Anthropogenic landscapes? Modelling the role of hunter-gatherers in interglacial ecosystems in Europe

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CHAPTER 2

AVAILABLE EVIDENCE FOR HUNTER-GATHERER IMPACT ON EUROPEAN ENVIRONMENT

Source

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Abstract

We review palaeoenvironmental proxies and combinations of these relevant for understanding hunter-gatherer niche construction activities in pre-agricultural Europe. Our approach consists of two steps: (1) identify the possible range of hunter-gatherer impacts on landscapes based on ethnographic studies; (2) evaluate proxies possibly reflecting these impacts for both the Eemian (Last Interglacial, Middle Palaeolithic) and the Early–Middle Holocene (Mesolithic). We found these paleoenvironmental proxies were not able to unequivocally establish clear-cut differences between specific anthropogenic, climatic and megafaunal impacts for either time period in this area. We discuss case studies for both periods and show that published evidence for Mesolithic manipulation of landscapes is based on the interpretation of comparable data as available for the Last Interglacial. If one applies the "Mesolithic" interpretation schemes to the Neanderthal record, three common niche construction activities can be hypothesised: vegetation burning, plant manipulation and impact on animal species presence and abundance. Our review suggests that as strong a case can be made for a Neanderthal impact on landscapes as for anthropogenic landscape changes during the Mesolithic, even though the Neanderthal evidence comes from only one high-resolution site complex. Further research should include attempts (e.g., by means of modelling studies) to establish whether hunter-gatherer impact on landscapes played out at a local level only versus at a larger scale during both time periods, while we also need to obtain comparative data on the population sizes of Last Interglacial and Holocene hunter-gatherers, as these are usually inferred to have differed significantly.

2.1 Introduction

Since the coining of the term Anthropocene for the current human-dominated geological epoch by Crutzen and Stoermer (Crutzen, 2002; Crutzen & Stoermer, 2000), the starting date for this period, as well as its geological relevance, has been under permanent debate. Suggestions for the beginning of the Anthropocene vary, from 13,800 BP when significant vegetation transformations and megafauna extinctions occurred, to the mid-twentieth century with the introduction of plastics and concrete production (Lewis & Maslin, 2015; Ruddiman, 2013; Smith & Zeder, 2013; Waters et al., 2016; Zalasiewicz et al., 2015). The absence of consensus among researchers concerning relevant types of evidence (e.g., greenhouse gases, isotopes caused by nuclear weapons detonations, biosphere modified by species extinctions and invasions, novel human-made "minerals" such as bricks, ceramic, concrete, asphalt), as well as the need for a "golden spike" (global boundary stratotype section), greatly complicate defining a starting point for the Anthropocene (Castree, 2017; Zalasiewicz et al., 2019). While the Anthropocene Working Group recently decided to use the stratigraphic signal of global distribution of primary artificial radionuclide signal due to atomic bomb explosions in the mid-twentieth century as the Anthropocene's "golden spike" (Anthropocene Working Group, 2019; Zalasiewicz et al., 2015), beyond the geological community, broader discussions stimulated by this "origins debate" still continue.

In the context of the debate about the status and chronology of the Anthropocene, questions about when and how humans began to shape the global earth system, including how human subsistence and land use strategies affected land cover, ecosystems and other aspects of their environments, are identified as priorities for research in archaeology and paleoecology (Ellis et al., 2021; Kintigh et al., 2014; Seddon et al., 2014; Thompson et al., 2021). An early (Pleistocene) date for the Anthropocene seems unjustified, in terms of the scale of human impacts in the Pleistocene past, and, as some hold, because of the ideological implications (Lane, 2015). However, this debate has highlighted the relevance of systematic studies of when humans began to have an impact on their landscapes, the spatial and temporal scale of these effects, and the nature of early impacts on the earth system.

Humans have a long prehistory of niche construction, defined as "the process whereby organisms, through their metabolism, their activities and their choices, modify their own and/or other species niches" (Odling-Smee et al., 2013). Given this definition, both agriculture and a foraging lifestyle can be considered human niche constructions. It is widely accepted that the emergence of agriculture strongly increased human impact on their environments, compared to that of

foraging societies (Delcourt, 1987; Kirch, 2005; Roberts et al., 2018; Ruddiman, 2013). Agricultural activities tend to replace diverse natural vegetation with relatively few domesticates with highly reduced habitat value for biodiversity, and can thereby increase species extinction rates and alter biogeochemical cycles (Lewis & Maslin, 2015); this makes the shift to agriculture very relevant to discussions of the origins and the character of the Anthropocene (Lindholm et al., 2020).

The focus of the current article is, however, on foragers, who also conduct both active and inadvertent niche construction (Smith, 2011). In this paper, hunter-gatherers (foragers) are defined as populations which mainly depend on food collection or foraging of wild resources (Ember, 2020). Foragers can and do actively transform land cover and ecosystems (Rowley-Conwy & Layton, 2011; Smith, 2011). In particular, the controlled use of fire, which is an important part of the technological repertoire of more recent forms of *Homo* (Alperson-Afil, 2017; Dibble et al., 2018; Gowlett & Wrangham, 2013; Roebroeks & Villa, 2011; Sandgathe et al., 2011), could have facilitated landscape transformations. Anthropogenic fire could possibly be as significant as or, in later stages, exceeding the impact of natural fires (Scherjon et al., 2015; Thompson et al., 2021; Whelan, 1995; Wrangham, 2009). In addition, Late Pleistocene faunal extinctions, in which human hunting is often implicated (Andermann et al., 2020; Sandom et al., 2014b; Smith et al., 2018), were associated with reduction of the structural diversity of vegetation (Bakker et al., 2016a; Berti & Svenning, 2020; Sandom et al., 2014a), changed fire regimes and likely a range of other ecosystem processes. Thus, studying hunter-gatherer impact on their surroundings is of interest in terms of anthropogenic ecosystem modifications in forager habitats as well as for contextualising and understanding the scale of Holocene agricultural transformation.

Identifying the possible impact of past hunter-gatherers on their environments to some degree calls for knowledge of "human free" or "natural" ecosystems, which arguably suggest the existence of a "natural palaeoenvironment". Such a term implies that environments exist in a stable natural state until disrupted by humans. However, all environments are constantly changing, determined by a myriad of factors such as climate, faunal activities, natural fire regimes and hominins. This makes it difficult to discriminate between "natural" and anthropogenic changes (Schreve, 2019). Nonetheless, the Eemian interglacial, sometimes seen as an analogue for present-natural vegetation (Svenning, 2002), provides an interesting case study in this respect.

The Eemian interglacial (Last Interglacial; ~130,000–116,000 BP) is the most recent (before the Holocene or current interglacial) in a series of Pleistocene interglacials–warm-temperate periods between glaciations (Schreve, 2019)–with a climate and vegetation comparable to the Holocene over major parts of

Europe (Svenning, 2002). On a finer scale, however, there were differences: the Eemian interglacial witnessed a higher sea level than the Holocene, making for a somewhat more Atlantic climate in western and central Europe than during the Holocene (Zagwijn, 1989). The Late Pleistocene extinction of various larger mammals occurred after the Eemian interglacial, and the absence of specific large herbivores such as elephant and rhinoceros during the Holocene may have decreased overall herbivore impact on vegetation during the current interglacial (Svenning, 2002). Study of Eemian vegetation structure may provide insights into the specific differences between the two interglacial periods and the factors responsible for these differences. At the same time, these differences make it challenging to understand the role of Neanderthal hunter-gatherers in this period.

The disappearance of megafaunal species during the latest Pleistocene and the Holocene was a complicated process that varied from region to region (Mann et al., 2019; Sandom et al., 2014b; Stewart et al., 2021; Wang et al., 2021), with likely overkill by *Homo sapiens* (Sandom et al., 2014b). Still, Neanderthals' game spectra were very much comparable to those of the first modern humans in Eurasia (Bar-Yosef, 2004; Wißing et al., 2019), and localised extinctions or potential reduction of populations of medium to large-sized herbivores do seem to correlate to much earlier Pleistocene hominin range expansions (Speth & Clark, 2006; Staesche, 1983; Surovell et al., 2005). In addition, besides their potential impact on megafauna, Neanderthals are considered to have possibly played a role in vegetation openness around the Last Interglacial Neumark-Nord 2 lake area site (Germany) (Roebroeks et al., 2021; Roebroeks & Bakels, 2015). While Neumark-Nord 2 provides us with an exceptionally high-resolution–but thus far unique–case (see below), it does suggest that Neanderthals elsewhere also could have transformed their surroundings on a local scale, e.g., via burning practices. However, their inferred small population sizes, and the low population densities that these imply, suggest a limited impact.

Despite the problems differentiating between natural and anthropogenic changes in past environments, the quantity of research devoted to pre-industrial human impacts on landscapes is increasing (Dietze et al., 2018; Hamilton et al., 2019; Thompson et al., 2021), as a result of increasing interest in the role of past humans in landscape transformations and the environmental consequences this may have entailed (Oldfield & Dearing, 2003; Thompson et al., 2020). However, specific research on the environmental impact of prehistoric hunter-gatherers is relatively rare, and hampered by both theoretical issues (a tendency to contrast hunter-gatherers and farmers) and methodological ones (Lightfoot et al., 2013). For example, detecting past hunter-gatherer burning of landscapes may be difficult because the effects may be limited at low population densities, and

tend to mimic or be completely concealed by natural fire regimes (Scherjon et al., 2015). Scherjon et al. (and comments therein) stress the need for more information combining various proxies, such as charcoal records and molecular markers, from well-sampled and well-dated sequences with archaeological records from the same area (ibid.). Standard requirements regarding the kinds of data that should be collected for such studies are lacking, and there are obvious taphonomic limitations on the range of data that can be collected and documented from prehistoric sites. In this regard, it is important to include a wide variety of relevant methods and proxies suitable for understanding hunter-gatherer impact, evaluate the strengths and weaknesses of various approaches and establish the character of the association between proxies and hunter-gatherer activity: hence this review.

The practice of interpreting past hunter-gatherer impact is best understood with the aid of concrete case studies, presented below, for the Last Interglacial and for the Holocene. The possibility that Mesolithic hunter-gatherers modified their environments has been explored since the late 1960s (Simmons, 1996; Woodburn, 1980; Zvelebil, 1994), and as a result a number of studies of relevant palaeoenvironmental evidence have been published. This possibility has also been considered for Upper Palaeolithic hunter-gatherers of the Last Glacial Maximum (Kaplan et al., 2016), but not, or very rarely, for earlier periods (see Thompson et al., 2021 for such an exceptional case-study from Lake Malawi, Africa). However, at least one Middle Palaeolithic case study seems to provide high-resolution evidence minimally indicative of Neanderthal impact on the local vegetation (Roebroeks et al., 2021; Roebroeks & Bakels, 2015).

