a particular species may be preserved in the fossil record, but it is lost when people fail to identify the remains to family/genus/species level.

3.1. Biomes

Biomes are global or regional biotic communities, characterized by the dominant vegetation types. The contemporary division of biomes from north to south is mainly regulated by temperature, whereas the east-west gradient is defined by changes in precipitation (May and McLean 2007; Dickinson and Murphy 2007). The compositions of plant and animal communities in present biomes can be of help in studies to the past environment. The modern analogues are especially helpful if species distribution is limited to only few biomes, and if the species are to some degree indicative of the past environment. The European continent is covered by of four dominant biomes: temperate broadleaf forest, Mediterranean zone, Boreal forest and tundra. In fig. 11a it can be seen that the temperate broadleaf forest biome is most widespread in continental Europe. This division into biomes is rather broad, while the fauna assemblages vary slightly in different zones of a biome. A more detailed version of the natural division into vegetation zones can be seen in fig. 11b. This figure shows the division of the biomes into smaller entities, defined as ecotones or ecoregions. Ecotones are derived from biomes, but these entities show more detailed information, because the division is based on a combination of vegetation zones and the presence of specific faunal communities.

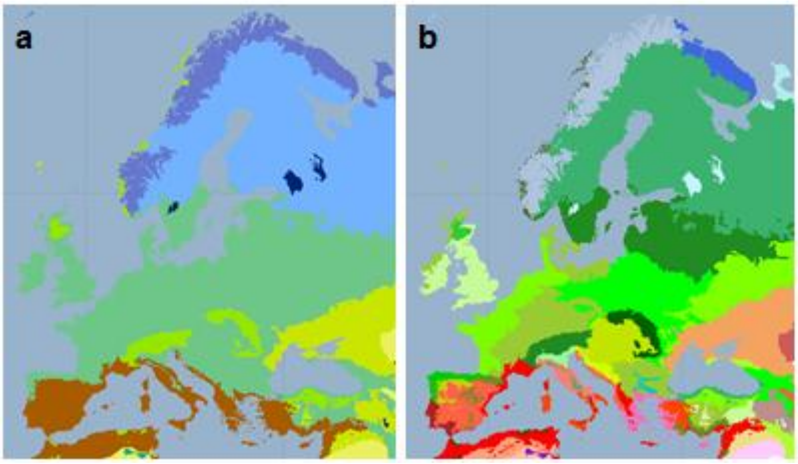


Figure 11 Divison of biomes (a) and ecotones or ecoregions (b) (source: WWF WildFinder, http://www.worldwildlife.org/science/)

The overall species composition in these biomes is similar. The biggest difference in species compositions can be seen in the tundra and taiga biomes in northern Scandinavia. Species diversity is more limited in these latitudes.

3.2. Species diversity and richness in contemporary ecology and the fossil record

Species diversity concerns the total number of taxa in a specific area, whereas species richness deals with the total number of individuals per area. It is both species diversity and species richness that are characteristic for different types of environments.

Species diversity is a highly variable entity in ecosystem ecology. Species diversity varies with climate, vegetation, soil physics and time (Begon *et al.* 2006). An important observation, especially in the European record, is the loss in species diversity from the Pleistocene to Holocene epoch. The greatest decrease is visible in the large herbivores. In this thesis, the term species diversity refers to the number of different species in a certain habitat or level, whereas the term species richness refers to the number of individuals of a particular species per habitat. Species diversity in the fossil record is more easily measured than richness, because it is less subjected to influence by sampling bias and excavation methods.

The number of species in a community is determined by many environmental variables, including the structural complexity of habitats, level of geographic isolation, habitat stress, closeness to margins of adjacent communities, and dominance of one species over others. These factors can have both negative and positive effects on richness (Solomon *et al.* 2008, 1159). Species richness is influenced by environmental conditions thus far that richness decreased with increasing levels of environmental stress. A low species richness is thus generally indicative for more extreme conditions (Solomon *et al.* 2008, 1159-1160). Species richness can also be influenced by dominance of species, outcompeting other species on basis of available resources (Solomon *et al.* 2008, 1160).

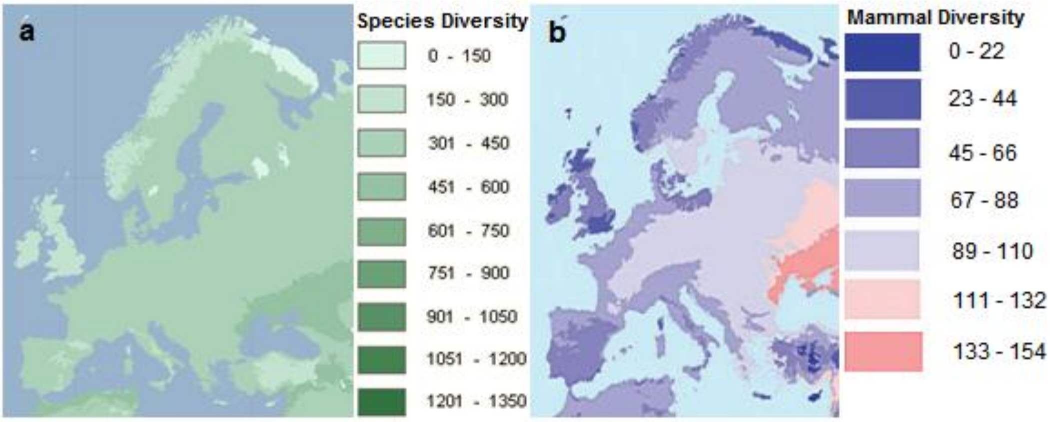


Figure 12 Total species diversity in number of mammalian and non-mammalian species (a) and relative mammal species diversity in number of species (b) (WWF WildFinder: http://www.worldwildlife.org/science/wildfinder/ ; after Olson et al. 2001, 936)

Patterns in species diversity and richness are based on ecological studies in various national parks of the world. The oberservations of richness and diversity are plotted against biomes and ecoregions. Overall species diversity and richness appear to be higher in continental regions, whereas diversity and richness is lower in regions with higher oceanic influence (fig. 12a). Mammal species diversity is relatively low in coastal and Nordic regions (fig. 12b). Towards the interior of the continent, this diversity increases. Schöningen is located in what is now an area with a relative mammal species diversity of 89-110 species. This is an averaged diversity, compared to the lower limits in high latitude and high altidude sites, and the highest limits in Central-Eastern Europe (Olson *et al.* 2001). A diversity of 89-110 species is relatively high in the European continent. This diversity spreads across Central Europe, the major mountaneous areas of Europe and (South)easten Europe. In the past the division of diversity patterns may have been different as a result of climatic fluctuations as well as changes in sea level.

Fig. 12b shows that the diversity in mammal species increases with longitude; diversity is higher in continental Europe (Southwestern Russia, the Ukraine and the Black Sea area) than in coastal Western Europe. In this respect, one could interpret from this observation that species diversity can be linked to oceanic influence and climate. Climatic fluctuations and related changes in sealevel in the past may thus have led to fluctuations in species diversity, as the position of sites changed relative to the distance to the sea.

Species richness of a particular area is more difficult to map in the fossil record than diversity, because of various limiting factors. In the fossil record, one has to deal with taphonomic processes, both of biotic and abiotic nature. Perhaps even more important than local taphonomy is the restricted sampling area. Even though the total sample of faunal remains may be relatively big, it only represents a small part of the original ecosystem.

Another factor that influences the fossil record is time averaging. As archaeological units may represent hundreds to thousands of years, the fauna will be accumulated over this long period. If, during this time span ecological changes have occurred, either long-term or short-term, the components indicative of ecological change can occur in the same stratigraphic unit. A disadvantage of this time averaging is the potential occurrence of species with conflicting ecological preferences (Behrensmeyer *et al.* 2002; Droser 2003).

A third influential factor, besides taphonomy and sampling size, is animal behaviour itself. Species diversity and species richness have an (in)direct influence on patterning of the fossil record. The presence and abundance of species depends on population densities, home ranges, competition and the abundance of resources.

The carrying capacity of an area is defined by the amount of resources available in the first order (vegetation). If these resources are abundant enough to sustain a variety of large herbivores, large carnivore diversity will also increase.

Carnivore density varies with the abundance and size of prey species; if few large prey species are present in an area, large carnivores like *Canis lupus* will be present at low population densities. Inversely, if large herds of large herbivores are present in the area, the carnivore population density and species richness will significantly increase, with the increased availability of resources.

If several ecological niches can be occupied because of an increased species richness (and diversity), more predator species can inhabit the area. Co-occurrences of large carnivores in contemporary European ecosystems are, depending on the carrying capacity of the region, wolf, lynx, bear and wolverine. Each of these species potentially hunt the same species, but their diet is generally broad, and can thus inhabit different ecological niches without too much competition.

It is important to remember in terms of diversity fluctuations that observed changes in diversity in the fossil record reflect a combination of changes in true biodiversity, changes in the quality and quantity of the fossil record, changes in paleontologic interest, and other biases (Bush *et al.* 2004, 666).

3.2.1. Species richness and range location

Generally, species richness and diversity is inversely related to the environmental stress of a habitat. Only the species capable of tolerating extreme conditions can live in environmentally stressed communities. Species diversity in high-latitude sites exposed to more extreme climates is lower than diversity in lower-latitude communities with milder climates. These observations lead to suggesting that species diversity in varying latitudes is influenced by the variation in solar energy. This observation is known as the *species richness–energy hypothesis* (Solomon *et al.* 2008, 1159-1160).

The degree of species richness and diversity can vary throughout different ecoregions. Ecoregions are usually not separated from each other by clear boundaries. If strict, naturally defined, boundaries are absent, the species from one ecoregion may disperse to the neighbouring region, if physiological tolerances allow. Species diversity is usually greater at the margins of communities than in the centers. This is caused by a gradual overlap of ecotones that contain ecological niches of the adjacent communities. The increase in diversity near edges of communities is known as the edge effect (Solomon *et al.* 2008, 1160). If three theoretical regions have a different species content, it could be expected that the overall species diversity is higher in the overlapping areas (Brown *et al.* 1996). However, this theory would not hold ground if the assumption is correct that species diversity is highest in the centre of a region, and decreases at the borders. In that respect, species diversity is not necessarily higher in overlapping ranges. Nevertheless, we must keep in mind that ecoregions are no static elements, and they can fluctuate over time in size. Long term climatic fluctuations in the Middle Pleistocene have certainly caused a fluctuation in range sizes, resulting in an ebb and flow pattern in the distribution of species. As ecoregions can be indicative of slightly differing climatic circumstances or vegetation, variation in species diversity in the archaeological record could theoretically be interpreted as a potential case of sampling at a former overlapping area between two or more ecoregions.

It is difficult, if not impossible, to retrace former boundaries of ecoregions in the fossil record. Despite the physical absence of these boundaries, overlap may be represented in the fossil record by a higher species diversity. The main problem with this interpretation is the absence of a detailed, standardized, fossil assemblage. Species diversity is not only a result of distribution within an ecoregion, but also fluctuates with climate. As the fossil record is deposited over a large time span, minor fluctuations in climate could have caused shifting ecoregion boundaries as well, captured in the fossil record.

It can be assumed that the species compositions in ecoregions is not limited by the size of an ecoregion, as each species has its own distribution range that stands apart from divisions in ecosystems. Depending on the tolerance levels of a species, a species has either a distribution limited within a specific ecoregion, or it can be distributed across the borders of several ecoregions. It is important to understand the theoretical ecoregional unit is not one single unit, but it could be seen as a unit in which many species, with varying ranges, live together under similar ecological conditions.

3.2.2. Species compositions – Pleistocene versus present

In research into past environments it is important to use a set of assumptions concerning animal behaviour. One of these assumptions is that mammal behaviour has not changed significantly over the course of the Pleistocene. In addition, one could define a set of basic principles, on animal behaviour in general. These basic principles are set out by Benton and Harper (2009) as follows:

- A species is adapted for and limited to a particular environment
- Individuals are directly and indirectly dependent on other organisms
- Species are adapted for a particular lifestyle

Differences in species distribution between the Pleistocene and present are generally triggered by changes in climate and other natural influences, but in modern societies climate is not the only factor that affects species distribution. Man has significant influence in the present distribution of animals and plants. It is on this account that comparing the Pleistocene assemblages with present-day distributions can show changes in distribution that are not directly related to natural influences. Human influence accumulated over time, with a peak in distortion in the present day. This can make it hard to define what the original, Pleistocene, habitat of a species was, or what the original preferred habitat was of a species. Human influence not only causes potential extinction and limited distribution of species, in some cases, mankind may help species to occupy larger territories.

In this research, the native species are distinguished from exotic species in modern biomes. Species distributions as seen in the modern world are presumably different from species distributions in the past. Nevertheless, present-day species distributions may prove helpful to indicate a possible species range of the past species. Predator-prey relations can also be informative for the levels of competition and abundance, as these systems of behaviour are assumed to have barely changed over the course of time.

3.2.3. Contemporary and fossil carnivore distribution

Only a few large carnivore remains are found in Schöningen 13 II, while a richer carnivore assemblage would be expected on the basis of the diversity of large herbivores as well as comparisons with archaeological sites and modern analogues. Their virtual absence or scarcity in archaeological sites raises the question as to what the chances are of finding fossilized carnivore remains in the record. The main issue with carnivores in the fossil record is probably the size of their home range and the high level of mobility that is difficult to retrace in a limited area that will be the archaeological site. As an example, the size of the excavated area of 13 II is approximately 3000 m^2, which is significantly smaller that the potential home ranges of *Canis lupus*. The estimated range size of this species varies between 60 and 85 km^2 (MacDonald an Barrett 1998). These range sizes depend on the type of environment. The maximum species density of wolves depends on the type and abundance of prey species. Usually wolves are solitary, but they hunt in packs where large sized prey are concerned. Species density may range up to 20 or 30 species per pack in extreme cases (large prey in herds), to as low as one individual, where the diet consists of mainly small mammals.

Species	Prey type (density-availability)	Population size	Range size
Canis lupus	Large herbivores	Max. 30	
	Medium herbivores (small deer)	<10	
	Small prey	1	1 per 50-60 km^2
Alopex lagopus	Voles, lemmings, eggs carrion	Small group (~5)	8-19 km^2
Vulpes vulpes		1 family per km^2	2-6 km^2 (agricultural land)
		1 family per 40 km^2 in barren uplands	4000 ha (Highlands), 40km^2
Ursus arctos	Elk, reindeer, bovids		
Gulo gulo	Reindeer, elk, roe deer	3,4	W: <2000km^2
	Rodents, birds, eggs	3,4	50-350, 600-1k
Lynx lynx	Hares, rodents		
	Reindeer, roe, chamois	1	2,5-1000km^2

Table 2 Large carnivore diet, population size and range size (data derived from MacDonald and Barrett 1998)

Table 2 shows the variation in carnivore diet and range size per prey type for most of the contemporary northwest European medium and large sized carnivores. Some of these predator species share an ecological niche, but can adapt in such a way that direct competition is not necessary.

What we see in this diagram is that predator density and home range size varies with the abundance and size of prey species. This fluctuation is especially significant in *Canis lupus*, where the population size can vary between one individual in regions where only small prey is present to packs of up to 30 individuals in barren lands where moose is the main prey species. The felids, in this context *Lynx lynx* are solitary, in contrast to canidae that live in groups if the prey size and density allows.

Knowing this variation in species density and range size, it becomes clear that finding fossilized carnivore remains in an archaeological site is highly dependent on chance. Indirect evidence for the presence of carnivores is more likely to be found, in the form of teeth marks on bones that are accumulated at the site.

4. Taphonomy

Understanding the various processes of degradation and taphonomy can provide insights into the distribution and presence of species in the archaeological record. There are a variety of taphonomical processes that can influence the deposited record, resulting in different patterns of preservation, presence and absence. The data as found in the archaeological record must not be taken for granted, but one must consider the potential of taphonomical processes that have resulted in a particular display of fossil material.

Taphonomy can be refered to as a study of the transition of organics from the biosphere into the lithosphere or geological record (Lyman 1994, 1). Taphonomy involves the formation of a maor part of the archaeological record (Lyman 194, 1). The term taphonomy was defined by Efemov (Olson 1980, 6). In his studies, he presented methods of analysis of the processes of destruction and preservation of continental sediments through time (Olson 1980 6). Behrensmeyer and Kidwell (1985) describe taphonomy as the study of processes of preservation and how they affect information. In taphonomical research, a variety of definitions is used. These include (Lyman 1994, 3-4):

> *Taphonomical agent*: the source of force applied to the bones. This is the immediate physical cause of modification to animal carcasses and skeletal tissues.
>
> *Taphonomical process*: the dynamic action of an agent on animal carcasses and skeletal tissues, such as downslope movement, gnawing and fracturing.
>
> *Taphonomical effect* or *trace*: static result of a taphonomic process acting on carcasses and skeletal tissues, the physical and/or chemical modification of a bone

The fossil record is by definition a biased sample of the past communities. It is likely that the fauna found in archaeological contexts is no direct reflection of the past ecosystem. Therefore, the faunal compositions from other archaeological sites that are used in comparative studies are no guarantee for representative proxies. The absence of species in the fossil record can be the result of environmental conditions, but it can also be the result of taphonomical processes of the species' ecology. The fauna compositions in the fossil record can be compared to other archaeological sites, but one must be aware of the taphonomical absence of species. To buffer fauna compositions in the archaeological record, modern analogues are applied as well. These records show a lower amount of bias than the Pleistocene records.

In research on the taphonomy of a site, one could ask several questions; which part of the evidence is found directly in the fossil record; what do the compositions in the fossil record tell us about potential taphonomic factors; what is the pattern of presence and absence; which part of the fossil record should be added theoretically to the physical record to make accurate assumptions; and do the sampling locations play a part in the presence or absence of species in the fossil record? Humans can have significant influence on the distribution patterns and modification of animal remains. Just as any other predator species, humans are known to modify and accumulate animal remains, resulting in a distortion of the natural assemblage.

The archaeological site of Schöningen 13 II provides evidence for the presence of hominins in the environment. This hominin presence may have influenced the natural signal of the faunal assemblages, but analogously the changes in the environment may have influenced the presence and activities of hominins. When attempting to reconstruct the environment, one has to acknowledge the fact that the archaeological assemblage is not a direct reflection of the past faunal assemblages. If this site is considered a hunting or butchering camp, the faunal assemblage at the site may show a bias towards the prey species that are part of the subsistence. As a result, the other species considered as natural background fauna may be underrepresented in the record. One of the basic goals in taphonomical research is to strip away the taphonomic overprint from the fossil record to obtain an accurate sample of the past community, and to determine the nature of the taphonomic overprint, whether it is natural or influenced by hominins.This information is needed to be able to analyse which taphponomical mechanisms were responsible for the formation of a specific fossil assemblage (Lyman 1994, 5). In order to reconstruct the past environment as accurate as possible in relation to the original deposited record, one must understand the different processes of taphonomy, comprising both biotic and abiotic factors. This understanding depends partly on the soil physics and also natural influences, such as the previously mentioned predator and scavenger bias and weather related circumstances.

The preservation of organic remains depends on a number of factors. If these factors are not favourable for the deposited material, it can degrade with time and leave no trace in the record. Usually calcareous soils tend to preserve well, whereas acidic soils are disastrous for preservation, especially of small animal bones.

Taphonomical processes can be divided into the categories *N-transforms* and *C-transforms*; natural transformations and cultural transformations (Lyman 1994, 5). The major changes in the background fauna and flora can be assumed to show little cultural influence, whereas the large mammal fauna that can be considered to be a part of the hominid subsistence does potentially implicate cultural transformations. The natural transformations of the fossil assemblage can be divided into biotic and abiotic factors.

Important biotic influences in the record, depending on the type of soil, can be microbial attack, dissolving and disintegrating parts of animal remains. Also bioturbation can have effects on repositioning artefacts and other remains. Apart from small and micro fauna, larger sized animals can also influence the distribution patterns in the deposited record, for example predators, or scavengers that accumulate their prey (Lyman 1994).

Abiotic, post-depositional factors that may influence the record can be assigned to weather and soil physics. Remains on the surface, exposed to all day to weather changes are likely to degrade faster than remains that are deposited and covered by substantial amounts of soil or water, protecting the material from external influences. Climatic factors are included in the abiotic factors. Movement in the record can be influenced by flooding, river movement, solifluction or aeolian action (Lyman 1994).

Both biotic and abiotic factors may affect a relatively small area in total, but if only segments of a site are excavated, it depends on the sample locations what abiotic and biotic factors play a role andwhat will be retrieved, and what the distribution of ecological components will look like.

4.1. Accumulation

Accumulation of the fossil record can be initiated by biotic and abiotic factors. Accumulation by water could be regarded as non-selective accumulation, whereas accumulation by hominins and other predators and scavengers are selective accumulators (Lyman 1994). Accumulation by natural bias, such as a flood, is often selected based on weight and density of the bone material; the heavier, dense material is likely deposited nearby, while smaller remains have the tendency to be washed away further from the other part of the assemblage (Lyman 1984; Lyman 1994; Behrensmeyer 1975). Patterns in flood accumulation may differ according to the type of deposit that is accumulated; whether it was a death assemblage, which already has been selected, or a living community, or a mix of both (Lyman 1994; Hanson 1980, 159).

There are several ways by which ecological data can get lost in the archaeological record. The soft-tissues can degrade and the remaining skeletal material can disintegrate due to the chemical features of the soil. Other ways in which the originally deposited assemblage may be destroyed are as a result of transportation by water and soil movement/mechanics. These modes of transportation can alter the faunal compositions in different ways. Transportation by slow moving water can result in the movement of the assemblage within a limited distribution area, whereas fast moving waters can disperse the assemblage across larges areas, scattering the original assemblage more than in the case of slow moving waters.

The Voorhies groups are based on experiments with disarticulated bones of *Ovis aries* and *Canis latrans*. It could be concluded from these experiments, that some skeletal elements are more likely to be moved by fluvial processes than others (Lyman 1994, 172). Voorhies groups can be described as sets of bones that display varying probabilities of being moved by fluvial processes (tab. 3; Lyman 1994, 172).

Behrensmeyer (1975) expanded the concept of Voorhies groups, by including interpretations on the structural density of bones and the size and shape of bones that influence the probability that a particular bone will be transported by fluvial actions (Lyman 1994, 172; Behrensmeyer 1975). The presence or absence of specific types of bones in an assemblage can thus provide information on the sedimentary history of bone assemblages.

I	I & II	II	II & III	III
Immediately moved, may float or bounce along bottom		Gradually removed, stay in contact with bottom		Lag deposit
Rib Vertebra Sacrum sternum	Scapula Phalange ulna	Femur Tibia Humerus Metapodial Pelvis radius	Ramus of mandible	Skull mandible

Table 3 Characteristics of Voorhies groups I-III. Dispersal rates described for the Voorhies groups related to the skeletal parts (after Lyman 1994, 172; Voorhies 1969)

4.2. Soil chemistry

To get an idea about the influences of soil physics on the preservation and degradation of animal remains, the article ‘Bone Degradation, Burial Medium and Species Representation: Debunking the Myths, an Experiment-based Approach’ by Nicholson (1996) is analysed. Nicholson conducted experiments to address the questions whether pH and drainage regime determine bone survival and whether bone decomposition processes proceed in similar rates in skeletons of a similar size from different animal groups (Nicholson 1996, 514). To analyse the effects, she used several sites with different soil conditions (acid, neutral and basic), where animal remains were buried. This study made it clear that soils with a neutral pH are the least destructive to faunal remains. Basic soils have a general preservation that is not as good as the preservation in neutral soils, but it is better than in acidic soils. In the different acid soils, preservation varied with pH level and drainage. The moorland site with a pH between 3,5-4,5 was most aggressive to the faunal remains; the fish remains had completely disintegrated, while bones from birds and rodents were still partly preserved, although the bone structure had changed. The preservation of fish was variable in the different sites; while preservation is generally limited in the highly acidic moorland site, preservation varied in the other acidic and neutral sites.

This experiment shows clear differences in preservation of acid and basic (alkaline) soils, where preservation in acid soils is limited. According to this pattern, and assuming the influences would have been the same in the past, one would expect the preservation of biotic remains in acid layers to be less prominent than preservation in more calcareous layers. To verify these assumptions, the faunal data should match the expected patterns.
A difficulty in assessing the link between soil chemistry and preservation of faunal content is the large amount of time that has passed since, in which many other degrading actors could have affected the other components. A lower species/individual (NISP/MNI) count in layers with acid environments, however, would show a certain correlation to preservation and pH of the soil. The results of this research can be used to interpret patterns of absence and degradation in the Schöningen 13 II assemblages.

4.3. Spatial distribution and preservation patterns

Patterns in species distribution and patterns in diversity can be a reflection of the past ecosystem, if the context is not disturbed. Post-depositional processes like flooding could either increase the original species diversity or decrease it. In theory, species richness at a site can be increased if a faunal assemblage is brought in from a different wider area, marking a different habitat. In the same way, local diversity can decrease if a flood or a process with similar impact moves a part of the fauna away from the original location. Because of the many different possibilities of fluctuations in diversity patterns, it is advisable to analyse whether there is evidence in the fossil record for the occurrence of a specific accumulating event.

The preservation of fossil remains depends on multiple factors, including the sedimentary context. From sedimentological analysis it can be interpreted that the sedimentary context of 13 II consisted of a lakeshore area, with fluctuating water levels (Thieme 2007; Van Gijssel 2006, 87). A question one might ask, is whether preservation near the palaeo-lakeshore is better than on the shore. There is a possible preservation bias in remains deposited in different environments. Remains deposited further upon the shore are likely to be less well preserved than remains deposited in an aquatic environment. In aquatic environments remains are sealed from external factors that may cause degradation of the material. The level of preservation in aquatic environments is not in every case per se better than on land deposition, depending on the salinity, acidity, velocity of the water stream and accumulation rate of sediments in the water body. It is evident however, that the species compositions in both types of environment can differ significantly. Also certain groups of animals can show a higher preservation rate in moist environments, such as insects.

Ecological abundance of the species are an important factor that may influence the presence and distribution in the fossil record. Ecologically abundant groups, for example small rodents, amphibians and birds, are not necessarily taphopnomically durable. Large carnivores on the contrary are less abundant, but have a higher preservation ratio, because of the bone size and structure. Large herbivores are assumed to be the most abundant group in the fossil record, because these taxa are relatively abundant in the ecological record, and have a high durability in the fossil record.

Apart from a variation in preservation through location of deposition, distribution patterns may also vary because of differences in size of the bone material. It is generally accepted that the larger and more compact a bone structure is, the better it will be preserved. In large mammals, mainly the long bones, costae and vertebrae will be preserved, either because of the size, or because of the bone density. Bones of smaller animals can generally only survive in more moderate conditions than large animal remains. Teeth and molars from a separate category in preservation, as dentine and emaille usually preserve better than bone remains. It is thus possible to find traces of small mammals in acidic environments, but nevertheless, the total of remains will be smaller for small mammals than large mammals.

4.4. Living community vs. death assemblage

Death assemblages of ecosystems are generally different in composition than the living communities, for example in age profiles. Death assemblages (thanatocoenoses), in its turn, also differ in composition from the deposited record as well as the preserved and the identified assemblages (fig. 13).

The biological community is defined as biocoenose. A thanathocoenose is a reflection of the deceased population o f the biocoenose. The transition from biocoenose to thanatocoenose involvesaccumulation and deposition of faunal remains (Lyman 2008, 23).

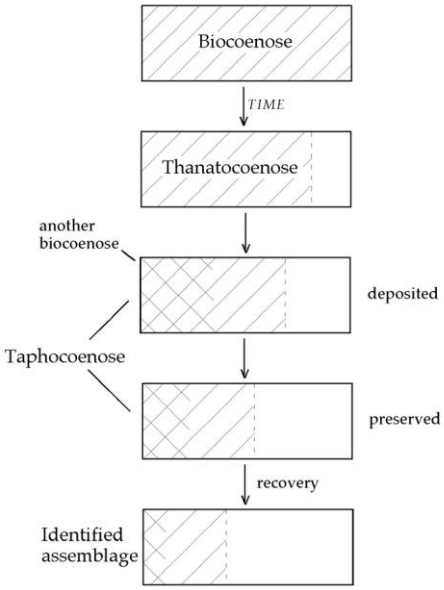


Figure 13 Schematic pathway from a biocoenose, the living community, to the identified assemblage (Lyman 2008, 23)

The taxonomic composition and abundances of the living assemblage (biocoenose) are the main goal of palaeoecological research. What palaeoecologists encounter in the fossil record, however, is an altered version of the death assemblage, or thanatocoenose (Lyman 2008, 22). Organisms in a death assemblage can form a statistical population, but as the death assemblage is no direct reflection of the living community, the organisms in the fossil record cannot be used directly to analyse the population structure in a past ecosystem (Lyman 2008, 22). The effective assemblage a palaeoecologist can use is the identified assemblage, which reflects the identified remains within a thaphocoenose (Lyman 2008, 23).

4.5. Sampling

The sample size and sampling location are of influence on the quantity and type of species that is recovered. Sampling locations in areas with better preservation circumstances can yield a higher species diversity and NISP than locations where preservation is limited (Lyman 2008). The richness of species in the fossil record thus partly depends on the ecological abundance of species as well as the archaeological preservation. Sampling location may also influence the pattern in species recovery. If the sampling location is similar throughout the levels, it can be assumed that the preservational circumstances are similar in these levels as well. In case of random sampling, a selection of the levels may show a bias towards species from other depositional contexts if these are not similar throughout the levels. If random sampling is applied with no substantial division of sampling in former aquatic and terrestrial habitats, the ratios of species from these contexts may vary due to differences in sampling location rather than changes in the physical environment. Besides sample location, the species-excavated area relationship also plays a part in the diversity of species in the fossil record. It can be assumed that the number of species found in an area depends on the total excavated area. The total number of species found in the fossil record will increase until an equilibrium of maximum number of species per area is reached.

Biases in sampling are described by Bush *et al*. (2004, 667) as alpha, beta and gamma biases. Biases can occur in the processes of preservation and sampling. The alpha bias is characterised by a distortion in the measurement of local diversity. The most important example of an alpha bias is undersampling, where not every preservable taxon is present in the record due to sampling limitations (Bush *et al.* 2004, 667).

Beta biases are the result of "*a failure to preserve or sample the full variety of habitats within a region*" (Bush *et al*. 2004, 668). These biases are created by either insufficient sampling or preservational circumstances, for example influenced by the structure of sedimentary environments or habitats.

Gamma biases result from comparing datasets of different types or regions (Bush *et al.* 2004, 668). Gamma biases are less significant in this thesis, as this bias concerns comparisons of different types of regions from a high variability in latitudes, with a higher amplitudal difference than the maximum latitudinal distance between sites used in this study (Bush *et al.* 2004, 668).

4.6. Time averaging and palimpsests

Communities from past ecosystems do not necessarily reflect similar compositions as modern ecosystem communities. Unknown compositions in the fossil record could on the one hand be indicative of time averaging of the fossil record, with unknown periods of deposition and stasis or erosion, or, on the other hand, compositions that show no link with present-day communities could be the common species composition of a certain period in time (Allison and Briggs 1991; Behrensmeyer 1992). It is difficult to distinguish between the two possibilities if the species diversity in fossil assemblages shares no or few modern analogues. In this paragraph the effects of time averaging and palimpsests on the fossil record are discussed.

Palimpsests usually refer to partial destruction or reworking of material traces because of taphonomical processes, superimposition of successive activities or the variable erasing of earlier traces in the fossil record and temporal overlapping of various activities in the record (Lucas 2005, 37; Bailey 2007, 203). Palimpsests can involve the total destruction of all (archaeological) information, with the exception of the most recent depositions. On the other hand, palimpsests can also involve the accumulation and mixing of successive, partially preserved remains, creating assemblages that differ from the original deposition in composition and diversity (Bailey 2007, 203).

Palimpsests can be divided into several categories (Bailey 2007):

> *True palimpsests*: True palimpsests are palimpsests in which virtually all traces of earlier activity have been removed, with exception of the most recent level of activity. It is difficult to distinguish true palimpsests from a single episode of deposition in the archaeological record. The presence of different material traces in the vincinity may indicate the potential existence of earlier levels that have been removed over the course of time (Bailey 2007, 203).
>
> *Cumulative palimpsests*: Characteristic for a cumulative palimpsest is that successive episodes of deposition remain superimposed, without loss of evidence, but re-working and mixing of the deposits make it difficult to separate the remains into single entities. The material variability in the individual levels within cumulative palimpsests is usually. Cumulative palimpsests differ from true palimpsests by a loss of resolution rather than a loss of material (Bailey 2007, 204).

