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

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CHAPTER 5

DISCUSSION

The aim of this study is to evaluate the hunter-gatherer impact on interglacial vegetation in Europe during the LIG and the Early Holocene by using the spatially-explicit HUMLAND ABM. The development of this model was central to this study, enabling to simulate the effects of climate, megafauna, natural fires, and human-induced burning on vegetation cover. Through a series of simulation runs, this research addressed objectives and the main research question, demonstrating the model's capability to quantify and trace different types of impact on vegetation. This approach offers insights into past dynamics of the European ecosystem and the role of hunter-gatherers in it. In addition, the results of this study establish a framework for future research in human presence within past landscapes using archaeology, paleoecology, and environmental modelling.

This chapter offers a summary and a discussion of the results in relation to the objectives outlined in Chapter 1. The first part discusses the review of available evidence from archaeological contexts regarding hunter-gatherer impact on landscapes. The detailed outcomes derived from this phase of the research were presented in Chapter 2 (Nikulina et al., 2022).

The second part focuses on the differences between the potential natural vegetation cover obtained via CARAIB and the pollen-based observed vegetation cover produced via REVEALS. The results of this comparison are crucial as they highlight discrepancies between the vegetation state before simulation runs (CARAIB) and the expected HUMLAND outcome (REVEALS), thereby setting the stage for further analyses. Identifying the factors that modify the vegetation conditions to align better with the REVEALS results is one of the key aspects of this study. The detailed methodology for the CARAIB–REVEALS comparison and incorporation of these datasets into the HUMLAND ABM can be found in Chapter 3 (Nikulina et al., 2024b). Section 5.2 focuses exclusively on the comparison results across all time windows as detailed in Chapter 4 (Nikulina et al., in press).

The HUMLAND ABM has been briefly introduced in Chapter 1, with additional model details, sensitivity analysis results and genetic algorithm experiments available in Chapter 3 (Nikulina et al., 2024b) and Chapter 4 (Nikulina et al., in press). Section 5.3 presents the limitations of this study and the challenges encountered during the development of this ABM. Section 5.4 summarizes and discusses the results of the sensitivity analysis (Nikulina et al., 2024b). The potential impact of Neanderthals and Mesolithic humans on vegetation for the most frequently generated scenarios is briefly discussed in Section 5.5, in accordance with Chapter 4 (Nikulina et al., in press). These scenarios are represented by various combinations of parameter values within the HUMLAND model. As a key outcome of this study, these scenarios were used to establish the relative continental level importance of different types of impact (humans, megafauna, climate, and natural fires) for interglacial vegetation. Section 5.6 provides the overall conclusion and outlines perspectives for future research.

5.1 Visibility of hunter-gatherer impact on landscapes within archaeological contexts

To present the available evidence and assess the visibility of foragers' impact in archaeological context, the categories of hunter-gatherer niche construction activities were identified based on ethnographic observations. Then, evidence for each category were listed and evaluated in terms of temporal relevance (i.e., whether this evidence could potentially be available for the LIG and Mesolithic contexts) and spatial resolution (i.e., the scales of processes visible in these proxies). Afterwards, the use and availability of proxies within discovered Neanderthal and Mesolithic sites were shown. The discussion on this review's outcomes focused on the validity and importance of current understanding of hunter-gatherer impact on interglacial landscapes in Europe.

Using ethnography-based review papers, the following categories for hunter-gatherer niche construction were identified: (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. The first category (Table 2.1) can be identified via biological indicators (e.g., pollen, charcoal, plant macrofossils, non-pollen palynomorphs, aDNA) and geochemical evidence (e.g., black carbon, levoglucosan). All biological indicators have a local scale resolution, which means that these proxies mostly reflect processes that occurred at or close to a specific location where hunter-gatherers were present. Some biological indicators reflect processes at a regional scale, making these proxies suitable for capturing regional-scale dynamics. Geochemical data is either difficult to detect or captures events on several scales from local to (sub-) continental which is the most general level of analysis. Thus, biological indicators are more suited for studies of hunter-gatherer vegetation burning because these fire events happened on local scales, and are visible via proxies with a local resolution.

The second category (Table 2.2) of hunter-gatherer activities, plant manipulation, can be identified via biological indicators (e.g., plant macrofossils, pollen), though these often indicate which plants were available for people rather than specific ways of plant manipulation. Discoveries of tools for soil-working, reaping and processing (e.g., digging sticks, hoes, mattocks and other tools) would provide more robust data for this category, as they represent direct evidence. However, such tools are rare for foragers' contexts, especially for the Pleistocene.

Similar to tools for plant manipulation, direct evidence of hominin impact on animal presence and their abundance (Table 2.3) consists of fishing and hunting constructions. However, such evidence is rarely available for study periods, particularly in Europe. Recently, a submerged stone structure was discovered in the Baltic Sea, with suggestions that it was used by Late Glacial and Mesolithic foragers for hunting (Geersen et al., 2024). Nevertheless, due to the limited availability of such evidence, other proxies should be used to assess animal presence within specific locations including pollen, non-pollen palynomorphs, aDNA and stable isotopes. It is important to note that these types of circumstantial evidence should be clearly linked to hominin presence and activity, because such proxies can reflect both the natural distribution of animals as well as anthropogenic impact on their presence. Faunal remains studied via zooarchaeological methods can clarify specific practices of hominins to hunt and process animals.

