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Anthropogenic Landscapes?

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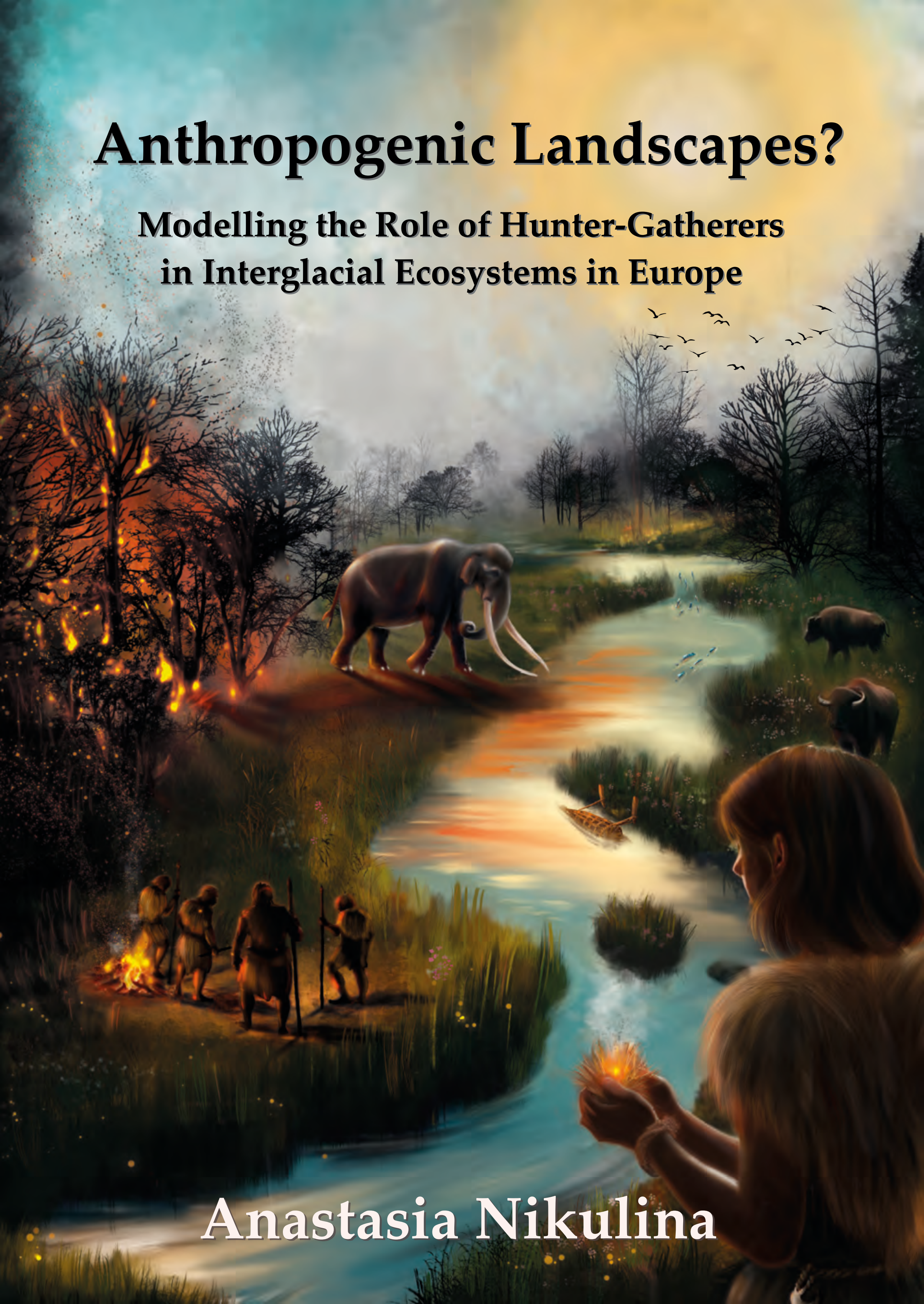

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PROEFSCHRIFT

ter verkrijging van
de graad van doctor aan de Universiteit Leiden, op gezag van
rector magnificus prof.dr.ir. H. Bijl, volgens besluit van het college
voor promoties te verdedigen op vrijdag 21 november 2025
klokke 11.30 uur

door
Anastasia Nikulina

geboren te Novosibirsk, Russia
in 1993

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Universiteit Leiden The Netherlands

TERRA NOVA

MARIE CURIE ACTIONS

The research is financed through the European Union's Horizon 2020 research and innovation programme within the TERRANOVA project, No 813904.

Printed by Gildeprint
Cover design by Darya Derzhavets
Layout by Douwe Oppewal

ACKNOWLEDGEMENTS

I owe deep gratitude to the many people who supported me throughout this PhD study and beyond. Each piece of advice and every dataset shared by these generous people has contributed to a unique mosaic of knowledge. This unwavering support was especially invaluable during times of upheaval, and I am profoundly thankful for the help and encouragement of each of you.

First and foremost, I would like to thank my supervisory team, especially Prof. Wil Roebroeks and Dr. Fulco Scherjon, for their endless support, belief in me, trust, and knowledge they shared with me. I am also grateful to Prof. Didier Roche, whose expertise was strategically crucial for this research. I wish to express my deepest gratitude to my late supervisor, Dr. Katharine MacDonald, for her constant support and invaluable knowledge. I extend my heartfelt thanks to her family for their support and for allowing me to benefit from her mentorship. I was incredibly proud and fortunate to work with such a great team. Thank you so much for everything!

I would like to extend my gratitude to every member of the Terranova project. I am particularly grateful to the researchers who contributed to the development of this project, specifically Dr. Sjoerd Kluiving and Prof. Jan Kolen. I am grateful to Dr. Angelina Zapolska, Dr. Maria Antonia Serge, Dr. Marco Davoli, and Dr. Elena A. Pearce, whose collaboration, mutual support, and shared efforts in publishing have been invaluable. I also would like to thank Prof. Jens-Christian Svenning, Dr. Florence Mazier, Prof. Ralph Fyfe, Dr. Dave van Wees, Prof. Marie-Jose Gaillard, Dr. Frank Arthur, Dr. Kailin Hatlestad, Emily Vella, Alexandre Martinez, Prof. Karl-Johan Lindholm, and Prof. Hans Renssen for the knowledge and support they provided throughout our work.

Of course, I would not have been able to even begin this study without the knowledge and skills I obtained at Novosibirsk State University. I would like to thank Prof. Ivan D. Zolnikov, Prof. Yaroslav V. Kuzmin, and Dr. Olga I. Novikova for everything you taught me. Your encouragement and belief in me have been invaluable! I also wish to thank all the members of the Laboratory of GIS and Remote Sensing at the Sobolev Institute of Geology and Mineralogy (Siberian Branch of the Russian Academy of Sciences), especially Dr. Darya A. Chupina and Dr. Nadezhda V. Glushkova, for their support and help. Special thanks to Dr. Hugues Plisson, Dr. Malvina Bauman, and Dr. William E. Banks for their help and encouragement.

I am very happy to have become part of the Leiden University community, where I have met many wonderful people. I especially want to thank every member of the Human Origins group for the inspiring discussions. I am very grateful for the unwavering support from the friends I made during my time in Leiden.

I also extend my gratitude to all the people listed in the acknowledgments of my papers. You were very responsive and helpful with various aspects of this study. Thank you so much for sharing your expertise with me.

I would like to thank my family for their endless support. My parents, Olga I. Kudashkina and Vyacheslav V. Nikulin, have always been an unlimited source of love, guidance, and motivation. I would also like to thank my granddad, Ivan P. Kudashkin, who always believed that I would become a doctor one day. Special thanks to my brothers and sisters, especially Svyatoslav V. Nikulin, Michail V. Nikulin, and his partner, Anastasia A. Nikulina. I am also grateful to my nephews and nieces, particularly Kirill M. Nikulin. I would also like to thank my partner's parents Brigitte Bruyère and Serge Coupas for their constant support while I was far from my hometown. I am also very fortunate to have amazing friends I made before starting this PhD research. We stayed in constant touch throughout these years. Thank you for your support despite the distances.

I am very grateful to my partner, Julian Coupas, for going through this challenging journey with me. Without your support, my ideas would never have become a reality. I would also like to thank our cocker spaniel, Vivaldi, for his unconditional love, fluffy companionship, and his persistent reminders to take regular walk breaks.

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SUMMARY

English

Human impact on the environment has extended over millennia, with evidence of anthropogenic landscape changes before the emergence of agriculture. Review of available archaeological evidence from both the Last Interglacial (LIG, ~130,000–116,000 BP; Neanderthals) and Early Holocene (~11,700–8000 BP; Mesolithic humans) archaeological contexts shows that a similar set of proxies is available for both periods. Despite available case studies and ethnographic observations of anthropogenic burning by hunter-gatherers, it remains challenging to ascertain whether these local-scale activities caused landscape changes at regional or even (sub-)continental scales.

To address this, a new spatially explicit open agent-based model (ABM) called HUMan impact on LANDcapes (HUMLAND) was developed to investigate the impact of hunter-gatherer activities on vegetation in Europe during the LIG and the Early Holocene. This model incorporates several sources of impact on vegetation: natural and anthropogenic fires, megafauna plant consumption, and climatic impact. The developed ABM integrates various datasets, including estimates of potential maximal megafauna plant consumption, digital elevation model, and distribution of large water bodies.

The developed ABM uses outputs from the CARbon Assimilation In the Biosphere (CARAIB) and Regional Estimates of VEgetation Abundance from Large Sites (REVEALS) models. CARAIB, driven by climate forcings and by assumptions about dynamics of vegetation, provides potential natural vegetation cover used as a starting point for simulation runs. REVEALS provides quantitative pollen-based regional vegetation abundance estimates. This dataset is used as target for HUMLAND runs. Comparing these datasets revealed significant differences, indicating that climate alone did not shape European landscapes during the study periods.

Sensitivity analysis showed that the intensity of human-induced vegetation changes depended on the number of forager groups, their vegetation preferences around campsites, and the size of impacted areas. HUMLAND was then combined with a genetic algorithm to generate scenarios of past vegetation change, using parameters identified by the sensitivity analysis, and an additional parameter for human-induced hunting pressure on megafauna. Finally, HUMLAND tracked and quantified the impact of humans, natural fires, climate and megafauna in the most common scenarios.

Comparisons between CARAIB–REVEALS data and genetic algorithm scenarios suggest that climate and megafauna were not the only factors determining

interglacial vegetation. Fires, specifically those caused by hunter-gatherers and their hunting impacts on megafauna, influenced European ecosystems. Ethnographic, archaeological, and modelling evidence indicates similarities in landscape impacts by Neanderthals and Mesolithic humans. Specifically, both groups impacted an area of similar size around their campsites and had comparable vegetation openness preferences. Additionally, minimum population estimates required to match HUMLAND outputs with REVEALS for the LIG are comparable to those of the Early Holocene.

This study provides the first quantification of Neanderthal and Mesolithic human impacts on interglacial vegetation, showing that both groups substantially shaped European landscapes. Although megafauna and climate were major factors during the LIG, Neanderthals influenced vegetation through fire use, making certain areas more attractive to herbivores because of increased nutrition and palatability of new plants. In the Early Holocene, humans directly transformed approximately 8–26% (with a maximum of 14–47%) of landscapes through burning, alongside indirect effects from hunting. Thus, European landscapes were shaped by human agency before the emergence of agriculture, highlighting the integral role of people and fires in interglacial ecosystems.

Nederlands

Aanwijzingen voor menselijke impact op hun omgeving gaan vele duizenden jaren terug, met goede data voor antropogene landschapsveranderingen van vóór de opkomst van de landbouw. Een studie van de archeologische sporen met betrekking tot de invloed van jagers-verzamelaars op hun omringende landschappen laat zien dat op lokaal niveau de aanwijzingen voor Neanderthaler-impact op landschappen tijdens het laatste interglaciaal (LIG, ~130,000–116,000 BP) vergelijkbaar zijn met die voor landschapsveranderingen door moderne mensen in het vroege Holoceen (~11,700–8000 BP). Het gaat hier om enkele geïsoleerde case-studies, en daarmee blijft het zeer moeilijk om vast te stellen of dergelijke lokale activiteiten in het verleden ook landschapsveranderingen op regionale, laat staan (sub)continentale schaal veroorzaakten.

Om dit te onderzoeken, is in deze studie een nieuw ruimtelijk expliciet agent-gebaseerd model (ABM) ontwikkeld, genaamd HUMan impact on LANDscapes (HUMLAND), dat beoogt de grootschalige impact van de activiteiten van jagers-verzamelaars op vegetatie in Europa tijdens het LIG en het vroege Holoceen te onderzoeken. Dit model bevat een serie geparametriseerde processen die invloed hebben op het landschap, zoals natuurlijke en antropogene branden, consumptie van vegetatie door megafauna en het klimaat. Hiertoe integreert HUMLAND verschillende datasets, waaronder schattingen van de maximale plantenconsumptie door megafauna, digitale hoogtekaarten en de ruimtelijke verspreiding van grote waterlichamen.

De output van twee klimaat modellen–CARbon Assimilation In the Biosphere (CARAIB) en Regional Estimates of VEgetation Abundance from Large Sites (REVEALS) vormen belangrijke invoergegevens voor het model. Het CARAIB-model wordt aangedreven door klimaatverandering en atmosferische CO_2-concentraties en aannames over de dynamiek van verschillende vegetatie soorten, terwijl REVEALS kwantitatieve, i.e., op pollen gebaseerde, regionale vegetatie reconstructies levert. De CARAIB-resultaten dienen als het startpunt voor alle simulaties, waarbij de natuurlijke omgeving wordt gereconstrueerd volgens dat model. Dan worden simulaties uitgevoerd met verschillende steeds verschillende waarden voor de model parameters. Vervolgens wordt REVEALS gebruikt om de HUMLAND-resultaten te vergelijken met de op basis van pollen gereconstrueerde vegetatiebedekking. Vergelijking van de CARAIB- en REVEALS-datasets onthulde aanzienlijke verschillen tussen beide modellen, wat aangeeft dat klimaat niet de enige factor was die het Europese landschap vormde tijdens de onderzochte perioden.