The aims of this paper are twofold: (1) to present the variety of available proxies relevant for studying past hunter-gatherer environmental impacts, and (2) to examine the presence and usefulness of the various types of evidence within specific geographical and chronological settings. The structure of the article is the following: (1) first we describe hunter-gatherer niche construction activities based on ethnographic observations; (2) we then list and evaluate proxies for each category of niche construction activity; (3) we illustrate the use of proxies in Middle Palaeolithic (Neanderthal) and Mesolithic archaeological contexts dating to the Last Interglacial (~130,000–116,000 BP) and Early–Middle Holocene (~11,700–6000 BP) respectively; (4) finally, we discuss the validity of current understanding of Neanderthal and Mesolithic hunter-gatherer impact on warm-temperate landscapes.

2.2 Ethnographic observations of hunter-gatherer impact on landscapes

Ethnographic records constitute an important source for understanding relationships between (sub-)recent hunter-gatherers and their environments and can help to build solid inferences about the possible antiquity of such relationships. However, we do need to acknowledge that the application of ethnographic data in this way faces important limitations: firstly, it is likely that only a small part of past diversity in foraging subsistence activities is reflected in the record of (sub-)recent hunter-gatherers (Bettinger, 2001). Secondly, it is clear that many (sub-)recent hunter-gatherers were part of larger socio-economic systems in which hunter-gatherer subsistence strategies were influenced by trade and communication across different regions, sometimes on a worldwide scale, as seen in the example of western European demand for South African bush products which directly impacted local hunter-gatherer hunting there (Stiles, 1992, 2001; Wolf, 2010). Thirdly, geographical biases and time limited observations restrict the scope of ethnographic records (Scherjon et al., 2015; Smith & Zeder, 2013). While an attempt has been made here to include a wide range of geographical and temporal ethnographic contexts, this only partially addresses these limitations. One of the reasons is geographical bias, with hunter-gatherers having disappeared from temperate parts of the world such as Europe, the region at stake here, long before ethnographic or ethnohistoric documentation started. Nevertheless, ethnographic data helps in interpreting decision-making behaviour leading to the creation of the archaeological record as well as the roles which ecological, biological, social and cultural settings play in these processes (Kelly, 2013).

The categories of hunter-gatherer niche construction practices listed below are not intended to cover the whole range of foraging and resource procurement activities in detail: these general categories were identified to illustrate possible ways in which hunter-gatherer activities can lead to landscape transformations and to structure the discussion of ethnographically documented niche construction and the relevant archaeological proxies. Based on review papers on ethnographic data (Rowley-Conwy & Layton, 2011; Smith, 2011), we identified the following categories for hunter-gatherer niche construction and effects on landscapes, to be discussed below: (1) modification of vegetation communities via burning; (2) small-scale plant manipulation; (3) landscape modification to impact animal presence and their abundance at specific locations.

Human-induced burning of vegetation communities, the first category, was a common practice which has been documented in all vegetation types except tundra (Scherjon et al., 2015), and with more cases for hunter-gatherers occupying forested or shrubland areas (Mellars, 1976). The ecological consequences of these practices are determined by the intensity, seasonality and frequency of burning and the fire resilience of plants, and mainly include improving the qualities and quantities of forage from a hunter-gatherer point of view (Anderson, 2005). Burning activities are often carried out for short-term purposes (e.g., hunting) but their repetitive character can have major long-term consequences, such as the creation of mosaic vegetation, with increase of biodiversity and reduced risk of habitat loss. Such an approach transforms an occupation area into a mosaic with diverse foraging and hunting options for humans at a relatively small spatial scale (Anderson, 2005; Bird et al., 2008).

The second category is small-scale plant manipulation, which does not imply plant domestication and cultivation of domesticated plants in a broad agricultural sense (involving human intervention becoming essential for replanting and the plant food making a large contribution to human diet). This category rather includes several smaller-scale activities such as broadcasting of wild annuals' seeds, and transplantation and in-place encouragement of fruit/nut-bearing species, plants that can be harvested for raw materials and perennial root crops via pruning, coppicing, thinning, clearing, weeding or fertilising (Feeney, 2019; Smith, 2011). While these actions can modify vegetation, it is often difficult to track which of these specific activities was carried out by hunter-gatherers in the deep past. Potentially, transformation of existing communities via these actions may be reflected in genetic transformations of some cultivated species (e.g., size of seeds, thickness of seed coats) (Greaves & Kramer, 2014; Rowley-Conwy & Layton, 2011; Smith, 2011).

In contrast to these strategies that encourage growth, trees may be killed to ensure firewood supplies, with implications for vegetation cover (Henry et al., 2008; Pryor et al., 2016). Construction of habitat improvement features (e.g., canals and dams, soil retention walls) has also been documented as a part of foragers' plant manipulation strategies, e.g., for Northern American hunter-gatherers (Anderson, 2005; Harrower, 2016). Other examples come from Australia where indigenous populations constructed small-scale water diversions, impoundments and dams (Jackson & Barber, 2016). Construction of such features can potentially leave more visible traces than small-scale activities involving plant transplantation, sowing or in-place encouragement.

The third category of hunter-gatherer niche construction consists of enhancing and/or expanding the geographic range of specific animal species and

the management of prey movements. These activities can include the construction of "clam gardens", fish weirs and traps, the transformation of fish streams via removing debris and translocation of fish eggs, and the use of fences to control herbivore movements (Rowley-Conwy & Layton, 2011; Smith, 2011). These types of resource manipulation have been documented ethnographically in various regions, particularly in North and Central America, Siberia, Africa and Australia (Anderson et al., 2019; Campbell & Butler, 2010; Deur et al., 2015; Khomich, 1966; McKey et al., 2016; Pascoe, 2014).

Controlled burning is also a tool for prey management. In particular, fire was used to drive animals and fish towards a specific location or temporarily paralyse prey to make hunting or fishing easier (Lytwyn, 2001; Roos et al., 2018; Scherjon et al., 2015). Recently burned areas are attractive for many herbivores because the increased visibility makes it easier to avoid predators and the new vegetation cover contains a higher nutrient level; these freshly burned areas also support hunting opportunities for some birds and insects (Allred et al., 2011; Bird et al., 2008; Eby et al., 2014; Herzog et al., 2016; Komarek, 1969; Mellars, 1976; Reid, 2012). People were then able to hunt prey animals attracted to recently burned areas (Scherjon et al., 2015). In addition, smoke from fireplaces around camps can provide animals such as reindeer with relief from biting insects, leading them to congregate within specific locations in the open air or inside specially constructed buildings (Groß et al., 2019).

Thus, hunter-gatherer subsistence strategies include a diverse set of niche construction activities, which allows foragers to be flexible, adaptable and able to withstand change and which also debunk characterisations of these populations as passive consumers of natural resources (Hitchcock, 2019; Kelly, 2013; Smith et al., 2013). While these activities could increase the local abundance of the plant and animal resources on which hunter-gatherers rely, these and other foraging and hunting activities could also depress resources (Feeney, 2019). We do not assume that all Pleistocene and Holocene groups of foragers engaged in all the types of activity described here in their daily practices. In addition, there is no consensus about which specific practices were incorporated in Neanderthal and Mesolithic strategies or differences/similarities between the niche construction activities of these two populations. To compare hominin impact on landscapes in these two periods, and begin to understand differences and similarities, we need to take the full range of possible activities into account. Therefore, the next section is devoted to the presentation and evaluation of proxies for each type of niche construction activity.

2.3 Types of evidence related to past hunter-gatherer niche construction activities

The following sections ("Proxies for Identification of Modification of Vegetation Communities Via Burning", "Proxies for Identification of Small-Scale Plant Manipulation by Hunter-Gatherers" and "Proxies for Landscape Modifications to Impact Animal Presence and Their Abundance in Specific Locations") are devoted to a review of proxies which correspond to three categories of hunter-gatherer impact defined on the basis of ethnographic studies ("Ethnographic Observations of Hunter-Gatherer Impact on Landscapes" section). Tables 2.1, 2.2, and 2.3 reflect the availability of different proxies in relation to their spatial scale (i.e., which scale is reflected in a specific type of evidence) and for the two time periods (the Last Interglacial and the Early–Middle Holocene). The local spatial scale is the most detailed, and this scale means that a proxy can be used to identify foragers' niche construction activities at a site and in close proximity to the site. The regional scale corresponds to a wider area, and this spatial scale can reflect processes around several sites within one region. The (sub-)continental level is the most general level

Table 2.1 Proxies and their maximum possible temporal representation (availability) and spatial scale (scale which is reflected in specific type of proxy) for reconstruction of burning of vegetation communities by hunter-gatherers (category 1).

Proxies	Temporal scales		Spatial scales		
	Last Interglacial	Early–Middle Holocene	Local	Regional	(Sub-) Continental
Pollen indicators	●	●●●	●●●	●●●	○*
AP/NAP	●	●●●	●●●	●●●	○*
Charcoal	●	●●●	●●●	●●●	○*
Non-pollen palynomorphs	●●	●●●	●●●	○	○
Plant macrofossils	●	●●●	●●●	●	○
DNA from sediments	●●	●●●	●●●	●●	○
Phytolith data	●●●	●●●	●●●	●	○
PAHs	●●●	●●●	●●●	●●●	●●●
Black carbon	○	●●●	●●●	●●●	●●●
Levoglucosan	●●●	●●●	○	●●●	●●●

*this spatial scale can be reached via integration of data from multiple sites
○ – absence of proxies
● – low availability/spatial resolution
●● – average availability/spatial resolution
●●● – high availability/spatial resolution

of analysis, and this level corresponds to proxies which reflect processes taking place at the scale of a large subcontinental area or a continent. It is furthermore important to highlight that taphonomic processes as well as research strategies can cause under- or overrepresentation and absence of proxies.

Table 2.2 Proxies and their maximum possible temporal representation (availability) and spatial scale (scale which is reflected in specific type of proxy) for reconstruction of plant manipulation organised by hunter-gatherers (category 2).

Proxies	Temporal scales		Spatial scales		
	Last Interglacial	Early– Middle Holocene	Local	Regional	(Sub-) Continental
Tools for plant manipulation	○	●●	●●●	●	○
Plant macrofossils	●	●●●	●●●	●	○
Pollen indicators	●	●●●	●●●	●●●	○
Phytolith data	●●●	●●●	●●●	●	○
Parenchyma analysis	○	●●●	●●●	○	○
Starch-grain analysis	●●	●●●	●●●	○	○

○ – absence of proxies
● – low availability/spatial resolution
●● – average availability/spatial resolution
●●● – high availability/spatial resolution

Table 2.3 Proxies and their maximum possible temporal representation (availability) and spatial scale (scale which is reflected in a specific type of proxy) for identification of landscape changes to impact animal presence and their accessibility in specific locations (category 3).