Available evidence from LIG and Mesolithic case studies show that it is challenging to identify which types of niche construction activities European hunter-gatherers from both periods had in common due to the scarcity of well-documented sites, especially for the LIG. A further issue lies in weaknesses in the argument connecting specific proxies with specific landscape modifying activities. For instance, when there is evidence for a correlation between hunter-gatherer presence and vegetation burning it is not possible to definitively establish whether this correlation reflects anthropogenic landscape changes or hominins occupied the area right after natural burning. This is because of the time-averaged nature of archaeological records, even for high-resolution data associated with hominin presence.

A similar set of proxies is available for both the LIG and Mesolithic case studies, and their examination reveals a comparable anthropogenic impact across both time periods (Table 2.4). The main evidence used to assess hunter-gatherer vegetation burning in these periods consists of changes in charcoal concentrations, pollen and macrofossils indicative of open/disturbed areas associated with hominin presence. Researchers have suggested that both Neanderthals and Mesolithic humans may have been responsible landscape transformations, with local-scale vegetation burning considered a potential common niche construction activity for both groups.

Regarding other niche construction activities, results of this review indicate that plant manipulation was another possible common niche construction activity among both Neanderthals and Mesolithic groups. This is supported by the identification of charred plant microfossils, stone tools with evidence of plant manipulation, and plant microremains from dental calculus at both Middle Palaeolithic and Mesolithic sites. Additionally, the (indirect) control of animal presence appears to be a similar activity for both Neanderthals and Mesolithic groups, as evidenced by the large numbers of animal bones found after butchering activities in archaeological contexts. 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 (e.g., coppicing) has also been suggested for the Mesolithic (Verpoorte & Scherjon, 2025), but it is often difficult to demonstrate.

Available evidence indicates that there are no substantial differences in the niche construction practices of Neanderthals and Mesolithic humans. Additionally, there is no definitive proof that the observed fire events were *intentional* outcomes of vegetation burning by populations in both periods. While this suggests that these populations influenced their landscapes on a local scale at least, it is not clear whether there is any difference on larger spatial scales.

To fill existing gaps in research about dynamic interglacial environments and the role of *Homo* in landscape changes, further studies and data are required. Future research could incorporate not only standard methods like palynological analysis and charcoal concentration estimates but also the extraction of less common proxies such as sediment aDNA, phytoliths, and parenchyma. Adopting this multi-proxy approach might help address the specific resolution limitations of each method, improve the visibility of the hunter-gatherer signal, and distinguish human-induced changes from those caused by other processes.

However, the possibilities for using a combination of proxies for such studies depend on taphonomic processes. In particular, the Neumark-Nord case study showed the benefit of extracting different types of evidence from one site, and that even sites from distant times can contain a wide range of proxies (Gaudzinski-Windheuser & Roebroeks, 2014; Nikulina et al., 2022; Roebroeks et al., 2021). It could be beneficial if there are more LIG contexts under such comprehensive study. Nevertheless, many European regions could benefit from already basic procedures such as palynological analysis of LIG samples. For example, most of the existing LIG pollen data is available for the Western and Central Europe while Southern, Northern and Eastern areas are not covered by such seemingly basic studies (Pearce et al., 2023; Nikulina et al., in press). There are many reasons for that including the overall higher research focus on some areas, taphonomic processes and overall preservation potential of different evidence within various settings.

There is more pollen evidence available for Early Holocene contexts compared to the LIG period (Nikulina et al., in press). It may therefore be beneficial to consider extracting less commonly found types of evidence from Mesolithic sites. On the other hand, it could be valuable to begin with a comparative study of existing local-scale palynological evidence across Europe. This approach would include comparing evidence from sites where human-induced fires were not indicated during foragers' occupation with those where anthropogenic burning was suggested. Researchers often emphasize human-induced vegetation changes and their visibility in relation to agricultural groups (Nikulina et al., 2022). Consequently, the impact of hunter-gatherers is often characterized as minimal or absent. Comparative studies have the potential to clarify whether it is accurate to characterize the local-scale impact of foragers in this way.

In addition, 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 to compare modelling results with empirical data.

5.2 Comparison of potential "natural" and pollen-based vegetation reconstructions

In this study, the differences between CARAIB and REVEALS were evaluated, and the mechanisms driving the observed differences were identified through ABM runs. This involved conducting a comparison between CARAIB and REVEALS initially. This analysis helped to quantify their disparities and establish objectives for the simulation runs. The detailed methodology developed for this comparison is described in Chapter 3 (Nikulina et al., 2024b).