Het onderzoek omvatte ook een gevoeligheidsanalyse van de model parameters om die factoren te identificeren die de intensiteit van door mensen veroorzaakte vegetatieveranderingen beïnvloeden: het aantal aanwezige jagers-verzamelaarsgroepen, hun vegetatievoorkeuren rond kampplaatsen en de grootte van het door hun activiteiten beïnvloedde gebied rondom een kamp. Vervolgens werd HUMLAND gecombineerd met een genetisch algoritme om scenario's van vegetatieverandering te genereren, met gebruik van de meest effectieve parameters geïdentificeerd in de gevoeligheidsanalyse en een extra parameter voor door mensen veroorzaakte jachtdruk op megafauna. Ten slotte volgde en kwantificeerde HUMLAND de impact van mensen, natuurlijke branden, klimaat en megafauna in de meest voorkomende scenario's.

Vergelijkingen van CARAIB–REVEALS en de scenario's gegenereerd via het genetisch algoritme suggereren dat klimaat en ook megafauna niet de enige factoren waren die de interglaciale vegetatie bepaalden. HUMLAND toont aan dat branden, met name veroorzaakt door jagers-verzamelaars, en impact van jager-verzamelaars op de verspreiding van megafauna door jacht ook een belangrijke rol gespeeld moeten hebben in het vormgeven van Europese ecosystemen.

Etnografische observaties en data uit archeologische casestudies, samen met de modelleringsresultaten, suggereren dat Neanderthalers en mesolithische mensen opvallende overeenkomsten vertoonden in hun impact op de omgeving. Specifiek hadden beide groepen invloed op een gebied van vergelijkbare grootte rond hun kampplaatsen, en deelden ze vergelijkbare voorkeuren voor vegetatieopenheid. Daarnaast vindt deze studie geen aanwijzingen dat de populatieomvang van jagers-verzamelaars tijdens het vroege Holoceen die van het LIG overtrof. Dit werpt twijfel op over de gangbare aanname dat jager-verzamelaars in het vroege Holoceen een grotere ecologische impact hadden vanwege hun hogere bevolkingsaantallen.

Met dit onderzoek werd voor het eerst de impact van Neanderthalers en mesolithische moderne mensen op interglaciale vegetatie modelmatig gekwantificeerd. De resultaten suggereren dat beide populaties een belangrijke factor vormden in de vegetatie dynamiek in interglaciaal Europa. Hoewel de grotere rol van megafauna en klimaat in vegetatie transformatie tijdens het LIG, beïnvloedden LIG jager-verzamelaars vegetatie veranderingen door het gebruik van vuur, waardoor bepaalde gebieden aantrekkelijker werden voor herbivoren. In het vroege Holoceen transformeerden jager-verzamelaars tot ~14–47% van de vegetatie op het continent, met name door vegetatie verbranding, naast hun indirecte impact door jacht. Zo werden Europese landschappen op grote schaal gevormd door menselijk handelen vóór de opkomst van de landbouw, hetgeen de integrale rol van mensen en hun vuurgebruik in interglaciale ecosystemen benadrukt.

Русский

На протяжении тысячелетий люди оказывали влияние на окружающую среду, о чем свидетельствуют археологические данные, относящиеся к периоду до появления сельского хозяйства. Археологические свидетельства демонстрируют, что схожие данные об изменениях окружающей среды охотниками-собирателями доступны как для археологических памятников неандертальцев во время ээмского периода (микулинское межледниковье; ~130,000–116,000 лет назад), так и мезолитических групп раннего голоцена (~11,700–8000 лет назад). Несмотря на существование этих археологических свидетельств и этнографических данных, сложно установить, вызывали ли эти локальные антропогенные влияния видимые изменения ландшафтов на региональном и континентальном уровнях.

Для решения этой проблемы в рамках данного исследования была разработана новая агентная модель (agent-based modelling) с ГИС (геоинформационные системы) компонентом. Данная модель называется "HUMLAND" (HUMan impact on LANDscapes; Влияние человека на ландшафты), и она может быть использована для изучения влияния охотников-собирателей на межледниковую растительность. Эта модель включает несколько типов влияния на растительность: природные и антропогенные пожары, потребление растительности мегафауной и воздействие климата. Кроме этого, в модель интегрировано несколько наборов пространственных данных, в том числе потенциальные оценки максимального количества потребляемой растительности мегафауной, цифровая модель рельефа и распределение крупных рек и озер.

Одними из ключевых данных являются результаты, полученные при помощи двух других моделей: CARAIB (CARbon Assimilation In the Biosphere; Ассимиляция углерода в биосфере) и REVEALS (Regional Estimates of VEgetation Abundance from Large Sites; Региональные оценки растительности из крупных объектов). Модель CARAIB реконструирует растительный покров на основе данных климата и динамики растительности. Вторая модель предоставляет количественные оценки растительности на основе данных палинологии. Результаты модели CARAIB использовались в HUMLAND в качестве отправной точки для всех симуляций, поскольку CARAIB моделирует растительность в естественных условиях (т. е., как теоретически может выглядеть район исследования при влиянии только климата на растительный покров). Палинологические данные использовались в качестве ожидаемых результатов для всех симуляций. При сравнении наборов данных CARAIB и REVEALS были выявлены существенные различия между ними. Это свидетельствует о том, что климат не был единственным фактором, который влиял на межледниковые ландшафты Европы.

После того, как модель HUMLAND была разработана, был проведен анализ чувствительности модели для определения факторов, которые влияют на интенсивность антропогенного влияния на растительность. Этот анализ показал, что интенсивность определяют три основных фактора: количество групп охотников-собирателей, их предпочтения в плотности растительного покрова вокруг стоянок и размер зоны воздействия вокруг них. Затем были созданы возможные сценарии изменения растительности. Для этого к HUMLAND был применен генетический алгоритм, разработанный для оптимизации моделей. Полученные сценарии представлены различными комбинациями значений параметров HUMLAND, которые были определены при анализе чувствительности как наиболее важные для интенсивности влияния охотников-собирателей. Кроме этих параметров, при создании сценариев был использован еще один параметр, который определяет то, насколько снижается интенсивность потребления мегафауной растительности из-за охоты. В результате статистического анализа были выявлены наиболее часто встречающиеся значения параметров, включенных в генетический алгоритм. Во время симуляций с этими значениями разработанная агентная модель отслеживала количество изменений растительного покрова, вызванных каждым типом влияния (естественные и антропогенные пожары, влияние климата и потребление растительности животными).

Результаты сравнения CARAIB и REVEALS и полученные значения параметров при разработке сценариев показали, что климат и мегафауна не были единственными факторами, определяющими динамику межледниковой растительности. Пожары, особенно вызванные охотниками-собирателями, и влияние людей на распространение мегафауны через охоту также играли значительную роль в формировании растительности. Этнографические наблюдения, данные из археологических памятников и результаты агентной модели показали, что у неандертальцев и мезолитического населения были сходства в том, как они влияли на растительный покров. Обе группы воздействовали на участки схожего размера вокруг своих стоянок и имели схожие предпочтения в отношении открытости растительности. Кроме этого, полученные результаты не поддерживают широко распространенную точку зрения о том, что численность населения во время ээмского межледниковья была существенно ниже, чем во время раннего голоцена в Европе.

В данном исследовании впервые было количественно оценено влияние неандертальцев и мезолитического населения на растительность. Полученные результаты показали, что обе популяции были важными компонентами межледниковых экосистем в Европе. По сравнению с неандертальцами, климат и мегафауна оказывали более видимое на континентальном уровне воздействие на растительность во время ээмского периода. Несмотря на это, неандертальцы играли важную роль в ландшафтной динамике, потому что эти охотники-собиратели вызывали пожары, после которых территории становились более привлекательными для травоядных из-за повышенной питательной ценности и распространения новых растений. В раннем голоцене мезолитическое население изменило в среднем 8–26% (с максимальными оценками до 14–47%) ландшафтов Европы. Это произошло в результате выжигания растительности и косвенного влияния на нее через охоту и сокращения интенсивности потребления растительности мегафауной.

Таким образом, ландшафты Европы были сформированы при существенном влиянии людей еще до появления сельского хозяйства. Результаты этого исследования подчеркивают, что охотники-собиратели и пожары имели важное значение для динамики межледниковых экосистем.

Français

L'impact humain sur l'environnement s'étend sur des millénaires, avec des preuves de la modification anthropique des paysages avant l'émergence de l'agriculture. Un examen des preuves archéologiques disponibles datant à la fois du dernier interglaciaire (~130,000–116,000 BP) et du début de l'Holocène (~11,700–8000 BP) révèle qu'un ensemble de proxies similaires est disponible pour les deux périodes. Malgré les études de cas disponibles et les observations ethnographiques des incendies provoqués par les chasseurs-collecteurs, il reste difficile de déterminer si ces activités à l'échelle locale ont causé des changements environnementaux à l'échelle régionale ou même (sub)continentale.

Pour résoudre ce problème, nous avons développé en libre accès un *agent-based model* (*ABM*) spatialement explicite, appelé *HUMan impact on LANDcapes* (*HUMLAND*) pour étudier l'impact des activités des chasseurs-collecteurs sur la végétation en Europe pendant le dernier interglaciaire et le début de l'Holocène. Ce modèle intègre plusieurs sources d'impact : les incendies naturels et anthropiques, la consommation de plantes par la mégafaune et l'impact climatique. De plus, *HUMLAND* intègre divers jeux de données, tels que des estimations de la consommation maximale potentielle de plantes par la mégafaune, des modèles altimétriques numériques ou encore la répartition des grands plans d'eau.

Le modèle ABM développé utilise les résultats des modèles CARbon Assimilation In the Biosphere (CARAIB) et Regional Estimations of VEgetation Abundance from Large Sites (REVEALS). Le modèle *CARAIB* est alimenté par les forçages climatiques et par des hypothèses sur la dynamique de la végétation, tandis que *REVEALS* fournit des estimations quantitatives régionales de l'abondance de la végétation basées sur la palynologie. Les résultats de *CARAIB* servent de point de départ pour toutes les simulations, établissant les conditions environnementales naturelles. En revanche, les résultats de *REVEALS* sont utilisés pour comparer les résultats de *HUMLAND* avec la couverture basée sur la palynologie. Des différences substantielles sont apparues lors de la comparaison jeux de données *CARAIB* et *REVEALS*, indiquant que le climat n'était pas le seul facteur ayant façonné les paysages européens pendant les périodes étudiées.

Nous avons réalisé une analyse de sensibilité du modèle *ABM* développé pour identifier les facteurs influençant l'intensité des changements de végétation induits par les humains : le nombre de groupes de chasseurs-collecteurs présents, leurs préférences en termes d'ouverture de la végétation autour des campements, et la taille de la zone impactée. Ensuite, nous avons combiné *HUMLAND* avec un algorithme génétique pour produire des scénarios potentiels de l'évolution de la végétation dans le temps. Ces scénarios sont représentés par différentes combinaisons de valeurs pour les facteurs les plus influents identifiés *via* une analyse de sensibilité, et un paramètre supplémentaire qui définit la diminution de la consommation de plantes par la mégafaune due à l'impact de la chasse. Enfin, pour les scénarios avec les valeurs de paramètres les plus fréquemment générées, l'*ABM HUMLAND* a suivi et quantifié les changements causés par chaque source d'impact.

La comparaison entre *CARAIB* et *REVEALS* et les scénarios générés *via* un algorithme génétique suggèrent que le climat et la mégafaune n'étaient pas les seuls facteurs déterminant la végétation interglaciaire. Les incendies, spécifiquement ceux causés par les chasseurs-collecteurs et leur impact sur la distribution de la mégafaune par la chasse ont également joué un rôle significatif dans l'évolution des écosystèmes européens. Les observations ethnographiques et les signaux des études de cas archéologiques, ainsi que nos résultats de modélisation, suggèrent que les Néandertaliens et les humains du Mésolithique ont eu un impact similaire. En effet, les deux populations ont impacté une zone de taille semblable autour de leurs campements et ont eu des préférences comparables en termes d'ouverture de la végétation. De plus, les estimations de population minimum nécessaires pour associer les résultats du modèle HUMLAND avec ceux du modèle REVEALS pour le dernier interglaciaire sont comparables à ceux du début de l'Holocène.

Pour la première fois, nous avons quantifié l'impact des Néandertaliens et des humains du Mésolithique sur la végétation interglaciaire. Nos résultats suggèrent que les deux populations étaient importantes pour la dynamique de la végétation en Europe interglaciaire. Bien que les rôles plus importants de la mégafaune et du climat dans l'évolution de la végétation au cours du dernier interglaciaire aient pu éclipser l'impact des activités néandertaliennes, les chasseurs-collecteurs du dernier interglaciaire ont influencé les changements de végétation par l'utilisation du feu, rendant certaines zones plus attractives pour les herbivores en raison de la valeur nutritionnelle accrue. Au début de l'Holocène, les humains ont eu un impact direct sur la transformation d'approximativement 8 à 26% des paysages (avec un maximum de 14 à 47%) par la combustion de la végétation et les effets indirects de la chasse. Ainsi, les paysages européens ont été façonnés par l'action humaine avant l'émergence de l'agriculture, soulignant le rôle intégral des humains et des incendies dans les écosystèmes interglaciaires.

CHAPTER 1

INTRODUCTION

1.1 Background

Throughout human history, relationships between people and their environments have been one of the fundamental drivers of changes in various systems including biological, techno-cultural, socio-economic, ecological, and digital. While the human-environment interactions span over millennia, the question when and how people started active changes of their environment is still highly debated especially in the light of the pressing environmental challenges confronting humanity.

As an attempt to emphasize the role of humans in environmental changes and to define the starting point of these processes the term "Anthropocene" was coined for the current human-dominated geological epoch (Crutzen, 2002; Crutzen & Stoermer, 2000). Since then, the beginning of this period, its geological relevance and which type of evidence should be used to define Anthropocene's starting point have been debated with suggestions varying from 13,800 BP when megafauna extinctions occurred, to the mid-twentieth century with the introduction of plastics and concrete production (Lewis & Maslin, 2015; Ruddiman, 2013; Waters et al., 2016; Zalasiewicz et al., 2015). These discussions also extend to whether the Anthropocene should be classified as an epoch or an event (Bauer et al., 2021; Gibbard et al., 2022).

The Anthropocene Working Group chose to identify the stratigraphic signal of the Anthropocene using the global distribution of primary artificial radionuclides from mid-twentieth-century atomic bomb explosions, and sediments from Crawford Lake near Toronto (Canada) as the Anthropocene's "golden spike" (global boundary stratotype section) (Anthropocene Working Group, 2019; McCarthy et al., 2023; Zalasiewicz et al., 2015). The proposal to recognize the Anthropocene as an official geological epoch was presented to the international Subcommission on Quaternary Stratigraphy which voted against it (Adam, 2024; Boivin et al., 2024). This decision to not formalize the Anthropocene as a geological epoch offers opportunities to study in depth the complex dynamics of human-environment relationships (Boivin et al., 2024). The 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, were identified as priorities for research in archaeology and paleoecology (Ellis et al., 2021; Kintigh et al., 2014; Seddon et al., 2014).