Proxies	Temporal scales		Spatial scales		
	Last Interglacial	Early– Middle Holocene	Local	Regional	(Sub-) Continental
Fishing and hunting constructions	○	●●	●●●	●	○
Pollen indicators	●	●●●	●●●	●●●	○
AP/NAP	●	●●●	●●●	●●●	○
Non-pollen palynomorphs	●●	●●●	●●●	○	○
DNA	●●	●●●	●●●	●●	○
Stable isotopes	●	●●●	●●●	●●●	●●●
Zooarchaeological data	●	●●●	●●●	○	○

○ – absence of proxies
● – low availability/spatial resolution
●● – average availability/spatial resolution
●●● – high availability/spatial resolution

Records from marine cores are often used in studies devoted to environmental changes through Pleistocene time (Kotthoff et al., 2011; Martín-Puertas et al., 2010). However, in virtually all cases, the transformation of landscapes by hunter-gatherers did not trigger visible changes in proxies documented in marine sediments, such as charcoal concentrations in deep sea or offshore cores (Daniau et al., 2009; Scherjon et al., 2015). Therefore, marine cores are not included in this review, only inland proxies are considered. It is also important to note that identification of human impact on landscapes is only possible when a clear correlation between hominin activities and proxies reflecting landscape changes can be established. In other words, in cases where we have several types of evidence for vegetation openness but where hominin presence could not be clearly identified, these events of vegetation transformation cannot be linked with anthropogenic impact.

2.3.1 Proxies for identification of modification of vegetation communities via burning

2.3.1.1 Biological indicators

To clarify the transformation of vegetation cover, relative or absolute abundances of remains from plants are required (Birks & Birks, 2016), and these can be obtained from palynological studies, analysis of non-pollen palynomorphs, plant macrofossils, DNA from sediments and phytoliths. Although pollen analysis is an important tool in research devoted to human-environment interactions, palynological data has thus far mainly been used to identify agricultural impact on past landscapes (Ledger, 2018), i.e., primarily crop cultivation and cattle grazing. Two major approaches have been used to identify these activities: the indicator species and the comparative approaches (Gaillard, 2013). These rely on the assumption that the ecological preferences of plants were the same in the past as at present or in recent times. The indicator species approach uses a number of pollen taxa (plant species, genus, groups of species or genus, families) that are related to anthropogenic activities such as agriculture (Behre, 1981; Gaillard, 2013). Occurrence and changes in the amount of these pollen indicators can be related to human impact, i.e., occurrence and changes in the extent of cultivated, hay meadow and/or grazing lands. Gaillard (2013) provides a list of tree and herb pollen taxa (with a few fern spores often included in pollen analyses) grouped into land-use/land-cover types. However, the number and proportions of pollen indicators also depend on the pollen productivity and dispersion characteristics of each plant taxon, the location of human activities in relation to the pollen site, and the type and size of the pollen site (Hellman et al., 2009; Hicks, 1992; Hicks & Birks, 1996). The comparative approach builds upon databases of modern pollen assemblages from

traditional agricultural landscapes and compares them with fossil assemblages (Gaillard et al., 1994; Mazier et al., 2006, 2009). For instance, the indicator species approach has been applied within Britain and Ireland to infer Mesolithic forest manipulation, including identification of secondary woodland taxa following disturbance (Warren et al., 2014) and open ground indicators (Bishop et al., 2015). Interpretation of such pollen evidence generally relies on the context of certain pollen assemblage and several lines of evidence within the pollen record, including decreases of tree taxa characteristic of mature woodland followed by sudden, regular occurrence or increases of pollen from other tree taxa and woodland herbs favoured by clearance during a short period. To the best of our knowledge, the comparative approach has not been used in studies of hunter-gatherers.

Deforestation and increases in landscape openness can be reconstructed from the relationship between the percentages of arboreal and non-arboreal pollen taxa (AP/NAP). This index is traditionally used to infer changes in landscape openness over time around a pollen site. Inferences about a human role in creating vegetation openness by burning are based primarily on correlation of AP/NAP ratios with evidence for human activity, the presence of proxies indicating burning and evidence for other factors (e.g., natural fire regime, megafauna activity). It has been shown, however, that this relationship is not straightforward and is strongly influenced by the character of the pollen assemblage, i.e., the composition and distribution of vegetation patches, the type and size of the pollen site (lake or bog, large or small) and inter-taxonomic differences in pollen productivity and dispersal characteristics (Cui et al., 2013; Hellman et al., 2009; Sugita, 2007a, 2007b; Sugita et al., 1999). Nevertheless, the combination of AP/NAP percentages with pollen indicators and other palaeoecological data can provide robust reconstructions (Svenning, 2002). Recent developments in quantitative reconstructions of past plant cover make it possible to provide more realistic reconstructions of past landscape openness at both local and regional spatial scale using the Landscape Reconstruction Algorithm modelling approach (LRA, Sugita, 2007a, 2007b). Among the pollen analytical methods reviewed above, the indicator species approach and the LRA are the most appropriate to identify possible forager activities such as small-scale crop cultivation, use of wild plants for consumption or building material and utensils (Gaillard, 2013; Gaillard et al., 1994; Regnell et al., 1995), and reconstruct landscape transformations such as changes in regional and local vegetation openness and composition (Nielsen et al., 2012; Nielsen & Odgaard, 2010; Trondman et al., 2015).

An important proxy for reconstructing hunter-gatherer burning of vegetation is the concentration of carbonised remains in samples derived from archaeological sites and their surroundings. Although evidence of the use of fire is rare for hunter-

gatherers and less evidence is available for the Palaeolithic than for the Mesolithic (Goldberg et al., 2017), an increased amount of charcoal above a baseline level (i.e., reference level relative to which higher/lower charcoal concentrations are identified) is often considered an indication of human impact (Ledger, 2018). Distinguishing anthropogenic burning is easiest in contexts where vegetation is not prone to burning and natural charcoal production is low (Scherjon et al., 2015). Correlation with proxies indicating vegetation change and human activity is also key. Charcoal particles can travel distances varying from local to regional, with the distance influenced by particle size and shape, characteristics of the fire and wind speed (Vachula et al., 2018; Vachula & Richter, 2018). However, hunter-gatherer burning is most likely to be detectable on a relatively small scale, particularly when population densities are low (Scherjon et al., 2015), and there are benefits to focusing on charcoal from depositional contexts (such as small lakes or colluvial settings) that reflect this scale. While both microscopic and macroscopic charcoal are of interest, the former is less often available/recorded: in the rest of this article, we do not distinguish the two size classes.

Charcoal records extend back to the Carboniferous period (Scott, 2000) and should be available equally for Palaeolithic and Mesolithic contexts. In interpreting charcoal peaks, it is important to take into account non-anthropogenic factors that affect abundance: fire characteristics, environment, meteorological conditions, taphonomy (e.g., sediment mixing, bioturbation) and time gaps between a fire episode and charcoal deposition (Duffin et al., 2008; Innes et al., 2004). The size of charcoal particles is also influenced by the pH of their encasing matrix: alkaline sediments lead to fragmentation (Braadbaart et al., 2009). Thus, interpretation of charcoal data in terms of anthropogenic factors is very problematic and any analysis should take into account the many factors related to the specific area, sampling site and methods used. In our analyses, we focus on charcoal data from contexts with a local-scale catchment, slow deposition rate, solid chronology and evidence of human activity-related proxies.

Percentages of non-pollen palynomorphs (e.g., fungi, zoological remains, plant fragments, algae) reflect the local ecological features of a site, because non-pollen palynomorphs are dispersed locally around the point of their origin (Cugny et al., 2010; Innes et al., 2013; Menozzi et al., 2010). Non-pollen palynomorphs can be preserved in Pleistocene (Bakels, 2012; Sandom et al., 2014a) and Holocene (Ryan & Blackford, 2010; Tunno & Mensing, 2017) deposits within all types of habitats. This makes non-pollen palynomorphs applicable for Middle Palaeolithic and Mesolithic studies. Non-pollen palynomorphs provide information about human-driven and natural processes (e.g., erosion, fire frequency, presence of pastures) (Gelorini et al., 2012; Haas, 2010; Revelles & van Geel, 2016). In particular, the presence of some

types of non-pollen palynomorphs, which appear after fires or can live within open habitats (Loughlin et al., 2018), constitutes one possible type of evidence of past fires.

Plant macroremains can be seen by the naked eye and identified under a microscope: diaspores (seeds, fruits, some large spores) and vegetative parts such as needles, leaves, buds, bud scales, flowers, bulbils and roots. Plants with low pollen production or vegetative reproduction can often be identified through plant macroremain analysis (Birks, 2001). These remains often indicate local processes when working with autochthonous assemblages from peat bogs and mires, with potential for more regional reconstructions based on allochthonous assemblages in specific environmental settings (fluvial and lacustrine deposits) when transportation is taken into account (Greenwood, 1991; Rawlence et al., 2014). Plant macroremains could be indicative of hunter-gatherer burning when they are charred, derived from open areas (i.e., are left by light demanding species) and/or from nutrient-rich, disturbed areas (i.e., are left by species that grow in burned areas), and if this type of proxy can be correlated with the presence of hunter-gatherers in the study area (Bos & Urz, 2003).

DNA from sediments is another type of proxy that can be used in studies of anthropogenic burning. DNA can be extracted from different contexts such as frozen soils, marine and lake deposits, peats, loess and archaeological sites. Biodiversity changes, vegetation alteration and climatic fluctuations can be clarified based on extracted DNA from sediments (Dussex et al., 2021; Giguet-Covex et al., 2014, 2019; Parducci et al., 2012; Rawlence et al., 2014). The current temporal limit of ancient DNA (aDNA) is up to 1 Mya for samples from ice and permafrost (Callaway, 2021). ADNA generally comes from plants and animals which were physically present at or near the sampling location and therefore reflect a local signal. However, regional processes such as long-distance dispersal of pollen can also affect results. Depending on the taxon of a plant identified via aDNA, corrections should be made in accordance with information about the pollen productivity of this taxon and long-distance dispersal. Currently, anthropogenic vegetation changes visible via aDNA have mainly been identified for past farming societies and their impact on landscapes via burning, logging and grazing (Dussex et al., 2021; Foster et al., 2020). ADNA allows one to identify plants to a high taxonomic resolution, and this approach is useful for small-scale vegetation changes (Niemeyer et al., 2017). Therefore, sedimentary aDNA could be useful in studies devoted to hunter-gatherer fire events.