CARAIB and REVEALS outputs were compared per time window in terms of the distribution of first PFTs and vegetation openness. The comparison was conducted for two LIG time windows (mesocratic I and mesocratic II) and for seven Early Holocene time windows, from 11,700 to 8200 BP, with a time step of 500 years. The results (Fig. 4.5) show that CARAIB consistently exhibits substantially higher percentages of grid cells dominated by trees compared to REVEALS. Additionally, a consistent trend was observed in mean vegetation openness estimates, with CARAIB showing significantly lower estimates than REVEALS. Thus, in the absence of impacts other than climate (as is the case in CARAIB), natural vegetation would tend to be denser with dominance of arboreal vegetation.

The differences between the CARAIB and REVEALS datasets are consistent between the LIG and Early Holocene, with the exception of the 11,700–10,200 BP period (Fig. 4.5). This deviation might be partially due to the glacial/interglacial cycle delaying the arrival of some tree species. Consequently, differentiating climate effects on vegetation from other processes during this period is challenging. As a result, HUMLAND runs were not conducted for this time frame.

Overall, the degree of difference between CARAIB and REVEALS datasets is similar and does not vary between the LIG and the Early Holocene (Fig. 4.5). The observed similarities between the CARAIB–REVEALS differences for the studied time periods are at least partially related to relatively coarse resolution of both models, shared characteristics and overall comparable vegetation development between the two periods. It is important to note that the relatively coarse resolution of this comparison likely smooths out, to some extent, inherent biases, uncertainties and limitations of the models that impact their outputs that were compared.

The primary differences between the LIG and the Early Holocene are the higher eustatic sea level in the LIG, differences in insolation, the composition of the megafauna community, and a different *Homo* population in Europe. Due to that, the contribution of certain elements to the overall functioning of the ecosystem would vary between the LIG and the Early Holocene, despite the similarities in the degree of CARAIB–REVEALS differences.

5.3 Challenges in development of the HUMLAND ABM

The development of the model faced several challenges. They were mainly related to the fact that this research was novel marking the first ABM to explore the impact of fire use by prehistoric hunter-gatherers on a continental scale.

One of the first challenges in this study was choosing an appropriate ABM tool for implementing the model. With a variety of tools available, such as *GAMA*, *NetLogo*, *Mesa*, and *Repast*, the decision was influenced by several factors including the learning curve, open-source availability, execution speed, the quality of documentation and availability of examples. To make an informed choice, existing publications comparing these tools (Abar et al., 2017; Antelmi et al., 2022; Railsback et al., 2006) were reviewed, tutorials were explored, and the implementation of some HUMLAND elements in each tool was tested.

NetLogo (Wilensky, 1999) was selected for its swift model development capabilities, facilitated by a user-friendly learning curve and effective visualization tools. As a widely recognized standard in ABM development, *NetLogo* offers many pre-existing solutions and application examples. It has an active user community, high levels of documentation, and this tool is the preferred choice for educational purposes. Its Geographic Information Systems (GIS) extension is important for handling spatial data used in this study. Moreover, the ease of integration with *R*, supported by specialized packages like *nlrx* for model optimization (Salecker et al., 2019), supported this choice. As *NetLogo* may exhibit moderate to slow performance with more complex models, the ALICE High Performance Computing facility at Leiden University was used to conduct several series of experiments, including the sensitivity analysis and the generation of scenarios via a genetic algorithm.

This study was conducted within the context of the Terranova project (Arthur et al., 2023; Davoli et al., 2023; Pearce et al., 2023; Serge et al., 2023; Zapolska et al., 2023a), where many new datasets were generated. The support from colleagues within the project was invaluable for this research. Despite having access to the necessary datasets (Table 3.1) and contact with their creators, integrating some of these datasets into a single ABM presented another challenge of this study. A particular difficulty resulted from the differences between the CARAIB and REVEALS models, which provide vegetation reconstructions in substantially different ways. The CARAIB model is driven by climate forcing and by assumptions about dynamics of vegetation, while REVEALS provides a quantitative pollen-based regional vegetation abundance. In collaboration with Terranova colleagues, we developed an approach to reclassify the datasets from CARAIB and REVEALS, enabling comparisons and making it possible to combine these datasets in HUMLAND (Nikulina et al., 2024b; Zapolska et al., 2023a). As a result, the two datasets were compared in terms of vegetation openness and distribution of dominant PFTs (herbs, shrubs, broadleaf, and needleleaf trees).

It is important to note that the PFTs used in this study were designed for continental-scale dataset comparisons, leading to merging certain categories, such as dwarf shrubs and shrubs. In addition, REVEALS reconstructs vegetation for the Holocene with 31 plant taxa and for the LIG with 30, omitting some taxa. Furthermore, bare ground, which cannot be reconstructed from pollen counts, limits the vegetation reconstruction. REVEALS results rely on various input parameters including original pollen counts and relative pollen productivity. For the LIG and Early Holocene, this study utilized REVEALS reconstructions based on research by Pearce et al. and Serge et al., with full methodological details in the respective publications (Pearce et al., 2023, 2024; Serge et al., 2023). Variations in REVEALS input parameters across different time periods and European regions are noted but not addressed within the scope of this PhD study.