Time averaging is described as the amount of time represented as a function of the sedimentary and taphonomic processes (Behrensmeyer 1992, 75). Because of the discrepancy in time resolution, biotic remains from different evolutionary stages and environments may be mixed. This may cause difficulties in interpreting non-contemporaneous ecological compositions (Behrensmeyer 1992, 76). Whether time-averaging influences our understanding of palaeocommunities depends on the scale of time-averaging and the quality of information that is required to answer the questions related to the palaeoenvironment (fig. 14; Behrensmeyer *et al*. 2000, 118). Effects of time averaging in the fossil record increase when the sedimentation rate is low. This results in a potential mix of several communities, indicative of succeeding periods of time, and perhaps of different climatic or environmental conditions.

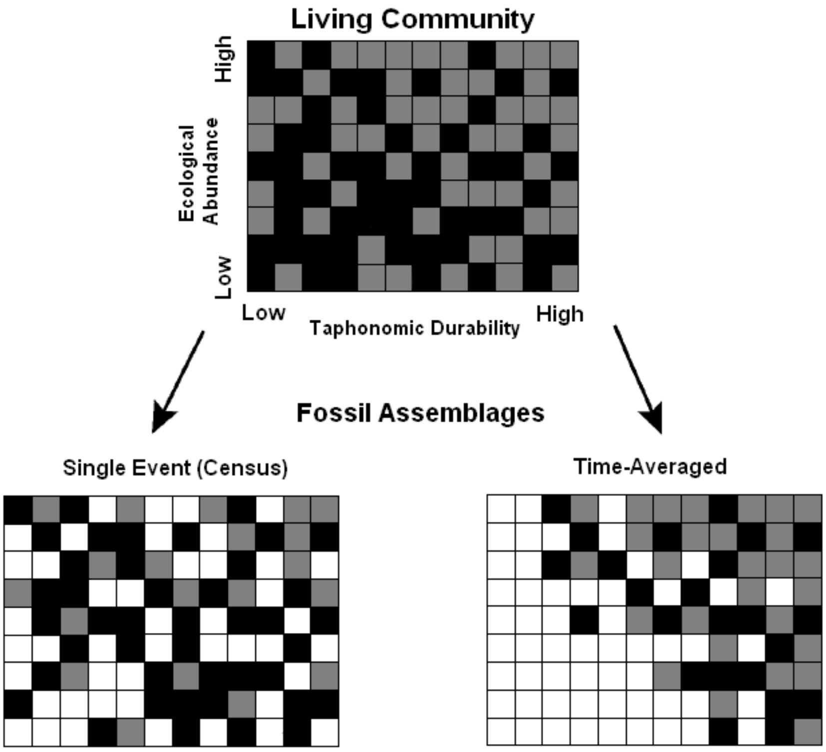


Figure 14 Schematic portrayal of changes in two types of fossil assemblages (single event (or catastrophic event) and time-averaged) compared to a hypotethical living community. The cells are characterised by two variables; ecological abundance and taphonomic durability. Black cells represent permanent residents and grey cells represent transient species. The white cells in the fossil assemblages represent absence of species due to taphonomical processes. The single event assemblages will cover most permanent species and some transient species, whereas this sample is more random in the time-averaged sample, which is biased toward higher durability of the remains and the more abundant species (after Behrensmeyer *et al.* 2000, 108)

The impact of temporal averaging depends on species dynamics, initiated by fluctuations in climate and environment. As faunal communities are dynamic entities that react to changes in the composition of the community, the faunal assemblage of a single site will vary with each fluctuation in environmental change. Temporal averaging can be minimised by a high sedimentation rate, because of the rapid burial of the depositions, protecting it from intermixture with later faunal assemblages (Behrensmeyer *et al.* 2000; Selden and Nudds 2004). But as this rapid sedimentation is often not the case in the majority of the (Middle) Pleistocene sites, we can expect a certain amount of temporal averaging in the various levels. The effects of time averaging could also be theoretically be reduced if archaeological sites are excavated in detailed units, minimising the time span of a level.

Time averaging of the fossil record would theoretically result in a diversification of the fossil assemblage, if the environment, and thus the faunal components, have changed over time (Lyons 2005, 170). However, according to Lyons (2005, 170), time-averaging may increase the probability that species are found at a site, because time-averaging allows accumulation of species. It depends on the amount of time represented within the time-averaged assemblages whether communities with different ecological tolerances are mixed. The way in which the faunal compositions changes depends on the intensity of the environmental/climatic change. The impact of this time averaging is clearly stated by Stearn and Carroll (1989, 379):

> *"…because fossil assemblages are described using time-averaged data, they cannot be accurate representations of the living community. The fossil assemblages will be less similar to the living community the greater the temporal variability of the living community and the longer the time averaged in the fossil assemblage."*

Minor fluctuations in climate and environment would result in a temporal diversification of the small (in)vertebrate fauna, because these species are more subjected to changes in environment. Climatic fluctuations with a higher impact, changing the local climatic envelope, would force also the movement of larger vertebrates, for example resulting in a shift from a typical forest adapted fauna community to a more steppe or tundra adapted fauna. In short, fauna compositions in a level that are similar to compositions from sites of the same age and region, likely indicate that the environment did not change significantly, whereas the co-occurrence of non-analogue species would indicate there were changes in the environment in the time span of the level.

4.7. Non-analogue communities

The fauna in fossil (Middle Pleistocene) records may show species compositions that are non-analoguous with present-day species compositions. As an example, species that live in different geographic regions at present, such as (cave) lion and reindeer, can occur in the same context in the (Middle) Pleistocene, because the climatic envelope of species may reflect a broader tolerance than the present distribution may relfect (Polly and Eronen 2011).

Whether the non-analoguous fauna represent a non-analogue composition or reflect a certain amount of time averaging of the fossil record is difficult to interpret. Examples of non-analogue fauna communities are depicted in fig. 15. In this figure, a clear distinction is made between the two major Pleistocene faunas; the interglacial *Elaphas* fauna and the glacial *Mammuthus* fauna. The extant species from this example often occur in different biomes in present-day environmental conditions. Good examples are *Hippopotamus amphibius* and *Saiga*, that were found in Pleistocene contexts in Europe, but have a modern distribution in Africa and Asia respectively. The species depicted in the center of fig. 15 are not associated with one certain faunal community, but their broad ecological tolerance allows the species to be able to cope with various environments.

It is widely accepted that the faunal communities depicted in fig. 15 reflect faunal communities that are non-analoguous in community structure, rather than non-analoguous in terms of environment and ecological preferences. Compositions of species that are environmentally incompatible may be indicative for time-averaging, rather than non-analogue communities based on community structure. Examples for time-averaging may be the co-occurrence of thermophilous species and species indicative for arctic conditions. A combination of for example musk ox (*Ovidbos moschatus*) and hippopotamus (*Hippopotamus amphibius*) is ecologically impossible. This co-occurrence would thus suggest time-averaging of succeeding stratigraphic layers, rather than representing a non-analoguous faunal community.

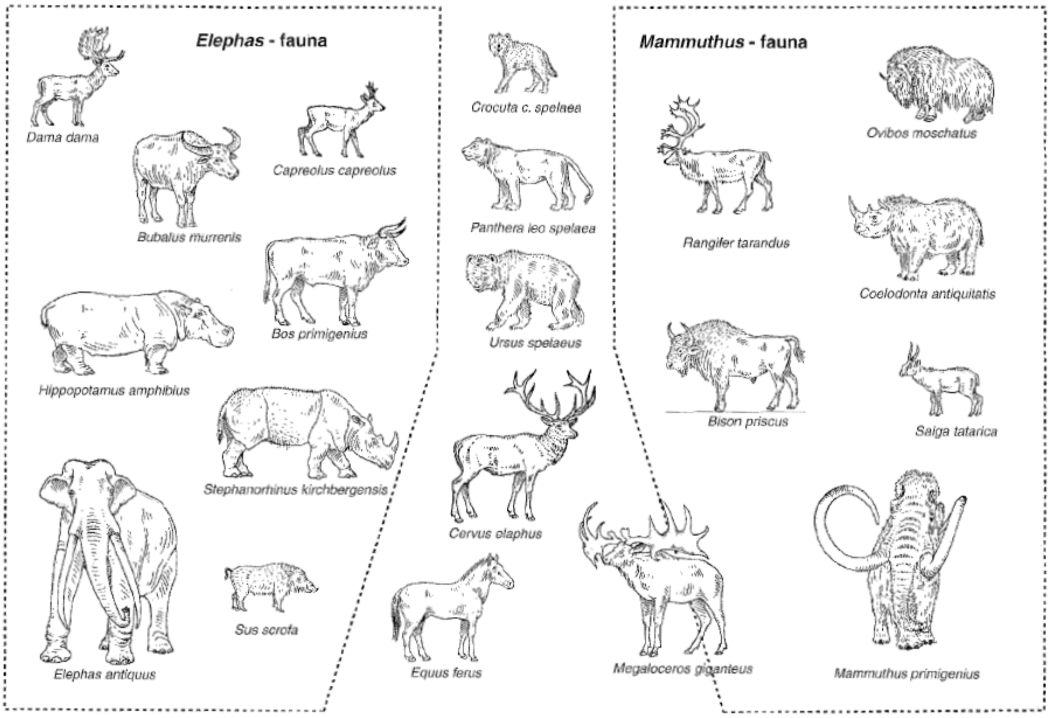


Figure 15 Mammal fauna communities in the Middle and Late Pleistocene. The *Elaphas* fauna is indicative for interglacial contexts, whereas the *Mammuthus* fauna is characteristic for glacial conditions. The fauna in the center can be found in association with both types of assemblages (Von Koenigswald 2007, 446; Von Koenigswald 2002)

The composition of species in the fossil record is not a direct reflection of the living community, if the remains reflect a time-averaged assemblage. Fossilised remains of catastrophic assemblage tend to display a community more similar to the living assemblage than time-averaged samples. The age class distributions in time-averaged fossil assemblages generally differ from the age classes in living communities. Natural death assemblages will display more adult individuals, while catastrophic assemblages would show a higher component of juvenile individuals.

If there is evidence of a catastrophic event, without significant taphonomic influence, the unknown community may prove to be showing a different community than is known in present-day ecosystems. The fossil assemblages could reflect a time-averaged sample of the palaeocommunity, but it could also reflect a less biased sample, determined by a catastrophic event. In this case, the fossil record reflects a different composition of death profiles than non-catastrophic time-averaged samples. Natural death assemblages often reflect exclusively the adult population, whereas catastrophic assemblages include individuals from all age classes according to the aging profile of living assemblages. A high amount of old individuals and a low amount of young individuals in a death assemblage is indicative of a natural death assemblages, whereas a high number of young and prime individuals are found in the assemblage, one would likely speak of the result of a catastrophic event.

5. Methods

In the previous chapters, the theoretical aspects of ecosystems and the reconstruction of past ecosystems is discussed. This chapter will focus on the available data and the methods that can be used for the analyses.

The data for this thesis consists of the floral and faunal data from Schöningen 13 II-1 to 13 II-4 that has been identified thus far. The flora has been examined by Brigitte Urban, while the fauna remains are identified by various researchers from the Landesambt für Denkmal Pflege, Sachsen-Anhalt and Leiden University. The flora will be used as supporting evidence for the climatic fluctuations throughout the profile of 13 II. The palynological data has already been analysed (Urban 2007a; Urban 2007b; Urban *et al.* 2011). In this thesis, the environmental characteristics derived from palynological data shall be used as an base of environmental characteristics to compare to the faunal data.

In order to make accurate reconstructions of past ecosystems it is crucial to understand general ecosystem functioning and species relations. To get a better understanding of the ecological patterns of the record in Schöningen 13 II, I shall use data from contemporaneous archaeological sites, as well as modern analogues. Modern analogues can give insight in predator-prey relations and species distributions in present-day biomes. The following flowchart shows the systematic pattern from ecosystem of the past, via the fossil record towards a reconstructed ecosystem.

Fig. 16 shows a schematic pathway from past ecosystem to reconstructed environment. Many external factors influence deposition, sampling and preservation, thus the composition of the ecosystem can be influenced prior to, during and after deposition. Elements that survived the process of fossilisation are subjected to another form of diversity loss by sampling and excavation. The reconstruction of past environments can be assessed by a variety of environmental proxies, including biotic and abiotic elements. The excavated remains will be subjected to various analyses that will lead to interpretations on the state of the past environment. These analyses can include comparison with fossil assemblages, modern analogues and other analyses, such as predator-prey ratios, that can be used to predict the presence of species in the fossil record.

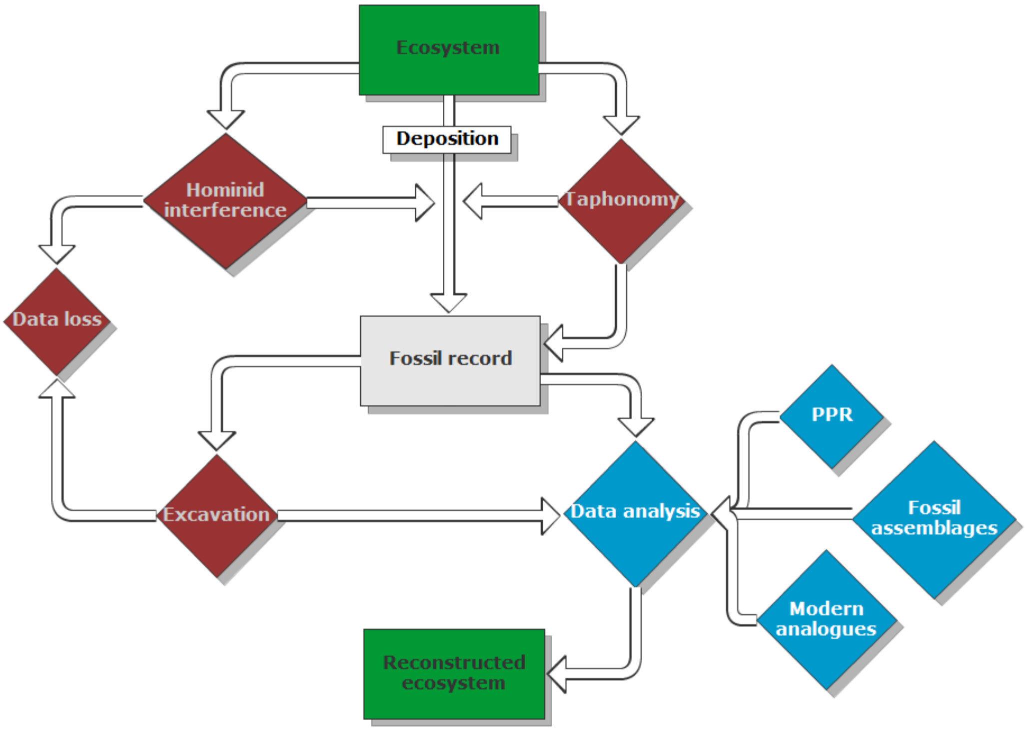


Figure 16 Schematic path from past ecosystem to a reconstructed ecosystem, via the fossil record. (diagram by Neeke Hammers 2012)

The various faunal groups can give different information about the past environment. The small mammal fauna is indicative of the type of vegetation and precipitation/humidity, amphibians are in general indicative of humidity, reptiles are indicative for temperature rather than humidity. Fish can be indicative for the type of water (salinity, chloridity, velocity, depth) and the density and type of water vegetation or bottom. The avifauna can be indicative for water conditions as well. Large mammal fauna is less indicative for climates, because of the broader level of tolerance. Carnivores take a rather peculiar place in the environment, because these species are rarely limited to specific biomes, but depend on the presence and abundance of prey species. The combination of environmental preferences of all these groups can give a detailed view of the past environment. Apart from the biotic elements, also abiotic elements can be crucial for the understanding of the fossil record. The data that are of use in this respect are pH values, stratigraphy and sedimentology. The patterns in presence, absence and diversity in the faunal record of Schö 13 II shall be compared to the available data on soil chemistry (Urban *et al.* 2011).

5.1. Reconstructing ecosystems from the fossil record

Pleistocene environments can be reconstructed with the aid of modern analogues, but it is important to remember that both the modern and fossil assemblages are likely to show bias. Modern analogues can be used if you assume that the environmental preferences of species have not changed over time. Nevertheless, it is important to keep in mind that present distributions can be influenced by man. If we are aware of the potential biases in both the fossil and the modern record, modern analogues can serve as a proxy to past environments.

While making reconstructions of the fossil record, one could ask which elements would have been present in the fossil record, and in which quantities or compositions these were found. Another question that comes to mind is whether diversity patterns and territorial relationships can be retraced in the archaeological record. To make accurate interpretations on the fossil record, one must include as many proxies as possible, that are analysed by a variety of methods. Important information for environmental reconstruction can include sample size, geology and (predator) accumulation. The analyses that can be applied are analyses of the environmental preferences, climatic development, predator and prey ratios and taphonomical analysis.

Most attention is paid to 13II-4, which will presumably produce the most detailed record, with a focus on the large mammal fauna. This discrepancy in research focus must be taken into account, in order to reconstruct the environment with as little bias as possible. Other factors that are important for the reconstructed environment are details on the geology and possible mineral content. Geology and the nature of soils is important for the understanding of the distribution of plants, as these depend on geological factors as well as climate.

As the fossil record is likely heavily fragmented, attention will also be paid to the composition of modern ecosystems, in order to create a better understanding of the past environment. Comparison with modern analogues, however, is not as straightforward as it may appear. Modern species distributions are in many ways influenced by human presence and interference. Also modern analogues cannot directly be linked to extinct species. Some extinct species either have no modern counterpart, or the species could be compared to a modern species in physiology, but a direct link cannot be established with certainty. These modern analogues will therefore be used as an aid to the understanding of past ecosystems, and not necessarily as direct comparison.

Information on species niches will be gathered as accurately as possible, including information on minimum and maximum temperatures, preferred habitat, species distribution, diet and type of biome. Possible dependence upon other species can also be noted. The species will be grouped per level to acquire detailed information on environmental changes between the levels of Schö 13 II.

For the study of the environment, one has to work backwards from the fossil record towards the possible past environment, but this cannot happen directly, as the archaeological record is likely to be fragmented and is not necessarily similar to the deposited record. First a few steps have to be taken to get the record straight and analyse the possible influences in the record, both taphonomical and ecological, to analyse what could have happened at the site. Modern analogues are included in this study to get a less biased view of species compositions in various ecosystems.

The knowledge from data recovered from the fossil record can be extended by applying a theoretical model. A study of several present day national parks has revealed specific patterns in species compositions along the different latitudes, altitudes and ecoregions.

5.2. Methods and data

Standard methods in palaeoenvironmental research focus on the presence of species in the fossil record and their environmental implications. The methods applied in this thesis will focus on the presence of species in the fossil record as well, but also the absence of species will be discussed. The data from Schö 13 II will be compared to modern analogues. The ecological preferences of the species in the fossil record are used to get an indication of the past environment and change of this environment throughout the site. Other methods used in this thesis are diversity analyses, predator-prey ratios and soil chemistry.

Because there is little numerical data for most of the species, I decided to analyse the data by using methods that allow comparisons of species diversity patterns rather than absolute counts in MNI (minimum number of individuals) or NISP (number of identified specimens). I am aware of the fact that the analysis of species compositions may therefore be less detailed, but if the proxies are used in a similar way, the comparisons between diversity patterns and environmental change can still be made.

Environmental preferences

The basic method in this study for environmental reconstruction is analysing the environmental preferences and habits of the faunal assemblage. These environmental preferences are derived from MacDonald and Barrett (1998), Mitchell-Jones *et al*. (1999), Boere *et al.* (2006) and Hutchins (2004). This application only works for species that are also present in extant communities. The goal of this method is to give an overview of the species preferences in the different levels. This analysis may prove whether or not there is significant change in environment between level 13 II-1 and 13 II-4.

Diversity patterns and species compositions

The species richness of large mammal fauna in Schö 13 II is limited, in particular when regarding the carnivore record. The referencing archaeological sites from similar age in Northwest Europe (Germany and UK) generally have a higher (carnivore) species diversity. The diversity patterns in the four levels of Schö 13 II, based on total species richness (including amphibians, reptiles, fish and mammals), will be compared to both diversity in archaeological sites and modern analogues. In the comparative analysis of diversity patterns, molluscs and birds are not included, because molluscan data was not widely available for both archaeological sites and modern analogues. Birds are excluded from the diversity studies, because the number of bird species in the modern analogues exceeds the number of bird species in the fossil record by far. Insect data is excluded from this research, because there was insufficient data available of this group to apply diversity analysis and environmental studies.

The modern analogues are included in this research, because the data on species compositions is less biased in present assemblages than in assemblages from the fossil record that are subjected to a variety of selective processes. The compositions in both modern analogues and fossil assemblages can also be used to analyse which species are absent in Schöningen, providing a comparative record to extrapolate the diversity in 13 II to more realistic compositions.

PPR

The predator-prey ratio (PPR) is a method which can be used to discover the relative ratio between the number of medium to large sized predators and large herbivores. This method will be used to get insight into the fluctuations in predator and prey assemblages through time. The PPR on itself is, however, not an indicator of the total number of predator and prey species in a site, therefore this ratio cannot be seen as accurate indicator. As a reference I shall use PPR values from both modern analogues and fossil assemblages, plotted against each other.

In order to get an idea about the structure of ecosystems and the related predator-prey compositions in various biomes, this thesis provides a case study of the mammal fauna compositions in sites across Europe. To analyse predator-prey relations additional sites are analysed: two African national parks (Nechisar, Ethiopia and Serengeti, Tanzania) and one American National Park (Yellowstone, Wyoming, USA). The European sites can be divided into temperate forest biomes, tundra, steppe and variations on these sites, including fluvial areas, high and low density woodlands and high altitude sites.

Soil chemistry

Many fossil assemblages reflect fluctuations in species diversity. This fluctuation could be the result of environmental change, but it is also possible that diversity loss is steered by taphonomical processes. For this case study I shall correlate the data from the soil analysis with the patterns of species diversity throughout the levels. Nicholson (1996) created a framework for the preservation of faunal remains in various soils. The observations from this work will be incorporated in the interpretation of patterns in preservation in Schö 13 II, which will be analysed by comparing the diversity of small vertebrates to the fluctuations in soil chemistry (pH and sedimentology), provided by Urban *et al.* (2011).

5.2.1. Archaeological sites

To analyse whether Schöningen 13 II reflects a fossil assemblage representative for the Middle Pleistocene, I compare the composition of this fossil record with that of six other sites from Early and Middle Pleistocene contexts. The sites selected for this research are Bilzingsleben, Hoxne, Swanscombe, Boxgrove 4C, Repolusthöhle and Untermassfeld. The first five sites date to the Middle Pleistocene and Untermassfeld to the Early Pleistocene. Despite the age discrepancy I decided to include this site because of the non-analogous large mammal composition. The site is especially remarkable for its high amount of large carnivore species.

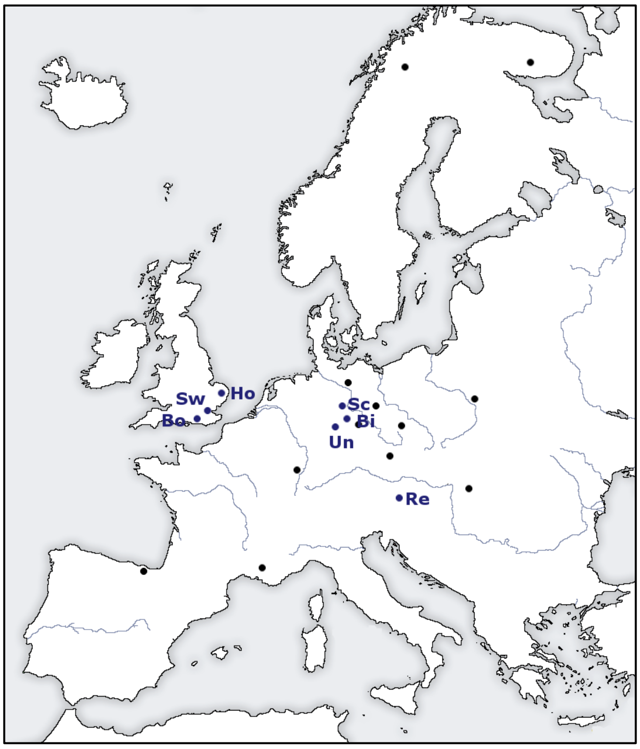


Figure 17 Site location of the archaeological sites (blue) relative to the modern analogue sites (black). Bi = Bilzingsleben, Bo = Boxgrove, Ho = Hoxne, Re = Repolusthöhle, Sc = Schöningen, Sw = Swanscombe, Un = Untermaßfeld.

The archaeological sites used as comparative sites in this study are chosen for their age and/or geographic position. It is expected that the large mammal assemblages in Middle Pleistocene contexts are comparable, but not necessarily the same. The similarity in large herbivore compositions in the archaeological sites could give information on the presence of certain carnivore species. The virtual absence of large carnivores in Schöningen does not fit the average pattern in Middle Pleistocene sites. The presence of large carnivores at contemporaneous sites with a similar large herbivore fauna could suggest a similar large carnivore assemblage at Schö 13 II.

Site	Country	Period	Type site	Latitude	Longitude
Bilzingsleben	Germany	Middle Pleistocene	Open air	51°N	11°E
Hoxne	United Kingdom	Middle Pleistocene	Open air	52°N	1°E
Swanscombe	United Kingdom	Middle Pleistocene	Open air	51°N	0 °E
Boxgrove	United Kingdom	Middle Pleistocene	Open air	50°N	1°W
Repolusthöhle	Austria	Middle Pleistocene	Cave	47°N	15°E
Untermaβfeld	Germany	Early Pleistocene	Open air	50^{0}N	10^{0}E

Table 4 Archaeological sites and their relative age

The archaeological sites in this thesis are selected on basis of the fossil content of the sites, as well as age and location. A total of six archaeological sites is included; three from the UK (Boxgrove, Hoxne and Swanscombe), two from Germany (Untermaßfeld and Bilzingsleben) and an Austrian cave site (Repolusthöhle).

Bilzingsleben

Bilzingsleben is a Middle Pleistocene site in Central Germany, approximately 130 km south of Schöningen. It is situated in the northern part of the *Mittelgebirge*, between the Harz mountains and the Thüringian forest, 50 km south of the North German *Tiefland* (Mania 1980, 44). Geologically, the site is situated on the edge of the Thüringer Basin. The surrounding sediments (sandstone, mollusc rich chalk) date from the Thüringian Trias (Mania 1980, 45). The archaeological site is positioned within the range of the Elsterian ice expansion, but it falls outside the range of the Saalian ice advance, in contrary to the Schöningen sites. The maximum range of the Elsterian ice expansion ended approximately 35km south of the site, whereas the Saalian ice extent reached the site to 30 km north o the location (Mania 1980, 47).

Hoxne

Hoxne is the type locality for the Hoxnian Interglacial (Ashton *et al.* 2008). This British interglacial is often correlated to Holsteinian Interglacial on the continent. The sediments represent lacustrine and fluviatile deposits. Chalky gravels and silts are the characteristic fill of the strata. The fill of Stratum B is interlayered and covered with coarser sandy gravels (Wymer and Singer 1993, 9-10). The Hoxnian data used in this thesis originates from Stratum B (Gladfelter 1993). The fauna at this level is indicative for interglacial conditions (Stuart *et al.* 1993).

Swanscombe

The archaeological site of Swanscombe is a fluviatile sequence in a former terrace of the Lower Thames river. The faunal data used in this thesis originated from the Lower Loam, a channel infill, superiposing the two underlying gravels (Basal Gravel and Lower

Gravel) (Ashton *et al.* 1995). The Lower Loam predominantly consists of clayey sands. the site is associated with the Hoxnian Interglacial, correlated to MIS 11 (Schreve 2001). The palynology of the site suggests temperate late interglacial conditions. This site yields a relatively rich mammal fauna, comparable to the Schö 13 II fauna.

Boxgrove

The archaeological site Boxgrove is correlated to the Cromerian Complex, dating to the early Middle Pleistocene. The site is situated in a chalk quarry on the West Sussex Coastal Plain (Roberts 1999, 26). The archaeological unit used in this thesis is Unit 4C. The Boxgrve sequence consists of Slindon silts and gravels ant the base, followed by various marine cycles of trangsgression and regression phases. These cycles are succeeded by the Slindon sits, Unit 4 (Collcutt 1999, 86). The sediments in this sequence mainly consist of muds. The lower boundary of this unit is difficult to establish because of post-depositional deformation (bioturbation) and chemical alteration (Collcutt 1999, 86). Unit 4C represents the final stage of the transition from marine to (damp) terrestrial conditions (Collcutt 1999, 87).

Repolusthöhle

Repolusthöhle is a Middle Pleistocene cave site in Austria. The site is dated to 200-220 ka (Fladerer 2000, 210). The faunal remains from this site were interpreted to represent an interglacial character, although some faunal elements are indicative of colder temperatures, for example *Rangifer tarandus*. The fauna of Repolusthöhle is rich, compared to other Middle Pleistocene sites (Döppes *et al.* 2008). This can be the result of specific preservational conditions, because of a $CaCO_3$-rich environment and accumulation in cave sites (Rosendahl *et al.* 2007, 455).

Untermaßfeld

Untermaßfeld is an Early Pleistocene site situated in the Thüringian Basin. The site yields a rich and diverse large mammal fauna, including an uncharacteristcly rich large carnivore fauna, but with a poor small carnivore assemblage. The remains of Untermaßfeld are presumably accumulated by a catastrophic event (Kahlke 2001, 943). Indicators for a catastrophic event are the age profiles of *Bison menneri* as well as the presence of species indicative for a wide variety of biotopes (Kahlke 2001, 972). This site is included to get insight in the potential number of predator species relative to prey species in fossil sites.

5.2.2. Modern analogues

In this thesis modern analogues are used as a proxy to analyse present day species compositions in various environments throughout Europe. These modern analogues are used as supplementary data to fossil assemblages, because the latter records may be biased due to taphonomical processes and sampling biases. The modern analogues are especially interesting for the non-mammalian fauna, because these elements are often underrepresented in the fossil record or in archaeological research in general. Modern compositions of these non-mammalian faunas could therefore aid in the understanding of ecological preferences and distribution patterns.

National Park	Country	Biome	Biome class	Latitude	Longitude
Lake Torne	Sweden	Tundra	VII	68°N	18°E
Laplandskiy	Russia	Taiga	VI	67°N	38°E
Elbe Flusslandschaft	Germany	Temperate broad-leaf forest	II	53°N	10°E
Bialowieza	Poland	Temperate broad-leaf forest	II	52°N	23°E
Spreewald	Germany	Temperate broad-leaf forest	II	52°N	14°E
Krkonoše	Czech Republic	Temperate mountain system	V	50°N	15°E
Vessertal	Germany	Temperate broad-leaf forest	II	50°N	10°E
Trebon Basin	Czech Republic	Temperate forest	I	48°N	14°E
Vosges du Nord	France	Temperate broad-leaf forest	II	48°N	7°E
Hortobágy	Hungary	Steppe	IV	47°N	21°E
Luberon	France	Temperate broad-leaf forest	II	43°N	5°E
Urdaibai	Spain	Coastal marine wetland	III	43°N	2°W

Table 5 Modern analogue sites. Data derived from Biological Inventories of the World's Protected Areas Database (http://www.ice.ucdavis.edu/bioinventory/bioinventory.html) and Olson *et al.* 2001). The biome classes are for this thesis assigned to the seven different biomes distinguished in the modern analogue sites

The modern analogues used for this comparative study are presented in table 5. The sites are selected on the type of environment and availability of biodiversity data. The 12 sites, between 68°N and 43°N, are situated in seven different biomes (fig. 18; tab. 5). The temperate broad-leaf forest biome is most abundant in this case study. The two northernmost sites, Lake Torne (68°N) and Laplandskiy national park (67°N) are characteristic for a tundra and taiga biome, with a relatively low species diversity. The majority of the sites is situated in the mid-latitudes of Europe (between 53°N and 47°N). Six of these eight sites are temperate (broad-leaf) forests, Krkonoše is defined as temperate mountain system and Hortobágy is defined as a (temperate) steppe biome. The southernmost sites, Luberon, France and Urdaibai, Spain are assigned to a temperate broad-leaf forest biome and coastal marine wetland biome.