Phytoliths are rigid, microscopic structures made of silica, present in some plant tissues and persisting after the decay of the plant. Although their production depends on taxa, phytoliths occur in many plants, especially grasses, sedges and

palms (Albert & Cabanes, 2007). Phytoliths often represent stable plant remains which decayed in place, reflecting local processes (Rovner, 2001). However, phytoliths can be transported via wind or water, and it is important to decide which of those present were formed in situ (Twiss, 2001). Phytolith analysis is often used in studies of farming societies (Piperno et al., 2009; Rosen & Weiner, 1994; Zhang et al., 2010) especially when it is not possible to identify cereals via pollen. Regarding hunter-gatherer impact on landscapes via fire, phytoliths are a tool to study vegetation openness, fire fuel and past burning regimes (Strömberg et al., 2018; Thompson et al., 2021). The inorganic nature of phytoliths makes them resistant to most types of impact including burning and suitable for identification of plants to taxonomic and anatomical levels (Esteban et al., 2018), even though diagenesis can influence preservation of phytolith morphology and hence limit identification, especially in alkaline settings (Braadbaart et al., 2020). Phytoliths have been used in studies devoted to fuel from fireplaces within foragers' sites (Albert & Cabanes, 2007; Esteban et al., 2018) and to burning of vegetation (Boyd, 2002; Roos et al., 2018) by hunter-gatherers.

2.3.1.2 Geochemical indicators

Past fire activity can be estimated via several geochemical proxies. It has been suggested that concentrations of polycyclic aromatic hydrocarbons (PAHs) in sediments reflect past fire activity (Brittingham et al., 2019). Differences between light (3–4 rings) and heavy (5–6 rings) PAHs can be used to separate the background signal from localised burning events. The limitation of this method is instrumental because detecting PAHs requires great sensitivity (Denis et al., 2012). Identification of PAHs has not become a standard research method in studies about hunter-gatherer impact on landscapes: a rare example of application focused on hominin burning during the Middle Palaeolithic (Brittingham et al., 2019).

Black carbon is a fire residue produced by incomplete combustion of organic matter (Brodowski et al., 2005; Kaal et al., 2008b). Black carbon has been used as a proxy for Holocene fire regimes and vegetation reconstruction in palaeoenvironmental and archaeological studies (Kaal et al., 2008a, 2008b, 2011). Moreover, black carbon appears to be much more abundant in soils and sediments than macroscopic charcoal (Kaal et al., 2008a). Concentrations of black carbon reflect local anthropogenic activities (e.g., cooking, heating) and regional natural processes (e.g., long-distance emissions carried by winds and rainfall) (Chen et al., 2018; Ramachandran & Kedia, 2010). Therefore, interpretation of black carbon concentrations in sediments can be difficult. Potentially, black carbon can be used in studies about hunter-gatherer burning during the Holocene, but links between

burning events on different scales and black carbon concentrations should be supported by data from other proxies.

Levoglucosan is a degradation product obtained from cellulose burning at temperatures more than 300°C (Kehrwald et al., 2012). Levoglucosan and its isomers, mannosan and galactosan, are considered robust indicators for biomass burning, because they can remain stable in the atmosphere for several days and can be transported over hundreds of kilometres (Sang et al., 2016; Schreuder et al., 2019). Levoglucosan then returns to the surface and becomes trapped in continental archives such as ice sheets (Kehrwald et al., 2012). Therefore, levoglucosan reflects regional and continental processes, rather than local-scale fire events such as hunter-gatherer burning practices.

In summary, burning of vegetation communities by hunter-gatherers can be identified via several types of proxies. All biological indicators (Table 2.1) reflect fire episodes on the local scale, and some of them do so on the regional scale. This makes biological indicators suitable for studies of hunter-gatherer vegetation burning, because these events were conducted on local scales, and, therefore, may be visible via proxies with a local resolution. Geochemical data is either difficult to detect or can reflect events on all three scales from local to (sub-)continental. Therefore, hunter-gatherer impact on vegetation can be difficult to identify via this group of proxies.

2.3.2 Proxies for identification of small-scale plant manipulation by hunter-gatherers

2.3.2.1 Tools as indicators of plant manipulation

Discoveries of tools unambiguously related to plant manipulation during the Pleistocene are very rare. Recent studies provided indirect evidence of such activities by hunter-gatherers from Ohalo II (Israel), at about 23,000 years ago: the earliest sickle blades for harvesting of cereals and proto-weeds (Snir et al., 2015). Combinations of different types of proxies (plant macrofossils and tools for plant processing) make this case study relatively unambiguous. While Neanderthals have been shown to be consumers of plant foods (Henry et al., 2011, 2014), stone tools interpreted as grinding stones are known from a number of Eurasian Upper Palaeolithic sites and suggest systematic exploitation of plant foods including grasses and tubers (Liu et al., 2013; Mariotti Lippi et al., 2015; Revedin et al., 2010).

In accordance with available data, hunter-gatherers included controlled, regular and intensive use of plant resources in their activities by the Late Mesolithic in Europe (Divišová & Šída, 2015), and even small-scale harvesting repeated over

many episodes and distributed over a landscape could cause landscape changes. Plant manipulations can be identified via the presence of tools for soil-working, reaping and processing: digging sticks, hoes, mattocks and other tools for procuring roots and tubers, clearing undergrowth, preparing the soil for planting and seeding, and grating/grinding plants (Zvelebil, 1994). Tools can be studied via use-wear analysis, and identified traces on surfaces can show that some tools were used on both plant and animal materials (Solheim et al., 2018), and some only on plants (Osipowicz, 2019). Evidence of surface transformation (e.g., ditches, channels) within sites can also reflect plant manipulations organised by foragers (Denham et al., 2004).

2.3.2.2 Biological indicators of plant manipulation

Biological indicators such as plant macroremains and microfossils (pollen, parenchyma, phytoliths and starch grains) do not necessarily represent plant manipulation. The presence of taxa outside their natural environment (i.e., archaeological sites can contain plant remains which were not local in the region where the site is located), overrepresentation of taxa, fragmentation of plants, their carbonisation and spatial distribution of remains within archaeological sites can help to clarify which species were available for hominins, and which plants were used (Divišová & Šída, 2015). In particular, analysis of plant macroremains from cultural layers shows important plant food resources for hunter-gatherers (Regnell, 2012). In addition to macroremains, pollen spectra can also reflect which plants were available for populations (Finsinger et al., 2006; Regnell, 2012). However, plant macroremains and pollen data do not indicate whether specific forms of manipulation were involved.

Phytoliths were mentioned above in relation to studies of hunter-gatherer impact on vegetation via burning. They are mainly used in studies of plant domestication and cultivation, because of morphological differences between phytoliths of domesticated and wild species (Piperno & Stothert, 2003; Zeder et al., 2006). The abundance of phytoliths in many plants (Albert & Cabanes, 2007) could make this proxy useful in studies of hunter-gatherer plant use, but there are currently much fewer studies of phytoliths for hunter-gatherer (Zurro et al., 2009) than for farming societies.

Parenchyma analysis examines tissue and individual cells of parenchymatous storage organs (Harris, 2013) and reflects local activities of populations (Fuller & Lucas, 2014). The parenchyma is a part of plant tissue found in most non-woody plants (Pryor et al., 2013). Due to variability in both morphology and physiology, it is possible to identify the plant species and determine if the plant was wild, domesticated or somewhere in between (Morris et al., 2016). Nevertheless,

parenchyma cells are often difficult to recognise and can be misinterpreted as burned cells from woody plants. If the parenchyma cells are recovered from a hearth, they may represent plant foods, but they may also have entered the record through animal dung burned as fuel (Pryor et al., 2013). Parenchyma has been recovered from Mesolithic and Epipalaeolithic contexts and some Upper Palaeolithic sites (e.g., Dolní Věstonice II) (ibid.). Their absence from earlier contexts may be related to the relatively recent archaeological use of this proxy (Fuller & Lucas, 2014). Regarding Mesolithic populations, parenchyma analysis has made it possible to identify categories of available plant food such as *Polygonum* (buckwheat and knotweed family), *Sagittaria el. sagittifolia* (arrowhead) from Całowanie (Poland) and roots of dicotyledon plants from Halsskov (Denmark) (Kubiak-Martens, 1996, 2002).

Starch-grain analysis studies have found organic residue preserved on stone tools (Harris, 2013; Piperno et al., 2004; Pryor et al., 2013) and in dental calculus (Henry et al., 2011; Pryor et al., 2013). These grains are plant microremains such as spores, pollen and phytoliths (Kovárník & Beneš, 2018). Starch grains are particularly significant because they can be found in all plants and are resistant to grinding and drying, can occasionally survive carbonisation (Cortella & Pochettino, 1994) and can thus provide a list of species used at an archaeological site (Messner et al., 2008). However, starch grains are rarely present (or recovered) from archaeological sites, and often unidentifiable if deteriorated or fragmented (Cortella & Pochettino, 1994). Starch grains have been identified in the dental calculus of Lower Palaeolithic hominins, with the oldest starch grains identified thus far, from the Sima del Elefante site at Atapuerca, Spain, being 1.2 Ma old (Hardy et al., 2017). More evidence is known from the Middle Palaeolithic, from sites such as Qesem Cave, Israel (Hardy et al., 2016); Shanidar Cave, Iraq; and Spy Cave, Belgium (Henry et al., 2011, 2014). Plant food was an essential dietary component for the occupants of these sites, and indications of heat modification, probably by boiling, of starch grains were identified in Neanderthal dental calculus at Shanidar (Henry et al., 2011, 2014). More details about plant procurement have been obtained for Upper Palaeolithic sites. Analysis of grinding tools from Grotta Paglicci (Italy) showed that humans consumed *Avena* (oats) and conducted thermal treatment before grinding. Data from Bilancino (Italy) and Dolní Věstonice (Czech Republic) supported evidence of advanced plant exploitation before the agricultural transition in Europe. In relation to the Mesolithic, starch-grain analysis made it possible to identify consumption of domestic cereals (*Triticum monococcum, Triticum dicoccum, Hordeum distichon*) before 8550 BP in the Balkans (site of Vlasac) (Kovárník & Beneš, 2018).

Thus, specific types of plant manipulation by hunter-gatherers can be identified based on specific tools for these activities. The majority of biological proxies only reflect which plants were available, and which species were consumed. Specific types of manipulation are often not possible to identify based on biological indicators alone (Table 2.2).

2.3.3 Proxies for landscape modifications to impact animal presence and their abundance in specific locations

The earliest archaeological evidence of fishing and hunting constructions are dated to the Early–Middle Holocene (Bailey et al., 2020; Lozovski et al., 2013; McQuade & O'Donnell, 2007; O'Shea & Meadows, 2009). Direct evidence of fishing is rare and fragmentary for the Mesolithic in comparison with later periods, and the best sources of information are sites with high moisture content. Fishing structures (fish fences, weirs, screens, traps) were used in specific types of fishing without active human participation (Lozovski et al., 2013; Lozovski & Lozovskaya, 2016) and served as a barrier to fish migration (Montgomery et al., 2015).