Another challenge of this study is related to CARAIB's limitations in capturing vegetation response to deglaciation. The outputs from CARAIB were derived from an equilibrium iLOVECLIM climate model. In this setup, both the vegetation and climate models were in equilibrium, thus failing to capture transient changes associated with deglaciation. As a result, HUMLAND was not executed for the earliest time windows (11,700–10,200 BP).

The comparison between CARAIB and REVEALS, along with generating HUMLAND results, was complicated by varying data availability for the LIG and the Early Holocene. Specifically, the Holocene has more comprehensive coverage in REVEALS reconstructions compared to the LIG, where estimates relied heavily on data from the regions which were glaciated during MIS 6. Additionally, difficulties arose because REVEALS LIG time windows could not be precisely aligned with specific CARAIB outputs, due to differences in dating quality and chronological resolution between the LIG and Holocene records. Therefore, continental-level CARAIB–REVEALS comparisons for LIG data and the extrapolation of LIG HUMLAND results across the entire continent should be approached with considerable caution.

The distribution of forager groups in the beginning of simulation runs presented another difficulty. Initially, the plan was to incorporate the observed distribution of LIG and Early Holocene archaeological sites into the HUMLAND model to locate campsites based on existing data. However, this approach proved challenging due to several reasons. Even with access to databases of archaeological sites (D'Errico et al., 2011; Hinz et al., 2012; Kandel et al., 2023; Manning et al., 2016; Vermeersch, 2020), selecting, standardizing, and verifying the accuracy of records across the continent for various time windows would be time-consuming but essential to obtain a consistent presence record from these varying sources. Moreover, the lack of archaeological sites in certain areas does not necessarily indicate the former absence of hunter-gatherers; it could merely reflect undiscovered sites as well as the destruction of former traces of occupation through erosive processes.

The possibility of incorporating hunter-gatherer population size estimates for the study periods into the HUMLAND model was explored. The population data for LIG Neanderthals is notably uncertain, with estimates for their census population size ranging from 5000 to 70,000 individuals (Bocquet-Appel & Degioanni, 2013), a range too broad to provide precise input for HUMLAND. These values come with the cautionary note that they should be regarded more as an order of magnitude than an exact value (ibid.). While the History database of the Global Environment (HYDE) offers Holocene population data, its latest update–despite incorporating radiocarbon data to mark the advent of agriculture–still lacks archaeological evidence for the Early Holocene, the period of our focus (Goldewijk et al., 2017; Goldewijk, 2024). Similarly, another dataset with estimates for the Holocene foragers is not archaeologically informed (Ordonez & Riede, 2022). Available aDNA estimates for the Mesolithic do not provide census population estimates for the entire European continent. Consequently, solid archaeological data for directly comparing census populations of the LIG and Early Holocene are lacking, and demographic reconstructions suitable for inclusion in HUMLAND for these periods do not exist.

Importantly, HUMLAND does not calculate the population sizes of foragers directly. Instead, it can suggest a potential minimal population size, as it excludes human groups that did not practice vegetation burning. The current study uses external population estimates (Goldewijk et al., 2017; Ordonez & Riede, 2022) for comparison purposes only. The obtained findings indicate that the Early Holocene population sizes generated by our ABM are consistently lower than those in existing literature, which combine various methods and datasets beyond this PhD study. This difference is acceptable because HUMLAND focuses solely on hunter-gatherer groups that burned vegetation, and not the entire population of European foragers.

Consequently, hunter-gatherer campsites have random distribution over the study area at the start of each simulation run. This decision, along with the use of the non-interpolated REVEALS dataset, which resulted in incomplete coverage for pollen-based estimates, prevented direct comparisons between the outputs of CARAIB, HUMLAND, and REVEALS on a grid cell by grid cell basis. To facilitate tracking human impact and comparing HUMLAND and REVEALS outputs despite incomplete REVEALS coverage and random distribution of campsites, mean percentages of PFTs and mean vegetation openness were calculated for all grid cells with REVEALS and CARAIB values. This method enabled comparison of the overall outputs from CARAIB, HUMLAND, and REVEALS without the complications of grid cell by grid cell analysis, simplifying the process and enhancing model efficiency. However, this approach allowed focus only on general patterns and the intensity of impacts at the continental scale, without delving into regional or local details.

Another challenge in developing HUMLAND was accurately representing the impact of megafauna on vegetation. Due to the difficulty in quantifying the effects of certain herbivory behaviours like trampling and bark stripping these aspects were not incorporated into the model. With the decline of megafaunal populations, the role of non-consumptive activities was probably lower and became less detectable at large scales. Fortunately, within the Terranova project, we obtained potential maximal estimates of megafauna plant consumption and CARAIB net primary production (NPP) (Nikulina et al., 2024b). While both datasets measure carbon, the former provides maximal potential values for megafauna metabolization of NPP, and the latter offers potential natural carbon values, excluding respiration. By merging these datasets, it became possible to quantify megafauna impact on vegetation via consumption. It is important to note that the maximum extent of animal plant consumption could have been greater than what is suggested by the potential maximum megafauna plant consumption dataset. This difference may stem from underestimates of natural densities and the reduced biomasses resulting from anthropogenic pressures on natural areas today.