Humans have a rich history 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). In accordance with this definition, agricultural practices and foraging lifestyles qualify as forms of human niche construction. It is widely recognized that the emergence of agriculture substantially intensified human impact on the environment compared to those of foraging societies (Delcourt, 1987; Kirch, 2005; Roberts et al., 2018; Ruddiman, 2013) defined as populations which mainly depend on food collection or foraging of wild resources (Ember, 2020).

Ethnographic observations show that hunter-gatherers influence their environment in several ways including modification of vegetation communities via burning (Nikulina et al., 2022; Rowley-Conwy & Layton, 2011; Scherjon et al., 2015; Smith, 2011). Besides ethnographic data, evidence from archaeological contexts show that fire use was an important part of the technological repertoire of the *Homo* lineage since at least the second half of the Middle Pleistocene (Gowlett & Wrangham, 2013; Roebroeks & Villa, 2011; Sorensen et al., 2018). Human-induced vegetation burning during the Late Pleistocene has been proposed as a potential factor for landscape changes in several case studies spanning various continents (Hunt et al., 2012; Pinter et al., 2011; Summerhayes et al., 2010; Thompson et al., 2021). Notably, the earliest evidence of human-induced vegetation burning was found at the Neumark-Nord site in Germany, dating back to the Last Interglacial period (LIG, ~130,000–116,000 before present; all dates are given in years before present (BP), where "present" is defined as 1950 CE) (Roebroeks et al., 2021). In addition, foragers using fire were suggested as main contributors to vegetation changes in Europe during the Last Glacial Maximum, potentially representing some of the earliest extensive anthropogenic alterations of Earth's systems (Kaplan et al., 2016).

While these Pleistocene cases are still debated, vegetation burning by hunter-gatherers during the Early–Middle Holocene (~11,700–6000 BP) is generally accepted (Davies et al., 2005; Dietze et al., 2018; Mason, 2000; Zvelebil, 1994), even though the quality of the data is not necessarily that different from the Palaeolithic evidence (Nikulina et al., 2022). There are more Early–Middle Holocene case studies than from Pleistocene contexts, with most of the evidence for the Early–Middle Holocene coming from Europe (Bos & Urz, 2003; Caseldine & Hatton, 1993; Gumiński & Michniewicz, 2003; Heidgen et al., 2022; Hjelle & Lødøen, 2017; Hörnberg et al., 2006; Innes et al., 2013; Kaal et al., 2013; Mellars & Dark, 1998; Milner et al., 2018; Sevink et al., 2023; Woldring et al., 2012). In addition, evidence suggests that humans had already altered natural fire regimes in Australia as early as 11,000 years ago (Bird et al., 2024).

Despite numerous case studies suggesting anthropogenic burning (intentional or not) by prehistoric hunter-gatherers, it remains challenging to establish whether these local-scale activities led to changes on regional and/or (sub-)continental scales (Nikulina et al., 2022). In addition, assessing the potential impact of past hunter-gatherers on their environments to some extent requires knowledge of "human-free" or "natural" ecosystems, which arguably points to the concept of a "natural palaeoenvironment". In the same vein, restoration for biodiversity conservation often requires a reference ecosystem or baseline (Burge et al., 2023) which is often referred to as a historical state before large-scale human exploitation of resources (Hildong-Rydevik et al., 2017). The search for such baselines is challenging due to the complexities of past environmental processes (Schreve, 2019). Thus, studying the impact of early human activities on their environment is crucial not only for archaeology and related fields but also for informing ecosystem restoration projects aimed at a sustainable future. By examining past human-environment interactions, we can better understand the landscape dynamics.

Landscapes are complex systems where heterogeneous components interact to impact ecological processes and might demonstrate non-linear dynamics and emergence (Newman et al., 2019). Modelling approaches offer excellent opportunities to explore how specific components of complex systems might interact, particularly when real-time experiments are not feasible.

Agent-based modelling (ABM) is often used to simulate real-world processes over time, to explore complex systems where multiple factors intertwine, and to suggest possible scenarios of system functioning (Romanowska et al., 2021). Importantly, the outcomes of ABM exercises can be compared to empirical data such as pollen-based vegetation reconstructions. The ABM approach has been applied in various contexts to examine past human-environment interactions and changes in land use and land cover caused by ancient societies (Boogers & Daems, 2022; Lake, 2000; Reynolds et al., 2006; Riris, 2018; Rogers et al., 2012; Santos et al., 2015; Saqalli et al., 2014; Scherjon, 2019; Verhagen et al., 2021; Vidal-Cordasco & Nuevo-López, 2021; Wren & Burke, 2019). In ABMs designed to study foragers, the role of fire used by hunter-gatherers to modify their habitats and its consequences is often overlooked (except for brief mentions in some studies such as Ch'ng and Gaffney (2013) and Snitker (2018)).

While acknowledging the potential for other modelling techniques, spatially explicit ABM is employed to address the unique challenges of this study, including the quantification of the potential impact of past hunter-gatherers within a dynamic environment where various processes influence human decisions to initiate vegetation changes. ABM allows to discern the earliest anthropogenic signals in landscape dynamics, moving beyond mere correlation between several proxy-based evidence. Additionally, it becomes possible to examine the interplay between scales, as we can observe how decisions at a local level influence broader landscape dynamics.

This study presents a spatially explicit ABM HUMan impact on LANDcapes (HUMLAND) with a primary emphasis on vegetation burning by hunter-gatherers.

This model explores key factors in continental-level interglacial vegetation changes during the LIG and the Early Holocene (~11,700–8000 BP, i.e., the period before the widespread adoption of agriculture in Europe). An important element of this study is assessment of differences between pollen-based reconstruction (inferred vegetation created by various processes including anthropogenic and natural fires, climatic fluctuations, megafauna presence, etc.) and dynamic vegetation model output (climate-based vegetation cover i.e., potential natural vegetation cover driven by climatic forces only).

1.2 Research questions

The primary research question addressed in this study is whether–and to which degree–hunter-gatherer activities could have impacted vegetation cover in Europe during the LIG and the Early Holocene. To address this question, six objectives have been set:

1) to review the currently available proxy-based evidence for past hunter-gatherer impact on interglacial environment in Europe (Chapter 2);
2) to evaluate the differences between potential natural vegetation as established via the CARbon Assimilation In the Biosphere (CARAIB) model and pollen-based vegetation obtained via Regional Estimates of VEgetation Abundance from Large Sites (REVEALS) for the study periods (Chapters 3 and 4);
3) to develop an ABM which is capable of tracking and quantifying different types of impact on vegetation (Chapter 3);
4) to identify the most influential parameters which define the intensity of human-induced vegetation changes (Chapter 3);
5) to generate potential scenarios of vegetation transformations due to megafauna plant consumption, anthropogenic and natural burning during the study periods (Chapter 4);
6) to track and to quantify the potential impact of Neanderthals and Mesolithic humans on vegetation for the most frequently generated scenarios (Chapter 4).

1.3 Datasets and research methodology

The research presented in this dissertation is multifaceted, positioned at the intersection between several disciplines including archaeology, ecology, and computer science. As a result, this study integrates various datasets developed within the broader research framework (Arthur et al., 2023, 2025; Davoli et al., 2023;

Pearce et al., 2023; Serge et al., 2023; Zapolska et al., 2023a, 2023b) to address the complexity of the main research question and objectives. Due to that, collaboration with other researchers on certain aspects was naturally involved. However, all work presented in this dissertation–including conceptualization, methodology, model development, validation, formal analysis, investigation, data curation, writing, visualization, project administration, and the open-access publication of all outputs–was carried out by the author. This is supported by the author's role as the first author on all relevant publications (Nikulina et al., 2022, 2024b, in press) and published models (Nikulina et al., 2023, 2024a). Contributions from co-authors are explicitly acknowledged in the statements of the respective publications, where permissible under journal guidelines.

1.3.1 Literature review of proxy-based evidence for hunter-gatherer impact on European environment

To meet the first objective of this study, the literature review was conducted (Nikulina et al., 2022). Firstly, hunter-gatherer niche construction activities were described based on ethnographic observations (Rowley-Conwy & Layton, 2011; Smith, 2011). Afterwards, proxies for each category of niche construction activity were listed and evaluated in relation to proxies' spatial resolution and availability for the LIG and Early Holocene contexts (Nikulina et al., 2022). Finally, the use of proxies within LIG and Mesolithic contexts was illustrated and compared between the two time periods (Bos & Urz, 2003; Innes & Blackford, 2003, 2017; Pop & Bakels, 2015; Roebroeks et al., 2021). Based on this, the validity of current understanding of Neanderthal and Mesolithic hunter-gatherer impact on interglacial landscapes was discussed (Nikulina et al., 2022).

1.3.2 CARAIB-REVEALS comparison and their integration into HUMLAND ABM

There is no accepted protocol for comparing the CARAIB and REVEALS models and for integrating them into a single ABM. The similarity between the two datasets is that they both produce quantitative output: CARAIB generates distributions of fractions for 26 plant functional types (PFTs), and REVEALS provides proportions for individual taxa. To meet the second objective, the approach was developed to compare CARAIB and REVEALS outputs, to include them into HUMLAND, and to compare ABM output with REVEALS estimates (Henrot et al., 2017; Nikulina et al., 2024b; Popova et al., 2013; Zapolska et al., 2023a). In accordance with this approach, CARAIB and REVEALS outputs were reclassified (i.e., transformed in accordance with the developed classification scheme) to compare them in terms of the distribution of dominant PFTs and vegetation openness. Because CARAIB and REVEALS assess vegetation openness differently, we use the term "vegetation openness" broadly, referring to vegetation density and its influence on visibility and activities of hunter-gatherers, such as movement. After reclassification, the datasets were compared per time window: two LIG (mesocratic I and mesocratic II) and seven 500-year-long Early Holocene (11,700–8200 BP) time windows (Nikulina et al., in press).

1.3.3 HUMLAND ABM

In this study a novel spatially explicit ABM HUMLAND was developed to track and to quantify different types of impact on vegetation in accordance with the third objective of this research (Nikulina et al., 2024b, in press). This ABM explores the impact on vegetation from different sources and operates at a temporal resolution of one year and a spatial resolution of 10 km × 10 km, with each simulation run consisting of 1000 steps. The primary observations made during simulation runs include the distribution of the dominant PFTs (percentage of grid cells covered by each of four PFTs: herbs, shrubs, needleleaf and broadleaf trees) and mean vegetation openness in percentage. These observations are collected only for grid cells that have both CARAIB and REVEALS values.

HUMLAND includes four types of impact on vegetation: climatic impact, human-induced and natural fires, and megafauna plant consumption. These types of impact on vegetation are considered among the most influential, widespread, and potentially visible on regional-(sub-)continental scales (Bond & van Wilgen, 1996; Nikulina et al., 2024b; Pringle et al., 2023; Whelan, 1995). HUMLAND has adjustable parameters for various impact types; these parameters can be modified during simulation runs (Nikulina et al., 2024b).

This model incorporates several datasets (Nikulina et al., 2024b) including potential maximal megafauna plant consumption (Davoli et al., 2023), digital elevation model (Danielson & Gesch, 2011; Gesch et al., 1999; https://www.usgs.gov/), Water Information System for Europe (WISE) (https://water.europa.eu/). While all datasets are integral to the development of the HUMLAND ABM, the outputs of the CARAIB and REVEALS models play an important role (Serge et al., 2023; Zapolska et al., 2023a, 2023b). CARAIB results serve as the starting point for all simulation runs, providing initial environmental settings. In contrast, the REVEALS model outputs used to compare HUMLAND outputs with observed vegetation cover. Specifically, the success of generated scenarios (Nikulina et al., in press) is measured by its ability to produce output similar to the REVEALS data.

1.3.4 Genetic algorithm

To meet the fifth objective, the genetic algorithm optimization technique was used to enable systematic and computationally efficient exploration of parameter space for generation of scenarios (Nikulina et al., in press). Each of them is represented by a different combinations of parameter values within the HUMLAND model.

The genetic algorithm is widely recognized as a useful approach for ABM optimization (Olsen et al., 2018; White et al., 2022), though application in archaeological research has been relatively limited (Scherjon, 2019). Optimization includes testing different designs and adjusting model elements (e.g., agent behaviours and parameter values) to obtain a desired output of a model (Turgut & Bozdag, 2023). In the current study, this output is a simulated vegetation cover that is similar to the past vegetation patterns represented by the REVEALS dataset.

Since CARAIB and REVEALS are compared in terms of the PFT distribution and vegetation openness, there two goals for the genetic algorithm runs: 1) to minimize differences in mean percentages of grid cells dominated by trees and 2) to minimize the differences in the mean vegetation openness between HUMLAND output and pollen-based (i.e., REVEALS) results. For each genetic algorithm goal, we assessed the feasibility of generating scenarios with and without human-induced fires. In all experiments humans influence the intensity of megafauna plant consumption via hunting pressure.

1.3.5 Quantification of Neanderthal and Mesolithic impacts on vegetation

To meet the last objective, parameter values with the highest frequency in HUMLAND scenarios where the output aligned with REVEALS reconstructions were selected. HUMLAND was run with the selected combinations of parameter values to quantify the number of modifications made by Neanderthals, Mesolithic groups, megafauna, natural fires, and climate (Nikulina et al., 2024b).

1.4 Thesis structure

The dissertation consists of a collection of three articles, accompanied by introductory and discussion chapters. Two papers have already been published in peer-reviewed journals, and one paper is currently in press. The findings of this research have been presented at various international conferences and workshops, leading to the publication of different aspects of this work in conference proceedings.

Chapter 2 presents the literature review of palaeoenvironmental proxies and combinations of these for understanding hunter-gatherer niche construction activities in Europe. LIG and Early Holocene case studies are discussed. The results of this review show that published evidence for Mesolithic manipulation of landscapes is based on the interpretation of data qualitatively comparable to those available for the LIG (Nikulina et al., 2022).

In the following chapter (3) the HUMLAND ABM is presented. This chapter includes the sensitivity analysis of the model and its first application. The results of this work support the hypothesis that European ecosystems were strongly shaped by human activities already in the Early Holocene (Nikulina et al., 2024b).