Almost no Mesolithic hunting fences have been discovered, but there are stone structures from the Great Lakes of North America (O'Shea & Meadows, 2009) and in the southeastern part of Jordan (al Khasawneh et al., 2019), likely dating to the Early Holocene. The low number of hunting fences discovered may be caused by their poor preservation, and dating difficulties as well as limited usage of such constructions by prehistoric hunter-gatherers and incorrect interpretations. Therefore, other evidence should be used to identify hunter-gatherer impact on animal presence and their abundance in specific locations. In particular, it can be identified via data related to changes in megafaunal populations due to overhunting, transportation of animals or other factors, which can however be difficult to rule out (e.g., climatic fluctuations). A decrease in the number of herbivores causes changes in vegetation cover such as distribution of shrubs and forests, higher absorption of solar radiation and rises in temperature (Boivin et al., 2016). To detect megafaunal presence and to assess changes in their distribution and density, pollen spectra, non-pollen palynomorphs, DNA, stable isotopes, and the amount and spatial distribution of faunal remains in layers within archaeological sites should be used as proxies.

As mentioned above ("Proxies for Identification of Modification of Vegetation Communities via Burning" section), changes in the amount of pollen indicators can be related to changes in the extent of grazing land. Increasing percentages of NAP relative to AP reflect increases in landscape openness. Pollen indicators and AP/NAP should be used together, and their quantitative changes can be caused by several factors including megafaunal presence. In addition to changes in

pollen spectra, animal presence can be identified via non-pollen palynomorphs (coprophilous fungi, eggs of parasites and beetles). These are deposited close to their point of origin (Cugny et al., 2010; Huang et al., 2020; Innes et al., 2013; Revelles & van Geel, 2016; Sandom et al., 2014a). Both pollen data and non-pollen palynomorphs have been used to identify the role of herbivores in landscape transformations, past mammalian behaviour and herbivore extinction processes in the past (Gill et al., 2013; Loughlin et al., 2018; Sandom et al., 2014b).

Another proxy for assessing animal presence is DNA. It can be used to understand human actions aimed at enhancing and/or expanding the geographic range of specific animal species and management of prey movements. DNA of animals can be extracted from sediments, and local presence of these species can be identified (Dussex et al., 2021; Haile et al., 2009). For example, parasite DNA from animal coprolites can chart the distribution of certain species and reflect human impact on them (Rawlence et al., 2014). DNA can be extracted from faunal remains, and this data can reflect the spatial distribution of animals based on geographic markers (Schlumbaum et al., 2008). Finally, past intense hunting pressure may have influenced population size and the distribution of targeted species. Studying the population dynamics of prey species through time using genetic studies can provide information about effective population sizes and whether one is dealing with a continuous "chrono-population" (individuals from older faunal assemblages are directly ancestral to the individuals from younger faunal assemblages) or whether faunal turnovers occurred, possibly as a result of hunting pressure. Such studies are in their infancy but are promising.

Stable carbon, oxygen and strontium isotope data are used in studies of megafaunal mobility, their geographic range and anthropogenic and climatic factors influencing animals (Swift et al., 2019). Geographically and temporally different populations and subpopulations have distinct isotopic values (Hoppe, 2004; Price et al., 2017). Isotopes vary in terms of spatial resolution: hydrogen and oxygen are "global-spatial" assays; carbon, nitrogen, sulphur and strontium are "local-spatial"; and multiple isotopes can be combined to increase spatial resolution (Wassenaar, 2008).

Faunal remains studied via zooarchaeological methods can clarify hominin impact on animal populations within site-adjacent areas. Such research pays considerable attention to taphonomy because this directly influences skeletal part representation, age and sex profiles, the visibility of markers caused by human activity and other evidence used for inferences about past human behaviour (diet, subsistence practices, animal husbandry, food distribution, social and cultural variation in foodways) (Boethius, 2018; Landon, 2005). Preservation of bones and their information content varies between regions due to differences in soils and

sedimentary geochemistry. Nevertheless, the general trend is characterised by the progressive loss of material through time (Surovell & Pelton, 2016).

Finally, human-induced burning can be used as a tool for prey management as discussed above. Therefore, proxies related to anthropogenic burning (Table 2.1) can be used in research related to past relationships between humans and animals. However, these proxies should be used carefully; apart from the ubiquitous problem of differentiating natural from anthropogenic fires, humans used fires for varied purposes. Therefore, evidence for hunter-gatherer burning per se does not equal human impact on animal populations; more evidence is needed to warrant conclusions here. Direct evidence of hominin impact on landscapes to impact animal presence and their abundance are fishing and hunting constructions, but their remains are rarely available for periods studied. Therefore, other proxies should be used to assess animal presence within specific locations: pollen indicators, AP/NAP, non-pollen palynomorphs, DNA and stable isotopes (Table 2.3). However, these types of evidence should be linked with hominin presence and activity, because such proxies can reflect both the natural distribution of animals and anthropogenic impact on their presence. Faunal remains studied via zooarchaeological methods can clarify specific practices which were used by hominins to hunt and consume animals.

2.4 Case studies

The following sections aim to illustrate the use of proxies in actual Middle Palaeolithic (Neanderthal) and Mesolithic archaeological contexts. These two types of contexts were chosen as an illustration because they were both formed under interglacial conditions with comparable climate (Svenning, 2002). The "The Visibility of Hunter-Gatherer Activity in Last Interglacial Records at Neumark-Nord" and "Impact of Mesolithic Hunter-Gatherers on Their Surroundings" sections focus on describing which proxies were extracted from both contexts and how they were interpreted for each of our categories of hunter-gatherer niche construction activities. We then assess whether the full range of proxies and best proxies are obtained and analysed in practice, and the extent to which this varies in older and younger contexts. We also discuss the strengths and weaknesses of the analysis of these proxies. A complete review of all relevant sites is beyond the scope of our paper, particularly for the Mesolithic; instead, we focus on case studies with large numbers of proxies that have a link to human activity. Finally, the current understanding of Neanderthal and Mesolithic impact on landscapes and common

niche construction activities for both Neanderthals and Mesolithic humans are discussed.

2.4.1 The visibility of hunter-gatherer activity in Last Interglacial records at Neumark-Nord

The visibility of hunter-gatherer activities during the Eemian is heavily limited due to taphonomical factors affecting Last Interglacial records and as a result of research bias (Nielsen et al., 2017; Roebroeks & Speleers, 2002). Neumark-Nord (Germany) is a rare example of a very rich and well-documented Last Interglacial location where different types of proxies (palaeoenvironmental and archaeological) were extracted from a landscape in which Neanderthals left a large amount of traces of their activities. At this location, the infill of two sedimentary basins has been submitted to a systematic investigation of Neanderthal activities and their environmental settings in an ~25 ha large Last Interglacial lake landscape. The infill is dated by a series of independent methods, including Thermoluminescence studies of heated flint artefacts, Amino Acid Racemization studies of Bithynia opercula and palaeomagnetic analyses of the Neumark-Nord 2 sequence (see, e.g., Sier et al. (2011) and Gaudzinski-Windheuser et al. (2018) for a summary of the dating evidence). The unique preservation at Neumark enables researchers to trace environmental change and human subsistence over a period of approximately 11,000 years, with a spatial and temporal resolution virtually unparalleled in the Pleistocene record. The Last Interglacial record of Neumark consists of a large water basin (NN1), recorded in a series of long-term rescue archaeology interventions by Dietrich Mania and his team during exploitation of a large brown coal quarry, and an adjacent smaller pool (basin NN2), studied in great detail during programmed excavations. Lake basin NN1 was about 24 ha large, while basin NN2 represents a small and shallow pond, of about 1.6 ha in size. The fine-grained sedimentary infill of the two basins covers the complete Last Interglacial cycle. Multidisciplinary analyses at NN2 and correlations with the record from NN1 enabled accurate and high-resolution localisation of Neanderthal occupations and faunal assemblages in a palaeoecological framework. The Neumark archaeological record contains high-density evidence for flint knapping, animal exploitation and fire use (at NN2) as well as low-density single activity death or kill sites, mostly accumulated during the first 7000 years of the Eemian. Comprehensive coverage of the Neumark palaeoecological and archaeological studies are assembled in Mania et al. (1990), Mania (2010), Meller (2010), Gaudzinski-Windheuser and Roebroeks (2014), Gaudzinski-Windheuser et al. (2018) and Kindler et al. (2020) (for various detailed studies of a wide range of proxies from Neumark-Nord see Mania, 2010; Meller,

2010; Bakels, 2012, 2014; Britton et al., 2012, 2019; García-Moreno et al., 2016; Milano et al., 2020).

Based on analysis of lithic assemblage and faunal remains, the NN2 site was characterised as a location where hundreds of medium-sized and large herbivores were processed during a well-constrained period of the Eemian Interglacial, with hominins revisiting the area over a period of minimally 2000 years (Pop et al., 2016) and with a striking absence of traces of carnivore modification of the abundant faunal remains (Gaudzinski-Windheuser et al., 2018). The frequency and the duration of the occupation events is still an open question (Pop, 2014). Samples for analysis of pollen, charcoal and animal remains were taken every 5 cm from the lithostratigraphic units of Hauptprofil 7 (Main profile 7) in a deeper part of the basin NN2 (Kuijper, 2014; Pop & Bakels, 2015). The rich archaeological find levels at the margins of the basin, located ~20 m from this profile, were easily positioned within the lithostratigraphy of Hauptprofil 7 thanks to the continuous exposures between the two locations (ibid.). Episodes with an open park-like forested area around the site were identified for NN2 during the period of hominin presence. It was suggested that such a type of environment could have been created via a combination of different types of disturbances: herbivores, aridity and Neanderthal fire practices (ibid.). This suggestion was based on pollen data (high percentages of herb pollen), charred plant macrofossils, macroscopic charcoal, thermally altered lithics (charcoal particles correlate with altered lithics) (Fig. 2.1) and faunal remains (most remains from the archaeological level NN2/2b belong to bovid and horse; wild ass, small cervid and roe deer may also be present, and several fragments attest to giant deer, wild boar, rhino and elephant) (Kindler et al., 2014). Kuijper's (2014) detailed study of the charcoal particles in the infill of the NN2 basin showed their presence all through the interglacial sequence, but with a very noticeable peak at the beginning of Neanderthal presence at the site, with ten times the amount of charcoal of any other peak in the sequence (Fig. 2.1, archaeological level NN2/3). Importantly, this charcoal peak and the beginning of a strong Neanderthal presence also coincide with significant changes in the vegetation: following the earlier (pre-Neanderthal occupation) expansion of taller deciduous forest, the landscape opens up, with a strong rise of upland herbs in the pollen curve and the beginning of a long *Corylus avellana* (hazel) period (Bakels, 2014; Gaudzinski-Windheuser & Roebroeks, 2014; Pop et al., 2016; Roebroeks & Bakels, 2015) (Fig. 2.1). Local-scale transformations of the natural landscape took place around the site when Neanderthals arrived, but it is not possible to establish if this correlation indicates causation (see below). The NN2 evidence however could reflect Neanderthal actions, specifically burning, to open up the area and attract game and increase plant food resources (Pop & Bakels, 2015; Roebroeks & Bakels, 2015). The hypothesis about creation of open habitats by

Neanderthals was supported via comparative study of the Neumark-Nord basins with the records from comparable Last Interglacial basins in the area: Gröbern, Grabschütz and Rabutz (Roebroeks et al., 2021). NN2 and these sites have common characteristics: similar soil conditions, basin forms, climatic conditions and presence of large mammals which preferred both closed forest conditions and open areas.