Modelling constant megafauna maximal consumption in each simulation step caused the first version of the HUMLAND model to overestimate vegetation openness, compared to REVEALS data. To address this, megafauna effects on regrowth was initially removed from HUMLAND. Due to that, megafauna impact on vegetation recovery was underestimated. In a subsequent HUMLAND update, megafauna's role was adjusted, and hunting pressure was included to align the results of megafauna impact closer to REVEALS findings. In the absence of human impact on megafauna, HUMLAND output would indicate greater vegetation openness compared to pollen-based estimates.

In HUMLAND 2.0 megafauna has preferences for secondary vegetation and open regrowth areas, enhancing the realism of animal impact on landscapes. In accordance with that, areas with greater openness tended to experience more substantial herbivore impact compared to relatively closed locations (Nikulina et al., in press). This adjustment ensures that megafauna affects all areas, including those regenerating. While HUMLAND can now produce outputs similar to REVEALS without anthropogenic fires, these scenarios remain rare (Table 4.3). Including human-induced fire in our simulation runs produced more outcomes similar to REVEALS data (Table 4.4).

Besides megafauna impact, simulating natural fires and other natural processes presented a challenge. Due to the absence of thunderstorm frequency data for the study periods, contemporary values for Europe were used (Enno et al., 2020; Nikulina et al., 2024b). Moreover, there is no data on average fire recurrence for the four broad PFTs categories used in our study. Due to that, continental-scale estimates of fire return intervals (FRI) were specifically calculated for HUMLAND via so-called "space-for-time" substitution (Archibald et al., 2013; Nikulina et al., 2024b). Besides FRI, there is no data on average recovery times for HUMLAND PFTs after disturbances. To overcome this challenge, continental-scale estimates for speed of vegetation regrowth were calculated via CARAIB. Further details on FRI intervals and regeneration speed are available in Chapter 3, based on (Nikulina et al., 2024b). In addition, HUMLAND does not account for other natural forest disturbances, such as disease outbreaks, treefall from senescence, and storms (Patacca et al., 2023; Seidl et al., 2011). Incorporating these factors into models like HUMLAND is challenging due to its continental scope and the use of four general

PFT categories, for which it is difficult to quantify the impact of such processes, particularly in the past. However, recognizing their potential influence is crucial for more localized applications of the model.

Thus, the development of the HUMLAND ABM encountered several challenges, from selecting the most suitable ABM tool to integrating diverse datasets and accurately representing different types of impacts on a continental scale. While the strategies used to address these difficulties have been shared, exploring alternative solutions would be valuable. This experience may serve as a useful resource for others in the field, and the development of different methodologies for these issues is highly encouraged.

5.4 Sensitivity analysis. Which factors defined the intensity of hunter-gatherers' impact on vegetation?

5.4.1 Summary of the sensitivity analysis methodology

To understand what defines the intensity of foragers' impact this study uses the LHS technique for sensitivity analysis, combined with PRCC. This analysis targeted parameters within the first version of the HUMLAND model: five parameters were related to human impact, and one to natural fires (Table 3.3). Further details on the sensitivity analysis methodology can be found in Chapter 3.

5.4.2 Discussion of sensitivity analysis results

LHS/PRCC results showed that the impact of hunter-gatherer vegetation burning on a continental-level was mainly influenced by three factors (Fig. 3.7). The intensity of these changes depended on the number of hunter-gatherer groups inhabiting the study area, thereby establishing a link between population size and the strength of anthropogenic impact. The extent of human-induced vegetation changes was also determined by the natural vegetation openness around campsites. This factor could be connected to the preferences of the hunter-gatherers when selecting the location for their campsites. The parameters associated with the mobility of hunter-gatherers included Accessible_radius, Campsites_to_move, and Movement_frequency_of_campsites. Among these, the first one held a greater influence on the model output than the latter two factors, which had minimal contributions to human-induced vegetation changes. This was because these parameters primarily allowed the vegetation a chance to recover and return to its natural state in HUMLAND. On the other hand, the accessible radius, with higher values, created a wider area around campsites that experienced constant anthropogenic impact without sufficient time for recovery. In other words, the movement frequency of campsites and their number that were relocated provided opportunities for vegetation to regenerate after anthropogenic impact.

5.5 Neanderthal and Mesolithic human impacts on vegetation: insights from HUMLAND ABM scenarios generated via genetic algorithm

5.5.1 Summary of the genetic algorithm methodology

This study uses a genetic algorithm to automatically generate potential scenarios represented by various combinations of parameter values within the HUMLAND model (Table 4.2). In the second version of this ABM, a genetic algorithm was used specifically for optimizing the most important parameters affecting human impact intensity, as identified through sensitivity analysis (Fig. 3.7). The parameter for hunting pressure, a new introduction in the second HUMLAND version, was also included in the genetic algorithm experiments.