Chapter 4 shows HUMLAND ABM application to two LIG and several Early Holocene time windows. In this work the developed model was combined with a genetic algorithm to explore possible scenarios for the past interglacial ecosystems functioning. The obtained results indicated that climate and megafaunal activities were not the only factors shaping European landscapes, with hunter-gatherers being important for interglacial ecosystems through both direct (via vegetation burning) and indirect (via hunting herbivores) pathways already in the LIG (Nikulina et al., in press).

CHAPTER 2

AVAILABLE EVIDENCE FOR HUNTER-GATHERER IMPACT ON EUROPEAN ENVIRONMENT

Source

Nikulina, A., MacDonald, K., Scherjon, F., A. Pearce, E., Davoli, M., Svenning, J. C., Vella, E., Gaillard, M. J., Zapolska, A., Arthur, F., Martinez, A., Hatlestad, K., Mazier, F., Serge, M. A., Lindholm, K. J., Fyfe, R., Renssen, H., Roche, D. M., Kluiving, S., & Roebroeks, W. (2022). Tracking Hunter-Gatherer Impact on Vegetation in Last Interglacial and Holocene Europe: Proxies and Challenges. *Journal of Archaeological Method and Theory 29,* 989–1033.

https://doi.org/10.1007/s10816-021-09546-2

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.

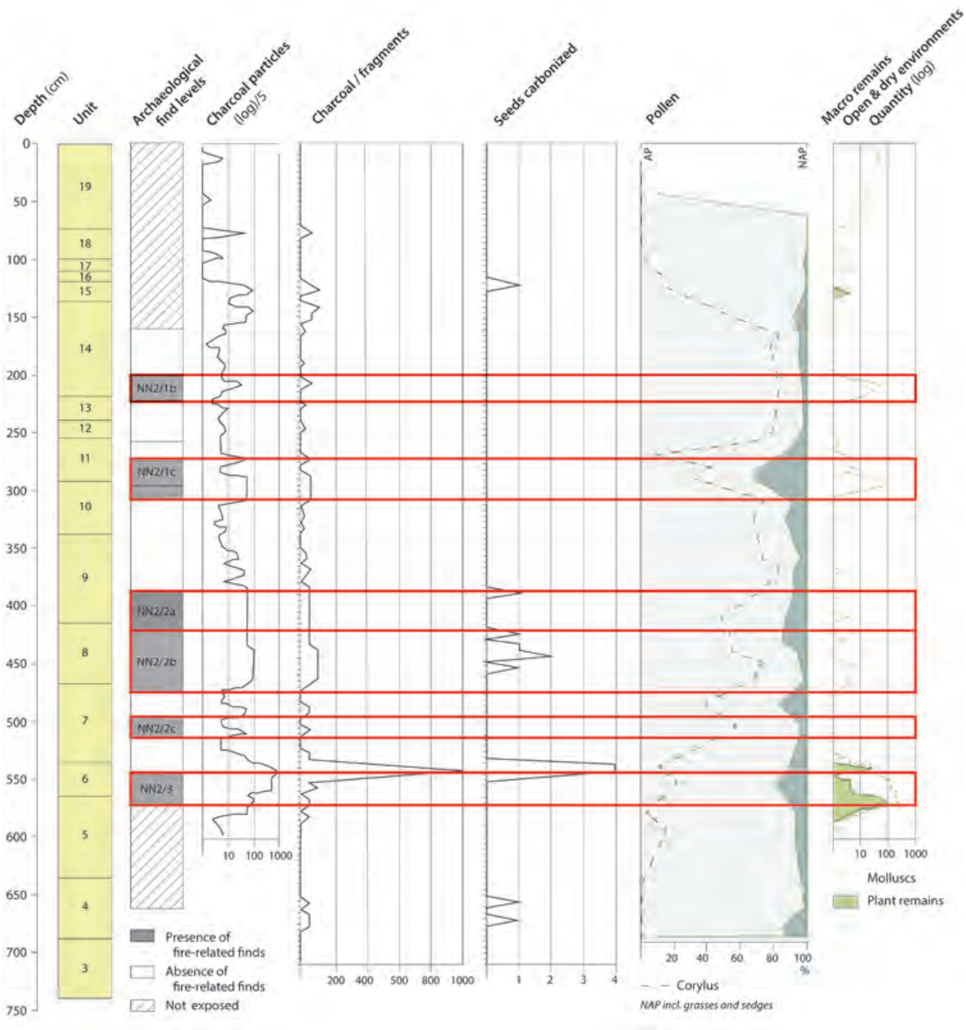


Figure 2.1 Neumark-Nord 2 (Germany) HP 7 sequence, with lithological units and the archaeological find levels (Sier et al., 2011), the stratigraphical distribution of charcoal particles, carbonised seeds (Kuijper, 2014), arboreal (AP) and non-arboreal pollen (NAP) and data regarding vegetation openness (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)

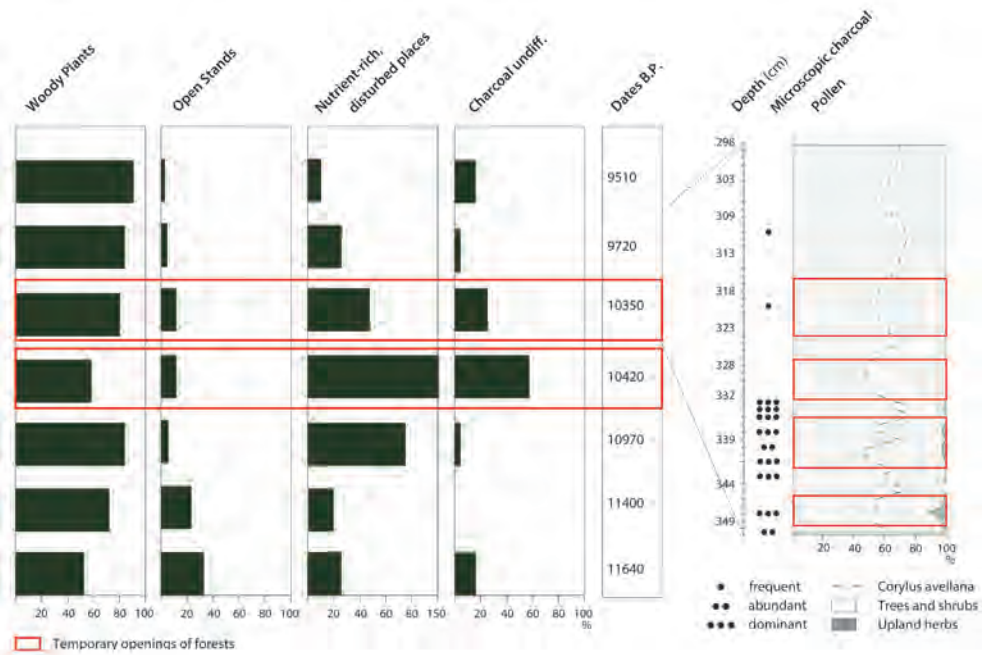


Figure 2.2 Pollen analysis (pollen percentage of trees, shrubs, upland herbs and Corylus avellana) from Weimar-Niederweimar II.2 profile and macrofossil evidence (percentage of wood, charcoal and remains from plants occupying open, disturbed and nutrient-rich areas) from different palaeochannel fills 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

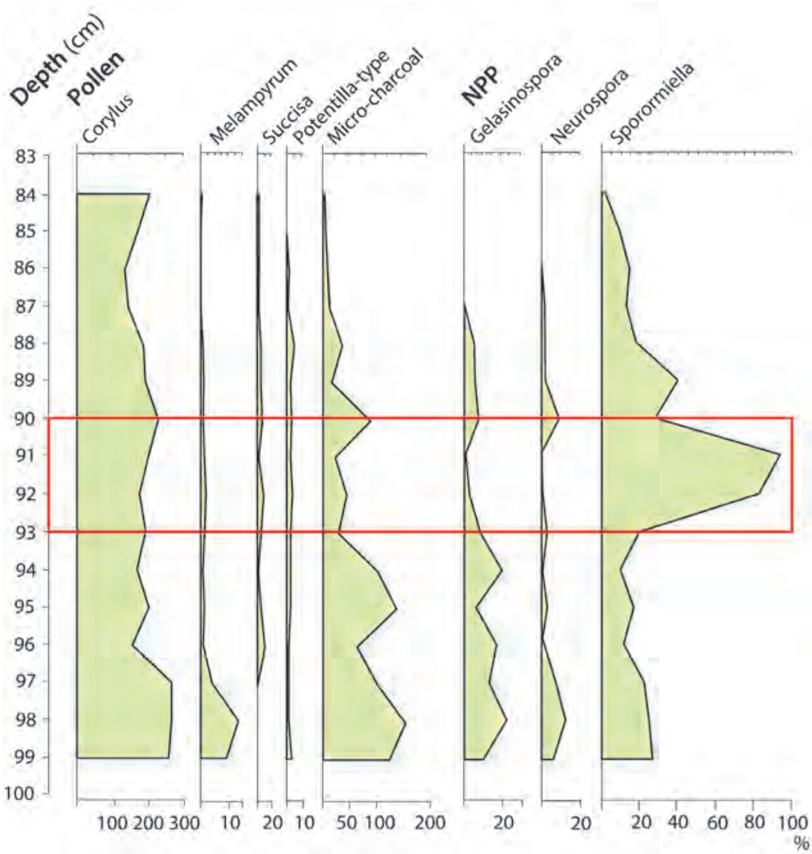


Figure 2.3 Pollen analysis (pollen percentage of *Corylus*, *Melampyrum*, *Succisa*, *Potentilla*-type and microcharcoal) and non-pollen palynomorphs (NPP) evidence (percentage of Gelasinospora, *Neurospora*, *Sporormiella*) from a profile at North Gill 5B (North York Moors within England and Wales). 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

We would like to thank Prof. Jan Kolen and Prof. Corrie Bakels (Leiden University, Leiden, the Netherlands) for inspiring discussions.

CHAPTER 3

HUMLAND ABM: MODELLING HUNTER-GATHERER IMPACT ON EUROPEAN LANDSCAPES

Source

Nikulina, A., MacDonald, K., Zapolska, A., Serge, M. A., Roche, D. M., Mazier, F., Svenning, J., van Wees, D., A. Pearce, E., Fyfe, R., Roebroeks, W., & Scherjon, F. (2024). Hunter-gatherer impact on European interglacial vegetation: A modelling approach. *Quaternary Science Reviews*, 324.
https://doi.org/10.1016/j.quascirev.2023.108439

Supplementary material

Appendices I and II

Data availability

HUMLAND ABM 1.0 is available via the CoMSES library (https://doi.org/10.25937/fxdq-fn86). The simulation results and the R project have been uploaded to the Zenodo repository (https://doi.org/10.5281/zenodo.10006039).

Abstract

This article focuses on hunter-gatherer impact on interglacial vegetation in Europe, using a case study from the Early Holocene (9200–8700 BP). We present a novel agent-based model, hereafter referred to as HUMLAND (HUMan impact on LANDscapes), specifically developed to define key factors in continental-level vegetation changes via assessment of differences between pollen-based reconstruction and dynamic global vegetation model output (climate-based vegetation cover). The identified significant difference between these two datasets can be partially explained by the difference in the models themselves, but also by the fact that climate is not the sole factor responsible for vegetation change. Sensitivity analysis of HUMLAND showed that the intensity of anthropogenic vegetation modification mainly depended on three factors: the number of groups present, their preferences for vegetation openness around campsites, and the size of an area impacted by humans. Overall, both climate and human activities had strong impacts on vegetation openness during the study period. Our modelling results support the hypothesis that European ecosystems were strongly shaped by human activities already in the Mesolithic.

3.1 Introduction

The history of anthropogenic impacts on the environment spans over millennia, with humans already engaging in landscape transformations before the emergence of agriculture (Ellis et al., 2016, 2021; Nikulina et al., 2022; Zapolska et al., 2023a). Ethnographic observations show that hunter-gatherers or foragers (i.e., groups that mainly depend on food collection or foraging of wild resources) (Ember, 2020) influence their surroundings in several ways including modification of vegetation communities via burning (Nikulina et al., 2022; Rowley-Conwy & Layton, 2011; Scherjon et al., 2015; Smith, 2011). This practice was identified for all vegetation types except tundra at different spatial scales and for diverse objectives including driving game, stimulating the growth of edible plants, and clearing pathways (Scherjon et al., 2015). Besides ethnographic data, evidence from archaeological contexts show that fire use was an important part of the technological repertoire of the *Homo* lineage since at least the second half of the Middle Pleistocene (Gowlett & Wrangham, 2013; Roebroeks & Villa, 2011; Sorensen et al., 2018). Human-induced vegetation burning during the Late Pleistocene has been proposed as a potential factor in several case studies spanning various continents (Hunt et al., 2012; Pinter et al., 2011; Summerhayes et al., 2010; Thompson et al., 2021). Notably, the earliest evidence of a local-scale impact of fire use was identified at the Neumark-Nord site in Germany, dated to the Last Interglacial (Eemian, ~130,000–116,000 BP) (Roebroeks et al., 2021). In addition, fire-using foragers were suggested as one of the primary drivers of vegetation openness in Europe during the Last Glacial Maximum, i.e., possibly constituting one of the earliest large-scale anthropogenic modifications of Earth's systems (Kaplan et al., 2016).

While these Pleistocene cases are still subject to debate, hunter-gatherer-induced vegetation burning during the Early–Middle Holocene (~11,700–6000 BP) is generally accepted (Davies et al., 2005; Dietze et al., 2018; Mason, 2000; Zvelebil, 1994), even though the quality of the data is not necessarily that different from the earlier ones (Nikulina et al., 2022). However, the number of case studies is higher for the Early–Middle Holocene than for the Pleistocene. Most of the Early–Middle Holocene evidence comes from Europe (e.g., Bos & Urz, 2003; Caseldine & Hatton, 1993; Gumiński & Michniewicz, 2003; Heidgen et al., 2022; Hjelle & Lødøen, 2017; Hörnberg et al., 2006; Innes et al., 2013; Kaal et al., 2013; Mellars & Dark, 1998; Milner et al., 2018; Sevink et al., 2023; Woldring et al., 2012).

Despite the presence of case studies for anthropogenic burning (intentional or not) of past landscapes by hunter-gatherers, it is still difficult to establish whether these local-scale activities caused changes at regional and/or even (sub-)continental scales (Nikulina et al., 2022). Furthermore, overall landscape dynamics do not only depend on humans, and rather represent the complex interplay of natural and cultural processes at different spatio-temporal scales (Tasser et al., 2009). Landscapes are complex systems where heterogeneous components interact to impact on ecological processes, and might demonstrate non-linear dynamics and emergence (Newman et al., 2019). Therefore, it is often challenging to identify specific types of impacts on landscapes using proxy-based reconstructions (e.g., palynological datasets).