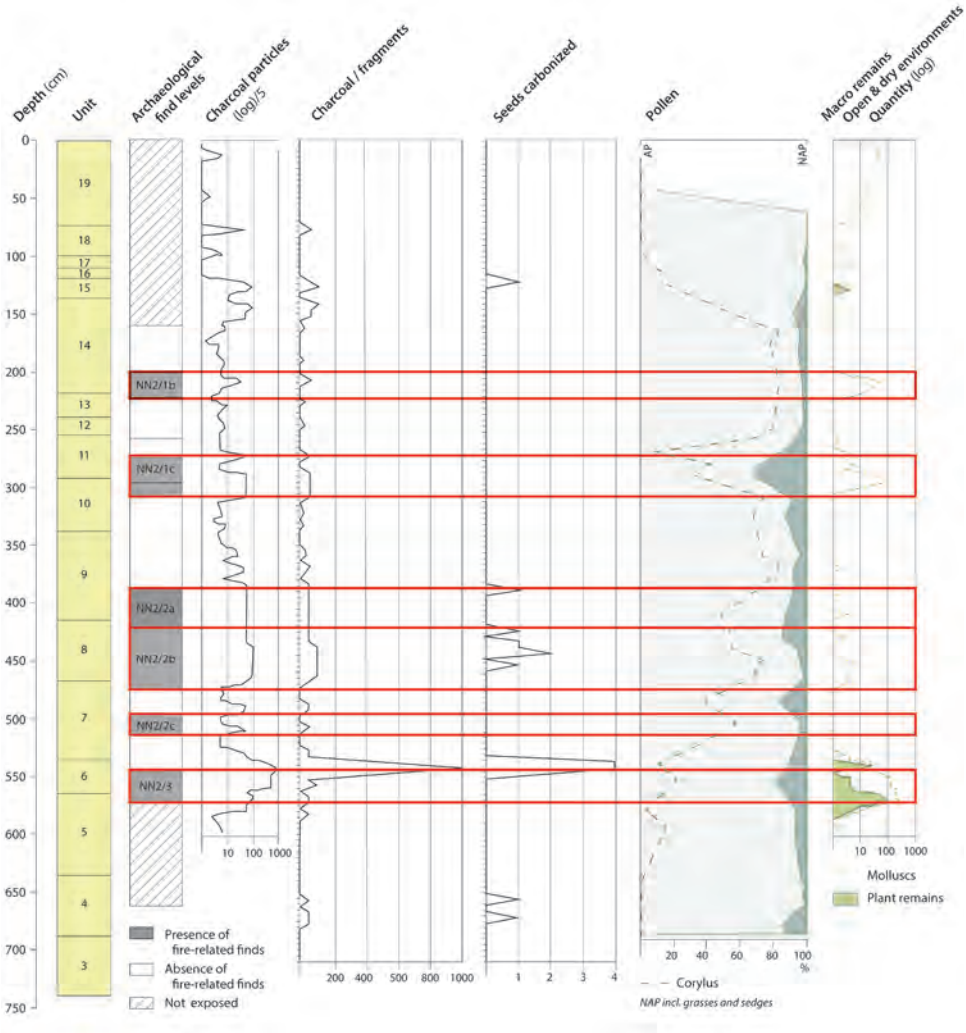

Figure 2.1 Neumark-Nord 2 (Germany) HP 7 sequence, with lithological units and the archaeological find levels (Sier et al., 2011), the stratigraphical distribution of charcoal particles, carbonised seeds (Kuijper, 2014), arboreal (AP) and non-arboreal pollen (NAP) and data regarding vegetation openness (Pop & Bakels, 2015); correlation of archaeological layers containing fire-related findings with vegetation openness episodes shown in red.

However, data from the Neumark-Nord area demonstrates unusual vegetation openness around basins, whereas there was relatively closed forest vegetation around other sites. Continuous vegetation openness around Neumark-Nord basins matches with 2000 years of Neanderthal presence, and, therefore, this vegetation change cannot be explained only by climatic shifts or megafauna impact.
Close-range hunting of large herbivores by occupants of this larger lake area was identified based on hunting lesions on fallow deer bones (Gaudzinski-Windheuser et al., 2018) at NN1. Neanderthals also played an almost exclusive role in bone accumulation at NN2 where large amounts of bone fragments with cutmarks accumulated (archaeological level NN2/2b, Fig. 2.1) (Gaudzinski-Windheuser & Roebroeks, 2014; Pop et al., 2018). Molluscs (discovered in units 18–16, 6, 4), fish (discovered in units 18–top 15, 6, 5, 4) and bird remains (egg fragments were discovered in units 19–17, 11, 6 and 5) are also abundantly present in the infill. The diet of the occupants may have included *Prunus spinosa* (blackthorn), *Quercus sp.* (acorn), and hazelnut, as their charred macroremains were discovered during excavations of archaeological level NN2/2 (Kuijper, 2014). Charred hazelnuts are also known from the neighbouring Last Interglacial archaeological site Rabutz (Toepfer, 1958). Based on analysis of coarse graveland cobble-sized stones transported by Neanderthals to the NN2 location, mainly quartzite and sandstone, some of these manuports were used for percussive tasks (lithic production and potentially bone processing) without contact with soft materials (e.g., nut processing) (Pop et al., 2018).

Thus, the subsistence activities of hunter-gatherers at Neumark-Nord were clarified based on a multi-proxy approach, applied to a series of sediments preserved in rather unique basin structures over large areas beneath a cover of Weichselian loess, with a spatial and temporal resolution unparalleled in the Pleistocene record. These taphonomically unique sediment traps allowed a detailed study of Neanderthal subsistence activities, identified via faunal remains with preserved anthropogenic traces, lithic assemblages and plant macrofossils. Local-scale transformations of the natural surroundings of the small lake of NN2 occurred when Neanderthals arrived, a correlation for which there are two plausible explanations: either Neanderthals started to frequent the location because the landscape had been opened up by natural fires as testified by the large charcoal peak in the lower part of the sequence (see Fig. 2.1) or their arrival opened up the landscape, e.g., by their use of fire (Pop & Bakels, 2015; Roebroeks & Bakels, 2015). Sedimentation of the infill of the central part of the NN2 basin was rapid and nearly continuous, with estimated sedimentation rates for the archaeology-yielding deposits varying from 0.11 to 0.24 cm/year (Sier et al., 2011), yielding a high-resolution NN2 sequence. That is why this case study provides

an example of the dynamic character of environments and how they can be transformed via the impact of several agents (hominins, herbivores and climate), with likely Neanderthal impact on surroundings. Currently, despite the large amount of high-resolution environmental data, it is not possible to identify which agent caused which types of changes at this particular location. Situating the local Neumark-Nord evidence within the wider regional record, by comparing it with similar Last Interglacial basins without an archaeological record, may enable better identification of the specific roles of the various actors, including large mammals and hominins (Roebroeks et al., 2021).

2.4.2 Impact of Mesolithic hunter-gatherers on their surroundings

It is widely accepted that Mesolithic populations impacted their surroundings via burning in different parts of Europe (Davies et al., 2005; Mason, 2000). Anthropogenic burning has been identified around such sites as Meerstad (The Netherlands) (Woldring et al., 2012), the Lahn valley complex (Germany) (Bos & Urz, 2003), Dudka Island (Poland) (Gumiński & Michniewicz, 2003), Star Carr (England) (Mellars & Dark, 1998; Milner et al., 2018), Dumpokjauratj and Ipmatisjauratj (Sweden) (Hörnberg et al., 2006), Vingen sites (Djupedalen, Vingeneset and Vingen terrace in Norway) (Hjelle & Lødøen, 2017) and the rock art park of Campo Lameiro (Spain) (Kaal et al., 2013). Table 2.4 shows that vegetation burning was mainly identified based on increased charcoal concentrations and the presence of pollen produced by species indicative of open/disturbed areas. These types of evidence were associated with archaeological records of human activity within and around sites, and therefore these burning events were interpreted as human-induced fire episodes (Bos & Urz, 2003; Gumiński & Michniewicz, 2003; Hjelle & Lødøen, 2017; Hörnberg et al., 2006; Kaal et al., 2013; Mellars & Dark, 1998; Milner et al., 2018; Woldring et al., 2012). As we can see, one type of evidence (pollen spectra) dominates in such studies; in fact, the data from the Lahn valley is outstanding because more types of proxies were related to human-induced burning there. Therefore, this case study is discussed in more detail below in accordance with the article published by Bos and Urz (2003).

Archaeological sites from the Lahn valley area in Germany were investigated at a high chronological resolution. Niederweimar 6 (NW6) and Niederweimar 8 (NW8) are two early Mesolithic archaeological sites discovered in 1994 during gravel mining. They are both located on river terraces along Holocene residual channels. Lithics and carbonised animal teeth were found within NW8, and a Mesolithic campsite was identified within NW6 where concentrations of artefacts and a fireplace were found. Geomorphological and palaeobotanical research was conducted in conjunction with pollen analysis and radiocarbon dating to reconstruct vegetation transformations in this area. Plant microfossils were

Table 2.4 Summary of main evidence associated with human-induced burning of vegetation around Mesolithic sites and the Last Interglacial site Neumark-Nord 2 in Europe.