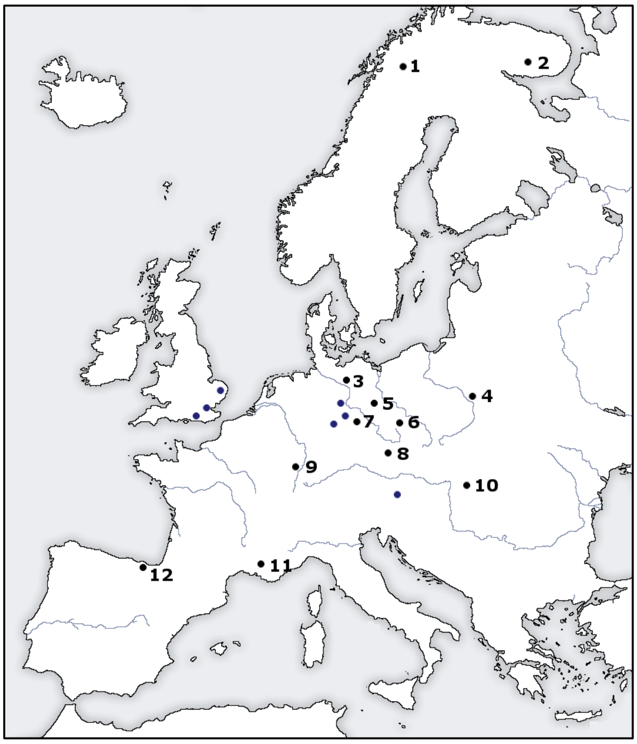


Figure 18 Site location of the modern analogue sites (black) relative to the archaeological sites (blue). 1. Late Torne, 2. Laplandskiy, 3. Elbe Flusslandschaft, 4. Bialowieza, 5. Spreewald, 6. Krkonoše, 7. Vessertal, 8. Trebon Basin, 9. Vosges du Nord, 10. Hortobágy, 11. Luberon, 12. Urdaibai.

6. Data

6.1. Palynology

The palynological record of 13 II is analysed and discussed by Brigitte Urban (Urban 2006; Urban *et al.* 2011). In this thesis, the signal in the palynological record will be compared to the environmental signal from the fauna. The pollen diagram represents both a subdivision of the record in the four separate levels and in Local Pollen Assemblage Zones (LPAZ) (tab. 6). In the floral record of Schö 13 II, including level Schö 13 II-5[3], there is evidence for 13 separate LPAZs. The LPAZ have as an advantage that each zone represents a single climatic stage within the interglacial sequence, and thus reflects a 'high definition' record of climatic changes in the past environment. The downside of the division in pollen assemblage zones is that these zones are not directly linked to the separate levels in 13 II, because the boundaries of these levels are defined by geological and sedimentological features, rather than by changes in the fossil record.

The faunal assemblages are separated per level, overlapping several LPAZ. It is therefore impossible to link the fauna with the flora on a detailed level.

Site level	**Climatic division**	**LPAZ**
13 II-4c/5	Reinsdorf Stadial C	RS III1
13 II-4	Reinsdorf Interstadial B	RS II
	Reinsdorf Stadial B	RS II, RS I2
13 II-3	Reinsdorf Interstadial A	RI 1
	Reinsdorf Interglacial A	RI 1, RI 2
13 II-2	Reinsdorf Stadial A	R3b, R4/5, RS I1, RS I2
13 II-1	Reinsdorf Interglacial	R3a, R3b

Table 6 Correlation of climatic divisions with local pollen assemblage zones (LPAZ)

The main characteristics of the Reinsdorf Interglacial are a climatic optimum characterised by a forest phase with the spread of *Tilia* before *Corylus*, which is only represented by low values, and by the occurrence of a late and less pronounced *Abies* phase. Furthermore, the Reinsdorf sequence shows two pronounced interstadials interrupted by stadial phases, characterised by a herb-rich and steppic environment (Urban 2006, 435).

6.1.1. Palynological characteristics per level

The floral pattern in Schöningen 13 II show a fluctuation in pollen throughout the profile (fig. 19). The first phase is interpreted as an interglacial optimum, based on the thermophilous taxa from level 13 II-1. In the second level, we can see a gradual decline of the

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[3] The level Schö 13 II-5 is included in the palynological and malacological research, but is largely excluded in research to the remaining groups. In this thesis, 13 II-5 is left out of the interpretations, because of the lack of data.

Alnus pollen, as well as a strong decrease in *Pinus* pollen, simultaneous to an equally strong increase in Poaceae.

Level 1

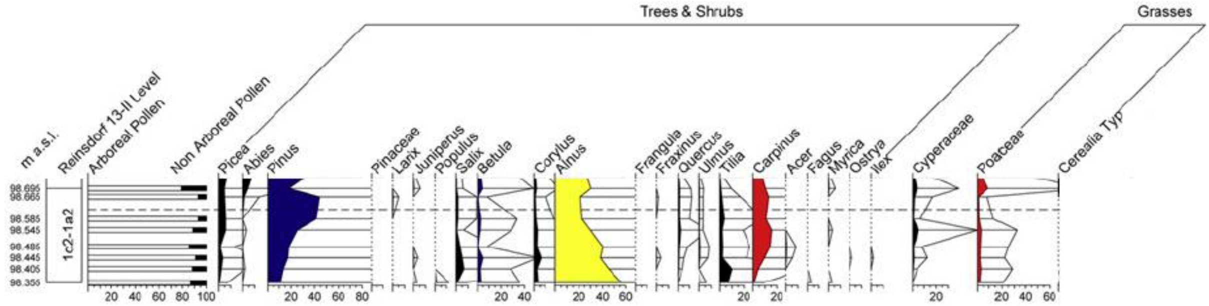

Figure 19 Pollendiagram of Schö 13 II-1 (after Urban *et al.* 2011, 133)

Level 13 II-1 coincides with LPAZ R3a and the lower part of R3b. In the palynological assemblage, two major groups of species are found that are indicative for slightly open deciduous forests and mesophilous mixed deciduous forests. The species indicative for a slightly open deciduous forest are *Acer campestre, Acer tataricum*, *Tilia cordata, Fraxinus excelsior, Prunus spinosa, Cornus sanguine* and *Crategus monogyna*. The elements indicative for mesophilous mixed deciduous forests are *Abies alba, Taxus baccata, Carpinus betulus, Sorbus torminalis, Berberis vulgaris, Sambucus nigra, Cerasus avium* and *Lonicera xylosteum* (Urban 2006, 425). The species *Linum austriacum* is indicative for temperatures 1.5-2 degrees higher than present.

The presence of slightly saline soil conditions are indicated by *Potentilla anserine, Rumex maritimus and Chenopodium rubrum,* whereas *Zanichellia palustris* is indicative for the presence of saline water. This evidence is supported by chemical data from the sediments.

The flora from 13 II-1 is characterized by an abundance of thermophilous, deciduous tree species. Characteristic for the Reinsdorf Interglacial is the low amount of *Taxus*, two pronounced *Tilia* phases, enclosing a *Corylus* phase. *Acer tataricum* and *Linum austriacum* are present in this phase, but these species have a present distribution in more southern areas (Johnson and More 2004).

Urban describes the environment of 13 II-1 as a *slightly open deciduous forest with mesophilous mixed deciduous forest elements* and light steppe elements (Urban 2006, 425). The proximity of the lake shore is characterised by a dense community of various tree species and an alder carr, indentified by the presence of many pollen from Alder, Ash, Birch and Oak. The soil preferences of the tree species is described in tab. 7. The majority of the species appears to be indicative for moist soils.

Species	soil preference	Current distribution
Acer campestre	nutrient rich loamy soils	Europe, Southwest Asia, North-Africa
Acer tataricum	moist soils	Austria to Caucasus
Tilia cordata	moist soils	Europe
Fraxinus excelsior	nutrient rich, moist soil	Europe, Caucasus
Prunus spinosa	loamy soils	Europe, North Asia
Cornus sanguine	loamy soils	Europe
Crategus monogyna	moist soils	Europe, West Asia
Abies alba	moist soils	south and central Europe
Taxus baccata	calcareous soils, mineral rich	Europe to south Sweden, east to Iran, south to North Africa
Carpinus betulus	clay soils	Europe, Asia Minor
Sorbus torminalis	loamy soils	south and central Europe
Sambucus nigra	avoids sandy soils	Europe, Southwest Asia, North-Africa
Cerasus avium	nutrient rich loamy soils	Europe, West Asia, North Africa
Ostrya carpinifolia	moist soils	southeastern France to Caucasus
Alnus glutinosa	moist soils	Europe, West Asia, North Africa
Pinus sylvestris	avoids calcareous soils	North, Central and Eastern Europe
Pinus nigra	calcareous soils	south Austria to Middle Italy and Balkan
Betula pendula	sandy soils	Europe, Northwest Asia
Betula pubescens	moist soils, depleted of calcium	Europe, West Asia
Picea abies	moist soils	South Sweden to the Alps and the Balkan

Table 7 Soil preferences and current distribution patterns of tree species from Schö 13 II. Data derived from Johnson and More 2004.

Level 2

In contrast to the preceding level, the clear increase in grasses and herbs and shrubs, is indicative for a change towards cool climatic conditions, characteristic for Reinsdorf Stadial A (fig. 20; Urban 2006, 425).

As well as in the underlying level, *Ostrya* is also present in level 13 II-2, but only in the lower parts of the sediments. The disappearance of this genus is simultaneous with the decrease in *Pinus* and *Alnus* pollen.

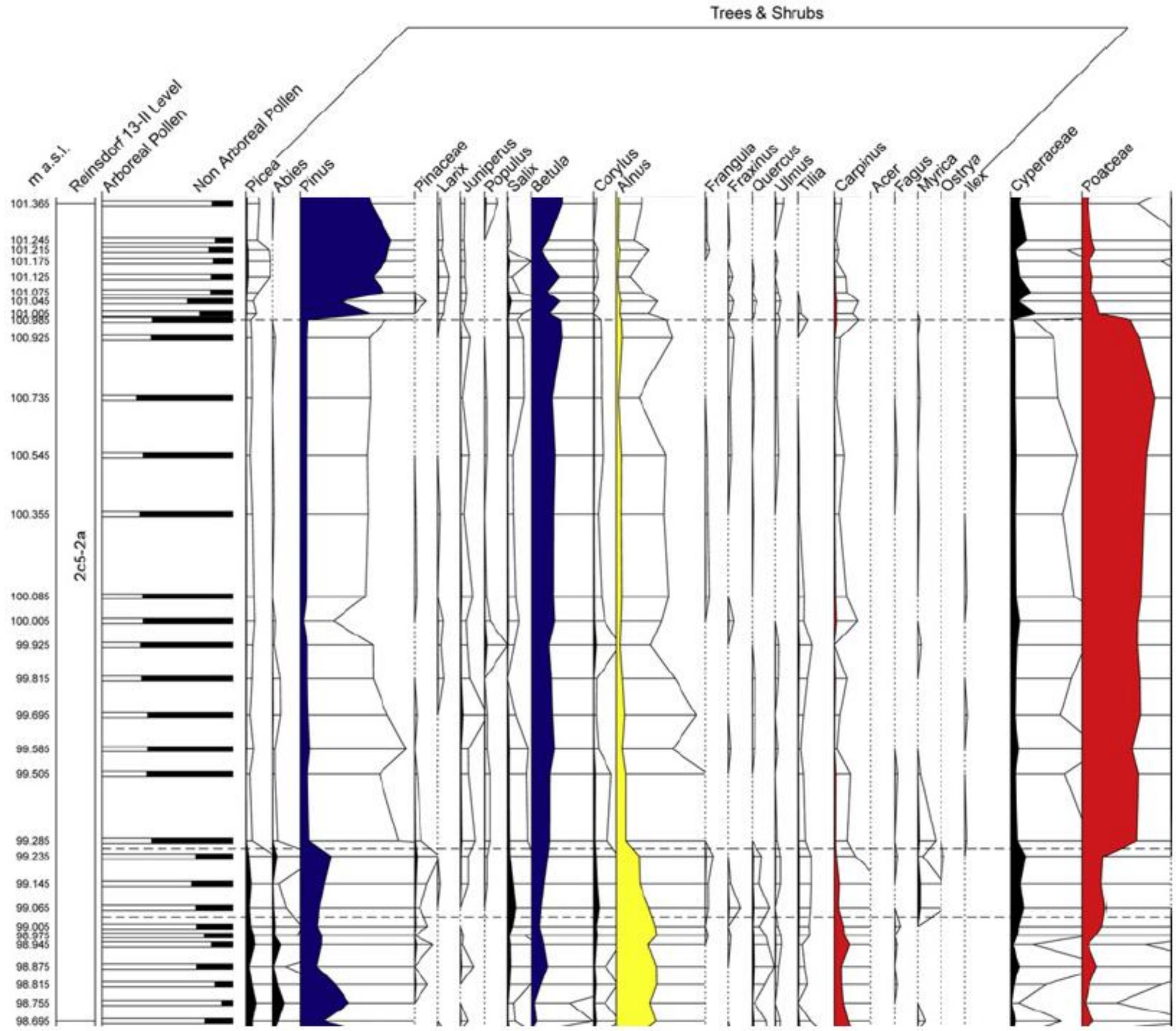

Figure 20 Pollendiagram of Schö 13 II-2 (after Urban *et al.* 2011, 133)

Level 3

The sediments of Schö 13 II-3 dominantly consist of organic mud and peat sediments, representing an interstadial period, Reinsdorf Interstadial A. The vegetation is dominated by *Pinus*, with *Betula*, *Alnus* and a few *Picea*. Trees that are indicative for a warm climate are more or less absent in this level (Urban 2006, 425).

Level Schö 13 II-3 is characterised by an increase in *Pinus* pollen and a decrease in Poaceae that starts in the upper part of level 13 II-2 (fig. 21). Despite this partial amelioration in climate, thermophilous species are almost absent. *Betula* remains relatively stable throughout the profile, but decreases slightly halfway in the profile.

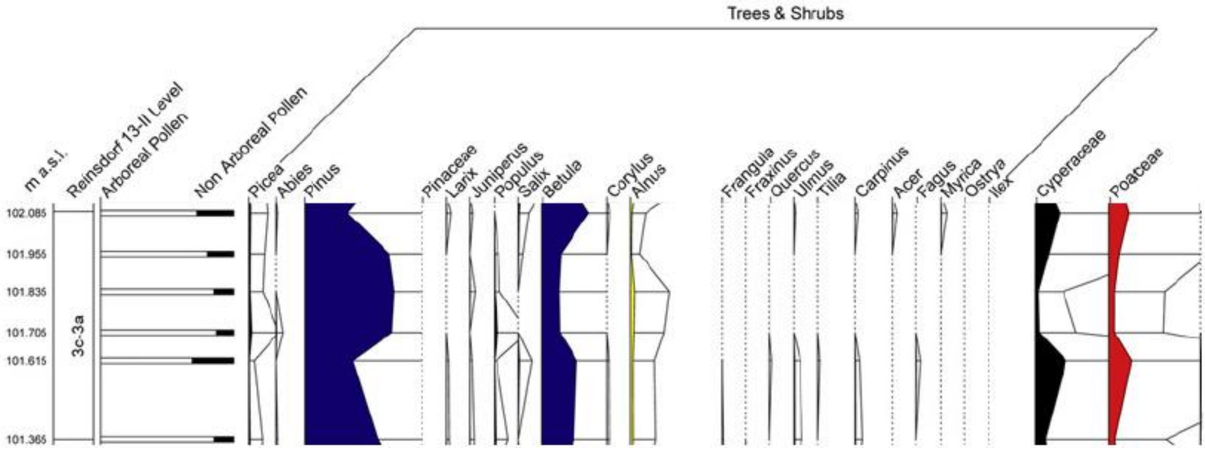

Figure 21 Pollendiagram of Schö 13 II-3 (after Urban *et al.* 2011, 133)

Level 4

Level 13 II-4 shows two stadials (Reinsdorf Stadial B and C), separated by an interstadial (Reinsdorf Interstadial B), which comprise a transition into 13 II-5. The onset of climatic deterioration in the lower part of level II-4 is reflected by a dominance of herbs indicating a steppe environment (fig. 22). The upper part of level II-4b is characterised by a *Pinus* forest, with *Betula* (Urban 2006, 425).

The dominant species in the pollen record associated with level Schö 13 II-4 are *Pinus* and *Betula*. This is similar to the flora composition in the preceding level. The species *Alnus*, *Picea* and *Larix* are scarce in this level. The environment is most likely characterised by an increase of moorland and a general change towards a dry herb- and grass-rich steppe environment. The fluctuations in the palynological record can also be interpreted as fluctuations in lake level.

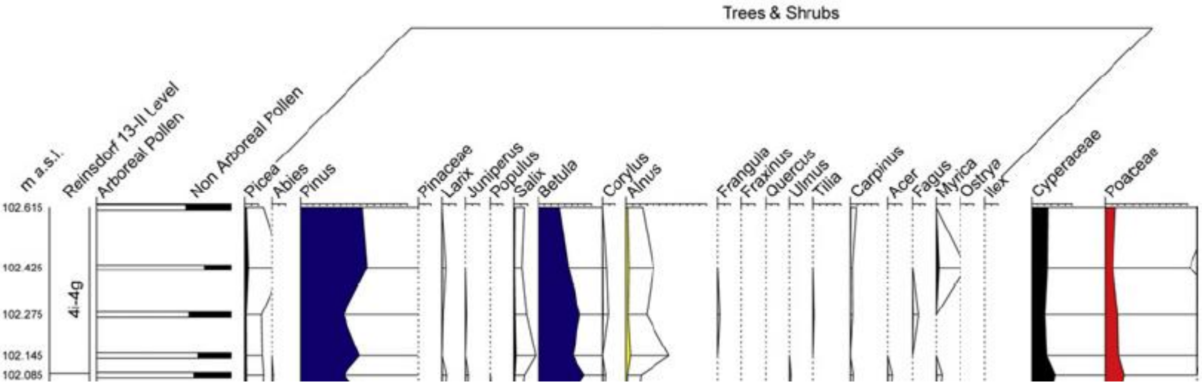

Figure 22 Pollendiagram of Schö 13 II-4 (after Urban *et al.* 2011, 133)

Level 5

The level environmental characteristics of Schö 13 II-5 are not discussed in this thesis, because there was not sufficient data available on a detailed account of the palynology as well as the mammalian and avian species in this level.

6.2. Non-mammalian fauna

Schöningen 13 II yielded a relatively rich fauna assemblage, including molluscs, amphibians, reptiles, birds, fish and mammals. The faunal data used in this thesis is analysed by various researchers. The mollusc fauna is analysed by Mania (2007), the herpetofauna and fish by Böhme (2007), and the avian and mammal assemblages are both analysed by students from the Faculty of Archaeology, Leiden University as well as researchers from the Landesambt für Denkmalpflege, Sachsen-Anhalt. In this chapter the different groups will be presented and the environmental and ecological characteristics and preferences will be discussed. Compared to other Middle Pleistocene sites, the non-mammalian fauna is relatively diverse, while the mammalian fauna is not exceptionally diverse. The faunal diversity per level is variable per group (tab. 8; fig. 23). Some groups show a clear trend in diversity declining with climate deterioration, while there is no significant pattern in other groups. It can be debated what influences this difference in diversity patterns. Differences could be caused by variation in ecological preferences or distribution, abundance, degree of fossilisation, external accumulation and preservation patterns.

	13 II-1	13 II-2	13 II-3	13 II-4
Molluscs	86	59	53	36
Amphibians	1	5	3	3
Reptiles	2	6	2	2
Birds	-	4	5	8
Fish	3	13	9	10
Small mammals	14	7	6	6
Large mammals	10	8	11	11
Total diversity	116	102	89	76
Vertbrate diversity	30	43	36	40

Table 8 Number of taxa per faunal group in Schö 13 II

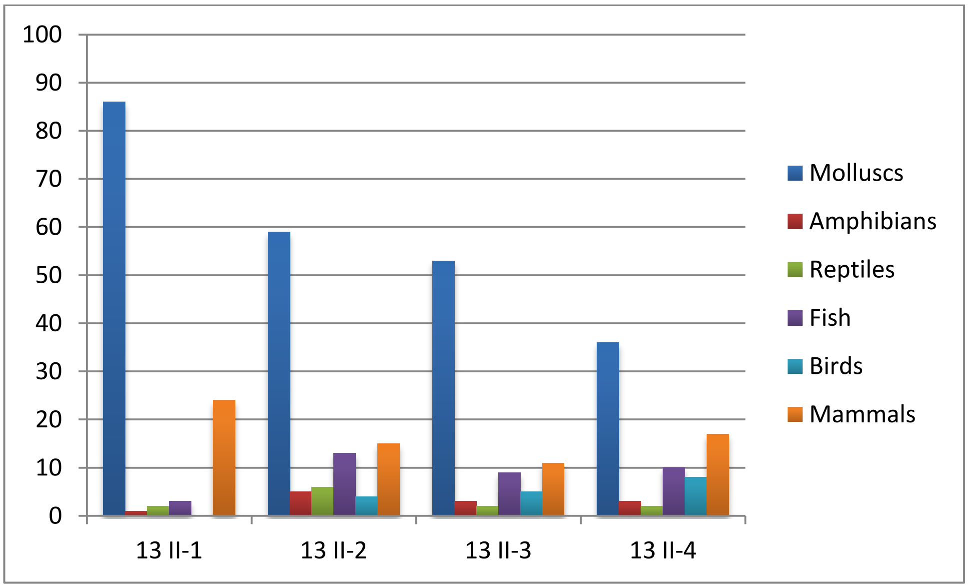

Figure 23 Graphic depiction of change in taxonomic diversity in Schö 13 II

6.2.1. Molluscs

Molluscs are often found in calcareous soils in a variety of environments (Claassen 1998; Mania 2007; Rousseau *et al.* 1992). It is generally assumed that the ecological preferences of molluscs have not changed significantly since the Middle Pleistocene (Mania 2007). Thus modern ecological data is used to interpret the past climate. In the total mollusc assemblage, a limited selection of species went extinct since the Middle Pleistocene. These species have more restricted environmental value, because the original context is not known. Mania (2007) argues that the most abundant mollusc species are autochthonous, while the less abundant species are parautochthonous, meaning that these species lived contemporaneously, but in different environments (Mania 2007, 100). In the Schöningen levels 13 II-1 to 13 II-6[4] a total of 106 mollusc species was found. 86 of these species were found in the interglacial optimum of 13 II-1 (tab. 9).

	13 II-1	13 II-2	13 II-3	13 II-4
Number of species	86	59	53	36
% forest fauna	30	18,5	18,5	11

Table 9 Number of mollusc species per level[5] and the percentage of forest adapted species

The decline in species richness is interpreted by Mania as a result of climatic deterioration, from interglacial optimum to cold steppe. In the first level, 26 species are indicative for a forested environment and dense vegetation. other species indicate swampy areas at the edges of vegetation rich, still water bodies. The dominant mollusc fauna is characteristic for mixed oak forests. Apart from the thermophilous forest fauna, some steppe dwellers are also present in the record (Mania 2007, 100-101). Indicating patches of open landscape situated within the forested landscape. The mollusc fauna in 13 II-1 is a mixture of local (middle European) and exotic species, that are at present native to south and southeastern Europe, alpine areas and the Balkan (tab. 10).

Local	Exotic
Helicodonta obvoluta	*Helicigona banatica*
Cochlodina obvoluta	*Aegopis verticillus*
Monachoides incarnate	*Pagodulina pagodula*
Helix pomatia	*Discus perspectives*
Cepaea hortensis	*Iphigena densestriata*
Cepaea nemoralis	*Cochlodina costata*
	Orcula doliolum
	Vitrea diaphana
	Vitrea subrimata

Table 10 Mollusc species (level 13 II-1) characteristic for local and exotic enviromments (derived from Mania 2007)

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[4] The levels Schö 13 II-5 and 13 II-6 are discussed by Mania (2007). The species from these two levels are not discussed in the thesis.

[5] The number of species is not mentioned for levels Schö 13 II-5 and 13 II-6, thus not included in table 9.

In the succeeding levels there is no evidence for the presence of molluscs in the cold phases of the climatic development, therefore the climatic reconstruction is based on (terrestrial) molluscs from the more temperate phases (Mania 2007, 102). The mollusc fauna from the more temperate warm phases have a general broader ecological niche, which allows these species to cope with colder temperatures in boreal forests and subarctic habitats as well (Mania 2007, 102). In all four warm phases, elements indicative for continental and boreal forests and steppe environments occur. Mania (2007) states that the development in mollusc fauna is synchronic to changes in the palynological record.

The percentage of species adapted to thermophilous forests declines per level. Where in level 13 II-1 30% of the total mollusc fauna is indicated as forest adapted species, this amount is significantly lower in level 13 II-2 and 13 II-3 with a percentage of 18,5%, and 11% in 13 II-4 (tab. 7).

6.2.2. Amphibians

Amphibians are generally indicative for the presence of water or other moist environments. Some species are an exception to this interpretation. However, although the species often have a distribution limited to moist environments, it is possible for most species to cover a wider area, further away from moist environments (Araújo *et al.* 208; Schlager 2004c, 6; Blain *et al.* 2009; Blain *et al.* 2010). Amphibians can be indicative for water quality, temperature and humidity.

The diversity of amphibians in Schö 13 II is limited to five identified species (tab. 11). All of these species occur in level 2, while a smaller selection of these species occurs in the other levels. The species identified in the fossil record are the more common amphibian species that at present occur in different habitats.

The identified species from 13 II are nowadays also found in different protected areas in Germany. The distribution maps provided by the WWF show the wide potential distribution areas of these particular species. In terms of climatic fluctuation, the amphibian assemblage from Schöningen is not particularly indicative for a specific climate. Considering landscape, the species have a higher indicative value.

Species	13 II-1	13 II-2	13 II-3	13 II-4
Triturus vulgaris		X	X	X
Bufo bufo		X	X	X
Pelobates fuscus		X		
Rana temporaria		X	X	X
Rana arvalis		X		
***Rana* sp.**	X			

Table 11 Distribution of amphibian species in Schö 13 II

Triturus vulgaris – smooth (common) newt

Triturus vulgaris is a small, smooth-skinned newt. At present, the smooth newt occurs in most of Europe, excluding the Iberian peninsula (fig. 24a). In the Pleistocene this was the most common species in Britain, and probably also in mainland Europe. Thus most Pleistocene species identified as *Triturus* sp. will likely represent *Triturus vulgaris*. In ecological terms, *Triturus vulgaris* lives in a wide variety of moist habitats (Holman 1998, 32-33). The species is generally indicative for still and shallow bodies of water with rich vegetation (Holman 1998, 33).

Figure 24 Present distribution of *Triturus vulgaris* (a), *Bufo bufo* (b) and *Pelobates fuscus* (c) (WWF Wild-Finder; http://www.worldwildlife.org/science/wildfinder/)

Bufo bufo – common (European) toad

At present, *Bufo bufo* is found in Europe (except for Ireland and some of the Mediterranean islands), and east to Lake Baikal in southern Siberia, the Caucasus and northern Iran (fig. 24b). The common toad has no specific environmental preferences. The species can be found in a wider variety of habitats than most European amphibian species. Exceptionally, it can occur in dry habitats (Holman 1998, 50).

Pelobates fuscus – common spadefoot

The present distribution of *Pelobates fuscus* is found in the temperate regions of Europe and parts of the Caucasus and southern Siberia (fig. 24c). The common spadefoot occurs mainly in areas with loose soil or sandy areas, in particular forests (Holman 1998, 44; Schlager 2004c, 124). The aquatic distribution of this species shows a preference to areas near shallow ponds or ephermal waters (Schlager 2004c, 124).

Genus *Rana*

The Pleistocene clade of the genus *Rana* consists of a minimum of ten species, including *R. arvalis, R. dalmatina, R. temporaria, R. graeca, R. bedriagae, R. cretensis, R. esculenta, R. lessonae, R. perezi, R. ridibunda* (Holman 1998, 56-66). Four of these species, *R. arvalis, R. dalmatina, R. temporaria* and *R. lessonae* have a broad distribution and occur at present in northwestern and central Europe. Only two different species are found in the archaeological record of Schöningen 13 II; *Rana arvalis* and *Rana temporaria*. These belong to the category with the highest ecological tolerance (Araújo *et al.* 2008).

Rana arvalis – moor frog

The modern distribution of *Rana arvalis* is spread throughout most temperate regions in continental Europe, excluding the British isles, the Mediterranean area and the tundra landscapes in (northern) Scandinavia (fig. 25a), although the species can occur above the Arctic Circle (Zeisset and Beebee 2008, 112). The species is commonly found in moist grasslands and in some wetland areas. *Rana arvalis* tends to occupy damper habitats than *Rana temporaria* when the two species occur together (Holman 1998, 60).

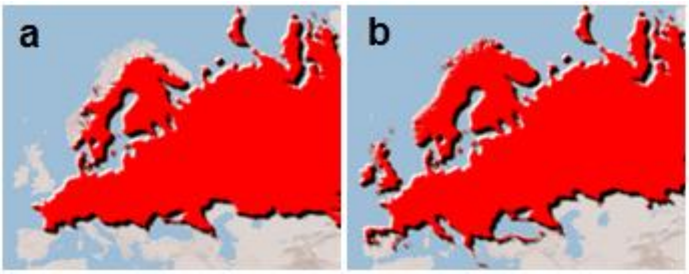

Figure 25 Present distribution of _Rana arvalis_ (a) and _Rana temporaria_ (b) (WWF WildFinder http://www.worldwildlife.org/science/wildfinder/)

Rana temporaria – common frog

The common frog has the most widespread distribution of all European amphibians, because of its broad environmental tolerance. The species can occupy more extreme environments than other species in this genus, and is considered the most cold tolerant herpetological species in Europe (Holman 1998, 63). It may occur in almost every moist habitat throughout its range (Holman 1998, 63). The present distribution of *Rana temporaria* is throughout Britain and Europe east to the Urals, but excluding most of Iberia, much of Italy, and the southern Balkans (fig. 25b). *Rana temporaria* is generally the only amphibian species that occurs in continental sites that indicate maximum glacial conditions (Holman 1998, 63).

6.2.3. Reptiles

Reptiles are cold-blooded animals that depend on specific climatic conditions to thrive. Most reptile species are therefore indicative for temperature (Schlager 2004d). The common pond tortoise, for example, is characteristic for July temperatures with averages around 17 degrees Celsius (Schlager 2004d). The nature and environmental characteristics differ per species and could provide extra detailed information on the character of the environment.

Emys orbicularis, common pond tortoise, are found rather often in interglacial contexts. These remains are more likely to survive the fossil record because of the fossilising capacities of their shields. Much less visible are remains of smaller reptiles such as lizards or snakes, as their remains are relatively small and less dense in bone structure. The species may, because of the taphonomic influence, appear to be one of the more common interglacial reptile species.

The diversity of reptile species in Schöningen 13 II varies between two species in 13 II-1, 13 II-3 and 13 II-4, and six species in 13 II-2 (tab. 12).

Species	13 II-1	13 II-2	13 II-3	13 II-4
Emys orbicularis	X	X		
Vipera berus	X	X	X	X
Lacerta vivipara		X	X	X
Anguis fragilis		X		
Lacerta agilis		X		
Natrix natrix		X		

Table 12 Reptile species in Schö 13 II

Emys orbicularis – European pond turtle

The European pond turtle is found in many aquatic habitats with unconsolidatd bottoms and abundant vegetation (Schlager 2004d). The types of aquatic habitats in which the species resides include rivers, streams, ponds, and marshes. The pond turtle has a limited distribution, with a northernmost limit in southern Scandinavia (fig. 26a). The species thrives in climates with an average summer temperature of 17°C (Schlager 2004d). Finding this species in the fossil record is indicative for a temperate climate.