Modelling approaches offer excellent opportunities to explore how complex system components might interact, particularly when real-time experiments are not possible. Spatially explicit agent-based modelling (ABM) is commonly used to explore complex systems where multiple factors intertwine, and to propose possible scenarios of system functioning (Romanowska et al., 2021). Importantly, the outcomes of ABM exercises can be compared to empirical data. The ABM approach has been applied in various contexts to study past human-environment interactions and land use/land cover changes, such as models for past societies that practiced agriculture and animal husbandry (Boogers & Daems, 2022; Riris, 2018; Rogers et al., 2012; Saqalli et al., 2014; Verhagen et al., 2021; Vidal-Cordasco & Nuevo-López, 2021), and for hunter-gatherer groups (Lake, 2000; Reynolds et al., 2006; Santos et al., 2015; Scherjon, 2019; Wren & Burke, 2019). In the case of ABM developed to study foragers, the use of fire by hunter-gatherers to transform foragers' habitats and the landscape consequences of these practices are usually not discussed (except for brief mentions of fire in some ABM case studies such as Ch'ng & Gaffney (2013); Snitker (2018)).

The goal of this study is to investigate multiple drivers of change within a system-based approach, including fire (natural and human-induced), herbivory and climatic impacts. In this study we develop a new spatially explicit ABM (HUMLAND: HUMan impact on LANDcapes) whose specific focus is the impact of hunter-gatherers on vegetation. To demonstrate the potential of our approach, we applied it to a 500-year long time interval from the Early Holocene (9200–8700 BP), drawing on novel datasets produced as part of a wider body of research (Arthur et al., 2023; Davoli et al., 2023; Serge et al., 2023; Zapolska et al., 2023a). Despite recognizing the challenges posed by plant migration and other processes linked to glacial/interglacial transitions during the Early Holocene (Dallmeyer et al., 2022; Giesecke et al., 2017), we deliberately chose this time interval, preceding the widespread adoption of agriculture in Europe (Gronenborn & Horejs, 2021; Hamon & Manen, 2021; Milisauskas, 2002). This choice aligns with our primary focus on vegetation burning conducted by hunter-gatherers. Our study emphasizes the comparison of digital vegetation model outputs with pollen-based reconstructions, and their integration into the HUMLAND ABM. Additionally, the study incorporates

continental-scale estimates of fire return intervals (FRI) and speed of vegetation regrowth in the current simulation, which were recently obtained specifically for this research. The article addresses the following sub-questions: 1) is it possible to create a modelling approach suitable for tracking and quantifying the intensity of different types of impact on interglacial landscapes at the continental level; 2) what defines the intensity of hunter-gatherer impact on interglacial vegetation?
3.2 Material and methods

3.2.1 Datasets used in the HUMLAND ABM

The simulation incorporates several datasets (Table 3.1). To standardize their spatial extent and resolution, Spatial Analysts and Data management *ArcMap* 10.6.1 toolboxes were used. The grid cell size of the input datasets was resampled to a common 10 km × 10 km spatial resolution via the "Resample" tool of the "Data management toolbox" with the "Nearest neighbour" resampling method.

Table 3.1 Datasets used in HUMLAND.

Dataset	Initial data type	Initial spatial resolution/ scale	Meaning, units	Source
GTOPO30	Raster	1 km	Digital elevation model, m	https://www.usgs.gov/
WISE	Vector	1:10,000,000	Distribution of large rivers and lakes	https://water.europa.eu/
CARAIB first dominant PFT	Raster	~26 km (0.25°)	PNV: first dominant PFT	http://www.umccb.ulg.ac.be/Sci/m_car_e.html
CARAIB vegetation openness			PNV: vegetation openness (%)	
NPP			PNV: NPP (excluding carbon used for respiration), g/m2	
Megafauna vegetation consumption	Raster	30 km	Potential maximal megafauna vegetation consumption (i.e., metabolization of NPP), kg/km^2 (converted to g/m^2)	Davoli et al., 2023
REVEALS first dominant PFT	Vector	~100 km (1°)	Observed first dominant PFT	Serge et al., 2023
REVEALS vegetation openness			Observed past vegetation openness (relative %)	
REVEALS vegetation openness standard errors			Standard errors for estimates of observed past vegetation openness	

The initial landscape before simulation runs (Fig. 3.1) was constructed via the following datasets: Global Topography 30 Arc-Second elevation dataset (GTOPO30), Water Information System for Europe (WISE) and three outputs of a dynamic vegetation model CARbon Assimilation In the Biosphere (CARAIB) (Danielson & Gesch, 2011; Dury et al., 2011; François et al., 2011; Laurent et al., 2008; Otto et al., 2002; Warnant et al., 1994). GTOPO30 is a digital elevation model (DEM) derived from several raster and vector sources of topographic information. We used this DEM to represent elevation data in the ABM. WISE is based on the information from the Water Framework Directive database. We assumed that this dataset represents distribution of major rivers and lakes during the study period, and we used these water bodies as natural barriers for the spread of fire in the model.

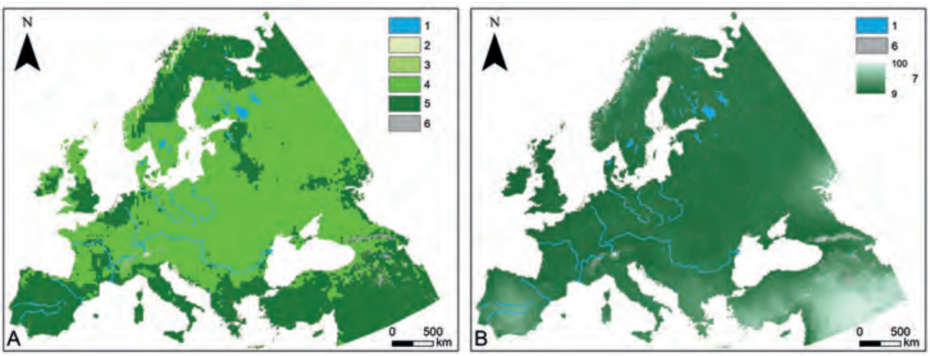


Figure 3.1 The reconstructed environment prior to the HUMLAND simulation runs for 9200–8700 BP: distribution of first dominant HUMLAND PFTs (A) and vegetation openness (B). Legend: 1–large rivers and lakes; 2–herbs; 3–shrubs; 4–broadleaf trees; 5–needle trees; 6–high mountains; 7–vegetation openness in percentages.

In the context of this research, the CARAIB dataset represents theoretical potential natural vegetation (PNV) distribution, driven by climatic conditions only (Zapolska et al., 2023a). As an input climate for running the CARIAB model, we used climatic variables simulated by the iLOVECLIM model (Goosse et al., 2010), revised by Roche (2013) and further expanded by Quiquet et al. (2018) with embedded online interactive downscaling (ibid.). Prior to the use of the iLOVECLIM-simulated climatic variables in the CARAIB model, they were bias-corrected using the Cumulative Distribution Function-transform (CDF-t) bias correction technique (Vrac, 2018; Zapolska et al., 2023b) and averaged over the studied period to get daily mean climate characteristics of our period of interest. CDF-t was selected as the bias-correction method, as it had demonstrated in previous testing within our specific setup (Zapolska et al., 2023b). CDF-t can be seen as an extension of the quantile-mapping (QM) method, allowing to account for climate change. As such, CDF-t mostly preserves the mean change of the variables to be corrected and, thus, behaves as the delta method in terms of means. As reference climate at present day for CDF-t calibration we used the EartH2Observe, WFDEI and ERA-Interim data Merged and Bias-corrected for the InterSectoral Impact Model Intercomparison Project (Lange, 2019). The CARAIB output dataset, used in this study, was previously published by Zapolska et al. (2023b), along with a full description of the modelling setup and the application of the CDF-t technique within this setup (Zapolska et al., 2023a, 2023b).

CARAIB outputs used in this study (Table 3.2) include distribution of fractions of 26 plant functional types (PNV PFTs), vegetation openness (PNV openness), leaf area index (LAI) and net primary productivity (PNV NPP) for the period 9200–8700 BP. Before being imported to the ABM, the mentioned CARAIB outputs were transformed (section 3.2.2). As the CARAIB dataset here represents climate-only forced vegetation, it is used in the current ABM as the starting point (i.e., before impact of humans, natural fires and megafauna) of each simulation and as target for vegetation regrowth after impacts (section 3.2.3).

To include megafauna (wild terrestrial mammals≥10 kg) impact on vegetation in our study, we calculated potential maximal vegetation consumption of the wild herbivore communities across the continent, as they were distributed and diversified prior to the extensive influence of humans. For this, we used the present-natural ranges estimated by Faurby and Svenning (2015), which were downscaled to a 30 × 30 grid-cell resolution by Davoli et al. (2023). Present-natural ranges are global estimates of mammal species distribution under climatic conditions similar to the Holocene. These ranges would be if *Homo sapiens* disturbance never occurred. In Davoli et al. (ibid.), these downscaled reconstructions were compared to species distribution reconstructions for the Last Interglacial to estimate differences between the two periods due to climate variability. The Early Holocene species pools were composed only of species occurring in Europe during this period in accordance with recent studies (Sommer, 2020). We considered these species pools and their distribution as representative of the potential maximum diversity of European herbivores in Early Holocene-like conditions without human impact, notably excluding species that went extinct in the Late Pleistocene, disregarding the reason for their extinction. Other comparable estimates of species distribution for the Early Holocene are not available, as the fossil record database is inherently scattered which potentially can lead to underestimation of faunal diversity (Crees et al., 2019). In the geographic space, we coupled the species pools with allometric estimates of plant consumption, in the form of consumed kg/km^2

Table 3.2 PFTs used in ABM (HUMLAND PFTs) and correspondence between CARAIB PFTs and REVEALS plant taxa.

CARAIB PFTs	Plant taxon / pollen morphological types	HUMLAND PFTs
Needle-leaved evergreen boreal/temp cold trees Needle-leaved evergreen meso mediterranean trees Needle-leaved evergreen subtropical trees Needle-leaved evergreen supra mediterranean trees Needle-leaved evergreen temperate cool trees Needle-leaved summergreen boreal/temp cold trees Needle-leaved summergreen subtropical swamp trees	*Abies* *Picea* *Pinus* *Juniperus*	Needleleaf trees
Broadleaved evergreen meso mediterranean trees Broadleaved evergreen subtropical trees Broadleaved evergreen thermo mediterranean trees Broadleaved evergreen tropical trees Broadleaved raingreen tropical trees Broadleaved summergreen boreal/temp cold trees Broadleaved summergreen temperate cool trees Broadleaved summergreen temperate warm trees	*Alnus* *Betula* *Carpinus betulus* *Carpinus orientalis* *Castanea sativa* *Corylus avellana* *Fagus* *Fraxinus* *Phillyrea* *Pistacia* deciduous *Quercus* t. evergreen *Quercus* t. *Salix* *Tilia* *Ulmus*	Broadleaf trees
Broadleaved evergreen boreal/temp cold shrubs Broadleaved evergreen temperate warm shrubs Broadleaved evergreen xeric shrubs Broadleaved summergreen arctic shrubs Broadleaved summergreen boreal/temp cold shrubs Broadleaved summergreen temperate warm shrubs Subdesertic shrubs Tropical shrubs	*Buxus sempervirens* *Calluna vulgaris* Ericaceae	Shrubs
C3 herbs (“dry”) C3 herbs (“humid”) C4 herbs	Amaranthaceae/Chenopodiaceae *Artemisia* Cerealia t. Cyperaceae *Filipendula* *Plantago lanceolata* Poaceae *Rumex acetosa* t. *Secale cereale*	Herbs

per year per species at 30 × 30 km resolution (Davoli et al., 2023). The methodology to reconstruct these values is extensively described by Davoli et al. (ibid.). After summarizing the vegetation consumption per species for all the species present, we obtained estimates of total megafauna potential maximal plant consumption, which were integrated with PNV NPP into the ABM to determine the extent to which vegetation changed as a result of potential megafauna impact (section 3.2.3.4).

Simulation outputs and CARAIB vegetation openness and distribution of first dominant PFTs were compared against proxy records of vegetation composition for the period 9200–8700 BP (section 3.2.2). Among existing empirical proxies of past vegetation, pollen records from lake sediments or peat deposits have the best potential for quantitative reconstructions of plant abundance. Regional Estimates of Vegetation Abundance from Large Sites (REVEALS) (Sugita, 2007a) is the only method so far that corrects the non-linear pollen–vegetation relationship by accounting for plant taxon-specific differences in pollen production, dispersal, and deposition (Prentice & Webb, 1986; Sugita, 2007a). It provides estimates of plant cover (in cover percentage of a defined area) for individual taxa. In recent years, datasets of pollen-based REVEALS plant cover were produced at a 1° × 1° grid cell spatial scale for large regions of the world, i.e., Europe, China, and North America–Canada (Cao et al., 2019; Githumbi et al., 2022; Li et al., 2023; Marquer et al., 2017; Serge et al., 2023; Trondman et al., 2015). Our study used REVEALS results from the most recent synthesis, which drew on a substantial number of pollen records (n = 1607) distributed across Europe (Serge et al., 2023). The dataset originally contains REVEALS estimates for 31 taxa, 25 consecutive time windows across the Holocene (11,700 BP–present), and 539 1° × 1° grid cells. For each cell, the REVEALS model has been run on all available pollen records (large and small pollen sites), and the mean REVEALS estimates of plant cover (and their standard errors) for the grid cell have been calculated for the 31 plant taxa (Table 3.2). The total cover of plant taxa within a grid cell is 100%. REVEALS cannot estimate the proportion of bare ground. The protocol for grid system, pollen data handling and REVEALS application was previously published (Githumbi et al., 2022; Mazier et al., 2012; Trondman et al., 2016).

The REVEALS dataset for the studied time window (9200–8700 BP) represents observed past vegetation cover, and, therefore, reflects vegetation cover impacted by all possible drivers, including megafauna, climate, anthropogenic and natural fires. In HUMLAND, REVEALS data is used as a target vegetation cover for the simulation output. Before being imported to HUMLAND, the used REVEALS and CARAIB outputs were transformed (section 3.2.2).

3.2.2 CARAIB, REVEALS and ABM output comparison

CARAIB and REVEALS are different modelling approaches, with dissimilar outputs (section 3.2.1). The similarity between the two datasets is that they both produce quantitative output: CARAIB generates distributions of fractions for 26 PFTs, and REVEALS provides proportions for individual taxa. The outputs of these models were compared in terms of vegetation openness and distribution of first dominant PFTs in the study area.