	Vingen sites	Meerstad	Lahn valley complex	Dudka Island	Star Carr	Dumpok-jauratj (?)	Ipmatis-jauratj (?)	Campo Lameiro (?)	NN2
Pollen of species occupying open/ disturbed areas	↑	↑	↑	↑	(?)	↑	↑	↑	↑
Charcoal	↑	↑	↑	↑	↑	↑	↑	↑	↑
Macro remains reflecting open environments (plant macrofossils of light demanding species, molluscs)	–	–	↑	–	–	–	–	–	↑
Plant macrofossils of nutrient-rich, disturbed vegetation	–	–	↑	–	(?)	–	–	–	–
Charred plant macrofossils	–	+	+	–	+	+	–	–	+
Date of suggested anthropogenic burning	7700–6200 BP	8200–7500 BP	10,420 BP; 10,350 BP	8500–7700 BP	11,300–10,600 BP	8400–8000 BP	8000–7600 BP	7600–6500 BP	Last Interglacial
Archaeological evidence supporting human presence	+	+	+	+	+	+	+	+	+
References	(Hjelle & Lødøen, 2017)	(Woldring et al., 2012)	(Bos & Urz, 2003)	(Gumiński & Michniewicz, 2003)	(Mellars & Dark, 1998; Milner et al., 2018)	(Hörnberg et al., 2006)		(Kaal et al., 2013)	(Gaudzinski-Windheuser & Roebroeks, 2014; Pop & Bakels, 2015; Roebroeks & Bakels, 2015)

↑ increase – no evidence (?) estimated/not certain

collected from different well defined and dated residual channel fills, and pollen data was collected from three sediment profiles along a transect at different distances (75–200 m) from the archaeological sites. Pollen samples were taken from palaeochannel fills of the river Lahn. Charcoal concentrations and NAP totals were calculated. Nineteen samples were AMS dated to obtain a chronostratigraphical framework which covers the period between 11,640 BP and 8830 BP. Mesolithic settlement existed in this area between around 10,940 BP and 10,360 BP.

Several proxies were combined to make hunter-gatherer landscape changes visible in the records. Correlation between different types of evidence was conducted via absolute dating, fluvial geomorphology and comparison of diagrams. As a result, large amounts of charcoal, high percentages of light demanding taxa and plants indicating a nitrogen- and nutrient-rich environment (i.e., disturbed surroundings and input of organic material) (Fig. 2.2), along with the presence of Mesolithic occupation traces in the area, were interpreted as evidence of human impact on landscapes via clearance and burning. In particular, high percentages of charcoal and macrofossils reflecting nutrient-rich and disturbed places, and the reduction of woody plant macrofossils around 10,420 BP (Fig. 2.2), were interpreted as indicating clearance and deliberate burning of the pine, birch and hazel-rich woodlands leading to the expansion of more open vegetation. The second phase of human impact in the oak, elm and hazel-rich woodlands took place around 10,350 BP, based on the identification of the second-highest charcoal peak along with a relatively high percentage of macrofossils from nutrient-rich and disturbed places. In addition, several periods of openness in hazel woodlands were discovered based on the pollen spectrum (Fig. 2.2). The presence of bones (some with cutmarks) of wild animals reflects the importance of hunting for occupants from the Lahn area. Hence, game attraction may have been one of the main reasons for vegetation burning. Ease of human movement could also be mentioned as a possible reason for fire practices. The discovery of hazelnut fragments (both charred and uncharred) in archaeological layers led the authors to the conclusion that promotion of the growth of edible plants such as hazel was one more reason for burning vegetation (ibid.). However, it is important to highlight that coppicing and pruning were important ways to promote edible plants, and these techniques were quicker ways to increase plant growth in comparison with vegetation burning (Bishop et al., 2015). Additionally, naturally good growing conditions could promote hazelnut growth (Groß et al., 2019).

Regarding plant manipulation, macrofossils of plants have been found in Mesolithic layers within sites in the Netherlands and Great Britain (e.g., *Ficaria verna*, lesser celandine), Denmark (e.g., *Allium cf. ursinum*, ramsons and *Conopodium majus*, pignut), and Poland (e.g., *Sagittaria cf. sagittifolia*, arrowhead)

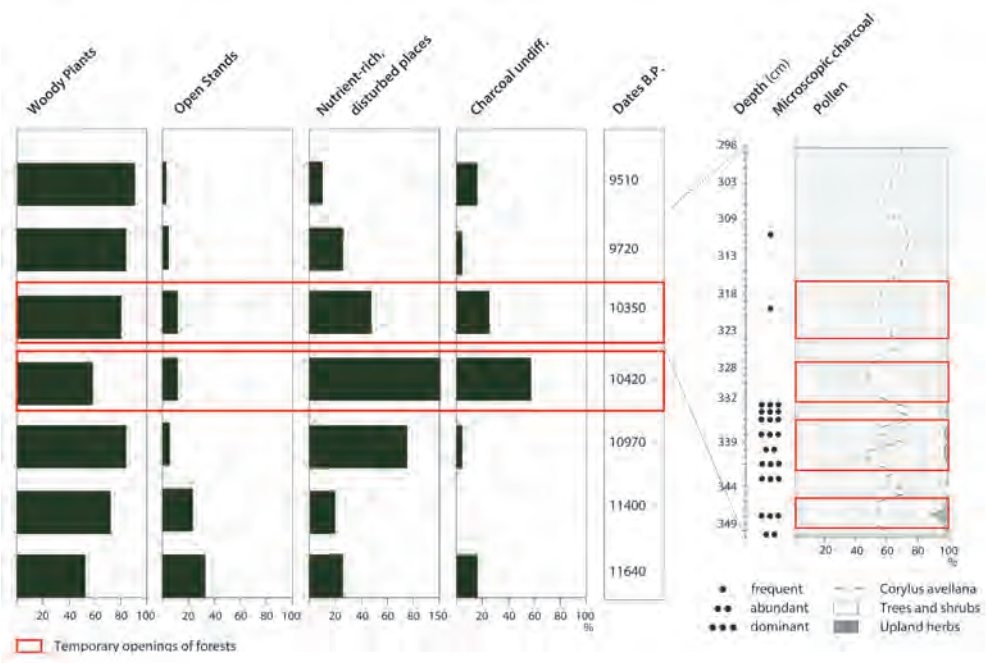

Figure 2.2 Pollen analysis (pollen percentage of trees, shrubs, upland herbs and Corylus avellana) from Weimar-Niederweimar II.2 profile and macrofossil evidence (percentage of wood, charcoal and remains from plants occupying open, disturbed and nutrient-rich areas) from different palaeochannel fills at Weimar-Niederweimar (Germany). The sequence shown here is dated to the Younger Dryas (11,640 BP, gravel layer), Preboreal (11,400–10,970 BP, gravel layer) and Boreal periods (10,420–9510 BP, sand/gyttja and gyttja layers); phases of Early Mesolithic anthropogenic impact within the Lahn valley area are shown in red (after Bos & Urz, 2003).

(Klooss et al., 2016; Kubiak-Martens, 2015). Due to the fact that tubers and roots of these plants were discovered as charred remains, researchers have concluded that these plants were part of the Mesolithic diet. Roots and tubers could have been abundant, starch-rich and easily available foods in temperate Europe. The starch content of these plants would have made a significant dietary contribution and made their enhancement worthwhile. Macrofossils of hazel and nut processing equipment were discovered in Mesolithic layers within different sites (Divišová & Šída, 2015; Groß et al., 2019; Holst, 2010; Regnell, 2012), and, therefore, this plant is currently considered one of the most important vegetable components of the Mesolithic diet. However, intensive exploitation of hazelnuts may be a response to good growing conditions rather than a result of human intervention (Groß et al., 2019). Not only nuts but also other parts of plants have been found in Mesolithic

assemblages which indicate that variable parts of plants were available for people, though specific types of plant manipulation are difficult to identify based on such evidence. Additionally, tools potentially related to Mesolithic plant manipulation were discovered within different European sites: wooden hoes and mattocks, antler artefacts interpreted as tools for a range of purposes including digging, and blades and microblades with traces of plant processing (Zvelebil, 1994). However, these tools could have been used for varied purposes, and unambiguous identification of their actual use is difficult to achieve. Mesolithic populations may have carried out small-scale plant manipulation for purposes other than obtaining food. In particular, the number of wooden artefacts discovered increased in the Mesolithic in comparison with preceding periods. Coppicing and forest clearing have been mentioned as possible methods to obtain wood materials of the properties required to produce tools or construct structures for variable purposes (Bamforth et al., 2018; McQuade & O'Donnell, 2007; Warren et al., 2014). Overall, it is difficult to distinguish unmanaged wood from coppicing remains left by humans (Out et al., 2013).

Animal presence within specific locations is often difficult to link directly with hunter-gatherer activity without evidence of special constructions (e.g., fences or traps) for the management of animal movements and distribution. Constructions for management of aquatic resources were identified within Mesolithic sites such as North Wall Quay in Ireland (McQuade & O'Donnell, 2007), and Zamostje 2 in Russia (Lozovski & Lozovskaya, 2016). The importance of aquatic resources for some Mesolithic groups was also supported via a combination of different proxies: several types of evidence were obtained as the result of zooarchaeological analysis interpreted in conjunction with ethnographic analogues (evidence of fish extraction in large quantities, year-round seasonality indicators, determination of species, etc.), archaeological (presence of mass catching equipment and a fish fermentation facility) and isotope studies (high dietary intake of aquatic resources by humans) in southern Scandinavia (Boethius, 2018). Terrestrial structures have not been discovered in Europe yet. An example of a study in which a link has been made to hunter-gatherer activity for terrestrial animals without the presence of special constructions is the North Gill site in England (Innes & Blackford, 2003). There are several exposed peat sections at the site, the base of which is rich in charcoal and contains evidence of fire disturbance. One of the previously defined basal disturbance phases at the site was studied via analysis of fungal spores in conjunction with already published charcoal and pollen counts. Samples were extracted from the basal disturbance phase at core North Gill 5B. Fungal spores were counted from the same slides as for the pollen and charcoal data derived from the basal disturbance phase at core North Gill 5B. Post-disturbance phases after

burning were reflected in pollen (abundance of *Melampyrum* as the initial post-fire flora), charcoal concentrations and fungi (*Neurospora* and *Gelasinospora*) counts (Fig. 2.3). An increased amount of dung fungus (e.g., *Sporormiella*) and pollen of *Succisa* and *Potentilla*-type during the post-disturbance transitional phases may reflect the presence of herbivores and intensive grazing. This data supports the view that recently burned areas were attractive for game. Two factors were