Figure 26 Present distribution of *Emys orbicularis* (a), *Anguis fragilis* (b) and *Lacerta vivipara* (c) (WWF WildFinder; http://www.worldwildlife.org/science/wildfinder/)

Lacerta agilis – sand lizard

The sand lizard occurs at present in most of Europe, north to northwestern England and southern Scandinavia, avoiding the colder tundra biomes in Scandinavia (fig. 27a). The species occurs in a variety of dry habitats. Generally the sand lizard inhabits regions that are more open than the ones inhabited by other *Lacerta* species. In the northern part of the distribution limits, the species occurs in sandy heathland, whereas it occurs in a wider variety of habitats in more southern sites.

Lacerta vivipara – viviparous (common) lizard

The viviparous lizard has the most widespread distribution of lizard species in the northern hemisphere. It occurs in a variety of regions with varying climate and environment. This species is one of the most cold-tolerant reptiles in the northern hemisphere, which can be found north of the Arctic Circle (fig. 26c). *Lacerta vivipara* is one of the two reptile species that are found in glacial contexts in the Pleistocene (Holman 1998, 84). In terms of habitat, the viviparous lizard prefers a rather moist environment, but it can occupy a variety of habitats, including heathlands and Alpine meadows (Holman 1998, 84).

Anguis fragilis – slow worm

Anguis fragilis is the only modern species in the genus *Anguis* (Holman 1998, 88). *Anguis fragilis* occurs in most areas of the European continent, with exception of southern Iberia and the northernmost latitudes (fig. 26b). This species prefers moist habitats with sufficient vegetation (Holman 1998, 89)

Figure 27 Present distribution of *Lacerta agilis* (a), *Natrix natrix* (b) and *Vipera berus* (c) (WWF WildFinder; http://www.worldwildlife.org/science/wildfinder/)

Natrix natrix – grass snake

The grass snake occurs in nearly all of Europe, ranging north to near the Arctic Circle in Scandinavia arid extending eastward to Lake Baikal (fig. 27b). It prefers moist habitats over dry ones, because the main diet consists of frogs and toads. *Natrix natrix* is the only snake species that has been found in a Pleistocene glacial site in Britain (Holman 1998, 121).

Vipera berus – common viper

At present, the adder occurs in much of Europe, with a focus on eastern Europe, Scandinavia and various regions in south and western Europe (fig. 27c). Adders occur in a wide variety of habitats in various latitudes and altitudes. The species prefers mesic habitats with meadows and moorland. It can be found at the edges of forests as well (Schlager 2004d, 459).The diet consists mainly of small mammals, with preference for voles. Occasionally birds, frogs, and lizards are part of the diet as well (Schlager 2004d, 459; Holman 1998, 127).

As the amphibians, the reptile fauna also shows a greater species diversity in Schöningen 13 II-2 than in the other levels. The other levels comprise two species. The presence of *Emys orbicularis* only levels Schö 13 II-1 and 13 II-2 could indicate a slight deterioration of the climate, as this species is more thermophilous than the other reptile species. Another possible explanation for the absence of *Emys orbicularis* in the record could be taphonomy.

The species *Vipera berus* and *Lacerta vivipara* appear in the topmost section; in levels 3 and 4. Three species, *Anguis fragilis*, *Lacerta agilis* and *Natrix natrix* appear only in the second layer.

There is no significant competition between the two snake species, *Vipera berus* and *Natrix natrix*, because both species feed on different animals. Whereas *V. berus* feeds mainly on small mammals (Holman 1998, 127), *N. natrix* feeds mainly on frogs and toads (Holman 1998, 121).

Emys feeds on frogs, salamanders, fish and worms. The diversity in amphibians is highest in level 2, in which *Emys* is also present. *Emys orbicularis* is not present in the following levels, while there are amphibians, and thus possible preys present.

6.2.4. Fish

Fish remains can give limited information on the terrestrial circumstances. Fish are indicative for the type of water they inhabit, in particular stream velocity, temperature, periods of freezing and potentially for hominin subsistence (Reitz and Wing 2008). Remains of fish that were not a part of hominin subsistence, are most likely to be found in former lakebeds, or flood plains.

Species	13 II-1	13 II-2	13 II-3	13 II-4
Esox lucius	X	X	X	X
Perca fluviatilis	X	X	X	X
Rutilus rutilus	X	X	X	X
Alburnus alburnus		X	X	X
Gobio gobio		X	X	X
Tinca tinca		X	X	X
Scardinius erythrophthalmus		X	X	
Leucaspius delineatus		X		
Carassius carassius		X	X	X
Lota lota		X		
Misgurnus fossilis		X	X	X
Pungitius pungitius		X		X
Cottus gobio				X
Gasterosteus aculeatus		X		

Table 13 Fish species in Schö 13 II

The assemblage of fish species in 13 II is more diverse than the amphibian and reptile diversity. Similarly to the amphibian and reptile fauna, species diversity is limited in 13 II-1 and is more diverse in the other levels. The diversity in 13 II-2 is the highest. Only few species are limited to one or two out of four levels (tab. 13).

Fish preservation depends on the size and abundance of the species and bone densities. More abundant and/or bigger species have a higher chance of preservation than smaller and less abundant fish. The patterns of presence and absence may thus be influenced partly according to this patterns, and not solely because of the presence due to climatological circumstances. Nevertheless, this does not reject the fact that the presence and absence of species could indicate shifts in climatic conditions.

***Esox lucius* – northern pike**

The northern pike is found in a variety of aquatic habitats, but it shows a preference for lakes, ponds and slow moving rivers with abundant vegetation. The shallow waters are occupied by the juvenile individuals, while the adults are often found in greater depths (Kottelat and Freyhof 2007). The habitat size of the species depends on the prey density. The main component of the diet is fish (Schlager 2004a, 383).

***Perca fluviatilis* – European perch**

The European perch inhabits a very wide range of habitats from estuarine lagoons and various types of lakes of all types to streams (Kottelat and Freyhof 2007). The occurrence of this species is thus not specifically indicative for the water quality and proximate environment.

***Rutilus rutilus* – common roach**

The common roach inhabits a wide variety of habitats as well. The species is mainly distributed in lowland areas. This species is most abundant in nutrient-rich lakes and large to medium sized rivers and backwaters (Schlager 2004a; Kottelat and Freyhof 2007). It occurs in water bodies of the freshwater or brackish type. It prefers water bodies with low water velocity, although it may occur in the backwaters of fast-flowing rivers. For spawning, the species requires dense submerged vegetation in various water bodies (Kottelat and Freyhof 2007).

***Alburnus alburnus* – common bleak**

The common bleak is indicative for open waters of lakes. Generally it tolerates little streaming in the water, showing preference to still water bodies. Spawning occurs, if possible, in shallow parts or along stony shores of lakes (Kottelat and Freyhof 2007).

***Gobio gobio* – gudgeon**

The preferred habitat for *Gobio gobio* is a fast-flowing river with a sand or gravel bottom, although it may also occur in still waters (Kottelat and Freyhof 2007). *Gobio gobio* is known to often appear in large numbers. The species' diet includes insect larvae, molluscs, and freshwater shrimps (Schlager 2004a).

***Tinca tinca* – tench**

The tench shows a preference for warm lakes and pools with abundant vegetation and muddy bottoms. Characteristic of this species is that it can tolerate low oxygen levels.

Their home range is limited, where the species generally lives solitary, or occasionally occurring in small groups. The species is omnivorous, feeding on aquatic invertebrates, insect larvae and algae (Schlager 2004a, 319).

***Scardinius erythrophthalmus* – common rudd**

The common rudd can be found in freshwater environments, particularly in lakes, rivers, marshlands and ponds. The preference of this species is pointed towards the presence of a soft, muddy bottom, dense vegetation and reedy margins. The diet of the species includes (aquatic) invertebrates and plants (Schlager 2004a, 318).

***Leucaspius delineatus* – moderlieschen**

The moderlieschen is often found in lowland riverine habitats especially oxbows and other water bodies only connected to rivers during floods (Kottelat and Freyhof 2007). The species is often found in ponds, steppe lakes and small water bodies not connected to rivers. It may occur in any habitat with few or no predators (Kottelat and Freyhof 2007).

***Carassius carassius* – Crucian carp**

The Crucian carp is usually restricted to densely vegetated backwaters and oxbows of lowland rivers. The species also occurs in small well vegetated lakes and channels (Schlager 2004a; Kottelat and Freyhof 2007). It tolerates high summer temperatures and very low oxygen concentrations in summer and under ice cover. Furthermore, it is able to survive in almost completely frozen water or almost-dry habitats by burying itself in mud (Kottelat and Freyhof 2007). For spawning, the species prefers dense submerged vegetation.

***Lota lota* – burbot**

The burbot occurs in freshwaters in northern North America and Europe and Asia. The species occurs north of 40° N with a northernmost distribution limit at 70-80^o N. the burbot is a bottom feeder that is found in a wide variety of freshwater lakes and rivers with a depth of 0,5 m to a depth of more than 230 m (Schlager 2004b, 36). The diet consists of aquatic invertebrates and other fish (Schlager 2004b, 36).

***Misgurnus fossilis* – weatherfish**

The weather fish is found mostly in slow moving waters of backwaters, side channels of lowland streams, rivers and lakes. The species is indicative for densely vegetated habitats with soft, muddy bottoms. The species may also occur in flooded meadows during spawning season (Kottelat and Freyhof 2007).

***Pungitius pungitius* – nine-spined stickleback**

The three-spine stickleback is predominantly found in brackish waters, but it can also occur in freshwater habitats, as the species has a broad environmental tolerance (Keivany and Nelson 2000; Kottelat and Freyhof 2007). Inland, the species is found in small freshwater streams and ponds, with provide dense aquatic vegetation (Schlager 2004b; Kottelat and Freyhof 2007).

***Gasterosteus aculeatus* – three-spined stickleback**

The nine-spined stickleback is widely distributed in tamperate marine waters as well as coastal rivers and freshwater lakes. This species can thus be indicative for brackish waters as well as freshwater. Adults are usually found in association with dense vegetation. The species feeds on a variety of aquatic invertebrates and insects. Sticklebacks are typical prey species for numerous other fish and water birds (Schlager 2004b, 141).

***Cottus gobio* – bullhead**

Cottus gobio is a cold tolerant species that can survive in small waterbodies (Englbrecht *et al.* 2000, 720). This species is often associated with river systems, but can also be found in lowland rivers and lakes in northern Europe and the Alpine regions. The species is physiologically limited by higher temperatures and lower oxygen levels (Hänfling *et al*. 2002, 1718).

6.2.5. Birds

Birds can be indicative for certain types of environments, but this depends on the habitat strategy of the species. If the species are (seasonally) migratory, individual remains may prove to be less informative of the characteristic environment than resident species. Water birds can be indicative for the salinity and vegetation composition of the water body, while land birds are less indicative for the environment, but these species can be indicative for the types of prey or diet.

Species	13 II-2	13 II-3	13 II-4
Anas acuta			X
Anas crecca			X
Anas platyrhynchos	X	X	X
Cygnus olor	X	X	
Aythya fuligula		X	X
Bucephala clangula			X
Tadorna tadorna	X	X	X
Rallus aquaticus			X

Table 14 Occurrence of bird species in Schö 13 II[6]

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[6] No bird species were assigned to level Schö 13 II-1

All species identified in Schöningen are characteristic for wetland environments (tab. 15). This is not surprising as it is known from the sedimentology and fish species that there was a lake in the vicinity of the site. A varying occurrence of bird species in the record can be indicative for local changes, but also for other, indirect factors not related to environmental change, for example related to taphonomy and preservation.

Environmental indicators could be species that have a smaller ecological niche than other species. The species limited to one single level are *Anas acuta, Anas crecca, Bucephala clangula* and *Rallus aquaticus*. The distribution of *Aytgya fulogula* is limited to levels 13 II-3 and 13 II-4, whereas *Cygnus olor* is found only in levels 13 II-2 and 13 II-3 (tab. 14).

Habitat	**freshwater**	**brackish**	**saline**	**forest**	**steppe**	**tundra**
Anas acuta	X	X	X		X	X
Anas crecca	X			X		
Anas platyrhynchos	X	X				
Cygnus olor	X					
Aythya fuligula	X	X				
Bucephala clangula	X	X		X		
Tadorna tadorna		X	X		X	
Rallus aquaticus	X	X			X	

Table 15 Aquatic and terrestrial preferences of the avifauna

Anas acuta – northern pintail

The northern pintail shows a preference for open grassland, steppe or tundra habitats with presence of freshwater, brackish or saline wetlands with shallow water (Snow and Perrins 1998). Wetland habitats include shallow freshwater marshes, marshy lakes, slow-flowing rivers and wet meadows (Del Hoyo *et al.* 1992). The winter habitat of the species can include inland lakes, tidal areas and brackish and saline marshes and lagoons (Del Hoyo *et al.* 1992). The species is omnivorous, feeding on plants, grasses, aquatic invertebrates, amphibians and small fish (Del Hoyo *et al.* 1992).

Anas crecca – common teal

The common teal is a characteristic wetland species, showing a preference for shallow freshwater lakes, ponds and marshes with abundant vegetation (Madge and Burn 1987; Del Hoyo *et al.* 1992). In the breeding season, the species prefers shallow permanent waters in the vicinity of woodlands with dense herb cover suitable for nesting (Del Hoyo *et al.* 1992). In winter, the species migrates to coastal environments.

Anas platyrhynchos – common mallard

The common mallard has a broad distribution and occurs in almost all (freshwater) wetland type areas, showing a preference for still to slow flowing waters with abundant vegetation (Del Hoyo *et al.* 1992; Snow and Perrins 1998). For foraging, the species requires water less than 1 m deep (Snow and Perrins 1998). In winter, the species can also be found in saline habitats of coastal areas (Madge and Burn 1988).

Cygnus olor – mute swan

The mute swan is often associated with freshwater wetlands in lowland areas, including lakes, ponds, marshes and slow-flowing rivers (Del Hoyo *et al.* 1992; Madge and Burn 1988). In some cases, the species can inhabit brackish wetland environments as well (Del Hoyo *et al.* 1992). The majority of the diet consists of aquatic plants and aquatic invertebrates (Del Hoyo *et al.* 1992; Snow and Perrins 1998).

Aythya fuligula – tufted duck

The tufted duck shows a preference for freshwater bodies of open water, lakes and ponds that have a depth of 3-5 m (Kear 2005). The species depends on abundant marginal vegetation (Kear 2005). In the winter season, the species is found in coastal areas, near brackish waters as well as freshwater lakes (Kear 2005; Snow and Perrins 1998).

Bucephala clangula – common goldeneye

The common goldeneye is commonly found at inland freshwater sites in the summer periods, and resides in coastal regions in the winter season. The species shows a preference for oligotrophic lakes with a limited amount of fish, in shallow waters of less than 10 meter deep, preferably four meters deep (Kear 2005; Snow and Perrins 1992; Bregnballe *et al.* 2006). The most common habitats include freshwater lakes, rivers and marshes surrounded by (coniferous) forests for nesting (Del Hoyo *et al.* 1992; Bregnballe *et al.* 2006). The diet consists predominantly of aquatic invertebrates, amphibians, small fish and aquatic plants (Del Hoyo *et al.* 1992).

Tadorna tadorna – common shelduck

Figure 28 Present distribution of _Tadorna tadorna_ (WWF WildFinder; http://www.worldwildlife.org/science/wildfinder/)

The common shelduck prefers saline habitats, mudflats and sandy estuaries in coastal regions (fig. 28), but the species also occurs in brackish lakes inland in steppe areas (Bregnballe *et al.* 2004; Burton 2006). The Asiatic populations and migration species are also found in freshwater habitats. The species generally feeds on molluscs and other aquatic invertebrates, as well as small fish and plants (Bregnballe *et al.* 2004).

***Rallus aquaticus* – water rail**

This water adapted species has a preference for still flowing shallow waters with dense marginal or aquatic vegetation. Characteristic for this species is the preference for wetlands with patches of drier areas and shrubs and trees in the proximity. Furthermore, this species requires a muddy ground for foraging (Snow and Perrins 1998). The water rail has a widespread distribution throughout Europe.

The modern occurrences of the bird species found in the archaeological record are presented in table 16a and 16b. In this comparison only 10 out of 12 sites are selected, because two sites did not yield any data on the presence of these particular bird species (tab. 16a – tab. 16b).

	Lake Torne	**Laplandskiy**	**Elbe**	**Bialowieza**	**Spreewald**
Anas acuta	permanent resident	present	present	irregular occurrence	summer migrant
Anas crecca	permanent resident	present	present	summer resident	permanent resident
Anas platyrhynchos	permanent resident	present	present	summer resident	summer migrant
Cygnus olor	no occurrence	no occurrence	present	summer resident	permanent resident
Aythya fuligula	permanent resident	present	present	resident	permanent resident
Bucephala clangula	permanent resident	present	present	resident	permanent resident
Tadorna tadorna	summer migrant	no occurrence	present	no occurrence	permanent resident
Rallus aquaticus	no occurrence	no occurrence	present	summer resident	permanent resident

Table 16a Occurrence, migration and residence patterns of bird species in national parks

	Krkonose	**Vessertal**	**Trebon basin**	**Hortobágy**	**Luberon**
Anas acuta	present	No occurrence	fall migrant	summer resident	no occurrence
Anas crecca	present	present	permanent resident	fall migrant	winter resident
Anas platyrhynchos	present	present	permanent resident	permanent resident	present
Cygnus olor	present	No occurrence	permanent resident	no occurrence	no occurrence
Aythya fuligula	present	No occurrence	permanent resident	summer resident	winter resident
Bucephala clangula	no occurrence	No occurrence	permanent resident	winter resident	no occurrence
Tadorna tadorna	no occurrence	No occurrence	summer migrant	winter migrant	no occurrence
Rallus aquaticus	present	present	permanent resident	permanent resident	present

Table 14b Occurrence, migration and residence patterns of bird species in national parks (continued)

There appears to be no strict division in northern and southern adapted species, in terms of migration and residence patterns.

6.3. Mammalian fauna

6.3.1. Small mammal fauna

Micromammals, including shrews and rodents, can be indicative for specific vegetation, humidity and climate. Some species have a habitat strategy that includes microclimates. These microclimates can broaden a species range by altering the natural tolerance; examples are species that make burrows and escape extreme conditions on the surface, like extreme weather etcetera. Some species might thus not be characteristic for one type of environment. Some small mammal species depend on specific types of vegetation. The most diverse group of mammals in Schöningen 13 II is the order of insectivora and rodents (tab. 17).

	13 II-1	13 II-2	13 II-3	13 II-4
Desmana moschata	X			X
Sorex minutus	X	X		X
Sorex araneus	X	X		
***Crocidura* sp.**	X			
***Neomys* sp.**	X			
***Dicrostonyx* sp.**	X			
Lemmus lemmus			X	X
Sicista betulina			X	
Castor fiber				X
Trogontherium cuvieri		X		X
Clethrionomys glareolus	X	X		
Arvicola cantiana terrestris	X	X	X	X
***Microtus* sp.**	X	X	X	X
Microtus arvalis/agrestis	X	X	X	X
Microtus agrestis	X			
Microtus gregalis	X		X	X
Microtus oeconomus	X		X	X
Microtus terricola subterraneus	X	X		X
***Apodemus* sp.**	X	X		
Apodemus sylvaticus	X	X		
Apodemus maastrichtiensis	X			

Table 17 Small mammal species in Schö 13 II (Data derived from Knul 2009, 51)

Desmana moschata – Russian desman

The habitat of the Russian desman is confined to ponds, streams and rivers, with still to slow moving water and abundant vegetation. In terms of diet, the desman feeds on amphibians, insects and crustaceans (Hutterer 2005). The present distribution of the Russian desman is limited to southwest Russia (Hutterer 2005). The distribution in fig. 29 shows a more widespread distribution, by including the potential species ranges based on habitat preferences and ecoregions.

Figure 29 Present distribution of the *Desmana moschata* (World WildFinder: http://www.worldwildlife.org/science/wildfinder/)

Sorex araneus – Eurasian shrew

The Eurasian shrew prefers damp and shady habitats with dense vegetation, such as reed beds. The species also tolerates a range of other habitats, including drier areas such as woodland, shrubs and sand dunes (Wilson and Reeder 1993; MacDonald and Barrett

1998). Found in temperate and northern Europe. Distribution limit reaches the Mediterranean area (Corbet and Harris 1991, 53). The species is found in most environments where low vegetation cover is available. It is most common in thick grass and deciduous woodland (Corbet and Harris 1991, 54). The common shrew is more abundant than the pygmy shrew (Corbet and Harris 1991, 62)

Sorex minutus – Eurasian pygmy shrew

The European pygmy shrew is indicative for damp areas with dense vegetation. It is not limited to a specific habitat, but the species does show preference for the afore mentioned characteristics. The species can inhabit a variety in niches, including swamps, grasslands, moorland, sand dunes, woodland edge, rocky areas, shrubland, and montane forests (Hutterer 1999; MacDonald and Barrett 1998). The Eurasian pygmy shrew has a similar distribution as the common shrew. The species is widespread in most types of habitats, altough the species shows a preference for areas with sufficient ground cover, preferring grassland over woodland (Corbet and Harris 1991, 62).

Neomys sp.

The genus *Neomys* consists of only two species; *N. anomalus* (Miller’s water shrew) and *N. fodiens* (water shrew). Both species have a broad distribution in present day Europe. The Miller’s water shrew is less adapted to or dependent on water than the water shrew. The preferred habitat of this species is grassland in the proximity of water or swamps (Spitzenberger 1999b; MacDonald and Barrett 1998, 33).

The water shrew mainly lives in the proximity of water, with a preference to fast flowing streams, but it can also occur near ponds. Occasionally, the species occurs in woodlands and grasslands (Spitzenberger 1999c; Corbet and Harris 1991, 65; MacDonald and Barrett 1998, 32).

Crocidura sp.

Genus *Crocidura* is worldwide the biggest genus of shrews. The diversity of the genus in mainland Europe, however is limited to three species; *C. leucodon, C. russula* and *C. suaveolens.* The habitat preferences of *C. leucodon* varies within the different parts of its geographic range. The preferences range from damp areas with dense vegetation and fringes of forests to open landscapes and moist habitats in mountainous areas. In the eastern distribution limits, the species can also be found in steppe areas and semi-deserts (MacDonald and Barrett 1998, 34)

C. russula is more restricted to the Mediterranean zone, where the species occurs in a wide range of habitats, including grassland, shrubland, open habitats, forest edges, mountainous areas and habitats in the proximity of rivers and streams (Corbet and Harris 1991, 74; MacDonald and Barrett 1998, 36). Populations of *C. suaveolens* from western and southern Europe inhabit a variety of habitats, including shrubland, sand dunes, rocky areas in mountains and heathland, but the species tends to avoid dense forests (MacDonald and Barrett 1998, 35). The distribution of *C. suaveolens* is centered in Southwest Europe, with an eastern distribution limit to central Germany (Corbet and Harris 1991, 73).

***Clethrionomys glareolus* – bank vole**

The bank vole has a widespread distribution in northwestern and eastern Europe. It prefers mixed deciduous woodland or areas with much shrub and herb growth, but can also occur in coniferous forests (Corbet and Harris 1991, 195; Spitzenberger 1999a). The species shows a preference for warm and dry areas (MacDonald and Barrett 1998, 243-244).

***Microtus agrestis* – field vole**

The field vole occurs in a wide range of habitats in West, Central and Northern Europe in grasslands, woodland (Corbet and Harris 1991, 205), upland heaths, dunes, marshes, peat-bogs and river-banks. The species tends to prefer damp areas (Zima 1999b).

***Microtus arvalis* – common vole**

The common vole is found in a wide variety of open habitats including moist meadows, forest steppe, moist forest and sometimes agricultural areas. It feeds mainly on the green parts of grasses and herbaceous plants (Zima 1999a; Wilson and Reeder 1993).

***Microtus gregalis* – narrow-headed vole**

The narrow-headed vole inhabits tundra, plains and mountain steppes and meadows. The species is commonly found in grassy areas in the forest zone and semi-deserts. A maximum density of the species is reached in cereal and grass steppes as well as alpine and water meadows (Wilson and Reeder 1993).

***Microtus oeconomus* – tundra vole**

The distribution of *M. oeconomus* is limited to Central Europe and northern Scandinavia (MacDonald and Barrett 1998; Van Apeldoorn 1999). It may also occur in some isolated areas in southern and middle Scandinavia. The species typically inhabits damp, densely-vegetated areas along the edges of lakes, streams and marshes, but the tundra vole can also be found in tundra, taiga, forest-steppe, and semi-deserts (Van Apeldoorn 1999; Wilson and Reeder 1993).

***Microtus (terricola) subterraneus* – European pine vole**

The European pine vole occurs in the middle latitudes of Europe, its range exending from the Atlantic coast in France to western Russia and the Balkan. The northern distribution limit is northeast of the Baltic states, while its southern distribution limit is found in the southern Balkan and northern Turkey (Shenbrot and Krasnov 2005; Kryštufek 1999). The species occurs in a wide range of habitats, including deciduous and coniferous forests, woodlands, meadows and mountainous areas. The species can tolerate both dry and damp conditions (Kryštufek 1999)

Arvicola cantania (terrestris)

Arvicola cantania is a Pleistocene water vole species. This species is often associated with interlacial conditions and temperate woodland faunas (Currant 1989, 27).

Apodemus sp.

The modern genus *Apodemus* includes five species; *A. agrarius, A. flavicollis, A. microps, A. mystacinus* and *A. sylvaticus*. *A. flavicollis and A. sylvaticus* are the most widespread species in this genus, occupying most of temperate Europe. *A. agrarius* has a more restricted distribution, limited to Eastern and Central Europe (MacDonald and Barrett 1998, 258-262). The species found in Schöningen are *A. sylvaticus* and the extinct *A. maastrichtiensis*.

Apodemus sylvaticus – long-tailed field mouse / wood mouse

Apodemus sylvaticus is a widely adaptad species, that inhabits a wide variety of niches including woodland, moorland, steppe, arid Mediterranean shrubland, and sand dunes, however its distribution is limited to the tree-line (MacDonald and Barrett 1998, 206; Montgomery 1999). The distribution of the wood mouse extends to the wooded and steppe zones in western Eurasia, but the habitat preferences do no allow the species to extend far into the coniferous zones (Corbet and Harris 1991, 223). The species is highly adaptable to most habitats, if these are not too wet. Habitats include grassland, heaths, bogs and sand dunes (Corbet and Harris 1991, 224).

Dicrostonyx sp. – collard lemmings

The modern genus *Dicrostonyx* consists of 11 species (Wilson and Reeder 1993). A limited selection occurs in modern assemblages in Eurasia, while the majority of the species occurs in the North American continent. Most *Dicrostonyx* species are characteristic for cool, dry environments, with a general distribution north of the Arctic Circle, and rarely occur in more southern regions than Scandinavia (Wilson and Reeder 1993). The presence of a *Dicrostonyx* species in 13 II-1 is thus not conform the expectations of the distribution of this species.

***Lemmus lemmus* – Norway lemming**

The Norway lemming is at present distributed in Scandinavia, occupying tundra biomes, but also woodlands with birch and pine (Hansson 1999; MacDonald and Barrett 1998, 241). Lemmings can create a microclimate by which the species is able to survive in a wider environmental area. The species is found in Schö 13 II-3 and Schö 13 II-4, the phases that show an onset to a deteriorating climate. Genus *Lemmus* is in the Pleistocene also known from interglacial contexts, from example Hoxne. The presence of this species in interglacial contexts is uncharacteristic, but a possible explanation raised for the occurrence of this species in non-analogue contexts is that the species potentially had a broader distribution in the Pleistocene, as compared to present distribution of this species (Stuart *et al.* 1993, 203). If lemmings occur in interglacial contexts, the species are often associated with the end of an interglacial phase (Stuart *et al.* 1993, 203).

***Sicista betulina* – northern birch mouse**

The northern birch mouse has a modern distribution in northeastern Europe and in some isolated areas in Northern and Central Europe (Pucek 1999). The habitat preference of the species is (birch) woodland, with a preference to damp or marshy areas (MacDonald and Barrett 1998, 278; Pucek 1999).

6.3.2. Large mammals

The large mammal fauna is often not indicative for specific climates, because of the general broad tolerance of the species. There are, however, some species that have a preference for specific biomes. *Sus scrofa*, for example, is described as a typical forest dweller. It has the tolerance to inhabit other habitats as well, but it will mainly be found in forests or woodland. The large herbivores are in general indicative for woodland or steppe environments. Most of these species are found in all of the four levels, with the exception of *Capreolus capreolus* and *Megaloceros giganteus*. The absence of these species is not necessarily a result of climatic or environmental changes; *Capreolus capreolus* is known to have a high environmental tolerance, and is in present times distributed across the entire European continent, from the Mediterranean sea to the near-Arctic regions in northern Scandinavia and Russia. *Megaloceros giganteus* is also found in stadial/(peri)glacial contexts, thus the absence of this species could be assumed not to be related to the cooler stadial phase in level 13 II-4.

Species	**13 II-1**	**13 II-2**	**13 II-3**	**13 II-4**
Ursus sp.	X			
Canis lupus		X		X
Vulpes vulpes				X
Mustela erminea			X	X
Mustela nivalis			X	X
Martes sp.	X		X	X

Elephantidae indet.	X			
Equus mosbachensis	X	X	X	X
Stephanorhinus kirchbergensis	X		X	X
Stephanorhinus hemitoechus			X	X
Stephanorhinus sp.	X	X		
Sus scrofa	X			
Cervus elaphus	X	X	X	X
Megaloceros giganteus	X	X	X	
Capreolus capreolus	X	X	X	
Bison priscus			X	X
Bos primigenius			X	X
Bos/Bison	X	X		

Table 18 Large mammal species in Schö 13 II, including small carnivores

6.3.2.1. Carnivora

***Ursus* sp.**

The genus *Ursus* was more diverse in the Middle Pleistocene than today. Ursid species that occured in the Middle Pleistocene are *Ursus arctos*, *Ursus spelaeus* and *Ursus denigeri*.

Ursus arctos is an omnivore that has a habitat preference for mixed woods, forests in mountainous areas, tundras and open pastures.The species needs some dense cover for shelter. Brown bears have a variable diet, consisting of grasses, herbs and berries as well as ungulates of varying size classes, including elk, reindeer and sheep. The home range of this species is variable. In Scandinavia the home range can vary from 25 km^2 to 150/1000-4000 km^2, whereas the populations in the Czech republic have more limited home ranges of 5 to 13-30 km^2. Population size in the European forest areas is also variable, with a generally low population density in Scandinavia of 1-11 individuals per 1000 km^2 and higher population densities in Italy; 135-190 individuals per 1000 km^2 (MacDonald and Barrett 1998, 105-106; Grzimek vol. 14, 303).

The cave bear, *Ursus spelaeus*, is known from the Middle Pleistocene in Europe. Remains are found in mainly karst regions of central Europe and the Mediterranean littoral zone (Martin and Klein 1984, 494). This species differes from *U. arctos* in behaviour, because the species was presumably less mobile and relied more on a vegetarian diet. Most fossil remains are found in caves, whereas little to no remains are found in alluvial, loam or loess deposits (Martin and Klein 1984, 495).

***Canis lupus* – wolf**

The grey wolf is a widely distributed carnivore species, it virtually inhabits all terrestrial biomes (fig. 30a). Its modern distribution excludes occurrences in western Europe, while in the Pleistocene the species was also present in these regions. The wide distribution indicates that the species is not restricted to and limited by specific biomes. Instead of climatic limitations, grey wolf distribution is steered by the presence and abundance of prey species (MacDonald and Barrett 1998). Despite the high tolerance, wolfs show a preference to open woodland, but they can also occur on tundras, in dense forests or mountainous areas. Prey species range from small rodents to large ungulates up to the size of moose. The core of the diet consists of large ungulates. Population size and density depends on the size and abundance of prey species (MacDonald and Barrett 1998).