Currently, there is no accepted protocol for comparing the CARAIB and REVEALS models and for integrating them into a single ABM. Therefore, prior to the comparison of dominant PFT distributions and their incorporation into HUMLAND, the datasets were transformed (i.e., reclassified) into categorical (qualitative) descriptions of dominant PFTs. Here we applied a classification approach described by Zapolska et al. (2023a), based on classification by Popova et al. (2013) and Henrot et al. (2017), which was further organized into four general categories: herbs, shrubs, needleleaf trees and broadleaf trees (Table 3.2).

The definition of common categories which would be relevant for both datasets on the continental scale is rather complex. These categories were chosen because both datasets contain information about types of plants (herbs, trees, and shrubs) and leaf types of present woody plants. Furthermore, the primary focus of the current study is the impact of fire on vegetation, and, therefore, the ABM classification should reflect differences in vegetation responses to fires. Needleleaf trees and broadleaf trees are generally characterized by different degrees of flammability. Coniferous forests are fire-prone communities because the crowns of trees are often densely packed, have low moisture levels, and litter accumulates due to low decomposition rates (Bond & van Wilgen, 1996). Deciduous plants are usually less flammable in comparison with coniferous species, mainly because living leaves have higher moisture content (Doran et al., 2004). Herbaceous plants such as grasses are easily ignited and burn rapidly during most of the year (Dennis, 1999), because dieback of grass leaves can produce a dense litter layer (Bond & van Wilgen, 1996). Shrubs are generally flammable, because they often grow in dense groups or thickets (Doran et al., 2004). As a result, shrublands can be subject to intense crown fires because of their higher fuel loads (Bond & van Wilgen, 1996). Thus, CARAIB and REVEALS PFTs are included in the current simulation and compared in terms of four general categories of the first dominant PFTs: needleleaf and broadleaf trees, shrubs and herbs. While the CARAIB model provides output in PFTs directly, REVEALS PFTs were calculated by summing the mean relative percentage cover of each associated taxon (Table 3.2).

After both datasets were reclassified, we calculated F1-score for their distribution of general PFTs used in HUMLAND. The F1-score is a metric often used to assess the accuracy of a classification model in machine learning. This value combines both precision (the accuracy of positive predictions) and recall (the model's ability to correctly identify all relevant instances). F1-score ranges between 0 and 1, where 1 represents perfect precision and recall, and 0 represents the worst performance.

Besides the first dominant PFT, we used CARAIB PNV and REVEALS outputs in terms of potential natural (CARAIB) and observed (REVEALS) vegetation openness in percentages. However, these two datasets estimate vegetation openness in a different way (Figure AI.1 showing these differences is available in Appendix I Supplementary data).

Vegetation openness in REVEALS was estimated via the percentage of an open land (OL) land-cover type, which combines the percentage of all herbs (Table 3.2) and *Calluna vulgaris* (Serge et al., 2023; Trondman et al., 2015). Since REVEALS estimates are based on pollen data, this approach cannot account for bare ground. However, REVEALS provides estimates of standard error values (uncertainties of the averaged REVEALS estimates) for every plant taxon per grid cell using the delta method (Stuart & Ord, 1994), based on the methodology from Sugita (Sugita, 2007a). Standard errors were obtained from the sum of the within- and between-site variations of the REVEALS results per grid cell (Githumbi et al., 2022). Therefore, it is possible to estimate the quality of data, and calculate possible maximal and minimal values for vegetation openness.

In CARAIB, simulated PFTs can co-exist on the same grid, forming two vertical levels: upper (trees) and lower (shrubs, herbs and bare ground). The primary focus of this study is on human activity. We therefore attributed bare ground and grass to open landscapes, and trees and shrubs to closed landscapes, based on the ability of each plant group to restrict human activity (e.g., human movements are impeded by closed vegetation dominated by shrubs or trees; and it is easier to move within open landscapes dominated by herbs). The maximum possible openness value for each of the two vertical CARAIB levels is 100% (i.e., the percentage of a level not covered by shrubs or trees), and, therefore, the maximum possible value for each grid cell is 200% (i.e., vegetation is completely open because only bare ground and/or herbs are present). Vegetation openness was first calculated for trees and shrubs separately, using formula (3.1):

$$\text{Monthly openness} = e\text{\^{}}(-0.5 * \text{LAI}) \tag{3.1}$$

where e–exponential constant, approximately equal to 2.718, and LAI–leaf area index for each month (leaf area/ground area in m^2/m^2).

Minimal Monthly openness represents vegetation at its full growth potential. Therefore, the minimum value of monthly openness per grid cell was used for further calculations. Because the REVEALS dataset provides one vegetation openness value per grid cell, we also assigned one CARAIB vegetation openness value to each grid cell. Under the assumption that upper and lower PFTs spatially align within a grid cell, we assumed the smaller openness value among the two to be representative of grid cell vegetation openness, as it indicates a fraction of an area where neither upper (trees) nor lower (shrubs) vegetation is present. As a result, both CARAIB and REVEALS have one vegetation openness value per grid cell. A two-sample t-test was applied to 500 randomly selected cells with both REVEALS and CARAIB vegetation openness estimates. The t-value is a measure used to assess whether the difference between the means of two groups is significant or if it could have happened by random chance.

In HUMLAND, more closed vegetation can only switch to more open vegetation after a disturbance event (e.g., fire, grazing). In our data comparison, where CARAIB shows a greater degree of openness in vegetation than REVEALS, we exclude these locations: the ABM will not be able to generate vegetation that is comparable to REVEALS as it is constrained by the CARAIB-prescribed PNV. As a result, the similarity between ABM output and REVEALS datasets can only be improved for grid cells where initial vegetation openness is equal to or lower than observed estimates. Secondly, there are several grid cells where climatic conditions only favour dominance of herbs or shrubs, but observed vegetation indicates dominance of trees. Besides that, shrubs cannot dominate grid cells where climatic conditions favour trees or herbs in HUMLAND. Such cases do not improve similarity between ABM output and REVEALS data, and, therefore, these grid cells were also excluded (Table AI.1 with more explanations about conflicting grid cells is available in Appendix I).

After the CARAIB and REVEALS datasets were imported to HUMLAND and conflicting grid cells were excluded, the mean percentage of each first dominant PFT and mean vegetation openness was calculated for all remaining grid cells with both CARAIB and REVEALS estimates. These mean values were used during ABM runs to assess the performance of the model, and to identify simulation runs which produced results similar to REVEALS. ABM outputs are considered similar to REVEALS estimates if the difference in the mean percentage of each first dominant PFT and mean vegetation openness does not exceed ±5% (the range of change is 10%). For such ABM outputs, we calculated F1-scores and t-values. These measures for ABM outputs and the CARAIB–REVEALS comparisons were obtained using *ArcMap* 10.6.1 and R (RStudio Version 1.3.1093, R Core Team, 2020) with the *caret* (Kuhn, 2008) and *tidyverse* (Wickham et al., 2019) packages.

3.2.3 Agent-based model

The current continental ABM was implemented in *NetLogo* 6.2.2 (Wilensky, 1999). The temporal resolution of the model is one year, and, therefore, seasonality is out of the scope of our research. Due to that and the spatial resolution of the model (10 km × 10 km), many types of impact on vegetation (e.g., droughts, cooling, and insect activity throughout a year) and the seasonal movements of hunter-gatherers are beyond the scope of this paper.

This model does include four types of impact on vegetation: climate, anthropogenic fires, thunderstorms, and megafauna plant consumption (activity diagram can be found in Appendix I, Fig. AI.2). Thunderstorms were included because lightning is one of the most general and widespread triggers of natural fire (Whelan, 1995). Another source of impact is climate, and it is included as a crucial element for vegetation regeneration after fires or vegetation consumption (section 3.2.3.1). Finally, megafauna are also a part of the current ABM, because their activity impacts litter accumulation, and high levels of megafauna plant consumption reduce fire occurrence in many areas (Bond & van Wilgen, 1996; Pringle et al., 2023). Simulation stops after 1000 steps.

3.2.3.1 Climatic impact

Each simulation step starts with climatic impact, which defines vegetation regrowth after fire events or megafauna vegetation consumption. Fire effects on vegetation and vegetation regrowth are difficult to predict due to variability of plant composition and fire characteristics such as frequency, intensity, and size (Johnson & Miyanishi, 2021; Zwolinski, 1990). Consequences of burning can vary from minor (e.g., fire scars and scorches) to complete vegetation replacement (Kleynhans et al., 2021). Due to the large study area, 10 km resolution and the primary focus on anthropogenic burning in the current model, all burning events replace vegetation of a grid cell by bare ground in HUMLAND. The mean number of years to recover is used to define the rate of vegetation regrowth after fires or vegetation consumption.

In the course of our research, we did not find estimates for the mean number of years to recover for four broad PFT categories used in this study (Table 3.2). Due to that, the mean number of years to recover was calculated via CARAIB. First, a maximum of five representative grid cells for each of 26 CARAIB PFTs (Table 3.2) were chosen. For the PFTs where less than five grid cells were found to be representative, we selected all the existing cells. A grid cell is representative if a selected PFT did not experience any evident competition with other PFTs within the grid cell, and after a certain number of years stabilized into an equilibrium state of dominance on the grid cell. Thus, extracted periods represent the number of years needed for a PFT to grow from the bare ground and establish as a dominant PFT on a grid cell in CARAIB.

After that, CARAIB PFTs were reclassified as four HUMLAND PFTs in accordance with Table 3.2, and we created frequency histograms for each of the general PFT categories. These histograms were analysed and outlier values were excluded. Afterwards, the mean values were calculated for each general PFT. These values represent the number of years which is required for each PFT to recover as it was before the fire episode or complete vegetation consumption by megafauna: seven years for herbs, 43 years for needleleaf trees and shrubs, 30 years for broadleaf trees.

Vegetation regrowth occurs for both dominant PFTs and vegetation openness. The first step of PFT recovery in ABM always starts with herbs, which replace bare ground after seven simulation steps in the model. Afterwards, herbs could be replaced by trees or shrubs in accordance with an initial dominant PFT estimated by CARAIB after the required mean number of years to recover.

Rate of vegetation openness recovery rate (V_{or}) is calculated in formula 3.2:

$$V_{or} = \frac{O_i - O_c}{\mu} \tag{3.2}$$

O_i is vegetation openness after impact done by fire or megafauna; O_c–CARAIB estimates of vegetation openness; and μ–mean number of years required for recovery of the initial vegetation openness before fire event or plant consumption. Every simulation step V_{or} is subtracted from current simulation openness until it reaches CARAIB vegetation openness estimates.

3.2.3.2 Anthropogenic fires

Humans impact landscapes after vegetation regrowth. There are five parameters which define human behaviour and the intensity of their impact: number of hunter-gatherer groups, accessible radius, campsites to move, their movement frequency, and openness criteria to burn. After human-induced burning, fire can spread depending on the probability of ignition of neighbouring cells (section 3.2.3.3).

The first parameter defines the number of groups in the study area during one simulation run, and, therefore, this parameter is associated with human population size. There are studies focused on relationships between fire regime, frequency and human population size in the past and the present at different spatial scales (Bistinas et al., 2013; Knorr et al., 2014; Sweeney et al., 2022). It was shown that both positive and negative relationships can vary from continent to continent (Bistinas et al., 2013). Such studies rarely focus on periods when foraging was the dominant subsistence strategy. Given the ambiguous nature of the relationships and the uncertainty surrounding the inclusion or exclusion of this parameter, we ultimately included it in HUMLAND. In the current model, one moving agent represents the whole group. The initial distribution of groups and their campsites is random at the beginning of each run. Humans cannot occupy and move on water bodies and high mountains (i.e., elevation above 2500 m a.s.l.).

The accessible radius parameter defines the territory within which humans move and set fires around campsites. In accordance with Binford's model (Binford, 1982), the area around hunter-gatherer sites includes a foraging radius and a logistical radius. The first one defines the area where most resources are obtained, and this zone rarely exceeds ~10 km (ibid.). The second radius defines the area used by task groups e. g., for raw material procurement or food collecting, special activities that could imply staying away from "base camp" from one night to much longer periods (e.g., hunting for four weeks or three months) (ibid.). The accessible radius parameter in HUMLAND defines the territory which includes both foraging and logistical radii. If the parameter value is set to 0, the group does not move from their basecamp site, and only impacts the grid cell where this campsite is located. Higher parameter values expand the accessible radius (e.g., accessible radius 3 would allow humans to move within 3 grid cells radius, ~40 km around their campsites including the grid cell with a campsite on it).

Due to the importance of seasonal movements for the hunter-gatherer lifestyle (Kelly, 2013), there are two parameters associated with the movements of campsites: Movement_frequency_of_campsites (the number of simulation steps after which groups can relocate a campsite) and Campsites_to_move (the percentage of hominin groups that relocate a campsite at certain step). Given the temporal resolution of the current simulation, hunter-gatherers' highest possible frequency of camp movements is every step (i.e., once per year). The search radius for the new grid cell to establish a site is twice the accessible radius. Any grid cell can be chosen for the new site, except the previously occupied one. The newly established accessible area can overlap with the previous one.

Since hunter-gatherers have different reasons to burn landscapes, and that this practice was documented in almost all vegetation types with more cases for foragers occupying shrublands and forests (Mellars, 1976; Scherjon et al., 2015), the openness criteria to burn was introduced. In the current simulation, humans only burn patches dominated by trees or shrubs with vegetation openness lower or equal to this criterion. Its low values minimize the number of positive decisions to start fire, and higher values increase human-induced fires, because even relatively open areas can be burnt by people in this case.

3.2.3.3 Thunderstorms

The model contains the parameter which defines the number of thunderstorms per simulation step. They randomly appear on grid cells within the study area. Fire starts depending on the probability of ignition of these cells. Fire can spread on the neighbouring grid cells following both human-induced and natural fires, and this process depends on the probability of ignition. In other words, thunderstorms do not always cause vegetation burning, and fire does not always spread after natural and human-induced ignitions. Thunderstorms can appear over water bodies and high mountains, but these areas cannot be burnt, and, therefore, they are natural barriers for fire.

The probability of ignition P(I) is calculated in formula (3.3). P(I) depends on time passed since the last burning episode (B) and natural FRI (F).

$$P(I) = \frac{T - B}{F} \tag{3.3}$$

T corresponds to the number of simulation steps (ticks) since the beginning of the simulation.