Our optimization goal was to minimize two differences: 1) the discrepancy between mean vegetation openness obtained from REVEALS and HUMLAND, and 2) the difference in the mean percentage of grid cells dominated by trees from REVEALS and HUMLAND. For each goal in each time window, 60 separate genetic algorithm experiments were conducted using different random seeds across the following three subgroups of experiments: 1) megafauna impact; 2) megafauna impact and natural fires; 3) megafauna, natural and human-induced fires. All experiments include hunting pressure by foragers and vegetation regeneration via climatic impact. This resulted in 360 genetic algorithm outputs per time window and a total of 2160 across all time windows.

Generated scenarios were considered to match REVEALS estimates if the output difference was 10% or less. This calculation served as an indicator of the overall success of each subgroup of experiments. Further details on the genetic algorithm methodology, results and their analysis are available in Chapter 4 (Nikulina et al., in press). The genetic algorithm set up is shown in Table 4.2.

5.5.2 Discussion of the genetic algorithm results

Integrating the genetic algorithm into this study improved the ability to generate and explore a diverse range of HUMLAND scenarios. This approach enabled efficient navigation through potential outcomes, providing insights into the complex interactions between Neanderthals, Mesolithic humans, and their environment. As shown in Table 4.3, even with relatively good Holocene REVEALS coverage, most of the scenarios without human-induced fires do not create output similar to the REVEALS. This result underscores the importance of anthropogenic activities, particularly burning by foragers, on European vegetation dynamics.

However, it was possible to reach REVEALS estimates without anthropogenic burning. In this case, hunter-gatherers had to decrease megafauna plant consumption by 20–25% during the LIG and by 80–90% during the Early Holocene (Fig. 4.6). Without reducing consumption through hunting, the simulated vegetation openness is different from what is shown in the REVEALS data; specifically during the LIG vegetation would be more open than pollen-based reconstructions show.

Although generated hunting pressure LIG values are lower than Early Holocene values, LIG hunting likely remained important due to larger megafauna populations before 100,000 BP. Strong empirical evidence indicates that Neanderthals were top carnivores, relying on terrestrial animals for protein and fat. HUMLAND scenarios suggest that even without landscape burning, foragers influenced vegetation by hunting prey, reducing faunal plant consumption. This indicates that interglacial landscapes could be shaped by *Homo* indirectly, even with limited anthropogenic burning. However, scenarios without human-induced fires seem less plausible (Table 4.3), given ethnographic and archaeological evidence of vegetation burning by Neanderthals and Mesolithic humans (Table 2.4).

When human-induced burning was included in the genetic algorithm experiments alongside other impacts, most generated scenarios matched REVEALS estimates (Table 4.4). The importance of human-induced fires was further supported by parameter values linked to the openness criteria for burning (Fig. 4.7A, B). The values obtained for this parameter in tree distribution scenarios indicate that Neanderthals and Mesolithic humans shared similar preferences for vegetation density around their campsites, as their values are close (within the range of 45–78%). This suggests that both populations likely engaged in burning practices across diverse landscapes, including those that were already relatively open (~78%).

On the other hand, scenarios generated for vegetation openness showed distinct Mesolithic and Middle Palaeolithic strategies. The obtained results indicated that in most cases Mesolithic humans engaged in burning activities across a range of vegetation openness (36–69%) while Neanderthals mostly engaged in less frequent burning, primarily targeting relatively closed areas with vegetation openness up to 23–48%. These differences could be related to variations in megafauna influence on vegetation during the study periods. Due to the more pronounced LIG herbivory impact in comparison with the Holocene, Neanderthals could practice fewer burning activities to achieve a comparable level of vegetation openness around campsites, aligning with the preferences of Mesolithic populations. In this interpretation of the modelling outcomes, both Mesolithic hunter-gatherers and Neanderthals had the ability to alter the vegetation around their campsites, and both groups could burn landscapes relatively often if necessary.

Modelling results for the areas impacted by foragers revealed similarities in the size of the regions affected by both populations (Fig. 4.7 E, F). Neanderthals impacted a relatively large area (~20–40 km). Mesolithic humans employed a more flexible strategy. They affected areas up to ~10 km around campsites and, in some cases, regions as large as those impacted by Neanderthals (~20–40 km).

Although estimating the *Homo* population size was beyond the scope of HUMLAND, the modelling results offer insights into the minimum population sizes of European hunter-gatherers needed to align HUMLAND outputs with REVEALS. Based on the average local group size of 25 in historical hunter-gatherer societies, our modelling suggests that Europe's population during the Early Holocene (10,200–8200 BP) ranged from 56,000 to 72,000 individuals. These values are lower than other estimates (Goldewijk et al., 2017; Goldewijk, 2024; Ordonez & Riede, 2022) because HUMLAND only includes groups with fire use.