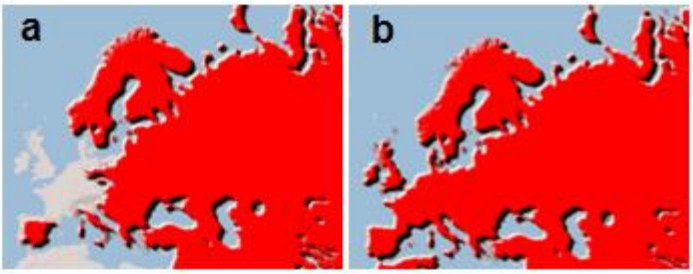

Figure 30 Present distribution of *Canis lupus* (a) and *Vulpes vulpes* (b) (WWF WildFinder; http://www.worldwildlife.org/science/wildfinder/)

Vulpes vulpes – red fox

The red fox occurs across the entire European continent (fig. 30b). As well as *Canis lupus*, the red fox is highly adaptable to many environments, including woodlands, tundra, moorland, mountains and dunes (Corbet and Harris 1991, 357). The main core of the diet consists of rodents and rabbits, but can also include invertebrates, birds and nestlings (Hutchins *et al.* 2004a, 279). Home range sizes varies from 40-60ha to 4000ha. The population size of red fox varies with the type of environment. At present, population density in farmlands is approximately one family per km^2, while the population density is higher in more urban settings with a density of up to five families per km^2. In barren environments, population density can decrease to one family per 10 km^2 (Lindsay and MacDonald 1986; MacDonald and Barrett 1998; Trewhella *et al.* 1988). A family consists of a male, one to six females and cubs, resulting in variable family sizes (Corbet and Harris 1991, 358).

Mustelidae

The mustelid family in Europe consists of ten species; *Lutra lutra*, *Meles meles, Gulo gulo, Martes foina, Martes martes, Mustela erminea, Mustela nivalis, Mustela nivalis, Mustela lutreola* and *Mustela putorius*. The mustelid family in Schöningen is limited to *Martes* sp., *Mustela erminea* and *Mustela nivalis*.

Mustela erminea - stoat

The ermine has the greatest distribution of all weasels. The species has a distribution in most of the biomes in Europe (Corbet and Harris 1991, 379). The species inhabits grasslands, forests, marshes, steppes and river valleys (King 1983). The diet is centred on rodents, especially mice, voles, and lemmings, but also consists of lagomorphs, birds and bird’s eggs (MacDonald and Barrett 1998, 109-110; Hutchins *et al.* 2004a, 327). The home range of the species varies between 2 and 200 ha, depending on prey availability and density.

The stoat is ‘found in any habitat, at any altitude that offers cover and prey’ (Corbet and Harris 1991, 379), including woodland, moors, marshes and mountains. The species tends to avoid open spaces (Corbet and Harris 1991, 379).

***Mustela nivalis* - weasel**

The weasel occurs in a wide variety of habitats in different biomes, generally a habitat that provides cover and prey. The species is mainly found in open forests, steppes and semi-deserts, whereas it tends to avoid deep forests, sandy deserts, and open spaces. The diet of this species varies with the habitat. Dietal elements are small mammals, mainly rodents (dominantly voles and mice), birds’ eggs, nestlings, insects and lizards. (MacDonald and Barrett 1998, 112; Hutchins *et al.* 2004a, 333).

The distribution of the weasel is similar to the distribution of stoat, but the distribution of the weasel is also extended to the Mediterranean (Corbet and Harris 1991, 389). The species is also able to inhabit a variety of niches, but it will be less common in areas where prey species are scarcer, for example on mountains or in woodland providing sparse ground cover (Corbet and Harris 1991, 389).

***Martes* sp.**

Martes martes is commonly found in the forest areas of Europe, with the exception of Spain, Greece and Eastern Europe (Hutchins *et al.* 2004a, 332; Corbet and Harris 1991, 371). The pine marten is found in a wide variety of habitats, including coniferous and deciduous woodland, open areas in forests, shrubs, moorland, temperate grasslands and coastal sites (Corbet and Harris 1991, 373). The species is mostly carnivorous, relying on a diet of small mammals for most of the year. The composition and proportion of the diet often change with the availability of resources, following season and local conditions (Hutchins *et al.* 2004a, 332).

6.3.2.2. Probiscidae

***Elephas antiquus* – straight-tusked elephant**

The straight-tusked elephant occurred in Europe from its first appearance during the Cromerian Complex to its extinction in Weichselian. *Elaphas antiquus* is a typical interglacial species, indicative for temperate grasslands and forestsed environments (Kúrten 1968, 135).

6.3.2.3. Perrisodactyla

Equus mosbachensis – Mosbach horse

Equus mosbachensis is a caballoid (true horse) species, occurring in Middle Pleistocene contexts. This species is atypical steppe adapted grazer, often associated with cool steppe environments with open forests (Eisenmann 1991).

Stephanorhinus kirchbergensis – forest rhino

Stephanorhinus kirchbergensis is one of the two dominant rhino species in the Middle Pleistocene. The forest rhino was indicative for open forests and shrubland. *Stephanorhinus kirchbergensis* is found co-occurring with the steppe rhino, *Stephanorhinus hemitoechus*, which is assumed to have different environmental preferences. The co-occurrence could indicate that both species were able to adapt to a broader niche than the preferred one (Guerin and Patou-Mathis 1996; Kútren 1968, 142).

Stephanorhinus hemitoechus – steppe rhino

The steppe rhino is associated with temperate grassland environments. The molar structure of this species indicates that it predominantly feeds on abrasive grasses (Kútren 1968, 143).

6.3.2.4. Artiodactyla

Sus scrofa – wild boar

Sus scrofa is found in many types of habitat including temperate woodlands, grassland, steppe and broadleaf forests. The species is found virtually across the entire European continent, with the exception of the northern latitudes in Scandinavia. Wild boars are omnivorous, feeding on plants, rodents and invertebrates (MacDonald and Barrett 1998, 197; Hutchins *et al.* 2004b, 288).

Cervus elaphus – red deer

The preferred habitat of *Cervus elaphus* is concentrated along open areas as well as densely forested areas for forage and cover. The species can inhabit a wide range of habitats, including open plains, hills, broadleaf and coniferos forests, marshlands, marshy river valleys and subalpine meadows (MacDonald and Barrett 1998; Hutchins *et al.* 2004b, 369). The feeding niche of *Cervus elaphus* is broader than in other species of cervids. The main diet consists of twigs, shrubs, branches, herbs and sedges and fruits (Hutchins *et al.* 2004b, 370). The home range of this species depends on the habitat. In woodlands, the home range is generally smaller than in more open areas. The size of the home range and population densities vary seasonally. Population density varies between 4-45 species per km^2 depending on the habitat (MacDonald and Barrett 1998).

***Megaloceros giganteus* – giant deer**

This giant deer had its origin in Europe, exploiting a large geographical area spanning Europe, Scandinavia, North-Africa, the Caucasus, Kazakhstan, southern Siberia and the Trans Baikal are. This indicates it must have been adapted to cope with a variety of environments and must be able to cope with drought (Martin and Klein 1984, 500)

***Capreolus capreolus* – roe deer**

Roe deer can inhabit a variety of landscapes of forested areas that are interchanged with open patches like steppe and meadows. Broadleaf forests, shrubs and tall grasses are used for shelter. The species is often not found in dense coniferous forests (MacDonald and Barrett 1998; Hutchins *et al.* 2004b, 388). The species feeds on a variety of herbs, fruits, grasses and cereals. The home range varies between 5-1000 ha, with average population densities of 15-25 individuals per km^2 (MacDonald and Barrett 1998).

***Bison priscus* – steppe bison**

The steppe bison, *Bison priscus,* is a widespread species in Middle Pleistocene assemblages. The species is found in a wide geographical area, indicating that *Bison priscus* was likely to be widespread across the steppes of Eurasia. Physical characteristics indicate that the species was adapted to living in dry and cool climates, associated with steppes and areas with open vegetation (Martin and Klein 1984, 501-502; Kúrten 1968, 186).

***Bos primigenius* – auroch**

In contrary to *Bison priscus,* aurochs are associated with open woodlands and temperate grasslands. The auroch is found less often in the fossil record than the steppe bison. It is assumed that *Bison priscus* lived in herds, while *Bos primigenius* had a more solitary lifestyle (Kúrten 1968, 188).

7. Analysis

In this chapter the faunal data from the four levels of Schö 13 II are analysed. A point of attention in this section are diversity patterns in the fossil record and in modern analogues, the species compositions, environmental indicative species and predator-prey relations in both fossil records and modern analogues.

7.1. Diversity

The mollusc fauna shows a clear declining trend in the species diversity of Schö 13 II. This pattern is not visible as such in the vertebrate assemblages (tab. 19). The large mammal diversity remains similar through the course of time, whereas the amphibians, reptiles and fish show an increase in species diversity towards Schö 13 II-2, and a gradual decline in 13 II-3 and 13 II-4. A clear pattern cannot be assigned to diversity changes of the bird remains, because this group lacks data from one of the levels. The total vertebrate species diversity alternates between 30 and 43 species. Levels 13 II-1 and 13 II-3 have a minimum species diversity of 30 species, while the diversity is higher in 13 II-2 and 13 II-4 with 43 and 40 species. A note has to be made that the absence of birds in 13 II-1 does influence the diversity patterns.

	13 II-1*	13 II-2	13 II-3	13 II-4
Vertebrates	30	43	30	40
Molluscs	86	59	53	36
Total assemblage	116	102	83	76

Table 19 vertebrate and mollusc diversity in Schö 13 II. * no bird species are assigned to level Schö 13 II-1

The total species diversity in Schöningen 13 II is not exceptionally high when compared to other archaeological sites. If you compare the mammal species diversity, including both small and large mammal species, the diversity in Schöningen 13 II is exceptionally low. Of the six comparative sites, Swanscombe and Hoxne have a comparable diversity, whereas the other sites have a higher diversity of between 30 and 43 mammal species (tab. 20). The variation is mainly caused by a higher diversity in small mammal species and large carnivores, as the amount of large ungulates is rather similar in the Middle Pleistocene sites.

Site	Climate type	Mammals[7]	Amphibians	Reptiles	Fish	Birds	Diversity
Untermaßfeld	Interglacial	43	7	2	-	7	52 (59)
Boxgrove	Interglacial	43	-	-	-	-	43
Swanscombe	Interglacial	23	-	-	-	-	23
Hoxne	Interglacial	20	-	-	-	-	20
Bilzingsleben	Interglacial	30	1	1	2	6	34 (40)
Repolusthöhle	Interstadial	35	-	-	-	-	35
Schöningen 13 II-1	Interglacial	24	1	2	3	-	30

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[7] Number of mammal species including Chiroptera

Schöningen 13 II-2	Stadial	15	5	6	13	3	39 (42)
Schöningen 13 II-3	Interstadial	16	3	2	9	4	30 (34)
Schöningen 13 II-4	Stadial	21	3	2	10	7	36 (43)

Table 20 Species diversity in archaeological sites. Numbers between brackets indicate the species diversity including the birds. Data derived from Kahlke and Dubrovo (2001), Kahlke and Cramer (2001), Roberts and Parfitt (1999), Mania (1980), Döppes *et al.* (2008)

Tab. 21 and tab. 22 show the number of species per order (and group). The diversity in the small mammal group, including insectivores, rodents, lagomorphs and small carnivores[8], varies between 9 and 26 species in the case study sites, while the diversity in Schö 13 II varies between 8 and 15 species. Rodents are the best represented order of small mammals, with a minimum of 6 species and a maximum of 14 species in the case studies, and a minimum of 6 and a maximum of 10 species in Schö 13 II. The other group that adds to the difference in diversity patterns is large carnivore group, with a maximum of two species in Schö 13 II, and a diversity between two and 10 in the archaeological case studies.

	Untermaßfeld	Bilzingsleben	Hoxne	Swanscombe	Boxgrove	Repolust-höhle
Insectivores	5	2	3	1	7	2
Rodents	11	10	7	6	14	9
lagomorphs	1	0	0	1	1	1
Small carnivores	1	2	1	1	4	3
Total small mammals[9]	**17**	**14**	**11**	**9**	**26**	**15**
Large carnivores	10	5	2	4	4	8
Perissodactyla	2	3	2	3	2	0
Probiscidae	1	1	0	1	1	1
Artiodactyls	7	7	5	6	4	8
Total large mammals	**20**	**16**	**9**	**14**	**11**	**17**
Total mammals	**37**	**30**	**20**	**23**	**37**	**32**

Tabel 21 small mammal and large mammal diversity per order in archaeological sites

	Schö 13 II-1	Schö 13 II-2	Schö 13 II-3	Sch ö 13 II-4
Insectivores	5	2	0	2
Rodents	10	6	6	8
lagomorphs	0	0	0	0
Small carnivores	0	0	2	3
Total small mammals	**15**	**8**	**8**	**13**
Large carnivores	1	1	0	2
Perissodactyla	2	2	3	3
Probiscidae	1	0	0	0
Artiodactyls	5	4	5	3
Total large mammals	**9**	**7**	**8**	**8**
Total mammals	**24**	**15**	**16**	**21**

Tabel 22 small mammal and large mammal diversity per order in Schö 13 II

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[8] Small carnivores are the carnivores up to an avegraged weight of 10 kg. This includes the mustelids, but excludes *Felis silvestris*, which is for this analysis included in the large carnovore group

[9] Chiroptera are excluded from this table to make a more direct comparison with the Schö 13 II assemblages

The diversity in the modern analogues is significantly higher than the Pleistocene counterparts, with the exception of the two northernmost sites Lake Torne and Laplandskiy. The total species diversity varies between 69 and 117 species in the temperate areas (tab. 23). The diversity of fish and amphibians is in modern contexts generally higher than in the Pleistocene sites. The variety in mammal species varies between 28 and 68 species, with an average of 45,4 species, which is higher than the richest mammal assemblage in the fossil record.

National Park	Biome	Biome class	Mammals	Amphibians	Reptiles	Fish	Diversity
Lake Torne	Tundra	VII	28	1	1	9	39
Laplandskiy	Taiga	VI	33	1	2	3	39
Elbe Flusslandschaft	Temperate broadleaf forest	II	25	12	6	29	72
Bialowieza	Temperate broadleaf forest	II	68	13	7	27	115
Spreewald	Temperate broadleaf forest	II	52	13	6	35	106
Krkonose	Temperate mountain system	V	68	6	6	7	87
Vessertal	Temperate broadleaf forest	II	33	13	6	17	69
Trebon Basin	Temperate forest	I	57	15	6	39	117
Vosges du Nord	Temperate broadleaf forest	II	52	12	6	23	93
Hortobágy	Steppe	IV	38	10	4	20	72
Luberon	Temperate broadleaf forest	II	48	8	17	22	95
Urdaibai	Coastal marine wetland	III	43	12	14	23	92

Table 23 Species diversity in European national parks

The avian diversity in modern contexts is significantly higher than the other vertebrate assemblages. This discrepancy is shown in fig. 31. Fig. 32 shows the relative vertebrate compositions with the exclusion of the avian assemblage. To be able to compare present compositions with the data from the archaeological record, birds are left out of the modern assemblages.

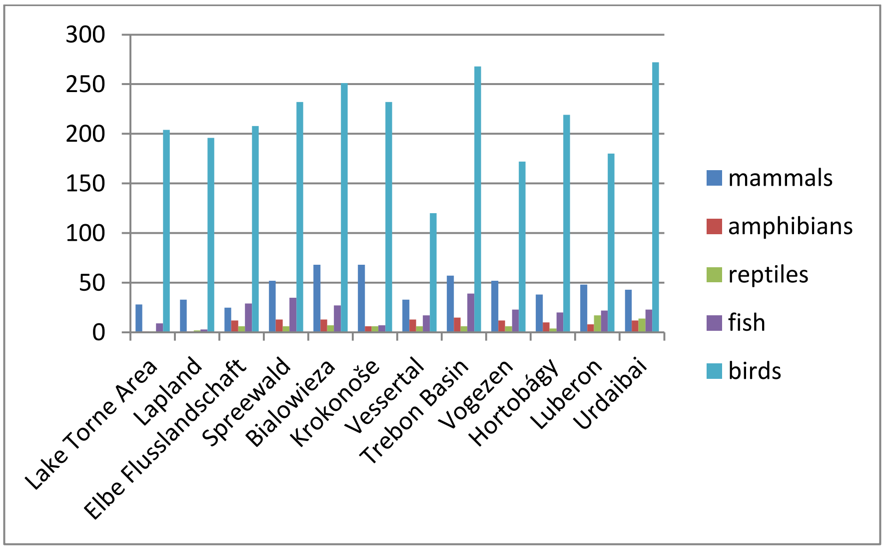

Figure 31 species composition based on total number of species including birds in European national parks

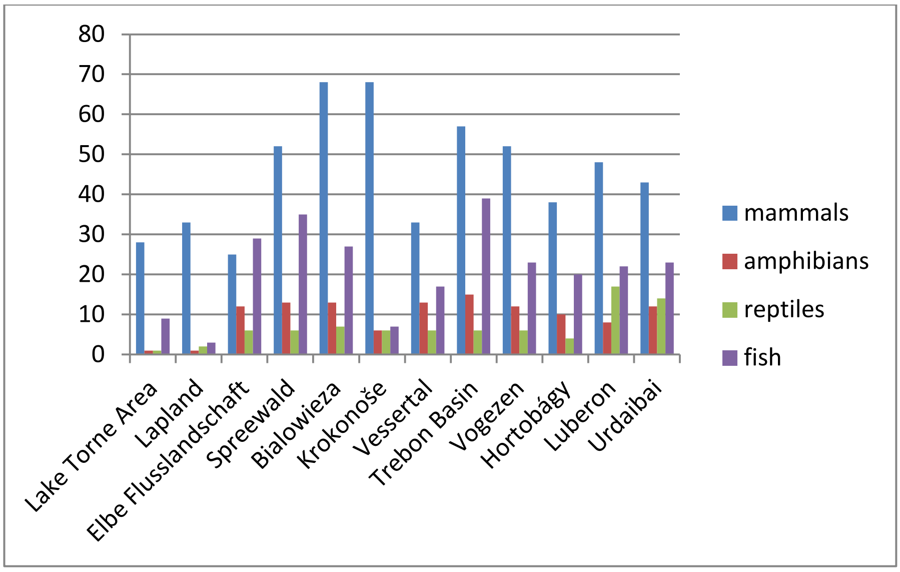

Figure 32 species compositions based on total number of species excluding birds in European national parks

7.1.1. Diversity as environmental indicator

Comparing diversity values in fossil assemblages with modern species diversity in a variety of biomes, the species diversity in Schöningen 13 II appears to be lower than expected. The minimum diversity in the modern analogues is 39 species in the most northern latitudes, in a tundra and taiga/boreal forest biome. Diversity in the temperate areas, in the temperate broadleaf forests, varies between 69 and 117 species. In the modern assemblages, the total species diversity shows some variation across the latitudes and biomes. The lowest diversity can be found in the northern latitudes, with a tundra and taiga biome. Species diversity is higher in the mid-latitudes, especially in the temperate broadleaf biome, but there is no further link between latitude and species diversity in the analysed sites. The reptiles are the group with the most clear diversity patterns based on latitude. Here, a low diversity is indicative for the northern latitudes, average diversity is characteristic for the mid-latitudes and the more Mediterranean-typed zones yield the highest species diversity. The amphibian compositions prove to be constant, with the exception of the two northernmost sites. Most fluctuation in diversity can be seen in the mammal and fish compositions. The diversity of these groups appears to influenced by other factors than climate.

The change in diversity patterns throughout site 13 II does not meet the pattern of expectation. The palynological record of 13 II-1 is clearly indicative for an interglacial optimum with temperatures approximately 1 to 2 degrees Celsius higher than present. These average annual temperatures are at present found in latitudes south from the location of Schöningen. The modern analogue sites that could fall in this range are Trebon basin, Vosges du Nord and Hortobágy. The species diversity in these regions is 117, 93 and 72. In these three sites, the mammal and fish diversity is significantly larger than the diversity in amphibians and reptiles, but there is still some variation in the amount of mammal and fish species. In Trebon and the Vosges, the mammal diversity is similar with 57 and 52 species, in contrary to 38 species in Hortobágy, whereas the fish diversity is more similar in the Vosges and Hortobágy than in Trebon basin (23 and 20 species against 39 species).

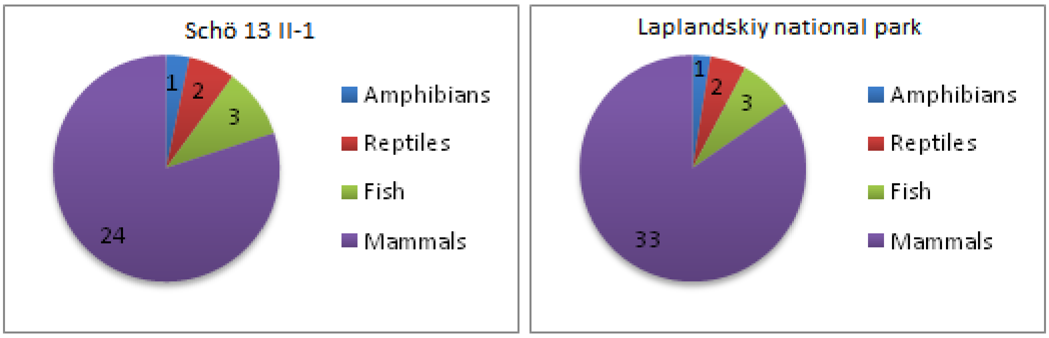

Figure 33 Species composition in Schö 13 II-1 and Laplandskiy national park, Russia

When analysing the diversity patterns of fossil assemblages and modern analogues, we can see that the species division in Schö 13 II-1 is highly similar to Laplandskiy natural reserve, Russia, which is part of a tundra biome (fig. 33). This comparison is based on the species diversity only, species content is not taken into account in this comparison. A conclusion based on this similarity in diversity patterns could be that the climate and environment in 13 II-1 were similar to the conditions in the Laplandskiy natural reserve. However, despite its low reptile diversity, there are remains found of *Emys orbicularis*, which is indicative for a MST (mean summer temperature) of ~17°C (Schlager 2004d). This shows that diversity patterns in archaeological sites cannot always be correlated to modern species compositions directly. Diversity patterns in the fossil record may be comparable to the modern record, but only after considering the potential factors that can influence the diversity patterns. The diversity patterns in modern analogue sites, however, do show fluctuations that can be of significant meaning for comparisons with the fossil record.

The fauna species diversity in Schö 3 II-3 looks slightly different in composition from the diversity patterns in Schö 13 II-4. Based on the palynological data, it can be seen that the floral components of the environment do not change significantly. If we assume that the palynological record is an indirect reflection of climate, it can be assumed that the environment was similar in both levels, including the faunal assemblage. The discrepancies we find in these levels could be the result of taphonomical processes rather than environmental change. Some slight discrepancies may occur in the faunal elements that are more sensitive to climatic and environmental change.

Species diversity is variable with climate and environment. There appears to be no direct relation between latitude and diversity, rather, these patterns vary with the type of environment and the related available resources and carrying capacity. To get insight in the relation between climate and/or environment and diversity patterns, the diversities in the modern analogue sites (fig. 34) are plotted to show fluctuations in various latitudes and environments. These patterns in diversity are compared to diversity in the four levels of Schö 13 II (fig. 35).

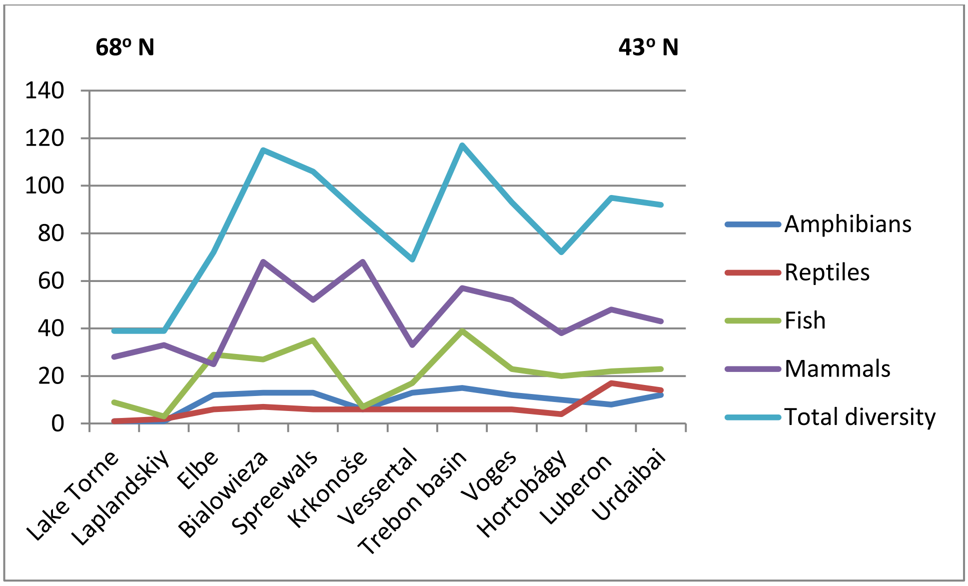

Figure 34 Species diversity in modern analogue sites

The diagram of the modern analogues shows the fluctuations in species diversity from high latitudes (68° N) to lower latitudes (43° N). The diagram shows that diversity is significantly lower in the two high latitude sites than in the other sites in temperate regions. The high fluctuation in diversity in the other sites is mainly caused by a fluctuation in fish and mammal diversity. The reptile and amphibian assemblages appear to be rather stable in the mid latitudes. Diversity fluctuations in the mid latitudes (58°N to 47°N) appear to be correlated to differences in environment, rather than climate. Diversity in these latitudes shows two peaks in Bialowieza, poland and Trebon Basin, Czech Republic. In these sites, the total diversity is high because of a combined high diversity in mammals and fish. Mammal diversity peaks in Bialowieza and Krkonoše, wehereas fish diversity is high in Elbe Flusslandschaft, Spreewald and Trebon Basin, each area characterised by a water rich environment.

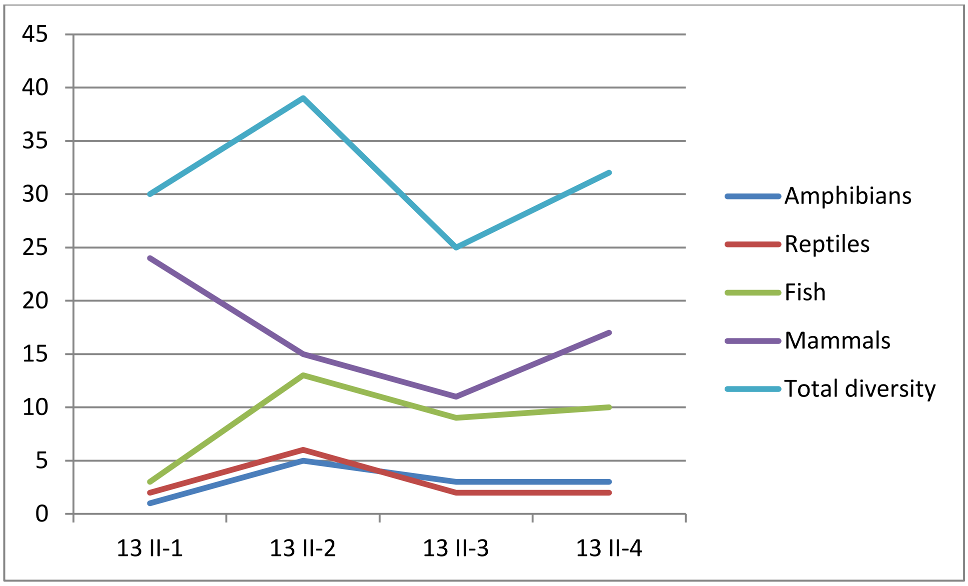

Figure 35 Species diversity in the four levels of Schö 13 II

The species diversity in Schö 13 II fluctuates throughout the four levels (fig. 35). The species diversity is significantly the highest in 13 II-2, and low in 13 II-1 and 13 II-3. In these diversities, the bird species are left out of the comparison, because of the absence of bird species in Schö 13 II-1. Fig. 36 shows estimated values for the diversity patterns in Schö 13 II. In this diagram, the number of species is adjusted by comparing the species in the fossil assemblage with the general patterns in species diversity in modern analogues and other fossil assemblages.

For the diversity estimates (fig. 36), the number of different species in modern analogue sites in various latitudes and environments is analysed, as well as diversity patterns in archaeological sites. The large mammal fauna diversity in the Pleistocene was significantly higher that today's diversity in this group, thus large mammal diversity patterns are based on diversities in archaeological sites, rather than the modern analogues. The diversity of the other groups (amphibians, reptiles and fish), is based on diversity patterns in modern analogues, as for these groups it is assumed that there are no significant differences in diversity between Pleistocene and modern assemblages. Modern analogues are used as comparative sits for these groups, because the archaeological record is often incomplete regarding the non-mammalian fauna. The amphibian and reptilian fauna in mid-latitude sites in modern analogue sites is rather stable, with an average of approximately 10 amphibian species and 6-7 reptile species. The diversity of reptiles is significantly higher in the Mediterranean sites. The number of amphibians and reptiles is thus adjusted to these levels, from a diversity of one to five species in Schö 13 II, to a value that is conform the expected diversity of approximately six species, considering both Pleistocene herpetological species compositions as well as modern diversity. The reptile diversity is adjusted to show a declining trend in diversity, starting with the highest diversity in Schö 13 II-1, with a similar diversity in Schö 13 II-2, to a low diversity in the (inter)stadial levels Schö 13 II-3 and 13 II-4. The number of fish and mammal species is highly variable troughout the modern analogues. Mammal species diversity is adjusted by analysing both archaeological sites and mder analogues, in small mammal, carnivore and large herbivore diversity.

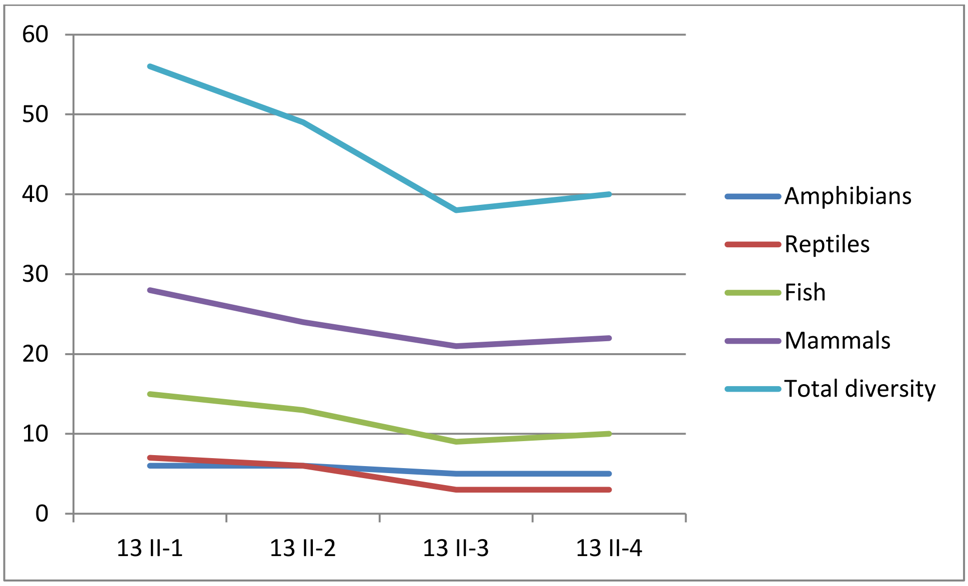

Figure 36 Estimated vertebrate species diversity in Schö 13 II

7.2. Amphibian and reptile introduction in Pleistocene interglacial cycles

Patterns in species diversity can give (restricted) information on the type of environment and climate. The next paragraph shall discuss the introduction and composition of herpetological species in past interglacials. The observations of herpetological successions in the Eemian Interglacial (Böhme 1999) shall serve as a base for the analysis of the Schö 13 II herpetological assemblage.

Böhme (1999) has described successions of herpetofauna during Pleistocene interglacials. The species to occur first in an interglacial is *Rana temporaria*, which can also occur in periglacial and potentially in glacial environments. Current distribution of the common frog reveals that the species has a high environmental and climatic tolerance, and is also present in northern latitudes, above the Arctic Circle. Species following the *Rana temporaria* in interglacial cycles are *Rana arvalis, Bufo bufo* and *Vipera berus*. Later in the interglacial cycle, *Anguis fragilis, Natrix natrix* and *Coronella ausriaca* can be found in the fossil record. The species *Triturus vulgaris, Lacerta vivipara* and *Lacerta agilis* are not assigned to a specific phase. These species are potentially introduced during late glacial phases (Böhme 1999). According to Holman (1988), *Lacerta vivipara* is also found in Pleistocene glacial sites (tab. 24). In this respect, one would expect to find this species co-occurring with the common frog, before the introduction of other herpetological species. In the Schöningen deposits there is no clear pattern in herpetofauna succession.