Estimating accurate FRI values requires long-term observations spanning multiple fire episodes over time. Globally, FRI can range from sub-annual values in frequently burning savannas to 1000 years or more in some temperate and boreal regions (Harrison et al., 2021). While direct observations over such long periods do not exist, indirect estimates can be derived by measuring char layers in sediment cores, ice cores, and tree rings. However, the spatial coverage of such estimates is limited. Another method to gain more insight in spatial patterns is by the use of so-called “space-for-time” substitution, based on remote sensing data of fire activity (Archibald et al., 2013). We used this substitution method to estimate the average fire-return interval for each 0.25 grid cell. It is assumed that the spatial and temporal variability in fire events is equal within a given grid cell, which allows for the interpretation of the spatial distribution of fire events as a measure for the temporal return time. For example, if a grid cell has burned for 25% in 20 years of the available satellite observation record, the resulting FRI is 20/0.25 = 80 years. In frequently burning savanna regions a grid cell could burn almost entirely each year, giving an FRI close to 1 year.

We used 2002–2020 MODIS burned area (BA) data from the MCD64A1 C6 product (Giglio et al., 2018) to calculate satellite-derived approximated FRI for four HUMLAND PFTs used in the current ABM. These PFTs were demarked using the annual PFT classification from the MCD12Q1 C6 land cover type product (Friedl & Sulla-Menashe, 2019). Evergreen and deciduous needleleaf forest classes were grouped as needleleaf trees, and evergreen and deciduous broadleaf forest classes were grouped as broadleaf trees. For each HUMLAND PFT, we first calculated the sum of 20 years of BA for each 500 m pixel, i.e., the fire frequency. We then calculated the average annual BA for each 0.25 grid cell by aggregation of the 500 m values. The FRI followed, by taking the reciprocal of the average annual BA. Afterwards, FRI values were obtained for grid cells where all four PFTs were present, and histograms of frequency distribution were created and analysed. Based on gaps and clear gradients between values on the histograms, the lowest and the highest FRI values were identified. These values were excluded, because we assumed that they reflect modern, relatively frequent fire use or delayed fire frequency due to fire management. For the remaining values, the mean FRI was calculated for each dominant PFT: 293 years for herbs, 286 for shrubs, 426 for broadleaf trees, and 246 for needleleaf trees. The obtained estimates were compared against the existing estimates derived from sediment sites dated to the Early–Middle Holocene in Europe (Dietze et al., 2018; Feurdean et al., 2013, 2017, 2019; Novenko et al., 2018; Pitkänen et al., 2001); summary of estimates from sediment sites can be found in Appendix I, Table AI.2).

3.2.3.4 Megafauna vegetation consumption

Megafauna constitutes the last agent which causes vegetation transformation in the model per simulation step. Only grid cells with fully recovered vegetation can be consumed by megafauna in HUMLAND. This assumption arises from our use of estimates for potential maximal megafauna plant consumption and the absence of data regarding partial consumption during the vegetation regrowth phase. After plant consumption, vegetation openness increases depending on the CARAIB NPP values and the maximal megafauna plant consumption estimates. We explicitly note that this assumption will underestimate megafauna impacts on vegetation regeneration in HUMLAND.

As our research primarily focuses on continental-level patterns for four broad PFT categories (Table 3.2), our analysis is conducted at a higher ecological scale than the plant taxon level. As a result, it is assumed that megafauna equally consume all PFTs present on a grid cell, i.e., besides the first dominant PFT megafauna consume the second, third and fourth dominant PFTs in equal proportions. Therefore, the first dominant PFT is replaced only if the vegetation was entirely consumed by megafauna and the vegetation openness value after consumption is 100%. In this case, the first dominant PFT would be replaced by bare ground.

The percentage of consumed vegetation (V_c) is calculated for each grid cell excluding water bodies and high mountains via formula (3.4):

$$V_c = \frac{V_m}{V_n} \times 100 \tag{3.4}$$

V_m and V_n values are obtained from datasets: V_m is a grid cell value for megafauna metabolization of NPP, and V_n is CARAIB NPP. After calculating the percentage of consumed vegetation in a grid cell, this value is combined with the vegetation openness value to enhance it following megafauna impact. The percentage of consumed vegetation influences the timing of reaching 100% in P(I) and, as a result, the effects of vegetation change caused by fires can be postponed due to consumption. Finally, the update of the first dominant PFT depends on the resulting vegetation openness achieved after vegetation consumption.

3.2.4 Experiments, observations, and analysis

The primary observations made during simulation runs include the distribution of the first dominant PFTs (percentage of grid cells covered by each of four general PFTs) and mean vegetation openness. We collected these observations only for grid cells that have both CARAIB and REVEALS values. The ABM output is considered similar to REVEALS data if the observations and REVEALS values vary within ±5% (the range of change is 10%).

Several sets of experiments were conducted, and every parameter combination had 30 runs whose outputs were analysed in R with the *ggplot2* (Wickham, 2016) and *tidyverse* (Wickham et al., 2019) packages. The adequacy of this number of runs is underscored by the minimal standard deviation observed across nearly all outputs (standard deviation values are in Tables AI.3, AI.4, AI.5, AI.7, and AI.8 of Appendix I).

During the first set of experiments, vegetation had only two types of impact: humans and climate; megafauna and climate; thunderstorms and climate. The main objective of these experiments was to isolate the impact of humans, megafauna, and natural fires, in order to determine whether it was possible to achieve REVEALS estimates without considering all agents together. Furthermore, this also served to establish the number of simulation steps required to reach equilibrium (i.e., state of a simulation when the values for primary observations do not significantly change anymore). During the first set of experiments, we also identified the highest achievable parameter values, as these are only attainable when exclusively one of the three impact types–megafauna, anthropogenic, or natural fires–is operative, leading to outcomes similar to REVEALS outputs. The identified maximum parameter values were integrated into the sensitivity analysis (see below).

Secondly, megafauna, thunderstorms, and climate impacted vegetation together. These experiments defined in which case the simulation reached the

REVEALS estimate without any role of humans. Finally, all four types of impact were combined to conduct a sensitivity analysis, to produce potential scenarios, and to identify the most influential agent in continental-level vegetation change.

A sensitivity analysis was performed via the *nlrx* R package (Salecker et al., 2019) to understand what defines the intensity of human-induced vegetation changes. Sensitivity analysis was conducted via the Latin Hypercube Sampling (LHS) technique developed by McKay et al. (1979), and Iman and Conover (1980). This method ensures that each factor is represented in a balanced manner irrespective of their importance (Saltelli et al., 2004). The technique involves dividing the ranges of parameter values into equally probable intervals and then sampling from each interval to ensure a representative sample of the input space. In this study, we conducted one LHS run, as multiple runs would demand a substantial amount of time and computational resources. LHS set up had two random seeds, and collected 160 samples for each run. Then, we used Partial Rank correlation coefficient (PRCC) which is widely used in sensitivity studies to measure the strength of a linear association between input and output (Hamby, 1994; Marino et al., 2008).

Once the most influential factors for human-induced vegetation change were identified via LHS/PRCC, the minimum, midpoint (average) and maximum values for these parameters were used to identify the first potential scenarios of vegetation change. Each parameter combination had 30 runs. A two-sample t-test for 500 randomly selected cells was conducted, and the F1-score was calculated for the REVEALS dataset and potential scenarios similar to REVEALS data.

3.3 Results

3.3.1 CARAIB and REVEALS datasets comparison

Out of the total 21,203 10 × 10 km grid cells with both REVEALS and CARAIB estimates, 25% of the grid cells were excluded from further analysis, as CARAIB predicts lower vegetation openness than the REVEALS results. Figures 3.2 and 3.3 show data comparison results after importing these datasets to HUMLAND and excluding the conflicting grid cells. There are more grid cells with the primary dominance of trees in the CARAIB dataset (Fig. 3.2 A, B) than in REVEALS (Fig. 3.2 C, D). F1-score for these two datasets is 0.001 with accuracy 0.51. Regarding the vegetation openness, REVEALS shows a more open landscape in comparison with CARAIB estimates (Fig. 3.3). The mean values for vegetation openness are 43% and 20%, respectively (Fig. 3.3C), and the t-value = -20.85 for 500 randomly selected cells (p-value < 2.2e-16, df = 998).

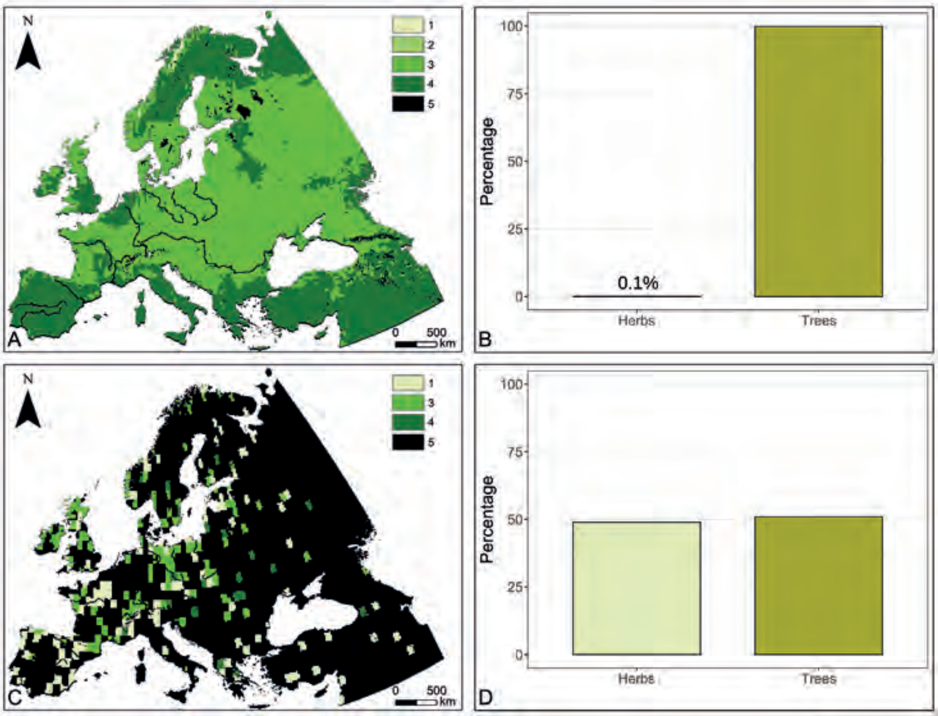


Figure 3.2 CARAIB (A) and REVEALS (C) first dominant HUMLAND PFT distribution accompanied with bar graphs of the proportions (100% on the bar graphs equals the number of grid cells with both REVEALS and CARAIB estimates) of CARAIB (B) and REVEALS (D) after excluding the grid cells where CARAIB predicts lower vegetation openness than the REVEALS results. Legend: 1–herbs; 2–shrubs; 3–broadleaf trees; 4–needleleaf trees; 5–no data.

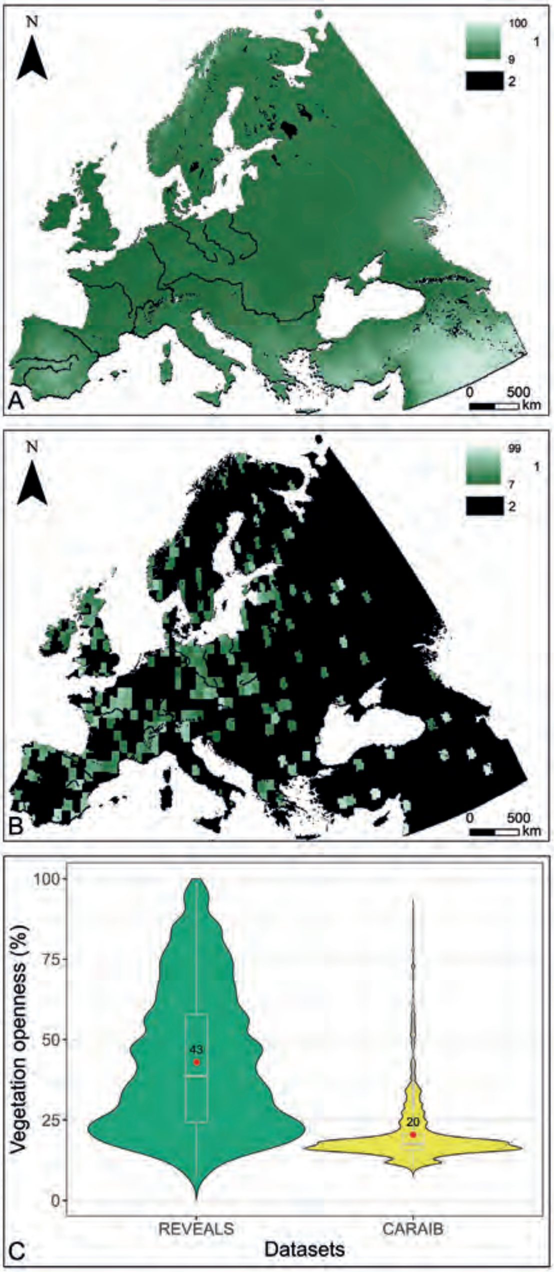


Figure 3.3 Vegetation openness of CARAIB (A) and REVEALS (B) with a summary of these datasets and their values' distribution only for grid cells with both REVEALS and CARAIB estimates (C) after excluding the grid cells where CARAIB predicts lower vegetation openness than the REVEALS results. In subfigure C the dot indicates the mean value for each dataset. Legend: 1–vegetation openness in percentages; 2–no data.

3.3.2 Natural fires and megafauna impact without human presence

The results of experiments when thunderstorms and megafauna impact separately without human presence showed that minimal impact of natural fires starts when 0.1% of all terrestrial cells have thunderstorms (Fig. 3.4 A, B). REVEALS trees (Fig. 3.4A) and vegetation openness (Fig. 3.4B) estimates are reached when 7% and 4.7% of all terrestrial cells are impacted by thunderstorms. These values are maximal for the parameter which defines the number of thunderstorms per simulation step. The equilibrium is reached after 450 steps (Fig. 3.4A and B).