For the LIG, HUMLAND estimates that a population of 48,000–82,000 individuals was needed to align ABM output with REVEALS. These estimates should be interpreted cautiously. The lack of pollen data for most of Europe prevents testing whether this population size produces ABM output similar to REVEALS data in regions where pollen counts are missing. A previous attempt to quantify the LIG census population suggested a broad range of 5000–70,000 individuals (Bocquet-Appel & Degioanni, 2013), but lacked specificity regarding geographic regions or temporal intervals within the extensive timeline of Neanderthal existence. It was also suggested that the LIG Neanderthal population may have increased due to growing ungulate populations and abundant plant resources under favourable interglacial conditions (Bocquet-Appel & Degioanni, 2013; Zilhao et al., 2024).

The available distribution patterns of LIG archaeological sites are likely very incomplete due to large-scale geomorphological processes and research bias. Unlike Mesolithic sites, the LIG archaeological evidence was impacted by a complete glacial–interglacial cycle which made those sites that escaped glacial destruction mostly inaccessible through deposition of covering layers. There are no distinctive stone tools produced by Neanderthals that can be attributed specifically to the LIG phase. Sites are identified as LIG based on a combination of stratigraphic data and various paleoenvironmental proxies.

Data-based estimates of LIG Neanderthal population size are unavailable, although some estimates, including those based on aDNA, exist for certain regions and time periods when Neanderthals were present (Li et al., 2024; Mellars & French, 2011; Rodríguez et al., 2022). It is important to highlight that genetic studies typically estimate effective population size (the number of reproductive individuals), not census populations. Local demographic estimates using aDNA for the Mesolithic period do not provide continental-scale census population estimates for the Early Holocene.

Thus, our modelling exercise indicates that the number of groups required to align the HUMLAND output with REVEALS is comparable for both the LIG and the Early Holocene. However, this does not exclude the possibility that the census population size differed between the two periods, with one potentially being larger than the other.

An additional challenge in assessing HUMLAND population size estimates and vegetation openness preferences is the lack of thunderstorm frequency data for the study periods. Modern values were used in the developed ABM. It is possible that HUMLAND minimal population estimates and vegetation openness values should be adjusted downward, as some vegetation burning in HUMLAND may be attributed to natural fires if thunderstorm frequency differed in the LIG and Early Holocene than currently. Further research is needed to expand REVEALS coverage, gather demographic data for comparison, and obtain specific estimates for factors like past thunderstorm frequency, which are crucial for understanding past vegetation changes.

To assess the extent of the area modified by each agent, the number of grid cells affected by each agent was calculated (Fig. 4.8) using parameter values from the ranges most frequently produced by the genetic algorithm. These results revealed that the combined influence of megafauna and climatic effects were important in transforming vegetation during the LIG period. However, scenarios without human-induced fires (Table 4.3) indicated that megafauna and climate alone did not produce results similar to REVEALS especially for the PFT distribution. Thus, although the mean number of modified grid cells by Neanderthals was lower (Fig. 4.8), their impact remained crucial to overall ecosystem dynamics.

During the Early Holocene, megafauna remained a key source of impact alongside climate in driving the transformation of vegetation openness in HUMLAND. Notably, herbivores did not change the PFT distribution during this time. Mesolithic humans were the second most influential factor after climate in shaping PFT distribution through fire use (Fig. 4.8). Simulation outcomes suggest that Mesolithic foragers transformed 26% of grid cells on average, reaching a maximum of 47% in PFT distribution, and altered vegetation openness in 8% of grid cells on average, with a maximum of 14%.

Ethnographic observations and evidence from archaeological case studies together with HUMLAND results suggest that Neanderthals and Mesolithic humans had substantial impact on interglacial vegetation. These populations could have a direct influence via vegetation burning and indirect impact via hunting herbivores, and, therefore, changing the intensity of megafauna plant consumption. This study also showed that both hunter-gatherer groups had similarities in their impact. This was indicated by parameter values obtained for sizes of impacted areas around campsites, minimal population estimates and shared preferences for vegetation density around campsites.

5.6 Conclusion. Future perspectives

Research presented in this dissertation focused on the deep history of human-induced landscape changes, specifically examining the early stages of these transformations in Europe when hunting and gathering was the main mode of subsistence. This study began with the review of available archaeological evidence of foragers' impact on landscapes. Published evidence for Mesolithic manipulation of landscapes was based on the interpretation of data similar to the ones available for the LIG. This review suggested that as strong a case could be made for a Neanderthal impact on landscapes as for anthropogenic landscape changes during the Mesolithic, even though the Neanderthal evidence came from only one high-resolution site complex, a unique large-scale exposure of a LIG landscape.

Expanding from this localized evidence, this study moved to a continental scale by comparing potential natural vegetation reconstructions (CARAIB) with pollen-based vegetation cover (REVEALS). The substantial differences between these datasets suggest that pollen-based vegetation cover cannot be attributed solely to climate. Other factors must have influenced vegetation dynamics during the LIG and the Early Holocene.