(Peri)glacial	**Early interglacial**	**interglacial**	**Unknown immigration****
Rana temporaria	*Rana arvalis*	*Anguis fragilis**	*Triturus vulgaris*
	Bufo bufo	*Natrix natrix**	*Lacerta vivipara*
	Vipera berus	*Coronella austriaca*	*Lacerta agilis*

Table 24 The introduction of herpetofauna in interglacials (after Böhme 1999) ****Anguis fragilis* **and** ***Natrix natrix*** **can also be found in earlier stages. **the immigration of these species is unknown; potentially arrival in the late glacial.**

In 13 II-1 only the genus *Rana* sp. is present. Considering the site's position on glacial sediments, the first phase could be considered as onset of an interglacial period, where *Rana temporaria* is the most likely species present. This pattern, however, does not match with the presence of *Vipera berus* and *Emys orbicularis*, as the latter species is indicative for relatively warm periods with July temperatures of ~17°C (Schlager 2004d).

13 II-1	**13 II-2**	**13II-3**	**13II-4**
Rana sp.	*Triturus vulgaris*	*Triturus vulgaris*	*Triturus vulgaris*
Vipera berus	*Bufo bufo*	*Bufo bufo*	*Bufo bufo*
Emys orbicularis	*Rana temporaria*	*Rana temporaria*	*Rana temporaria*
	Rana arvalis	*Lacerta vivipara*	*Lacerta vivipara*
	Pelobates fuscus	*Vipera berus*	*Vipera berus*
	Vipera berus		
	Natrix natrix		
	Lacerta vivipara		
	Lacerta agilis		
	Anguis fragilis		

Table 25 The occurrence of herpetological species in Schö 13 II

A later arrival of the species *Anguis fragilis*, *Natrix natrix* and *Coronella austriaca* in interglacial stages implies that these species have a more restricted ecological niche than the other herpetological species. The absence of these species in Schö 13 II-3 and 13 II-4 could be the result of a deterioration of the climate, but the absence of these species in Schö 13 II-1 is not in line with this interpretation, because of the interglacial character of this level. The absence of a high diversity in herpetological species in this level can however be the result of taphonomic influences, rather than climate. The higher diversity in herpetofauna in 13 II-2 can be assigned to the interglacial conditions at the base of this level (tab. 25).

13 II-1	Interglacial
13 II-2	Full interglacial
13 II-3	Early interglacial[10]
13 II-4	Early interglacial

Table 26 Climatic determination based on the occurrence of herpetological species

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[10] The climatic determination based on the presence of specific amphibian and reptile species in Schö 13 II-3 and 13 II-4 suggests an early interglacial phase; species characteristic for late glacial environments are absent from the Schö 13 II-3 and 4 contexts. In chronological perspective, these phases should be considered late interglacial.

On basis of the pollen sequence, level 13 II-1 is interpreted as full interglacial phase, based on the presence of several thermophilous tree species, some of which are nowadays exotic to northwestern Europe. The base of this level is situated on glacial deposits of the Elsterian glaciation. The direct succession of the interglacial phase immediately on top of the glacial deposits suggests there is an hiatus between these Quaternary deposits.
This hiatus could explain the discrepancy of the amphibian successions of the Schöningen levels as compared to Böhme's interpretations during the interglacials in general. However, one would expect with level 13 II-1 being a full interglacial, as defined in the pollen record, that the amphibian and reptile fauna would be more diverse, as an interglacial optimum is not likely the first phase in a cycle. The presence of solely *Rana* sp. in this level does not coincide with the environmental signal revealed by the pollen. The amphibian and reptile record of the second level, however, is more diverse and could match with Böhme's description of the succession of herpetofauna in interglacial phases. The major part of 13 II-2 is characterised by a distinct climatic deterioration, however, the lower part of this level is, according to the pollen zones, still part of the interglacial phase, and could thus explain the diversity in amphibians and reptiles (tab. 26).
The higher diversity of herpetofauna in level 2 could be ascribed to the warm phase at the base of the level. This diversity in species would not be expected in phases with stadial conditions. If compared to present day herpetofauna diversity, higher latitude areas in Scandinavia and Russia show a low diversity in amphibian and reptile species of only two or three species, whereas sites in central Europe show a general higher diversity of six to eight reptile species and a maximum of 15 amphibian species, depending on the amount of water present.

The highest species diversity would be expected in interglacial optima. One would therefore expect the highest diversity in species in level 1 and level 2, despite the severe climatic deterioration in this period. The lower species diversity in level 3 and 4 is according to the expected pattern of herpetofauna diversity.

The low species diversity in the interglacial optimum 13 II-1 could be the result of taphonomic factors. This level is characterised by a low pH in the upper part of level 13 II-1, which could cause the limited preservation of amphibians and reptiles. Potential explanations for the low diversity that would not fit the evidence from this site, are temporal averaging of the fossil assemblage or the assumed hiatus in this level. The onset of the interglacial phase is missing in 13 II, as seen in the palynological record, but the absence of the lower part should not have influenced the species diversity in the upper part of level 13 II-1.

A hypothetical explanation for the absence of many species in the lower part of the record could be that the succession of amphibian species in an interglacial phase differs with each interglacial. As Böhmes analysis of herpetological successions in early interglacials is based on the Eemian interglacial, it is possible that the Reinsdorf interglacial shows a different pattern in succession, with a less diverse herpetofauna.

The theory that I support here to explain the low number of herpetological species, is diversity loss due to taphonomy, in particular chemical weathering through low pH values. The average pH is higher in the second level than in Schö 13 II-1. Level 13 II-2 also has the highest level of sediment deposition, likely resulting in a longer period in which species could have accumulated.

The general observations in the interglacial herpetological succession and diversity, discussed by Böhme (1999), are not seen in Schö 13 II. One would expect the fauna in an interglacial optimum to be fully developed, and thus more diverse. Yet, the diversity of non-mammalian fauna in 13 II-1 is very low, compared to contemporaneous sites and modern analogues.

The signal in the reptile fauna is different from the amphibian fauna. Once again, the diversity is low in levels 1, 3 and 4, and high in level 2, but in this case, the first level does provide evidence for a thermophilous species, *Emys orbicularis*, which would be expected in this phase. Despite the presence of this species, the diversity is lower than expected. In modern analogues it can be seen that reptile diversity increases with a decreasing latitude, and related increase in temperature. A species diversity of 1 or 2 species is characteristic for areas around the Arctic Circle. In latitudes between 58^{o}N and 47^{o}N, species diversity is raised to 4 to 7 species, with an average of 5,9 species. In the most southern areas with a latitude of 43^{o}N, the diversity is significantly higher with 14 and 17 species respectively. Given this data from modern analogues, I would argue for an expected species diversity of a minimum of six species, with peaks to approximately 10 species. This pattern of expectation would indicate that the archaeological record is incomplete.

7.3. Soil chemistry

The non-mammalian record shows high fluctuations in species diversity. Where the fish and herpetofauna in level 1 show the lowest species diversity, and the diversity in level 2 is the highest. The diversity of levels 3 and 4 are averaged between those of level 1 and 2. Fluctuations in species diversity could be related to fluctuations in climate or other environmental changes. If there is no clear sign of climatic change, the difference in diversity could be related to external (taphonomical) factors. As discussed above, the faunal diversity signal in level 1 is not in line with the expected diversity in relation with the climatic signal in the palynological record.

The low diversity of especially the amphibians, fish and reptiles do not fit the pattern of expectation for an interglacial optimum. In modern analogues it becomes clear that the reptile diversity is more diverse in species count than the number of species found in 13 II-1. The presence of the European pond turtle, *Emys orbicularis*, is indicative of warmer temperatures, but the diversity does not fit the expected pattern. The scarce amphibian and fish faunas of 13 II-1 do not consist of any temperature dependent species. The solo-appearance of *Rana* sp. and the presence of the three most common and tolerant fish species could lead to the interpretation that the deposits are from a stadial phase, rather than a typical interglacial. Whereas the diversity of non-mammalian fauna in Schö 13 II-1 is low, it is significantly more diverse in 13 II-2. Due to these discrepancies in the record it could be interesting to analyse also potential taphonomic factors that could have influenced the limited species diversity.

While remains from mainly large mammals tend to preserve rather well, remains from the smaller animals tend to preserve only under specific conditions. Soil chemistry is one of the influencing factors in preservation of gracile materials. Organic remains tend to preserve better under anaerobic and acidic conditions. Acidity in the soil is marked by the fluctuation of pH, correlated to the $CaCO_3$ content in the sediments. The layers corresponding to a lower pH could show signs of better preservation of organic remains, depending on the type of remains.

Small mammal diversity is higher in level 13 II-1 than in the succeeding levels, thus this is not in line with the species diversity of the other categories. It is possible that the species diversity in this category is relatively high, because the molars are well preserved, and have a general better preservaion than the remains of herpetofauna and fish.

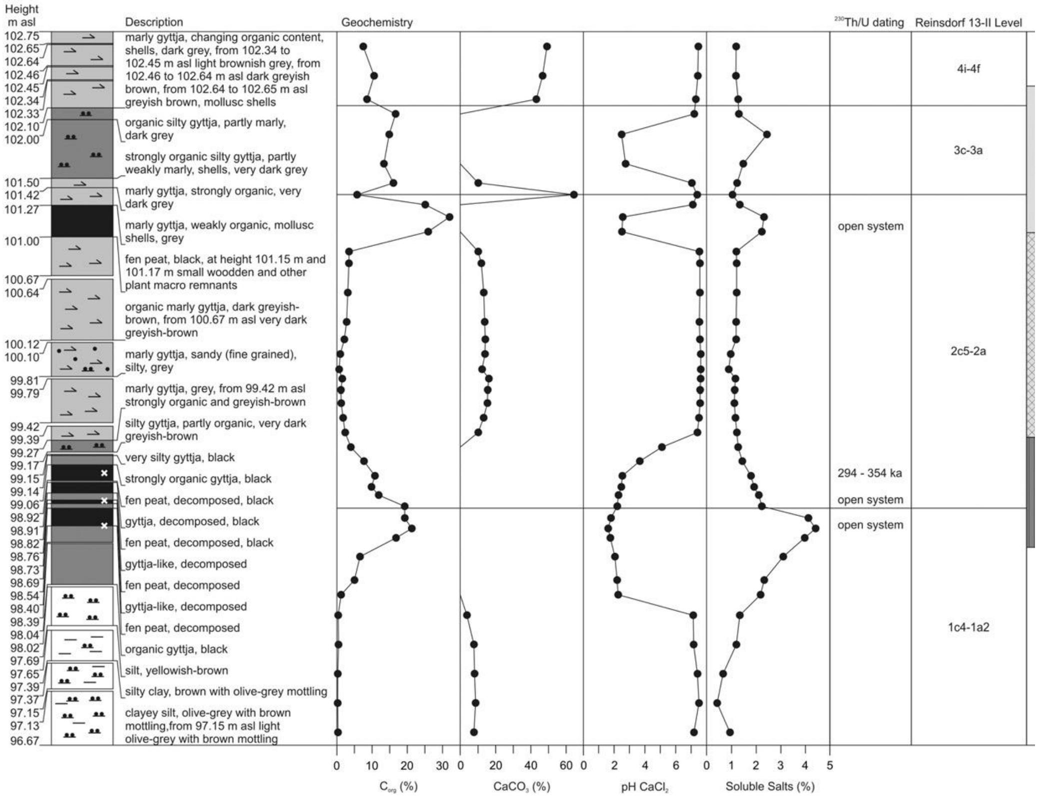


Figure 37 Geochemical properties of the sediments in Schö 13 II, including pH, $CaCO_3$, carbon content and soluble salts (Urban *et al*. 2011, 131)

In fig. 37, the soil analysis of the stratigraphy shows the variation of $CaCO_3$ content in the soil, which is correlated to pH values. It is possible that this chemical fluctuation will have had effect on the fossil assemblage by variation in the speed of decomposition of organic matter, resulting in an increased or decreased level of preservation. A question one could pose regarding this fluctuation is whether the variability in $CaCO_3$ content and pH values is visible in the floral and faunal components. A decrease in organic matter in layers with a lower $CaCO_3$ content would be an expected pattern in the predicted taphonomical patterns.

The study by Nicholson (1996) shows that the diversity loss in soils with a neutral pH in calcareous soils is minimal, whereas acid moorlands with pH values between 3,5 and 4,5 were most aggressive. Apart from the pH values, the depth of burial and presence or absence of cover is also important in the preservation of biotic remains. The characteristics of the soil determine the drainage regime and the availability of oxygen. Together with temperature and precipitation, this determines the rate of microbial activity, responsible for the deterioration of organic material.

Level 13 II-1 has a relatively high sediment accumulation of 2,03 m. In this level, the pH value varies between 7,3 in the lower half of the level and 1,8 in the upper half. Around 97.69m asl (above sea level) shift from around 7 to 2, fluctuating between 1.8 and 2.2

until the start of level 2. Depending on the depth, one would expect a good preservation of material deposited in the lower half of the level, and a poor preservation of material in the upper half of the level. Level 13 II-2 shows the longest sedimentation interval of 2,67 m with a pH of around 7,6. This pH value remains stable throughout the middle section of this profile (fig. 37). The majority of this level reflects a neutral to slightly basic pH, with pH extremes in the lower and upper part of the level. The preservation can be expected to be overall good, because of the general neutrality in pH. The upper and lower levels have a low pH value, and thus generated a potential diversity loss. Level 13 II-3 is a short phase with low pH values, averaged on 5, with fluctuations between 7 and 3. The expected preservation in this of the smaller remains level is poor, with a potentially related lower MNI, NISP and species diversity. Level 13 II-4 is an equally short phase as level 13 II-3. The pH in this level is neutral to basic. It can be expected that the preservation in this level is better than the preservation in the preceding level, including a potential higher species diversity.

Levels 3 and 4 show a similar depositional depth, but have opposing pH values; the sediments in level 3 are overall acid, while level 4 is neutral to basic. Apart from the probable research bias to 4, as compared to 3, these two levels would be a good case study to test whether the acidity in the soil affects preservation of bone material. This could be tested by analyzing which remains are still present. For example whether there is a bias towards larger mammalian and avian bones in 3, and a higher diversity in species in level 4.

In the levels 1, 2 and 3, one could expect a diversity loss based on the low pH values. Diversity loss is more likely in levels 1 and 3, because these levels are smaller than level 2, where a large part of the level is buffered with a neutral pH.

7.3.1. Results

The variation in pH values is summarised in tab. 27. The levels that have the lowest average pH are Schö 13 II-1 and Schö 13 II-3. The average pH value in Schö 13 II-2 is below 7 as well, but a significant part of the level shows a neutral pH value. The total height of sedimentation in this level is 2,67 m, of which approximately 1,70 m represents a pH near 7. This is higher than in the other levels.

Height (in m a.s.l.)	Site	pH min.	pH max.	pH average	Sedimentation (m)
96,67-98,70	Schö 13 II-1	1,6	7,3	4,3	2,03
98,70-101,37	Schö 13 II-2	2,3	7,4	5,74	2,67
101,37-102,10	Schö 13 II-3	2,4	7,4	5,0	0,73
102,10-102,75	Schö 13 II-4	7,2	7,3	7,3	0,65

Table 27 Variation in pH values related to depth in Schö 13 II. The average value of the pH is based on the values of all measuring points per level (after the data provided by Urban *et al.* 2011)

Both the levels 13 II-1 and 13 II-3 show a lower diversity than 13 II-2 and 13 II-4 that have longer sedimentary sequences with a neutral pH. The diversity in 13 II-1 is lower than expected for the non-mammalian fauna, whereas the diversity of 13 II-3 is relatively low because of the few herpetological species and small mammal species. The diversity in 13 II-1 is below expectation because of the interglacial character; one would expect to find a higher diversity in the non-mammalian faunas. The absence of these species could relate to the low pH values in this level. The low diversity of herpetological species in 13 II-3, however could be the result of both the climatic conditions as well as soil chemistry. The relatively high diversity in non-mammalian fauna in 13 II-2 is probably related to the neutral pH values in most of this level.

In the material analysis by Berkholst (2011), the preservation of the various faunal remains is discussed. When combining the data on the preservation of the faunal remains, a clear pattern can be established. The remains in Schö 13 II-1 show variable preservation, varying between a bad preservation of heavily weathered and fragmented remains to a general good preservation. In general, the material from Schö 13 II-2 is described as well preserved, whereas the majority of the remains originating from Schö 13 II-3 is defined as badly preserved and/or weathered. This pattern of preservation is in line with the expected preservation based on pH values in these levels. The acidity in levels 13 II-1 and 13 II-3 suggest a general bad preservation, whereas the dominant neutral pH in 13 II-2 suggests a general good preservation of the remains (tab. 28).
As the large mammal remains are affected by soil acidity, it can be expected that this also influences the small vertebrate remains. The low diversity reptiles, amphibians and fish in level 13 II-1 could thus be assigned to soil acidity, as explanation for this observation.

	Schö 13 II-1	**Schö 13 II-2**	**Schö 13 II-3**
Canis lupus	-	Well preserved	-
***Elephantidae* indet.**	Severely weathered	-	-
Equus caballus	weathered	Well preserved	Average preservation
Stephanorhinus kirchbergensis	Well preserved (molars)	-	-
Stephanorhinus hemitoechus	-	-	Well preserved (molars)
***Stephanorhinus* sp.**	Well preserved	Well preserved	Well preserved
Sus scrofa	Well preserved	-	-
Cervus elaphus	Well preserved, fragmented	Well preserved, fragmented	Badly preserved, severely fragmented
Megaloceros giganteus	Average/poor preservation	Average/poor preservation	Average/poor preservation
Capreolus capreolus	Bad preservation, severe flaking	Well preserved, fragmented	Average/poor preservation
***Cervidae* indet.**	Average/poor preservation	Average/poor preservation	Bad preservation, flaking
Bos/Bison	Well preserved	Well preserved	Averaged preservation

Table 28 Preservation of large mammal remains (bones and molars) per species/genus/family in Schö 13 II-1, 13 II-2 and 13 II-3 (based on data provided by Berkholst 2011, 29-60)

7.4. Middle Pleistocene environments in Schöningen 13 II

The environment of past ecosystems can be analysed by grouping the environmental preferences of all species present in a startigraphic unit. In order tan o get accurate reflection of the past environment, it is important to have as little time-averaged assemblages per unit as possible, as these time-averaged samples can yield faunal and floral data from contrasting environments.

The habitat preferences of the faunal species in Schö 13 II show gradual change in the four succeeding levels. There is a clear shift in the amount of woodland species and species that thrive in a water rich environment. The forest and woodland habitats appear to decline with the climatic change, whereas the number of species related to water rich environments increases. Also the amount of species not related to a specific habitat increases over time. This could lead to the interpretation that these species tend to avoid forested environments.

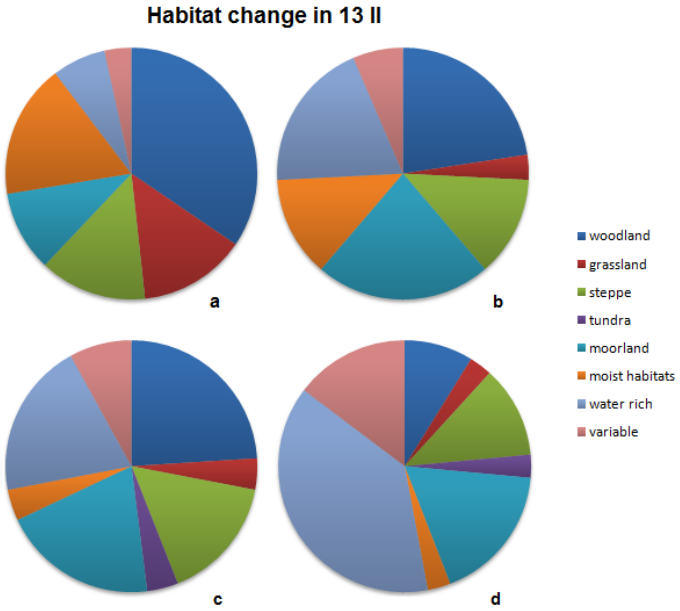


Figure 38 Change in environmental preferences per level. a = Schö 13 II-1, b = Schö 13 II-2, c = Schö 13 II-3, d = Schö 13 II-4.

Even though the amount of woodland and grassland species generally decreases over the course of time, the number of steppe adapted species does not increase. This change in composition suggests an advance of the lake level, or increase in marshland, towards 13 II-4 and a deterioration of the climate, where the openness of the environment has increased. An increase in steppe environments, however, is not supported in terms of a significant increase of steppe adapted species, but rather by the decrease in forest and woodland adapted species.

The proxies for the aquatic environment indicate that there is little change in the composition of water dependent species (fish, amphibians, pond turtle, water birds). The freshwater species remain dominant in the succeeding levels, as well as the amount of species that are also associated with brackish or saline water conditions (tab. 29). The species that can occur in brackish or saline environments are not restricted to these environments, but can also cope with freshwater environments. Thus, this analysis shows that the water body was dominantly a freshwater body with little water movement (tab. 30). The salinity conditions have not changed significantly over time, as there are no species found that are characteristically limited to brackish or saline environments, without a tolerance for freshwater environments. Because of the continental position of Schöningen, it is unlikely that the brackish and saline conditions are of Pleistocene marine origin. The brackish or saline soil conditions at this site could be caused by chemical influences of the nearby saltdome.

	13 II-1	**13 II-2**	**13 II-3**	**13 II-4**
freshwater	2	13	11	13
B+F	2	4	3	3
F+B+S	0	1	0	1
F+S	0	0	0	1

Table 29 Species preference for salinity (B+F = brackish and freshwater, F+B+S = freshwater, brackish and saline, F+S = freshwater and saline)

Species	**Vegetation**	**Bottom type**	**Water body**
Triturus vulgaris	abundant vegetation	no preference	still, shallow waters
Pelobates fuscus	abundant marginal vegetation	no preference	still
Emys orbicularis	abundant vegetation	soft bottoms	ponds
Anas acuta	abundant marginal vegetation	no preference	various
Anas crecca	abundant vegetation	no preference	shallow, permanent waters, marshes, freshwater lakes
Anas platyrhynchos	dense vegetation	no preference	shallow water
Cygnus olor	abundant vegetation	no preference	freshwater lakes, ponds
Aythya fuligula	abundant marginal vegetation	no preference	eutrophic waters, 3-5m deep
Bucephala clangula	abundant vegetation	no preference	freshwater lakes, rivers, ponds deep marshes
Tadorna tadorna	little vegetation	no preference	brackish inland lakes
Rallus aquaticus	dense vegetation	mud bottom	fresh and saline swamps, fens, marshes, lakes
Esox lucius	abundant vegetation	no preference	Lake, pond, slow-moving rivers
Perca fluviatilis	little vegetation	no preference	estuaries, streams
Rutilus rutilus	dense vegetation	sand or gravel bottom	lake, lowland streams, brackish coastal lagoons
Alburnus alburnus	little vegetation	no preference	open water lakes, rivers
Gobio gobio	little vegetation	sand or gravel bottom	fast-flowing rivers, still waters
Tinca tinca	little vegetation	mud bottom	warm lakes and pools
Scardinius erythrophthalmus	abundant vegetation	soft bottoms	lakes, rivers, marshland, ponds
Leucaspius delineatus	little vegetation	mud bottom	river, oxbow lake, water bodies

			connected to rivers
Carassius carassius	dense vegetation	mud bottom	well-vegetated lakes, oxbows, backwaters
Lota lota	little vegetation	sand or gravel bottom	lakes and rivers
Misgurnus fossilis	dense vegetation	mud bottom	backwaters of lowland streams, rivers and lakes
Pungitius pungitius	dense vegetation	soft bottoms	freshwater streams and ponds, brackish water
Cottus gobio	abundant vegetation	gravel bottom	river systems, lowland rivers, lakes
Gasterosteus aculeatus	abundant vegetation	no preference	Freshwater lakes, coastal and marine waters

Table 30 Preferences of (semi-)aquatic species that occur in the record of Schö 13 II for vegetation, bottom and water type.

The preferences of species living in and living from an aquatic habitat are shown in tab. 30. The dependence on vegetation is variable, but the majority of the species prefers an aquatic habitat with abundant to dense vegetation. The species are indicative for soft bottoms of mud or sand. The preferred type of water bodies varies per species, but all species are indicative for either ponds, lakes or marshlands.

7.5. Mammal species compositions in Schö 13 II

The composition of mammal species has changed over the course of time in 13 II (fig. 31). The number of rodentia remained relatively stable, as well as the diversity in perrisodactyla, whereas there is a fluctuation in the other groups, mainly the insectivore, carnivore and artiodactyla.

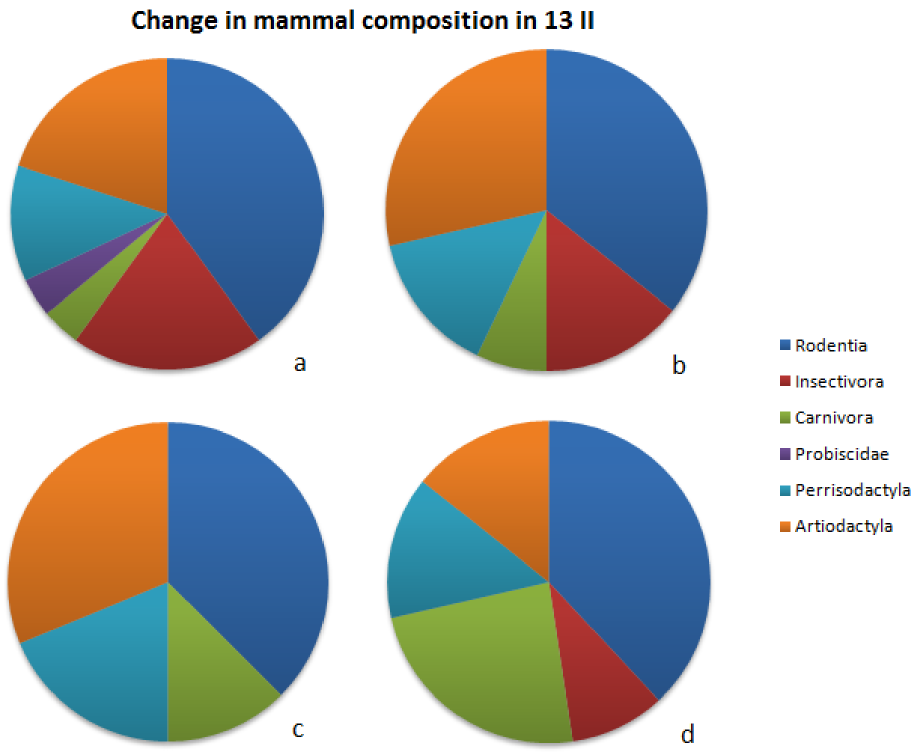


Figure 39 Change in mammal composition throughout 13 II-1 (a), 13 II-2 (b), 13 II-3 (c) and 13 II-4 (d)

The slight changes in artiodactyl diversity may be the result of the identification to genus level, rather than species level, slightly reducing the total number of identified species.

Large herbivore diversity in Middle Pleistocene sites is greater than modern large ungulate diversity. Fig. 40 and fig. 41 show the difference in diversity (number of different species) and the division of size classes in the fossil record and in modern analogues. The Middle Pleistocene fauna can be divided into five size classes, as described by Brugal and Croitor (2007). The number of size classes in modern assemblages is limited to three size classes (II, III and IV) in Bialowieza and two size classes (II and III) in the other modern analogue parks.

I (0-20)	II (20-100)	III (100-400)	IV (400-750)	V (800-1k)	VI (>1000)
	Capreolus capreolus	*Dama dama*	*Bison menneri*	*Megaloceros giganteus*	*Stephanorhinus hemitoechus*
	Sus scrofa	*Cervus elaphus*	*Bison priscus*		*Stephanorhinus kirchbergensis*
	Ovis amon	*Alces alces*	*Bos primigenius*		*Paleoloxodon antiquus*
		Rangifer tarandus	*Equus caballus*		*Elephantidae* indet.
		Capra ibex	*Equus ferrus*		*Stephanorhinus hundsheimensis*

Table 31 Division of modern and fossil Probiscidae, Perissodactyla and Artidactyla species in size classes, weight in kg (size classes after Brugal and Croitor (2007); species division based on Brugal and Croitor (2007) and MacDonald and Barrett (1998))

The size class division in fig. 40 shows that there is some variation in the composition of large herbivores in the archaeological sites. The total diversity varies between five species in 13 II-4 to 11 species in Bilzingsleben. Despite the variation in diversity, there is no significant difference in the overall composition of the size classes in the archaeological sites.

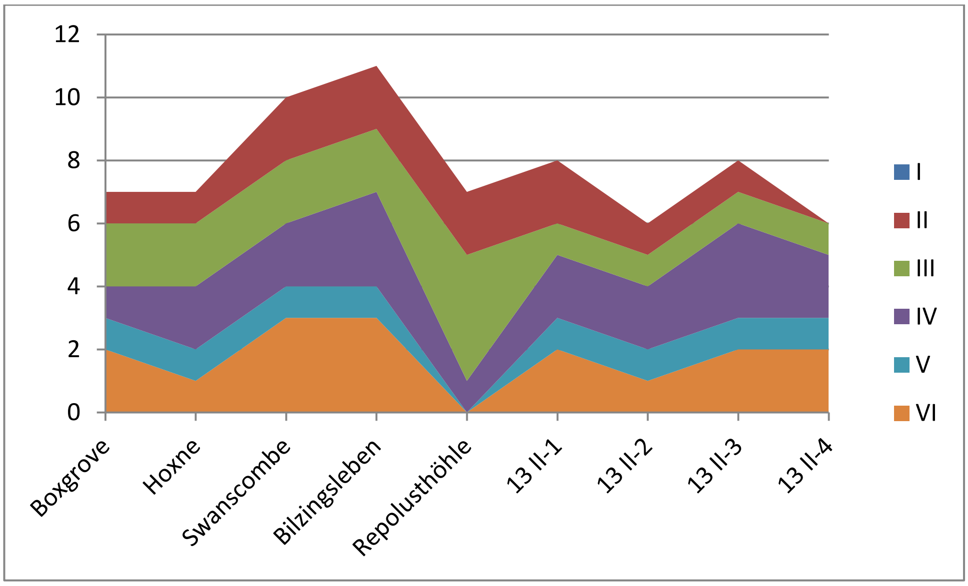


Figure 40 Division of Probiscidae, Perissodactyla and Artiodactyla size classes (Brugal and Croitor 2007) in archaeological sites

Diversity in modern analogue sites (fig. 33) is more limited, with a maximum diversity of six large mammal species in Trebon Basin and a minimum of one in Urdaibai and hortobágy.