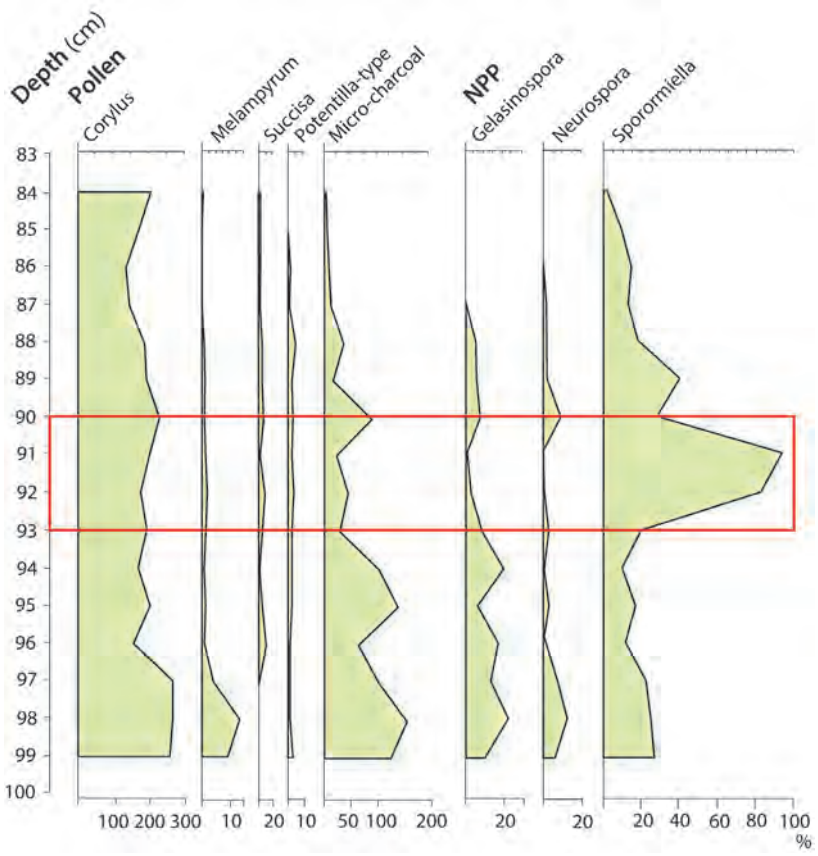

Figure 2.3 Pollen analysis (pollen percentage of *Corylus*, *Melampyrum*, *Succisa*, *Potentilla*-type and microcharcoal) and non-pollen palynomorphs (NPP) evidence (percentage of Gelasinospora, *Neurospora*, *Sporormiella*) from a profile at North Gill 5B (North York Moors within England and Wales). This evidence reflects post-disturbance phases after burning and intensive grazing during the Late Mesolithic at North Gill. The profile consists of amorphous peat resting on sand at 100 cm. The inferred age of the basal peat lies within the Late Mesolithic based on dates available for a section a few tens of meters away from North Gill 5 (5270 BP) and higher section of this site (4540 BP at 73 cm) (after Innes & Blackford, 2003). Red shows the phase with the highest herbivore concentrations; this follows a phase with intensive burning.

considered causes of burning events leading to an increase in grazing activities: anthropogenic burning and climatic impact (ibid.; Innes & Blackford, 2017).

Therefore, data from several European archaeological sites has been interpreted by researchers as evidence of vegetation burning organised by hunter-gatherers during the Mesolithic. Such evidence mainly includes increases in charcoal concentrations and pollen of species occupying open/disturbed areas while Mesolithic people were present in the areas. Anthropogenic burning was mostly local and during favourable conditions for the spread of fire could impact surroundings more dramatically. The high importance of plants in the Mesolithic diet was mainly identified based on the presence of charred and not charred plant remains within cultural layers. Specific types of plant manipulation could be suggested based on tools discovered in different archaeological sites in Europe. Mesolithic people also used aquatic and terrestrial animal resources, but the direct evidence (e.g., traps, fences) of hunter-gatherer impact on animal presence and their abundance in specific locations is only available for the former. Non-pollen palynomorphs and pollen spectra reflected high grazing activity, but a strong link between human activity and high concentrations of herbivores around a specific site has not been established.

2.5 Discussion

Currently, identifying what niche construction activities Last Interglacial and Early–Middle Holocene hunter-gatherer populations had in common is complicated due to the scarcity of well-documented sites, especially for the Last Interglacial. A further issue lies in weaknesses in the argument connecting proxies with landscape management activities: anthropogenic burning provides a good example.

Anthropogenic burning of the immediate surroundings of Eemian and Mesolithic camp sites was identified in a series of inferential steps. Firstly, proxies were observed reflecting changes in the vegetation cover. Secondly, further interpretation emphasises that these vegetation transformations were caused by burning. A next step in the interpretation linked these fire events to hominin activity, and to hominin firing of the landscape. Finally, this burning was interpreted in terms of intentional landscape transformation by hunter-gatherers.

The first and the second steps are reproducible and relatively easy to support with empirical data, built on various proxies ("Proxies for Identification of Modification of Vegetation Communities Via Burning" section) and their analyses. The transition from the second interpretation step towards linking the specific fire with human activity is much more difficult, but can ideally be inferred

on the basis of a high-resolution archaeological context and/or setting of the proxies. However, due to the time-averaged nature of the archaeological records even for high-resolution data associated with evidence of hominin presence, it is not possible to definitively establish if this correlation reflects anthropogenic landscape changes or hominins occupied the area right after or during landscape changes caused by natural factors. The last step, leading to the conclusion about intentional hunter-gatherer landscape management, is the most difficult, because this step needs to be supported by robust evidence regarding the intentions of past populations. In the absence of such robust data, the Eemian and Mesolithic case studies lack a solid link between data and conclusions about the intentional nature of anthropogenic burning, be it Last Interglacial or Early–Middle Holocene in age.

What one can minimally observe is that a similar set of proxies was available for both the Last Interglacial and the Holocene case studies. The main evidence used to assess hunter-gatherer vegetation burning in these periods are increases in charcoal concentrations, as well as pollen and macrofossils indicative of open/disturbed areas when hominins were present (Table 2.4). Both Neanderthals and Mesolithic humans were considered by researchers as possible agents of landscape transformations, and currently local-scale vegetation burning could be considered a common niche construction activity for both Neanderthals and Mesolithic populations.

Regarding other niche construction activities, we suggest that plant manipulation and control of animal presence were common activities for Neanderthals and Mesolithic populations, because charred plant microfossils, stone tools with evidence of plant manipulation (e.g., from the Middle Palaeolithic site of Payre in France; Hardy & Moncel, 2011; Osipowicz, 2019), plant microremains from dental calculus (Cristiani et al., 2016; Henry et al., 2011, 2014) and large numbers of animal bones accumulated through butchering activities were identified within both Middle Palaeolithic and Mesolithic sites. Additionally, management of aquatic resources by Mesolithic populations has been demonstrated based on several types of evidence including fish traps and faunal remains. Manipulation of wood raw materials has also been suggested in the Mesolithic, but is difficult to demonstrate.

Given the available evidence, one cannot postulate significant differences between the categories of niche construction practices conducted by Neanderthals and Mesolithic humans, and likewise there exists no unambiguous proof that the observed fire events were the intended outcomes of vegetation burning by populations during both periods. While this suggests that both populations influenced their landscapes on a local scale at least, it is not clear

whether there is any difference on larger spatial scales. Currently, the main way of assessing possible larger-scale differences lies in estimates of population sizes, but these are notoriously difficult to establish. Additional studies are necessary to assess whether repetitive landscape transformation activities on a local scale could have caused shifts in vegetation composition on regional – and possibly (sub-) continental–levels during the Eemian and the Holocene, and which population densities of hunter-gatherers are needed for such changes to become visible on such scales.

To fill existing gaps in research about dynamic interglacial environments and the role of *Homo* with different demographic settings in landscape changes, further research endeavours could include not only standard procedures such as palynological analysis and estimation of charcoal concentrations, but also extraction of less common proxies (e.g., DNA from sediments, phytoliths, parenchyma and other evidence mentioned in the "Types of Evidence Related to Past Hunter-Gatherer Niche Construction Activities" section). However, the possibilities for using a combination of proxies for such studies depend on taphonomic processes and on data availability determined by previous research. Such a multi-proxy approach could potentially help to overcome the specific resolution limitations of each method, to make the hunter-gatherer signal more visible, and to separate human-induced changes from transformations caused by other processes (climatic fluctuations, megafauna activities, etc.). Modelling efforts might be helpful in making the transition from local to regional to (sub-)continental research. Depending on the modelling type, local-scale evidence could form one of the inputs into a model, or could be used later at a validation stage.

2.6 Conclusion

Three categories of hunter-gatherer niche construction activities were described in accordance with ethnographic observations: (1) modification of vegetation communities via burning; (2) small-scale plant manipulation; (3) landscape modification to impact the presence of large animals and their abundance in specific locations. Every niche construction practice can potentially be identified via several types of evidence. However, the actual visibility of these activities depends on several factors. These include the impact of taphonomic processes on the extraction and analysis of evidence (i.e., over-representation of some proxies or indicators and underrepresentation or complete absence of others); spatial scale (i.e., reflection by some proxies of past processes on local and regional scales, others on (sub-)continental scales); temporal representation (i.e., the tendency for

younger things to be better represented than younger things in the archaeological record); and research strategy during field studies which defines further analysis.

Case studies showed that similar sets of proxies (mainly charcoal concentrations, pollen and macrofossils of species reflecting open and disturbed areas) exist for possible Neanderthal and Mesolithic firing of vegetation. Anthropogenic (intentional) changes of vegetation during the Mesolithic are commonly accepted on the basis of these proxies. The Neumark-Nord case study illustrated that data exists for the Last Interglacial that in terms of their information quality match the best Mesolithic cases known. Hence, Last Interglacial Neanderthals' impact on their surroundings was occasionally very much comparable to that of Mesolithic hunter-gatherers. However, the absence of unambiguous methods to clearly distinguish between hominin, climatic and megafaunal local impact on vegetation during both periods forces us to be careful in interpreting these firing activities. In general, many studies have inferred a relationship between observed proxies for vegetation transformation via burning and hominin activities identified based on the archaeological context and/or setting of the proxies. These correlations were then translated into conclusions about hunter-gatherer intentional landscape transformations via burning. However, the intentional nature of anthropogenic landscape changes is difficult to verify, even in high-resolution cases. The currently available data and amount of research could allow researchers to consider local-scale vegetation burning as a common niche construction activity for both Neanderthals and Mesolithic populations. Other suggestive niche construction activities organised by foragers during both time periods are plant manipulation and impact on animal presence and their abundance.

In short, given the significance of the Eemian interglacial as an "analogue for present-natural vegetation" for the Holocene, clarifying the role of fire using Neanderthals in the past landscapes under scrutiny is important. To identify the extent of past hunter-gatherer impact on surroundings, more precise estimates of population sizes are necessary, hence the need for further research. In addition to long-established research methods (e.g., pollen analysis and the study of charcoal particles), future research endeavours should try to make use of less common techniques such as sediment DNA, phytoliths and starch grains. Studies of past hunter-gatherer landscape changes should mainly rely on evidence with a local spatial resolution (Tables 2.1, 2.2, and 2.3), reflecting the scale at which hunter-gatherer activities had an impact. The transition from local to regional to (sub-) continental research can be made via modelling which can include information obtained from proxies as an input to models or as the way to test modelling results. Additional studies are necessary to assess whether repeated activities by hunter-gatherers causing landscape transformation on a local scale led to shifts

in vegetation composition on regional and (sub-)continental scales, or not, and which population density of foragers could cause such significant changes.

2.7 Acknowledgements

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