Developing the HUMLAND ABM made it possible to assess human impacts on vegetation and examine the observed CARAIB–REVEALS differences. Sensitivity analysis revealed that the extent of anthropogenic vegetation changes primarily depended on the number of groups, their preferences for vegetation openness, and the impacted area's size around campsites. By incorporating the genetic algorithm, a range of potential scenarios for past ecosystem changes was explored. This step showed that both Mesolithic and Neanderthal groups may have had similarities in their impacts and in preferences for vegetation openness around campsites. Based on simulation outcomes, it was concluded that climate and megafauna were not the sole factors shaping interglacial landscapes. Hunter-gatherer vegetation burning and anthropogenic impacts on megafauna distribution through hunting were also key elements of past European ecosystems.

This study holds substantial practical implications and makes important contributions across several disciplines. It enriches archaeology by examining the interactions between hunter-gatherers and their environments across Europe, focusing on the relationships of two different *Homo* species with megafauna and exploring hunter-gatherers' paleodemography. This research also enhances our understanding of paleoecology, addressing the influences of natural fires, climate, and megafauna on the dynamics of interglacial ecosystems. Furthermore, it advances computational archaeology through the development of a novel open-access ABM. This includes comprehensive steps such as sensitivity analysis and the application of a genetic algorithm for scenario generation, a technique still rarely used in the ABM domain. This study also highlights the potential of combining traditional evidence such as pollen data with simulation techniques to reconstruct landscape dynamics, offering tools for predicting the outcomes of human impacts on ecosystems. The insights, challenges, and ideas of this study can benefit other interdisciplinary projects that focus on large-scale analyses, combinations of different types of data and techniques.

The practical implications of this research go beyond academia, offering insights that can guide modern conservation strategies. This study demonstrates that humans have been a fundamental part of interglacial ecosystems, substantially shaping European landscapes long before the emergence of agriculture (Ellis et al., 2016, 2021; Nikulina et al., 2022, 2024b; Zapolska et al., 2023a). Contrary to the notion that the LIG and the Early Holocene were times of absent or very low human impact, this study revealed substantial human influences. HUMLAND results showed LIG Neanderthals initiated vegetation changes via fire use, making certain areas more attractive to herbivores. These hunter-gatherers indirectly influenced vegetation through hunting, which may have reduced megafauna population and, consequently, animal pressure on vegetation (Nikulina et al., in press). In the Early Holocene, humans transformed on average ~8–26% (with maximum of 14–47%) of European landscapes through non-agricultural vegetation burning, in addition to continuing to affect vegetation indirectly through hunting (Nikulina et al., 2024b, in press). These results highlight the importance of recognizing long-term human impacts on landscapes in efforts to conserve biodiversity and maintain landscape resilience under ongoing climate change.

To address research gaps in archaeological and palaeoecological records, future studies should adopt a multi-proxy approach, incorporating both established methods, like palynological and charcoal analyses, and relatively less conventional proxies, such as sediment aDNA, phytoliths, and parenchyma. This methodology could improve detection of hunter-gatherer signals and help distinguish between anthropogenic and natural changes. Given that hunter-gatherer landscape impacts are often seen as minimal or absent compared to agricultural groups, a comprehensive, multi-proxy study across Europe could clarify this characterization. Furthermore, additional studies are needed in underrepresented areas and on sites occupied by Neanderthals to provide a fuller picture similar to that at Neumark-Nord.

While demographic estimates were beyond this study's scope, it is evident that more robust paleodemographic research is needed. Existing population estimates are either nonspecific to the LIG or lack archaeological input even for the Early Holocene estimates. Developing a detailed, archaeologically informed database for the LIG and Early Holocene could allow more accurate demographic models.

To enhance the precision and reliability of future modelling exercises on early human impact on landscapes, the quality of used datasets is one of the key elements. HUMLAND could be refined with more accurate past thunderstorm frequency data, contingent on advancements in related fields. Local-scale research is important for studying past human-environment interactions to test whether patterns observed at the continental level are also visible at the local scale. Improving the quality of proxy-based reconstructions, such as REVEALS, necessitates an expansion in the spatio-temporal coverage and density of sites from which proxies are sampled. In addition, it is required to combine different types of proxies (e.g., plant and animal macrofossils, phytoliths, charcoal, etc.) in conjunction with pollen-based local-scale modelling. Furthermore, dynamic vegetation models which generate datasets that could be included in models like HUMLAND require improvements to minimize inherent biases and limitations. Finally, it could be useful to extend the developed approach to other time periods and continents by merging CARAIB, REVEALS and the HUMLAND ABM. The Americas are of particular interest due to the relatively late arrival of *Homo sapiens* there, enabling comparisons between true "human-free" and "humans present" periods. These enhancements provide us with a strong foundation to uncover the complex dynamics of the relationship between people and their environment.