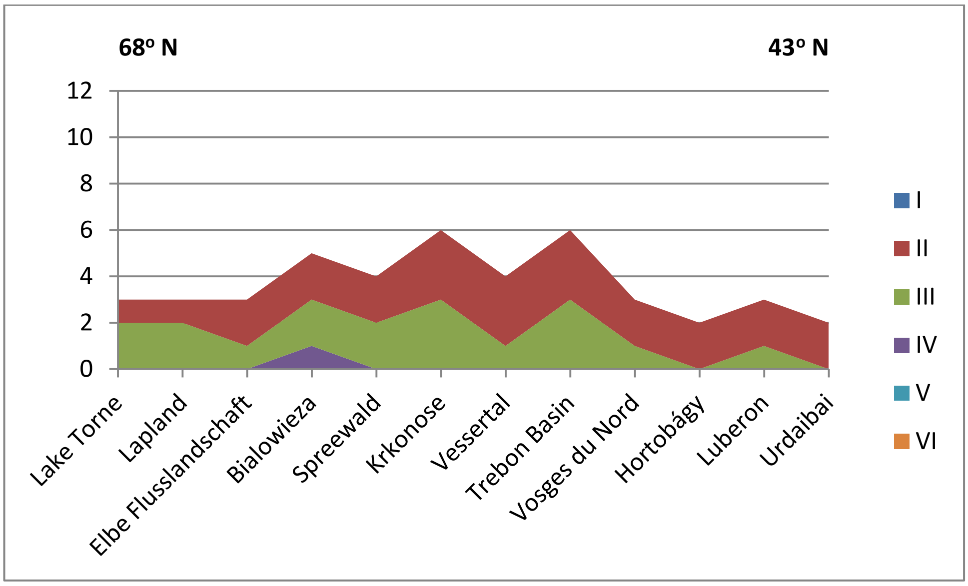
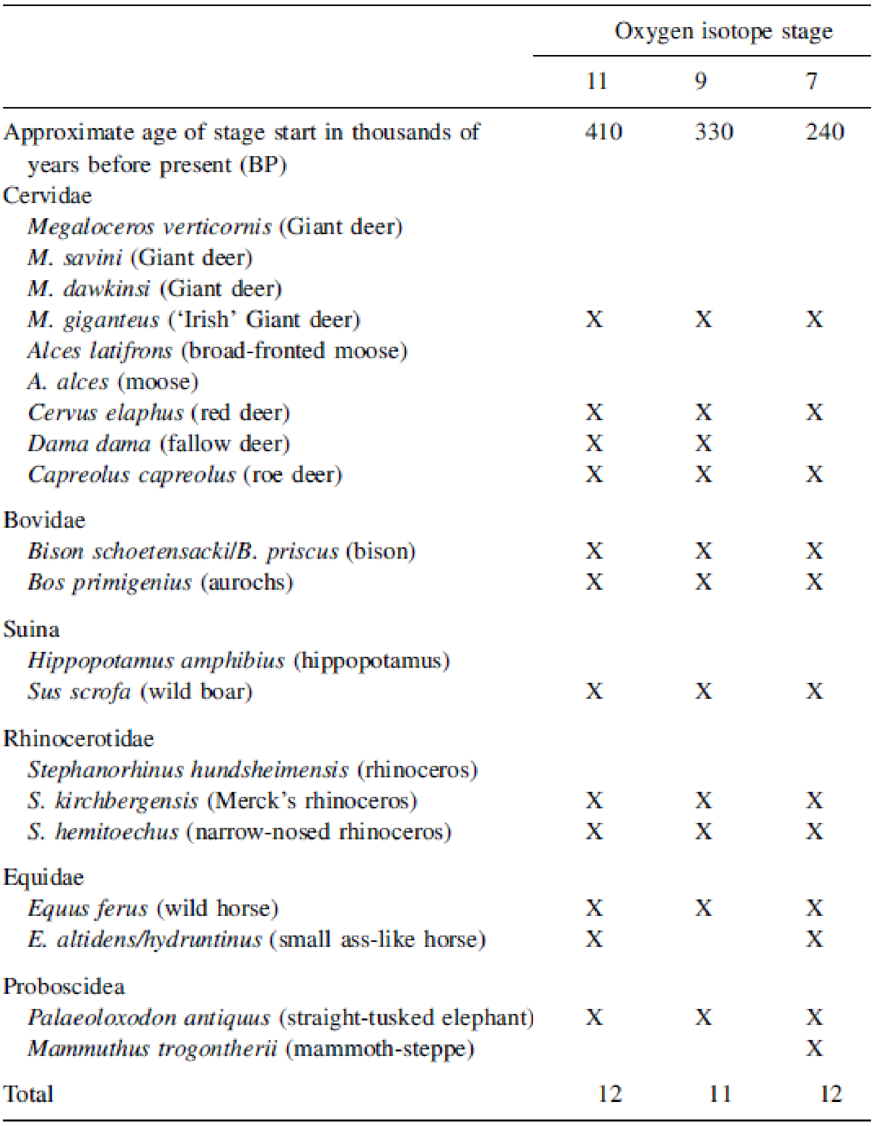


Figure 41 Division of Artiodactyla size classes (Brugal and Croitor 2007) in modern analogues

The diversity of large herbivores in Schö 13 II is not exceptionally high. The diversity of large prey species, including Perissodactyla, Probiscidae and Artiodactyla, in Schö 13 II is similar to the diversity in Boxgrove, Hoxne and Repolusthöhle. This diversity is higher in Swanscombe and Bilzingsleben (fig. 40). The large mammal, non-carnivore, species content is overall similar throughout the sites. In all sites, genus *Equus* is present, as well as genus *Stephanorhinus* (tab. 32). The number of Perissodactyla in the archaeological sites varies between two or three species. More diversity is seen in the number of Artiodactyla, which varies between three and seven species. In Schö 13 II, two Perissodactyla species are found in levels 13 II-1 and 13 II-2, and three species in 13 II-3 and 13 II-4. The number of Artiodactyla alternates between six and eight species; six species in 13 II-2 and 13 II-4, and eight species in 13 II-1 and 13 II-3.

The herbivore diversity in the archaeological sites is in general higher than the diversity in modern European assemblages (fig. 41). In the case of Schö 13 II-2 and 13 II-4, the diversity of these sites is comparable to the maximum artiodactyl diversity in the European sites.

The similarity in large ungulate communities and occurrences in the oxygen isotope stages 11, 9 and 7 is depicted in fig. 42. Many of these species occur in Schö 13 II and the archaeological sites used as a case study.



	Oxygen isotope stage		
	11	9	7
Approximate age of stage start in thousands of years before present (BP)	410	330	240
Cervidae			
Megaloceros verticornis (Giant deer)			
M. savini (Giant deer)			
M. dawkinsi (Giant deer)			
M. giganteus ('Irish' Giant deer)	X	X	X
Alces latifrons (broad-fronted moose)			
A. alces (moose)			
Cervus elaphus (red deer)	X	X	X
Dama dama (fallow deer)	X	X	
Capreolus capreolus (roe deer)	X	X	X
Bovidae			
Bison schoetensacki/B. priscus (bison)	X	X	X
Bos primigenius (aurochs)	X	X	X
Suina			
Hippopotamus amphibius (hippopotamus)			
Sus scrofa (wild boar)	X	X	X
Rhinocerotidae			
Stephanorhinus hundsheimensis (rhinoceros)			
S. kirchbergensis (Merck's rhinoceros)	X	X	X
S. hemitoechus (narrow-nosed rhinoceros)	X	X	X
Equidae			
Equus ferus (wild horse)	X	X	X
E. altidens/hydruntinus (small ass-like horse)	X		X
Proboscidea			
Palaeoloxodon antiquus (straight-tusked elephant)	X	X	X
Mammuthus trogontherii (mammoth-steppe)			X
Total	12	11	12

Figure 42 Ungulate faunas in British interglacials grouped per occurrence in oxygen isotope stages (OIS), 11, 9 and 7 (after Bradshaw *et al.* 2003, 269)

7.6. Carnivores in the fossil record

The diversity of carnivores in Schö 13 II is exceptionally low if compared to other north-west European sites from a similar age. In the Middle Pleistocene of Europe, using the age of Schö 13 II as a reference (± 300ka), there a maximum diversity of approximately 10 different large carnivore species (Brugal and Croitor 2010, 100) A comparison is made with six other Early and Middle Pleistocene sites. The carnivores identified to species level in Schö 13 II reach a maximum of two identified large carnivore species per level, whereas the number of large carnivores ranges between two and 10 in the other archaeological sites.

An analysis of several Lower and Middle Pleistocene sites shows that there is a diversity in the large mammal species compositions, in particular in the ratio of Probiscidae, Perissodactyla and Artiodactyla to large carnivores. The biggest differences compared to the low number of (large) carnivores in Schö 13 II are found in the sites Untermaßfeld and Repolusthöhle. In both sites, a high number of carnivores is found (10 large carnivore species in Repolusthöhle and nine species in Untermaßfeld).

The other archaeological sites in the case study reveal a large predator diversity of about two to four species, whereas Untermaßfeld has the highest species diversity with 10 large predators (tab. 32).

	Untermaßfeld	**Bilzingsleben**	**Hoxne**	**Swanscombe**	**Boxgrove 4C**	**Repolusthöhle**
Ursus sp.			X			
Ursus spelaeus		X		X		
Ursus denigeri					X	X
Ursus rodei	X					
Ursus arctos						X
Canis lupus		X		X		X
Canis mosbachensis						X
Canis lycaonoides	X					
Vulpes vulpes		X				X
Cuon alpestris sp.						X
Panthera leo			X	X		
Panthera leo spelaea		X				X
Panthera pardus						X
Panthera onca gombaszoegensis	X					
Puma pardoides	X					
Lynx lynx						X
Lynx issiodorensis	X					
Felis silvestris				X	X	X
Crocuta crocuta					X	
Pachycrocuta brevirostris	X					
Acinonyx pardinensis pleistocaenicus	X					
Megantereon cultridens adroveri	X					
Homotherium crenatidens	X					
Mammuthus trogontherii	X					
Equus ferrus			X	X	X	
Equus mosbachensis		X				
Equus wuesti	X					
Equus sp.	X					
Stephanorhinus etruscus	X					
Stephanorhinus hemitoechus		X		X		
Stephanorhinus kirchbergensis		X		X		
Stephanorhinus hundsheimensis					X	
Stephanorhinus sp.			X	X		
Hippopothamos amphibius						
Sus scrofa	X	X		X		
Cervus elaphus		X	X	X		X
Cervus nestii	X					
Megaloceros sp.		X				

Megaloceros giganteus			X	X		
Dama sp.		X			X	X
Dama dama			X	X		
Eucladoceros giulii	X					
Capreolus capreolus		X	X	X	X	X
Capreolus cusanoides	X					
Bos/Bison			X			
Bison sp.					X	
Bos primigenius		X		X		
Bison menneri	X					
Bison priscus		X				X
Alces carnutorum	X					
Rangifer tarandus						X
Rupicapra rupicapra						X
Capra ibex						X

Table 32 Large mammal species (carnivores, Probiscidae, Perissodactyla, Artiodactyla) in Early and Middle Pleistocene archaeological sites

The presence of carnivores in 13 II-4 can be explained if the accumulation of the horse remains was a single event, not accumulated over time. If this had been a single event, it is likely that carnivores will be attracted to the carcasses that remain near the site. This pattern would fit with the general habits of carnivores that tend to avoid human contact, but are attracted to food remains. Thus, if the hominids have left the site after the single event hunting, while leaving parts of the carcasses, an increase in carnivore presence could be expected, and thus validating the presence of these species in the archaeological record. The absence of large carnivores in other levels could be the result of more active inhabitation of the site by hominins, limiting the presence of large carnivores.

The Schöningen sites reveal very little evidence of predator species. The maximum number of identified carnivore species/genera is five, which is found in level 13 II-4. The carnivore species found in this level are *Canis lupus*, *Vulpes vulpes*, *Martes* sp., *Mustela erminea* and *Mustela nivalis*. The wolf is the only species to regularly hunt larger ungulates. *Vulpes vulpes* and the species of the Mustelid family generally hunt small mammals, with a focus on rodents. The presence of only one type of large predator reveals that there was little competition for the prey species in the proximity of the site, as all predators could feed from their own, not widely overlapping, niche.

A study of the predator assemblages in archaeological sites and modern analogues shows that areas with more than one large herbivore species are occupied by more than one large predator, often a combination of the families of canidae, felidae and ursidae. Co-occurring large predators in modern European contexts are *Canis lupus*, *Ursus arctos* and *Lynx lynx*.

In seven out of ten archaeological sites (including the four levels of Schö 13 II), the number of herbivores is higher than the total amount of carnivores. In Untermaßfeld, the amount of large herbivores to the total amount of predators is the same, yet Boxgrove is similar to the other sites in terms of the ratio of total number of carnivores to large carnivores, whereas in Untermaßfeld, the small carnivores are absent, and thus the total amount of carnivores is almost the same as the amount of large carnivores (tab. 32).

The absence of many predator remains in Schö 13 II can be explained by the size of the species' home range. Whereas the total excavated area of Schöningen 13 II is 3000m^2, the home range of large predators like *Canis lupus* exceeds the size of the excavated area. The chance of finding fossilized remains of *Canis lupus* is reduced by the combination of range size, taphonomical processes and human bias.

7.7. Predator-prey ratios in Schö 13 II compared to fossil assemblages and modern analogues

The virtual absence of carnivore remains in the Schöningen record is a striking observation. The diversity in potential prey species is relatively high, which would suggest the presence of various large predator species

In modern sites the number of large herbivore species varies between two and six species, whereas the large herbivore fauna of the archaeological sites has a diversity varying between four and eleven species. The carnivore species diversity ranges between one and six species in modern analogues, as opposed to two to ten species in fossil assemblages (fig. 43).

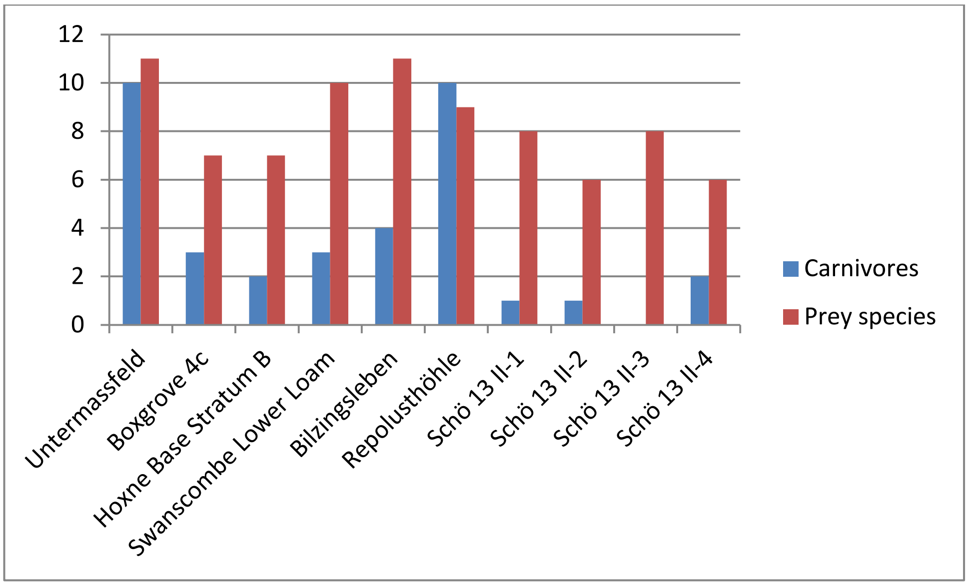


Figure 43 Large herbivore and carnivore composition in Middle Pleistocene archaeological sites

The Predator-Prey ratios in Schöningen are generally low, as only in level 13 II-1, 13 II-2 and 13 II-4 a limited number of remains of medium and large carnivores were identified to genus level. It is therefore impossible to calculate a more accurate PPR value for these sites. The large herbivore community, albeit not abundant, is relatively diverse in numbers of species. The number of prey species relative to the number of large carnivore species is reflected in tab. 33. The predator-prey ratios for the archaeological sites can be found in tab. 34 and tab. 35. The PPR values in Schö 13 II are significantly lower than in other Middle Pleistocene sites.

	Repolusthöhle	**Bilzingsleben**	**Hoxne**	**Swanscombe**	**Boxgrove 4C**
Herbivore size class					
I	0	0	0	0	0
II	1	2	1	2	1
III	2	2	2	2	1
IV	1	3	2	2	2
V	0	1	1	1	0
VI	0	2	1	2	1
Carnivore family					
Canidae	4	2	0	1	0
Felidae	4	1	1	2	1
Ursidae	2	1	1	1	1
Hyaenidae	0	0	0	0	1

Table 33 Size class division of Artiodactyla, Perissodactyla and Elephantidae compared to large carnivore compositions in archaeological sites

	Medium / Large Carnivore[11]	Large mammalian prey[12]	PPR
Repolusthöhle	10	4	2,5
Bilzingsleben	4	10	0,4
Swanscombe	4	9	0,44
Hoxne	2	7	0,286
Boxgrove	3	5	0,6
Untermaßfeld	10	11	0,91
Average	**5,5**	**7,67**	**0,86**

Table 34 Number of medium and large sized carnivores relative to large herbivores and omnivores in archaeological sites

	Medium / Large Carnivore	Large mammalian prey	PPR
Schö 13 II-1	1	8	0,125
Schö 13 II-2	1	6	0,167
Schö 13 II-3	0	8	0
Schö 13 II-4	2	6	0,167
Average	**1**	**7**	**0,114**

Tabel 34 Number of medium and large sized carnivores relative to large herbivores and omnivores in Schö 13 II

The PPR values and large mammal ratios in modern sites are depicted in tab. 36 and tab. 37. The artiodactyl fauna of Schö 13 II consists of *Cervus elaphus*, *Capreolus capreolus*, *Bos/Bison* and occasional *Sus scrofa*. *Cervus elaphus* and *Bos/Bison* are present in every level. Similar Artiodactyla compositions are found in the Spreewald area and the Elbe Flusslandschaft nature reserve. Considering the presence of *Bison/Bos*, the composition of these artiodactyl species also shares resemblance with Bialowieza national park.

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[11] Medium and large carnivores include species with an average body weight ≥ 10 kg, including *Felis silvestris,* excluding genus *Meles*.

[12] Large mammalian prey species include the orders Probiscidae, Perissodactyla and Artiodactyla

The main difference between Spreewald and Elbe and Bialowieza national park is the number and type of predators present. Bialowieza has the highest variety in predator species. 16 out of 19 predators are present in this national park. Of these species, three fall in the classification of large predators, six are considered medium size and seven fall in the range of small predators. In stark contrast, the identified predators in the Elbe Flusslandschaft are limited to four species, one medium sized and three small sized. The artiodactyl fauna of Bialowieza is associated with a high carnivore diversity, including three large predator species that focus on ungulates in their diet.

	Medium / Large Carnivore	Large Herbivore	PPR
Lake Torne	5	3	1,67
Lapland, Russia	5	3	1,67
Bialowieza	5	5	1
Elbe Flusslandschaft	1	3	0,33
Spreewald	2	4	0,5
Vessertal	1	4	0,25
Krkonose	5	6	0,83
Voges	3	3	1
Trebon Basin	3	6	0,5
Hortobágy	1	2	0,5
Urdaibai	1	2	0,5
Luberon	4	3	1,33
Average	**3**	**3,67**	**0,83**

Table 36 Number of medium and large sized carnivores relative to large herbivores in European national parks

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Herbivore size class												
I	0	0	0	0	0	0	0	0	0	0	0	0
II	1	1	2	2	2	3	3	3	2	2	2	2
III	2	2	1	2	2	3	1	3	1	0	0	1
IV	0	0	0	1	0	0	0	0	0	0	0	0
Carnivore family												
Canidae	2	2	1	2	2	2	1	2	1	1	1	2
Felidae	1	1	0	2	0	2	0	1	2	0	0	2
Ursidae	1	1	0	1	0	1	0	0	0	0	0	0
Mustelidae	1	1	0	0	0	0	0	0	0	0	0	0

Table 37 Size class division of Artiodactyla and Perissodactyla compared to large carnivore compositions in modern analogue sites. 1. Lake Torne (Tornetrask), 2. Laplandskiy, 3. Elbe Flusslandschaft, 4. Bialowieza, 5. Spreewald, 6. Krkonoše, 7. Vessertal 8. Trebon Basin, 9. Voges du Nord, 10. Hortobágy, 11. Urdaibai, 12. Luberon

The biggest differences in species diversity between Pleistocene sites and modern analogues can be found in the large herbivore diversities. Whereas the average diversity is limited to 3,67 species in modern analogues, the average in fossil assemblages is 7,67 species. A more limited difference can be found in the medium and large carnivore species diversity, where modern analogues have an average diversity of three species, compared to the 5,5 species in fossil assemblages.

The averaged PPR in fossil assemblages and national parks is similar; 0,86 in fossil assemblages and 0,83 in national parks. However, if we exclude the non-analogous sites Untermaßfeld and Repolusthöhle, the average PPR has decreased to 0,43. This can be explained by the high herbivore diversity in Middle Pleistocene contexts.

The diversity of large carnivores and herbivores in Europe, Africa (Serengeti and Nechisar) and North-America (Yellowstone) is depicted in fig. 44. In this diagram the discrepancy between the European continent and the African and American continent become clear. The diversity in the African sites is in general composition more similar to the Middle Pleistocene assemblages (fig. 43) than the contemporary European assemblages. Considering the similarities in structure of the record of both the African savannah sites and the Middle Pleistocene sites, one could expect that a higher variety of carnivores was present in Middle Pleistocene Schöningen.

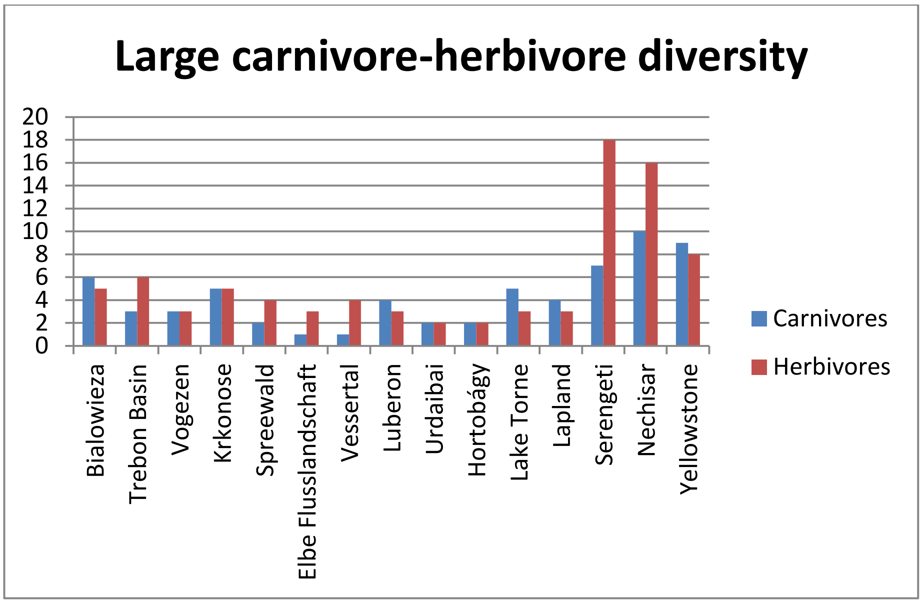

Figure 44 Composition of large herbivores and large carnivores in national parks

8. Environmental conclusions

As the fauna data is divided into the four levels 13 II-1 to 13 II-4, I gathered the environmental data from these four levels to use this as a base for comparison of the environmental conditions in the site. The following table shows the general difference between the levels in environment based on vegetation and the mollusc fauna, and it displays the species numbers per group and level.

	13 II-1	**13 II-2**	**13 II-3**	**13 II-4**
LPAZ	R3a	R3b, R4/5, RS I1, RS I2, RI 1	RI 1	RI 1
Dominant vegetation	Quercetum Mixtum phase: thermophilous forest with exotics	Carpinus-Picea-Abies phase, Pinus-Ericaceae phase, increase in Poaceae, birch carr	birch forest, steppe	Steppe environment
Mollusc fauna	Quercetum mixtum, thermophilous forest, steppe elements	continental/boreal forest, steppe elements	continental/boreal forest, steppe elements	continental/boreal forest, steppe elements
Modern analogue link	Bialowieza	Elbe Flusslandschaft	Hortobágy	Hortobágy
Total vertebrate diversity	30	42	30	43
amphibians	1	5	3	3
reptiles	2	6	2	2
mammals	24	15	16	21
large carnivores	1	0	1	2
PPR	0,44	0,00	0,5	0,67

Table 35 Environmental preferences and differences in diversity in Schö 13 II-1 – 13 II-4. The environmental preferences based on the palynology and mlluscan fauna are described, as well as close links with modern analogue sites are noted

8.1. Level 13 II-1

Level 13 II-1 is complicated in terms of species absence and presence. The species diversity in this level is highly variable. Diversity is significantly limited in the fish, amphibian and reptile assemblages, while the mollusc and small mammal diversity is high. Why diversity in this level is low for the herpetofauna and fish assemblages can only be guessed. One of the few plausible explanations for the limited species diversity is the low pH value in level 1 (pH=~2/3), as discussed above. In terms of climate, as derived from the palynological record, one would expect a more diverse species record, especially in the reptile and amphibian assemblage.

The mollusc fauna from 13 II-1 has a rich forest assemblage. The species are indicative for a well vegetated lake shore with reed beds and shrubs. The aquatic molluscs from this level indicate a waterbody that is vegetation rich with still to lightly flowing water. The majority of this assemblage consists of thermophilous species, indicative for mixed oak forests. The occurrence of species that are now exotic to Central and Western Europe together with other thermophilous species supports the interpretation that the temperature in 13 II-1 was higher than present. Next to the high amount of thermophilous species, steppe adapted species also occurred, indicating the presence of open spaces in the forested areas.

The amphibian fauna in 13 II-1 is limited to *Rana* sp. The most plausible *Rana* species in this level are *R. temporaria*, *R. arvalis*, *R. lessonae* and *R. esculanta*, as these species occur in the same region at present. With this level being associated with an interglacial optimum, one would expect to find a more diverse amphibian record, including other anurids and salamanders. The limited diversity of amphibian species would, out of the context of the other fauna species, suggest a more boreal type of landscape and climate, rather than a temperate to warm broadleaf forest biome.

The reptiles in 13 II-1 are *Vipera berus* and *Emys orbicularis*. The reptile assemblage, as well as the amphibian assemblage, is less diverse than one would expect in an interglacial optimum. Modern analogues for the same latitudes indicate that reptile diversity has a minimum of four and a maximum of seven species. Despite the low diversity, 13 II-1 does provide evidence for a warmer phase by the presence of *Emys orbicularis*, which is indicative for average summer temperatures of 17^{o}C.

No bird remains are clearly associated with level 13 II-1. The bird species with a determined context are found in levels 13 II-2, 13 II-3 and 13 II-4. Some bird species are from an unknown context, which could theoretically include 13 II-1, but as this is not certain, the birds are left out of the environmental interpretation of 13 II-1.

The fish fauna in 13 II-1 is limited to *Esox lucius* (common pike), *Perca fluviatilis* (European perch) and *Rutilus rutilus* (common roach). The co-occurrence of these three species as the only fish species in modern contexts is indicative for harsh and cold climates (Olin *et al*. 2010). These species have a widespread distribution across the entire European continent. Because of the broad tolerance of these species, they cannot be used as a dominant reference for the environmental conditions.

The small mammal assemblage is most diverse in this level. 12 species are identified to species level, and five to genus level. The majority of these species is indicative for damp habitats with dense or abundant vegetation, whereas a few species prefer drier habitats with less vegetation. Two species in this level, *Dicrostonyx* sp. and *Microtus gregalis* are not characteristic for the climate that is associated with this level, but are rather indicative for steppe and tundra environments. Species in the genus *Dicrostonyx* have a current distribution in northern Eurasia and north America north of the Arctic Circle and are seldom found in regions further south than Scandinavia (Wilson and Reeder 1993). Species in the genus *Lemmus* are at present found in tundra biomes as well as pine and birch forests, but it is suggested by Stuart *et al.* (1993, 203) that species in the genus *Lemmus* had a broader distribution during the Pleistocene. Yet, these explanations do not fit with the interglacial optimum character of Schö 13 II-1. As both these species were found at the base of Schö 13 II-1, it is, however, possible that both species originate from the underlying (peri)glacial deposits, but occur in the interglacial deposits due to taphonomical processes. In this respect, it is important to remember that the interglacial sequence of Schö 13 II does not show a complete cycle, but starts in an interglacial optimum, following a hiatus of the deposits between the Elsterian glacial and the Reinsdorf Interglacial.

The large mammal fauna of Schö 13 II-1 is relatively rich with eight large mammal species in the orders Probiscidae, Perissodactyla and Artiodactyla. The species unique to this level are *Sus scrofa* and *Elephantidae* indet., presumably *Elaphas antiquus*. These species would be expected in the interglacial optimum of 13 II-1. *Sus scrofa* is commonly associated with forested environments. *Bos primigenius* also fits the environments associated with this level, as this species is assumed to prefer milder, more vegetated environments than the more steppe adapted *Bison priscus*. The species, *Equus mosbachensis*, *Stephanorhinus kirchbergensis* and *Stephanorhinus hemitoechus* are associated with more steppic environments. *Megalorceros giganteus*, *Cervus elaphus* and *Capreolus capreolus* are typical woodland dwellers, but can also occur in a wider variety of habitats. These species and the steppe dwellers are common in Middle Pleistocene assemblages.

8.2. Level 13 II-2

Level 13 II-2 is characterised in the palynological record by a strong decrease in tree pollen and a related increase in Poaceae pollen. At the end of level 2, at the boundary between LPAZ RS I2 and RI 1, this process inverses abruptly, resulting in an increase in *Pinus* pollen and a decrease in Poaceae. The lowest part of this level represents a remnant of the tree-rich last phase of the Reinsdorf Interglacial. The environment as based on the pollen has thus changed from a phase with interglacial conditions to a more steppe adapted area. It is likely that the woodland and forest adapted species in this level are found in the lower parts of the level, correlated with the interglacial phase. Based on the palynological data in Schö 13 II-2, a deterioration in climate is interpreted, which is not clearly reflected in the faunal assemblage from this level, presumably due time-averaging of the record, mixing the interglacial deposits with deposits from the cooler phases.

Whereas the pollen diagram shows full interglacial conditions in level 1, on basis of the abundant presence of *Alnus* and *Betula*, the pollen in level 2 show a fluctuation from climatic deterioration to a gradual amelioration, indicating that the fauna from level 2 is a temporal mixture/time averaged sample of various climatic phases and fluctuating environments. The stratigraphic levels from which the faunal remains originate can thus unfortunately not be regarded as climatologically/environmentally distinct levels, but they instead represent more complex levels that comprise time averaged faunal records that are not indicative for one single type of environment.

The species diversity in this level is significantly higher than in 13 II-1. This holds mostly for the herpetological and fish assemblages. These groups also have a higher diversity than in the succeeding levels. The highest diversity in amphibians and reptiles would be expected in the interglacial optimum in 13 II-1. The diversity and composition in reptile species of 13 II-2 is similar to compositions in modern national parks in temperate latitudes. The diversity in amphibians is similar to or slightly lower than in modern sites.

The small mammal fauna in 13 II-2 is less diverse than in 13 II-1. The species found in this level are the more general species with a relatively broad distribution. Environmentally, these species are indicative for grasslands or damp, moist or water rich habitats. The large mammal fauna is less diverse than in 13 II-1, because of the absence of *Elephas* sp. and *Sus scrofa*. Otherwise, there is little change in the composition of large herbivores.

Of the three identified avian species in this level, *Anas plathyrchos* is the most common. *Cygnus olor* has a more limited distribution, excluding the northern and southern latitudes of Europe, whereas *Tadorna tadorna* is a summer migrant in Lake Torne and Trebon Basin; whereas it is a winter migrant in Hortobágy and present on a regular basis in Spreewald and Elbe Flusslandschaft. The avian species indicate a rather temperate climate.

The large mammal fauna in Schö 13 II-2 is similar to the species composition in preceding level, with the exception of *Sus scrofa* and *Elephantidae* indet.. The three cervid species, *Cervus elaphus*, *Megaloceros giganteus* and *Capreolus capreolus* are all present in this level. Species indicative for steppe environments, with the exception of *Equus mosbachensis,* are absent in this level. Bovid and rhino remains are found in this level, but as these are not identified to species level, it is not certain whether these species would represent a more forested environment, or if the total assemblage is yet changing towards a more steppe adapted fauna. No carnivore remains were found in this level, despite the diversity of large prey species.

8.3. Level 13 II-3

The palynological record in 13 II-3 is a continuation af the pollen in the upper level of 13 II-2. There is a fluctuation in *Pinus* pollen and a slight increase in *Betula* pollen as well as Cyperaceae. 13 II-3 is associated with an interstadial phase. The fauna diversity has decreased in comparison to the previous level. The herpetofauna has decreased in diversity to three amphibian species and two reptile species. These compositions are in present analogues indicative for steppe and tundra environments. The small mammals in this level are indicative for moist and damp habitats, as well as steppe (*Microtus gregalis*) and tundra (*Lemmus lemmus*). The avian fauna is similar to the species in 13 II-2, but is extended with the presence of *Aythya fuligula*. This species is not specifically characteristic for more stadial environments, as the species is at present found in the northern as well as southern latitudes of Europe.

The large mammal fauna consists of nine species, including one large predator *Canis lupus*. The other larg mammal species in this level are the three cervids, *Cervus elaphus, Capreolus capreolus, Megalocers giganteus,* which are also found in Schö 13 II-1 and 13 II-2. Both large bovid species, *Bos primigenius* and *Bison priscus* are found in this level, as well as the two rhinoceros species, *Stephanorhinus kirchbergensis* and *Stephanorhinus hemitoechus*. The number of steppe indicators, including *Bison priscus*, *Stephanorhinus kirchbergensis* and *Equus mosbachensis*, has increased, compared to the previous two levels. It could be interpreted that the environment, based on the large mammal fauna is changing towards a cooler and more open landscape, with woodland environments still present.

8.4. Level 13 II-4

The environmental characteristics of 13 II-4 are similar to the environmental conditions in 13 II-3. The herpetofauna species are the same, and the fish species are largely similar. A difference in this level compared to the preceding level is the presence of the species *Cottus gobio,* which is a stenothermous species, adapted to cold climates. The presence of this species is likely indicative for the cooler climatic conditions. The small mammal fauna is more diverse than in 13 II-3, but is similar in composition, including the species *M. gregalis* and *L. lemmus*, that are indicative for cool and dry landscapes. The steppe adapted *Microtus gregalis* also occurs in the interglacial optimum level of 13 II-1, but as discussed before, the presence of this species at the base of Schö 13 II-1 is more likely the result of taphonomy, originating from a cooler phase underlying the Schö 13 II-1 deposits, rather than the actual occurrence of the species during an interglacial optimum.

The species *Capreolus capreolus* and *Megaloceros giganteus* are absent from Schö 13 II-4. The absence of these species is often interpreted to reflect a decline of the forested environment. When analysing the distribution of *Capreolus capreolus* in modern analogues, it can be seen that this species has a broad distribution, and equally broad tolerance for a wide variety of environments. An increase of the steppe environment can thus not necessarily be linked to the absence of this species. Other large mammal species that occur in this level are the steppe dwellers *Bison priscus*, *Equus mosbachensis*, and *Stephanorhinus hemitoechus*. Species generally associated with a woodland or temperate grassland environment; *Cervus elaphus* and *Stephanorhinus kirchbergensis* are also found in this level. The number steppe adapted species has increased in this level relative to the more woodland adapted species.

9. Summarizing conclusions and discussion

The floral assemblage of 13 II indicates that the environment has changed over time from a dense forest with mesophilous and steppe elements to a cooler climate with a more open landscape. This pattern of environmental change is also visible in the mollusc fauna that show a decrease of forest adapted species and a gradual increase of steppe adapted species, including a higher total assemblage cold tolerant species. The other fauna elements are more problematic in terms of indicating environmental change. The diversity and compositions of the herpetofauna are not in line with the environmental change that can be seen in both the flora and the mollusc fauna. If the faunal groups would be analysed individually, the environmental conclusions would be contradictory on various levels. The vertebrate fauna composition in level 13 II-1 differs most from the expected pattern in diversity. In this respect, the palynological assemblage can record fluctuations in the past climate with greater detail than the faunal assemblages. The level of environmental accuracy in the various groups of fauna is variable. The mollusc assemblage proves to be indicative of environmental change, whereas the individual change in the other faunal groups is less clear. When the environmental preferences of various species are analysed, there is a relatively clear change in the environment; the diversity in forest and woodland adapted species decreases, whereas the diversity in aquatic adapted species increases. This could indicate that the climate deteriorated gradually over the course of time and that the lake, or marsh environments expanded towards level 13 II-4.

The variation in the faunal groups is influenced by different factors. The limited diversity of fish, amphibian and reptile species in 13 II-1 can be explained by the acidity of the soil and the relative short period of deposition. It is assumed that the period of deposition in 13 II-1 is shorter than in 13 II-2, because of the difference in sedimentation in both levels. The general scarcity of carnivore remains on the other hand is more likely a result of ecological nature than a result of taphonomical processes or hominin action. Hominin action may play a role in the carnivore scarcity, but in the context of 13 II-4 this is not the sole explanation, as the carnivore diversity of 13 II is the highest in 13 II-4, the level with the highest concentration of archaeological activity. What could have happened at this stage is that the killing of the horses was a short term event, where much hunting remains were left at the site, attracting carnivores, thus explaining the higher diversity of carnivores in this level. The archaeological signal at 13 II-4 contradicts this view, because the level of archaeological activity is assumed to be the highest in this level, which would theoretically imply a low amount of carnivores. The carnivore diversity in 3 II-4, however, is higher than in the other levels. The higher amount of species diversity in 13 II-4 could be formed because of taphonomical factors in the lower levels, or because the carnivores were attracted to the herbivore carcasses, provided by the hominids.

The change in the faunal assemblage can be a result of both natural and artificial influence. The interpretation on the state of the palaeoenvironment of Schöningen thus depends on the forming factors. Human influence is most likely to be seen in the medium and large mammal fauna. Non-analogue accumulations, such as the density of horse remains in mainly Schöningen 13 II-4, in combination with the many butchering marks provides likely evidence for accumulation by hominin actors.

Fluctuations in small vertebrates (micro mammals, amphibians and reptiles) are less likely caused by hominin interaction. Therefore these elements are likely a better estimate for fluctuations in the past environment, or the differences in diversity are a result of taphonomical factors. The background fauna in Schö 13 II shows a slight deterioration in climate over the course of the four levels. This deterioration can also be seen in the palynological samples of Schö 13 II, that show the climatic fluctuations in more detail. The non-mammalian vertebrate fauna of Schö 13 II-1 appears to be affected most by taphonomical processes, and thus shows a biased sample of the past environment. the non-mammalian vertebrates in Schö 13 II-2 to 13 II-4 show a declining trend in species diversity, related to a deterioration in climate. The micromammals do not show a clear declining trend in diversty, but the composition of the species, and their related environmental preferences change over time. The environmental preferences of the species change from a dominance of forest and woodland adapted species, to grassland and steppe adapted species.

The ecological elements in Schöningen 13 II are in some elements similar to modern analogues, but the context differs when we compare the herbivore compositions that are substantially diverse in the Middle Pleistocene. Most of the faunal elements from the other groups are still present in modern contexts. Despite the similar occurrences in both the fossil record and modern analogues, the actual compositions in species diversity are not similar. As demonstrated, the diversity patterns in 13 II-1 match the patterns of Laplandskiy national park, but the environments are significantly different. It is most likely that taphonomical factors have altered the fossil record, e.g. soil acidity, thus making it difficult to compare species compositions of past and present contexts.

As mentioned earlier, the virtual absence and scarcity of (large) carnivores is uncharacteristic for environments with many large herbivores. The modern analogues have shown that a minimum of two large carnivore species are usually present in national parks with either a higher diversity of large herbivores or large densities. In the Middle Pleistocene the large carnivore diversity can be assumed to be slightly higher in Schö 13 II, with three or four carnivore species, considering the general higher diversity of large carnivores in other archaeological sites of similar age. The large herbivore diversity in Schö 13 II is similar to the diversity in other archaeological sites, suggesting a higher variety in large carnivores would have occurred at the site.

The pattern of environmental change in 13 II as seen in the flora and fauna shows a change from an interglacial optimum to a stadial phase in an onset to glacial conditions. This fluctuation in combination with the new U/Th datings provided by Urban *et al.* (2011) of ~300 ka in the lower level of 13 II-2 would place the Reinsdorf Interglacial in MIS 9. As of yet, little is known about the environment of post-Holsteinian interglacials, in particular MIS 9 environments. Therefore it is important to get an accurate reconstruction of the environment of the Reinsdorf Interglacial in Schö 13 II, providing information on the environmental characteristics of a regional interglacial phase, succeeding the Holsteinian Interglacial, and preceding the Drenthe ice advance.

In this research, the palynological record as well as the mollusc fauna provided the most detailed information on the environment and the gradual climate change. The herpetological species are in theory practical indicators of change in either climate or (aquatic) environment, but due to an incomplete record in 13 II-1, a full comparison within this group was not possible. The amphibian species had a diversity varying from one species to six species. In modern sites in Central Europe, this diversity is averaged around 10-12 species. A total diversity of six species in Schö 13 II-2 is thus relatively low compared to modern analgues. The environmental consequences of the low diversity of species would lead to the interpretation that the restricted diversity in Schö 13 II-1 is comparable to high latitude sites in Northern Europe. The reptiles in Schö 13 II-1 and 13 II-2 were characterised by the presence of *Emys orbicularis*, which is indicative for interglacial conditions. The absence of this species in this succeeding levels, 13 II-3 and 13 II-4 could be seen as a marker for a general cooling in temperature. The fish proved to be indicative for various types of salinity, water, velocity, depth, vegetation and the type of bottom, but less so for climate. One species that can be considered climatologically indicative, is the species *Cottus gobio*, a stenothermous fish that can tolerate freezing temperatures, but of which the distribution is restricted by higher temperatures. The presence of this species in Schö 13 II-4 is a good indicator for a relatively cold climate in this level. The majority of the small mammal species was indicative for vegetation type and humidity, and indirectly for climate. Schö 13 II-1 contained small mammal species mainly indicative for temperate, forested environments, whereas this has changed in Schö 13 II-4 to the presence of more steppe adapted species, such as *Microtus gregalis*. *Lemmus lemmus,* also found in 13 II-4, is indicative for tundra environments The large mammal fauna from Schöningen 13 II is similar to the large mammal species in contemporaneous sites, with the exception of large carnivores, which are virtually absent in Schö 13 II. Most of the species have a broad tolerance range that can extend the preferred habitat ranges. Also, some species co-occur while the assumed environmental preferences are different. This is the case for *Stephanorhinus kirchbergensis* and *Stephanorhinus hemitoechus* and for the bovid species *Bos primigenius* and *Bison priscus*. The co-occurrence of these species can indicate that the species had a relatively broad tolerance, or that the environment contained elements favourable for bth species. Therefore this fauna category is not characteristic for the environment, but the large mammal fauna can be indicative for the type of predator-prey community.

The ecological basis of this thesis consisted of both palynological data and fossil fauna assemblages. The various fauna compositions from the different levels showed that the record is not always an accurate reflection of the past environment. In the case of the Schöningen 13 II sites, there were enough environmental proxies to form a buffer for potential incomplete assemblages. Without a sufficient buffer, the environment may be interpreted in a wrong way, providing different ecological conclusions. An example is the limited diversity in fish and amphibians in 13 II-1. In modern analogues, these limited compositions would be indicative for areas in the northern latitudes, thus comparable to environments with an ‘interstadial’ character rather than the characteristics of an interglacial optimum. In this case, there was sufficient other data to indicate the interglacial climate; palynology, molluscs and reptiles. In other sites, were the total species diversity is more limited, or where only a selection of species are analysed (for example only mammals or herpetofauna) it might be problematic to make accurate interpretations of the past climate and/or ecosystem.

In this thesis I posed various explanations for limited species diversities and the absence of particular species in the fossil record. These explanations are based on a combination of modern data and data from modern ecosystems. Both the fossil and modern data are biased; the fossil data by taphonomical processes and sampling and excavation, and the modern data is subjected to sampling, as well as influences by humans. As Middle Pleistocene environments are significantly different from today’s environments and human influenced ecosystems, it is difficult to examine to what extent past ecosystems are similar in composition and functioning to modern ecosystems.

When making interpretations on the past environment, it is important to keep all biases, both in the fossil record as well as in the contemporary assemblages, in mind. Also, this thesis has shown that the various ecological proxies cannot give proper environmental information, when used on their own. It is thus crucial for the understanding of climatic fluctuations in the past, to examine as many proxies as possible, and to analyse the possible forms of bias, including natural bias (taphonomy, species behaviour and ecology) and human-induced biases, concerning sampling and excavation, but also the identification of species.

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List of figures

List of tables

Appendix I

Vertebrate species occurrences in Schöningen 13 II

	13 II-1	13 II-2	13 II-3	13 II-4
Fish				
Esox lucius	X	X	X	X
Perca fluviatilis	X	X	X	X
Rutilus rutilus	X	X	X	X
Alburnus alburnus		X	X	X
Gobio gobio		X	X	X
Tinca tinca		X	X	X
Scardinius erythrophthalmus		X	X	
Leucaspius delineatus		X		
Carassius carassius		X	X	X
Lota lota		X		
Misgurnus fossilis		X	X	X
Pungitius pungitius		X		X
Cottus gobio				X
Gasterosteus aculeatus		X		
Amphibians				
Triturus vulgaris		X	X	X
Bufo bufo		X	X	X
Rana sp.	X			
Rana temporaria		X	X	X
Rana arvalis		X		
Pelobates fuscus		X		
Reptiles				
Vipera berus	X	X	X	X
Lacerta vivipara		X	X	X
Emys orbicularis	X	X		
Anguis fragilis		X		
Lacerta agilis		X		
Natrix natrix		X		
Mammals				
Desmana moschata	X			X
Sorex minutus	X	X		X
Sorex araneus	X	X		
Crocidura sp.	X			
Neomys sp.	X			
Dicrostonyx sp.	X			
Lemmus lemmus			X	X
Sicista betulina			X	
Castor fiber				X
Trogontherium cuvieri		X		X
Clethrionomys glareolus	X	X		
Arvicola cantiana terrestris	X	X	X	X
Microtus sp.	X	X	X	X
Microtus arvalis/agrestis	X	X	X	X
Microtus agrestis	X			
Microtus gregalis	X		X	X
Microtus oeconomus	X		X	X
Microtus terricola subterraneus	X	X		X
Apodemus sp.	X	X		
Apodemus sylvaticus	X	X		
Apodemus maastrichtiensis	X			
Canis lupus		X		X
Vulpes vulpes				X
Martes sp.			X	X
Mustela nivalis				X

Mustela erminea			X	X
Elephantidae indet.	X			
Equus mosbachensis	X	X	X	X
Stephanorhinus kirchbergensis	X		X	X
Stephanorhinus hemitoechus			X	X
Stephanorhinus indet.	X	X		
Sus scrofa	X			
Cervus elaphus	X	X	X	X
Megaloceros giganteus	X	X	X	
Capreolus capreolus	X	X	X	
Bos primigenius			X	X
Bison priscus			X	X
Bos/Bison	X	X		

Appendix II

Large mammal fauna from archaeological sites

	Bilzingsleben	**Hoxne**	**Swanscombe**	**Boxgrove 4C**	**Repolusthöhle**
Canis lupus	X		X		X
Canis mosbachensis					X
Vulpes vulpes	X				X
Cuon alpestris sp.					X
Panthera leo		X	X		
Panthera leo spelaea	X				X
Panthera pardus					X
Lynx lynx					X
Felis silvestris			X	X	X
Ursus sp.		X			
Ursus spelaeus	X		X		
Ursus denigeri				X	X
Ursus arctos					X
Crocuta crocuta				X	
Equus ferrus		X	X	X	
Equus mosbachensis	X				
Stephanorhinus hemitoechus	X		X		
Stephanorhinus kirchbergensis	X		X		
Stephanorhinus hundsheimensis				X	
Stephanorhinus sp.		X	X		
Cervus elaphus	X	X	X		X
Megaloceros sp.	X				
Megaloceros giganteus		X	X		
Dama sp.	X			X	X
Dama dama		X	X		
Capreolus capreolus	X	X	X	X	X
Bos/Bison		X			
Bison sp.				X	
Bison priscus	X				X
Bos primigenius	X		X		
Sus scrofa	X		X		

Appendix III

Species list of archaeological sites

	Untermaßfeld	Bilzingsleben	Hoxne	Swanscombe	Boxgrove	Repolusthöhle
Fish						
Silurus glanis		X				
Tinca tinca		X				
Amphibians						
Triturus cf. *cristatus*	X					
Triturus cf. *vulgaris*	X					
Bufo bufo	X	X				
Bufo cf. *viridis*	X					
Hyla cf. *arborea*	X					
Rana arvalis	X					
Rana cf. *dalmatina*	X					
Rana temporaria						
Reptiles						
Chalcides sp.	X					
Eublepharis sp.	X					
Natrix natrix		X				
Birds						
Anas platyrhynchos		X				
Bucephala clangula		X				
Cygnus olor		X				
Cygnus sp.	X					
Anser sp.	X					
Haliaëtus albicilla		X				
Haliaëtus sp.	X					
Francolinus alpeki	X					
Strix alucu		X				

Turdus sp.	X	X				
Corvus sp.	X					
Garrulus aff. *glandarius*	X					
Insectivora						
Erinaceus sp.	X				X	
Desmana moschata			X			
Neomys sp.					X	
Sorex araneus		X	X			X
Sorex minutus			X		X	
Sorex runtonensis	X				X	
Sorex ex gr. *margaritodon*	X					
Sorex savini					X	
Talpa europaea	X				X	X
Talpa minor	X			X	X	
Talpa sp.		X			X	
Rodentia						
Sciurus cf. *whitei*	X					
Sciurus sp.					X	
Spermophilus sp.		X				
Spermophilus ex gr. *primigenius*	X					
Spermophilus cf. *citellus*						X
Marmota marmota						X
Hystrix cf. *vinogradovi*						X
Myopus schisticolor					X	
Lemmus lemmus			X		X	
Clethrionomys glareolus		X	X		X	
Pliomys episcopalism	X				X	
Arvicola arvaloides				X		
Arvicola cantiana		X	X	X		
Arvicola terrestris					X	
Microtus subterraneus					X	
Microtus agrestis		X	X	X	X	
Microtus arvalis		X		X	X	X
Microtus oeconomus				X	X	

Microtus thenii	X					
Microtus sp.					X	
Pitmys arvaloides			X			
Muscardinus avellanarius					X	
Sicista cf. *Betulina*					X	
Apodemus flavicollis		X				X
Apodemus maastrichtiensis					X	
Apodemus sylvaticus					X	X
Castor fiber	X	X	X	X		
Trogontherium cuvieri	X	X	X			
Glis glis		X				
Glis sackdillingensis	X					
Cricetus major						X
Cricetus cf. *runtonensis*	X					
Clethrionomys glareolus		X				X
Clethrionomys cf. *hintonianus*	X					
Clethrionomys hunasensis						X
Mimomys savini	X					
Mimomys pusillus	X					
Lagomorpha						
Oryctolagus cuninculus				X		
Lepus timidus					X	
Lepus sp.	X					X
Carnivora						
Canis lupus		X		X	X	X
Vulpes vulpes		X				X
Ursus arctos						X
Ursus denigeri		X			X	X
Ursus spelaeus				X		
Ursus sp.			X			
Mustela erminea					X	
Mustela lutreola					X	
Mustela sp.					X	
Mustela nivalis						X

Martes martes				X		X
Martes sp.		X				
Meles meles		X				X
Meles sp.					X	
Lutra lutra			X			
Crocuta crocuta					X	
Felis sylvestris		X		X	X	X
Panthera leo			X	X		
Panthera leo spelaea		X				X
Panthera pardus						X
Lynx lynx						X
Panthera onca gombaszoegensis	X					
Acinonyx pardinensis pleistocaenicus	X					
Puma pardoides	X					
Lynx issiodorensis	X					
Megantereon cultridens adroveri	X					
Homotherium crenatidens	X					
Pachycrocuta brevirostris	X					
Meles hollizeri	X					
Ursus rodei	X					
Canis lycaonoides	X					
Canis mosbachensis	X					X
Cuon alpinus sp.						X
Artiodactyla						
Bison menneri	X					
Bison priscus		X				X
Bison sp.					X	
Bos primigenius		X		X		
Bos/Bison			X			
Rangifer tarandus						X
Megaloceros giganteus			X	X		X
Megaloceros sp.		X				
Cervus elaphus		X	X	X	X	X
Dama dama			X	X	X	

Dama sp.		X				
Capreolus capreolus		X	X	X	X	X
Capreolus cusanoides	X					
Alces carnutorum	X					
Cervus s.l. *nestii vallonnetensis*	X					
Sus scrofa	X	X		X		X
Eucladoceros giulii	X					
Hippopotamus amphibious antiquus	X					
Rupicapra rupicapra						X
Capra ibex						X
Perissodactyla						
Stephanorhinus etruscus	X					
Stephanorhinus hundsheimensis					X	
Stephanorhinus hemitoechus		X		X		
Stephanorhinus kirchbergensis		X		X		
Stephanorhinus sp.			X	X		
Eauus ferus			X	X	X	
Equus mosbachensis		X				
Equus wuesti	X					
Equus sp.	X					
Probiscidae						
Mammuthus trogontherii trogontherii	X					
Palaeoloxodon antiquus		X		X		
Elephantidae indet.					X	X

Appendix IV

Species lists of 12 national parks and protected areas in Europe (data gathered from the Biological Inventories of the World's Protected Areas database)

	Lake Torne	Lapland	Elbe Flusslandschaft	Bialowieza	Spreewald	Krkonose	Vessertal	Trebon Basin	Voges	Hortobágy	Luberon	Urdaibai
Fish												
Abramis ballerus			X									
Abramis bjoerkna				X	X					X		
Abramis brama			X	X	X			X	X	X	X	
Alburnoides bipunctatus								X	X		X	
Alburnus alburnus			X	X	X					X	X	
Anguila anguila			X	X	X		X	X	X		X	X
Aristichthys nobilis					X							
Aspius aspius			X		X			X				
Barbatula barbatula					X							
Barbatus barbatus												X
Barbus barbus					X				X		X	
Barbus bocagei												X
Barbus meridionalis											X	
Chelon labrosus												X
Chondrostoma nasus								X			X	
Chondrostoma toxostoma											X	X
Carassius auratus				X	X			X		X		
Carassius carassius			X	X	X		X	X	X	X		
Carassius gibelio			X									
Cobitis taenia			X	X	X			X		X		
Coregonus albula							X					
Coregonus lavaretus multispinatus	X	X						X				
Coregonus peled								X				
Cottus gobio						X	X	X	X			
Cottus poecilopus	X			X								
Ctenopharyngodon idellus			X	X	X			X				

Cypriunus carpio			X	X	X		X	X	X	X		
Dicentrarchus labrax												X
Esox lucius	X	X	X	X	X			X	X	X		
Eudontomyzon mariae				X								
Gasterosteus aculeatus			X	X	X		X		X			
Gobio gobio			X	X	X		X	X	X			
Gymnocephalus gerbuus			X	X	X			X		X		
Hypophthalmichthys molitrix			X		X		X	X		X		
Lampetra fluviatilis				X								
Lampetra planeri			X		X	X	X	X	X			
Lepomis gibbosus								X	X	X		
Leucaspius delineatus			X		X		X	X				
Leuciscus cephalus			X		X			X	X	X		
Leuciscus idus			X	X	X			X				
Leuciscus leuciscus			X	X	X			X	X			
Leuciscus souffia											X	
Lota lota	X			X	X			X				
Micropterus salmoides								X			X	
Misgurnis fossilis			X	X	X			X		X		
Nemacheilus barbatulus cau				X		X	X	X	X			
Oncorhynchus mykiss					X	X		X			X	
Perca fluviatilis	X	X	X	X	X		X	X	X	X	X	
Phoxinus phoxinus	X		X			X	X	X	X		X	X
Platichtys flesus												X
Pomatoschistus microps												X
Pomatoschistus minutus												X
Pseudorasbora parva								X				
Pungitius pungitius			X	X	X							
Rhodeus sericeus			X	X	X					X		
Rutilus rutilus			X	X	X		X	X	X	X	X	
Salmo trutta	X				X	X	X	X	X		X	X
Sander lucioperca					X					X	X	
Salvelinus alpinus murta	X											
Salvelinus fontinalis						X	X		X			
Scardinius erytrophthalmus			X	X	X			X	X	X	X	
Silurus glanis					X			X		X		

Solea vulgaris												X
Thymallus thymallus	X							X	X			
Tinca tinca			X	X	X		X	X	X	X	X	
Vimba vimba			X					X				
Zingel asper											X	
Amphibians												
Alytes obstetricans							X				X	X
Bombina bombina			X	X	X			X		X		
Bombina variegata								X	X			
Bufo bufo			X	X	X	X	X	X	X	X	X	X
Bufo calamita			X	X	X		X	X	X		X	X
Bufo viridis				X	X			X				
Discoglossus hispanicus												X
Hyla arborea			X	X	X		X	X	X	X		X
Hyla meridionalis											X	
Pelobates cultripes											X	
Pelobates fuscus			X	X	X			X		X		
Pelodytes punctatus											X	X
Rana arvalis			X	X	X		X	X		X		
Rana dalmatina							X	X	X	X		
Rana esculanta			X	X	X			X	X	X		
Rana iberica												X
Rana lessonae			X	X	X		X	X				
Rana perezi											X	X
Rana ridibunda			X	X	X					X		
Rana temporaria	X	X	X	X	X	X	X	X	X			X
Salamandra salamandra						X	X		X		X	X
Triturus alpestris						X	X	X	X			
Triturusd cristatus			X	X	X	X	X	X	X	X		
Triturus helveticus							X		X			X
Triturus marmoratus												X
Triturus vulgaris			X	X	X	X	X	X	X	X		
Reptiles												
Anguis fragilis			X	X	X	X	X	X	X		X	

Chalcides chalcides											X	
Coluber viridiflavus											X	
Coronella austriaca			X	X	X	X	X	X	X		X	
Coronella girondica											X	
Elaphe longissima											X	
Elaphe scalaris											X	
Emys orbicularis			X	X	X					X	X	
Lacerta agilis			X	X	X	X	X	X	X	X		
Lacerta viridis											X	
Lacerta vivipara	X	X	X	X	X	X	X	X	X			
Malpolon monspessulanus											X	
Natrix maura											X	
Natrix natrix			X	X	X	X	X	X	X	X	X	
Podarcis muralis									X		X	
Podarcis taurica										X		
Psammodromus hispanicus											X	
Tarentola mauritanica											X	
Timon lepidus											X	
Vipera aspis											X	
Vipera berus		X		X		X	X	X				
Insectivora												
Crocidura leucodon					X				X	X		
Crocidura russula									X		X	X
Crocidura suaveolens					X	X		X		X	X	X
Erinaceus concolor				X		X				X		
Erinaceus europaeus					X	X	X	X	X		X	X
Neomys anomalus				X		X	X	X				X
Neomys fodiens	X	X	X	X	X	X	X	X	X	X	X	X
Sorex alpestris						X						
Sorex araneus	X	X		X	X	X	X	X	X	X		
Sorex coronatus												X
Sorex minutissimus		X		X								
Sorex minutus		X	X	X	X	X	X	X	X	X		X
Sorex caecutiens	X	X		X								
Suncus etruscus											X	

Talpa europaea				X	X	X	X	X	X	X	X	X
Rodentia												
Cricetus cricetus						X				X		
Sciurus *vulgaris*	X	X		X	X	X	X	X	X		X	X
Spermophilus citellus						X		X		X		
Myopus schisticolor		X										
Lemmus lemmus	X	X										
Chionomys nivalis											X	
Clethrionomys glareolus	X	X	X	X	X	X	X	X	X	X		X
Clethrionomys rufocanus	X	X										
Clethrionomys rutilus	X	X										
Pteromys volans				X								
Arvicola sapidus											X	X
Arvicola terrestris	X	X		X	X	X	X	X	X	X		
Micromys minutus			X	X	X	X		X	X	X		X
Microtus agrestis	X	X		X	X	X	X	X	X		X	X
Microtus arvalis				X	X	X		X	X	X		
Microtus duodecimcostatus											X	
Microtus gerbei												X
Microtus lusitanicus												X
Microtus oeconomus	X	X		X	X							
Microtus subterraneus						X	X	X		X		
Mus musculus				X	X	X	X	X	X	X	X	X
Myocastor coypus					X						X	
Myoxis glis				X		X					X	X
Ondatra zibethicus	X	X		X	X	X		X	X	X	X	
Muscardinus avellanarius				X		X	X	X	X			
Sicista Betulina				X								
Apodemus agrarius			X	X	X	X				X		
Apodemus flavicollis				X	X	X		X	X	X		
Apodemus sylvaticus				X	X	X	X	X	X	X	X	X
Apodemus uralensis										X		
Castor fiber	X	X	X	X							X	
Rattus norvegicus		X		X	X	X		X	X	X	X	X
Rattus rattus					X						X	X

Eliomys quercinus					X				X		X	X
Marmota marmota						X						
Lagomorpha												
Oryctolagus cuninculus					X	X		X			X	
Lepus capensis						X		X	X		X	
Lepus europaeus				X	X		X			X		
Lepus timidus	X	X		X								
Carnivora												
Canis lupus	X	X		X	X	X		X			X	
Vulpes vulpes	X	X	X	X	X	X	X	X	X	X	X	X
Ursus arctos	X	X		X		X						
Mustela erminea	X	X		X	X	X	X	X	X	X		
Mustela eversmanii						X				X		
Mustela lutreola				X								X
Mustela nivalis	X	X	X	X	X	X	X	X	X	X	X	X
Mustela putorius				X	X	X	X	X	X	X	X	X
Mustela vison	X	X		X	X	X		X				X
Martes foina				X	X	X	X	X	X	X	X	X
Martes martes	X	X	X	X	X	X	X	X	X			
Meles meles			X	X	X	X		X	X	X	X	X
Lutra lutra	X	X		X	X	X		X		X	X	
Felis sylvestris				X		X			X	X	X	X
Lynx canadensis		X										
Lynx lynx	X			X		X		X	X		X	
Alopex lagopus	X	X										
Genetta genetta											X	X
Gulo gulo	X	X		X								
Nyctereutes procyonoides				X	X	X		X				
Procyon lotor					X		X		X			
Perissodactyla												
Eauus caballus				X								
Artiodactyla												

Alces alces	X	X		X	X	X		X				
Bison bonasus				X								
Cervus elaphus			X	X	X	X	X	X	X		X	
Dama dama								X				
Capreolus capreolus	X	X	X	X	X	X	X	X	X	X	X	X
Rangifer tarandus	X	X										
Capra ibex						X						
Ovis ammon						X	X	X				
Rupicapra rupicapra						X						
Sus scrofa			X	X	X	X	X	X	X	X	X	X

Appendix V

Occurrences of extant species in Schöningen 13 II and present-day biomes

Species	level	Biomes
Fish		
Esox lucius	1, 2, 3, 4	I, II, IV, V, VI, VII
Perca fluviatilis	1, 2, 3, 4	I, II, IV, VI, VII
Rutilus rutilus	1, 2, 3, 4	I, II, IV
Alburnus alburnus	2, 3, 4	II, IV
Gobio gobio	2, 3, 4	I, II
Tinca tinca	2, 3, 4	I, II, IV
Scardinius euryth.	2, 3	I, II, IV
Leucaspius delineatus	2	I, II
Carassius carassius	2, 3, 4	I, II, IV
Lota lota	2	I, II, VII
Misgurnis fossilis	2, 3, 4	I, II, IV
Pungitus pungitus	2, 4	II, IV
Cottus gobio	4	I, II, VII
Gasterosteus Aculeatus	2	II
Amphibians		
Rana sp.	1	I, II, III, IV, V, VI, VII
Triturus vulgaris	2, 3, 4	I, II, IV, V
Bufo bufo	2, 3, 4	I, II, III, IV, V
Rana temporaria	2, 3, 4	I, II, III, V, VI, VII
Rana arvalis	2	I, II, IV
Pelobates fuscus	2	I, II, IV
Reptiles		
Vipera berus	1, 2, 3, 4	I, II, V, VI
Lacerta vivipara	2, 3, 4	I, II, V, VI, VII
Emys orbicularis	1, 2	II, IV
Anguis fragilis	2	I, II, V
Lacerta agilis	2	I, II, IV, V
Natrix natrix	2	I, II, III, IV, V
Mammals		
Neomys sp.	1, 2	I, II, III, IV, V, VI, VII
Crocidura sp.	1	I, II, III, IV, V
Sorex araneus	1, 2	I, II, IV, V, VI, VII
Sorex minutus	1, 2, 4	I, II, III, IV, V, VI
Microtus agrestis	1	I, II, III, V, VI, VII
Microtus arvalis	1, 2, 4	I, II, IV, V
Microtus oeconomus	1, 4	IV, VI

Microtus subterraneus	1, 4	II, VI, VII
Apodemus sylvaticus	1, 4	I, II, IV, V
Clethronomys glareolus	1, 2	I, II, III, IV, V
Canis lupus	2, 4	I, II, V, VI, VII
Vulpes vulpes	4	I, II, III, IV, V, VI, VII
Martes sp.	3, 4	I, II, V, VI, VII
Mustela erminea	4	I, II, IV, V, VI, VII
Mustela nivalis	3, 4	I, II, III, IV, V, VI, VII
Cervus elaphus	1, 2, 3, 4	I, II, IV
Capreolus capreolus	1, 2, 3	I, II, III, IV, V, VI, VII
Sus scrofa	1	I, II, III, IV, V