The impact of megafauna plant consumption did not have a significant effect on the vegetation (Fig. 3.4C and D), because the percentage of consumed vegetation never exceeds 1%. The obtained modelling results thus show that megafauna does not significantly change the distribution of dominant PFTs and

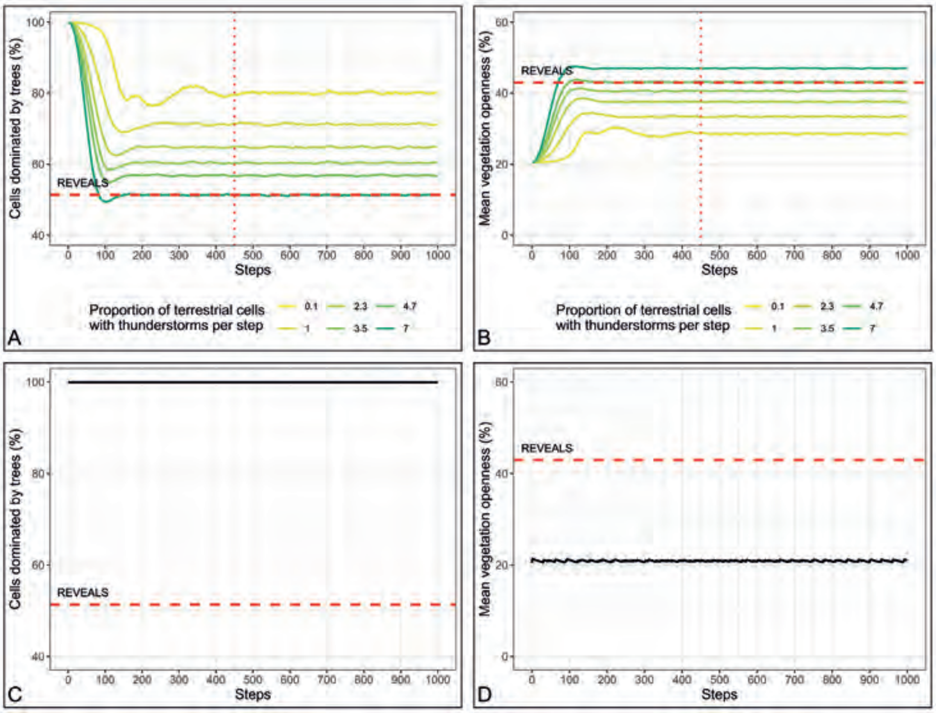


Figure 3.4 Percentage of cells dominated by trees (A) and mean vegetation openness (B) after natural fires caused by thunderstorms and impact of climate, and percentage of cells dominated by forest (C) and mean vegetation openness (D) after megafauna vegetation consumption and impact of climate. Each line depicted on the experiment output graph represents the mean of 30 simulation runs. The horizontal dashed line indicates REVEALS estimates, and the vertical dotted line shows the step when simulations reach equilibrium.

mean vegetation openness on the continental level. Due to the low intensity of megafauna impact, the experiments with a combination of the three types of impact (thunderstorms, climate and megafauna) did not lead to different maximal and minimal Territory_impacted_by_thunderstorms parameter values, in comparison to the results obtained when thunderstorms and climate impact vegetation without megafauna presence.

3.3.3 Anthropogenic impact on vegetation without natural fires and megafauna plant consumption

Several sets of experiments with only anthropogenic and climatic impacts were conducted to define maximal and minimal values for five parameters associated with human-induced vegetation change. Firstly, the Number_of_hunter-gatherer_groups parameter was varied, while others remained constant (Openness_criteria_to_burn = 50, Campsites_to_move = 50, Movement_frequency_of_campsites = 500, Accessible_radius = 5). Human induced vegetation changes start when there is only one group present (Fig. 3.5), and, therefore, this is the minimal value for this parameter. REVEALS openness estimates were reached when 3128 groups impact vegetation and REVEALS percentage of cells dominated by forest was reached with 3167 groups (Fig. 3.5). Thus, the maximum parameter value for Number_of_hunter-gatherer_groups is not lower than 3167.

Fig. 3.5 demonstrates a noticeable difference in simulation outcomes between the minimum (1) and maximum (3128 and 3167) values of the Number_of_hunter-

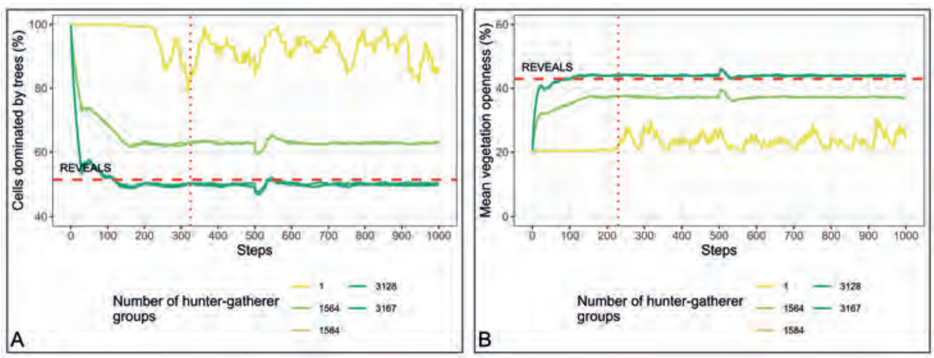
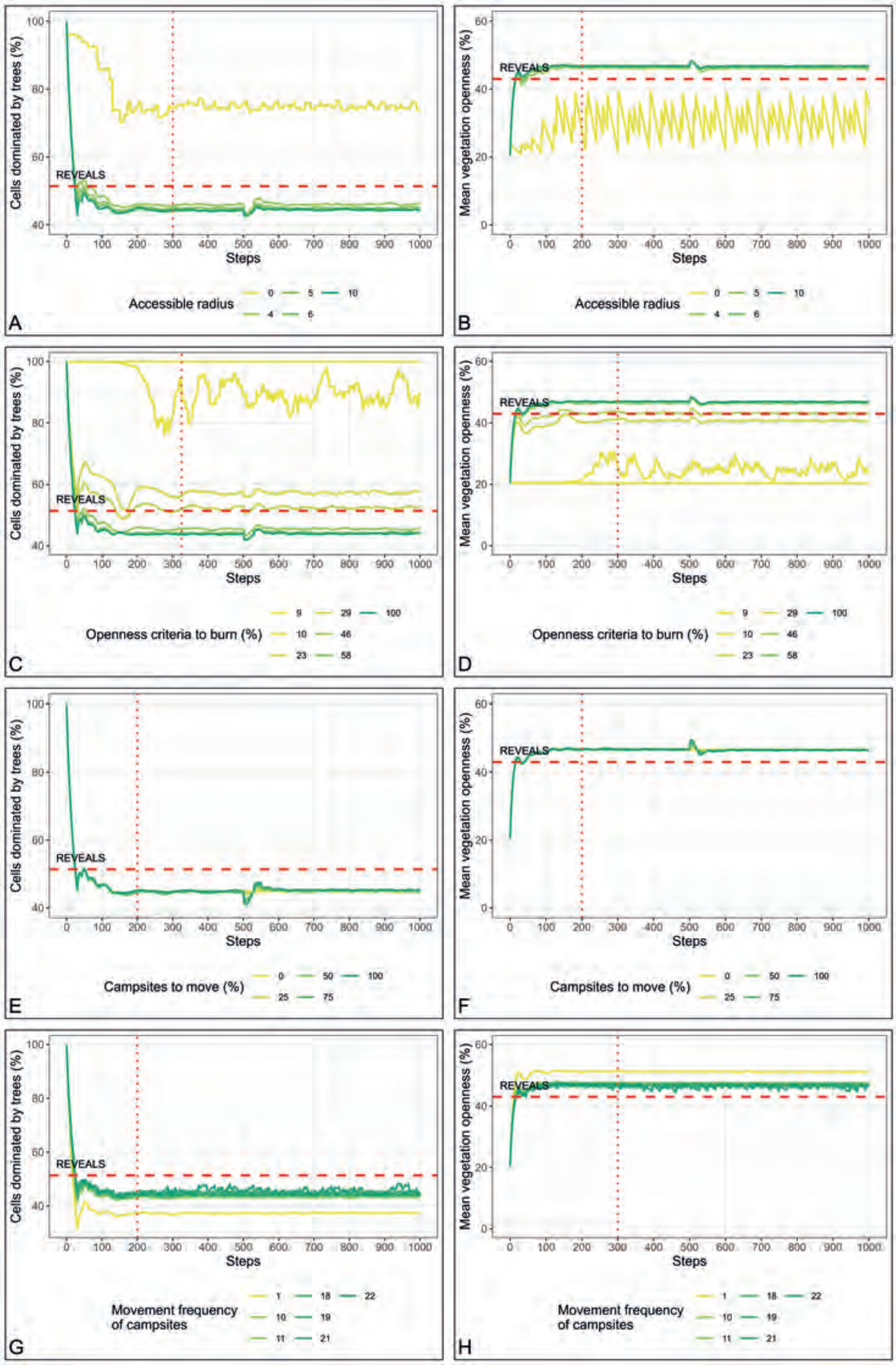


Figure 3.5 Percentage of grid cells dominated by trees (A) and mean vegetation openness (B) caused by different numbers of hunter-gatherer groups and climatic impacts. Each line depicted on the experiment output graph represents the mean of 30 simulation runs. The horizontal dashed line indicates REVEALS estimates, and the vertical dotted line shows the step when simulations reach equilibrium.



Cells dominated by trees (%)
Mean vegetation openness (%)
REVEALS
Steps
Accessible radius
0 5 10 4 6
Openness criteria to burn (%)
9 29 100 10 46 23 58
Campsites to move (%)
0 50 100 25 75
Movement frequency of campsites
1 18 22 10 19 11 21
A
B
C
D
E
F
G
H

Figure 3.6 Results of experiments conducted for 4000 hunter-gatherer groups: A–percentage of grid cells dominated by trees after the accessible radius was varied; B–mean vegetation openness after the accessible radius was varied; C–percentage of cells dominated by trees after the openness criteria to burn was varied; D–mean vegetation openness after the openness criteria to burn was varied; E–percentage of grid cells dominated by trees after the percentage of moving campsites was varied; F–mean vegetation openness after the percentage of moving campsites was varied; G–percentage of grid cells dominated by trees after the movement frequency was varied; H–mean vegetation openness after the movement frequency was varied. Each line depicted on the experiment output graph represents the mean of 30 simulation runs. The horizontal dashed line indicates REVEALS estimates, and the vertical dotted line shows the step when simulations reach equilibrium.

gatherer_groups parameter, highlighting its significant impact on the model output. To further understand the impact of other parameters on the model output and track its behaviour in relation to different human population sizes, we varied the parameters related to anthropogenic burning for 100, 1000, and 4000 groups. The experimental results for 4000 groups are presented in Fig. 3.6, as this value was determined to be the maximum parameter value. This was because the majority of simulation outputs for 4000 groups exceeded REVEALS estimates. The graphs with the results of experiments for 100 and 1000 groups can be found in the appendix.

The variation of values for Accessible_radius parameter produces different model outputs when this parameter is set to 5 or lower (Fig. 3.6A). The simulation results do not change significantly when the radius has higher values. Additionally, we found that the simulations reach their equilibrium after 200 to 300 steps.

The parameter Openness_criteria_to_burn must not be set lower than 9%, as this corresponds to the minimum threshold for vegetation openness of the CARAIB dataset (Fig. 3.1B). When this parameter is set to 58% the model output in terms of the mean percentage of cells dominated by trees does not change significantly. Similarly, the mean vegetation openness does not change significantly when Openness_criteria_to_burn is set to 46% (Fig. 3.6 C, D). Therefore, 58% is the maximum possible value for the Openness_criteria_to_burn parameter. After 300 steps, the simulations reach their equilibrium.

The results remain largely unaffected by variations in the Campsites_to_move parameter (Fig. 3.6 E, F), i.e., its low and high values produce similar results. On the contrary, values between 1 and 21 for the Movement_frequency_of_campsites parameter led to different results (Fig. 3.6 G, H), and the equilibrium is reached after 200 steps. If this parameter has values higher than 21, the output does not vary.

As a result of this research step, the model behaviour was examined in relation to climatic impact together with the separate impacts of each agent: humans, thunderstorms, megafauna, or the combination of the latter two. We identified the maximum and minimum parameter values, and the number of steps required to reach equilibrium. These estimates served as the foundation for setting up the sensitivity analysis.

3.3.4 Sensitivity analysis: combined impact of humans, megafauna, climate and natural fires on vegetation

Table 3.3 provides a detailed overview of the sensitivity analysis experiment that was undertaken to assess the extent to which different parameters influence the model outcomes. The analysis was based on the findings presented in Sections 3.3.2 and 3.3.3. Several parameter settings in the sensitivity analysis, such as Territory_impacted_by_thunderstorms, Accessible_radius, and Movement_frequency_of_campsites, correspond to the maximum and minimum values identified in these sections. We set the maximum value of Number_of_hunter-gatherer_groups to 4000, as experiments with separate impact of humans and climate revealed that this parameter's maximum value is not less than 3167, and most of the simulation outputs exceeded REVEALS results when this parameter was set to 4000. Experiments showed that the maximum value for the Openness_criteria_to_burn parameter varies greatly depending on the Number_of_hunter-gatherer_groups value. Due to this, Openness_criteria_to_burn was set to 100% in the sensitivity analysis to explore all possible combinations for this parameter with other settings. Moreover, we assigned 100% as the maximum value for Campsites_to_move to confirm that this parameter is relatively less important for HUMLAND output despite the value of this parameter.

Table 3.3 Details of the sensitivity analysis experiment.

Parameter	Variable/constant	Min	Max
Territory_impacted_by_thunderstorms	Variable	0.1	7
Megafauna	Constant	True	
Number_of_hunter-gatherer_groups	Variable	1	4000
Accessible_radius	Variable	0	5
Openness_criteria_to_burn	Variable	9	100
Campsites_to_move	Variable	0	100
Movement_frequency_of_campsites	Variable	1	21

The sensitivity analysis considers the combined impact of all agents, including constant presence of megafauna in all simulations. In Figure 3.4, we identified the maximum starting point for equilibrium during simulations with the separate impact of each agent at step 450. As a result, we took the primary measurements– mean vegetation openness and the percentage of grid cells dominated by trees– between steps 450 and 1000 for the sensitivity analysis.

As we can see in Figure 3.7, four parameters (Number_of_hunter-gatherer_groups, Accessible_radius, Openness_criteria_to_burn, and Territory_impacted_by_thunderstorms) have greater influence on the model output than parameters associated with campsites' movements (Campsites_to_move and Movement_frequency_of_campsites). All the parameters, except for Movement_frequency_of_campsites, exhibit PRCC values with p-values<0.05, indicating their statistical significance within LHS/PRCC analysis. Thus, the choice of 160 samples for two random seeds proved to be appropriate as it yielded statistically significant results. For the Movement_frequency_of_campsites parameter, the p-values are 0.17 (mean vegetation openness) and 0.14 (grid cells dominated by trees in

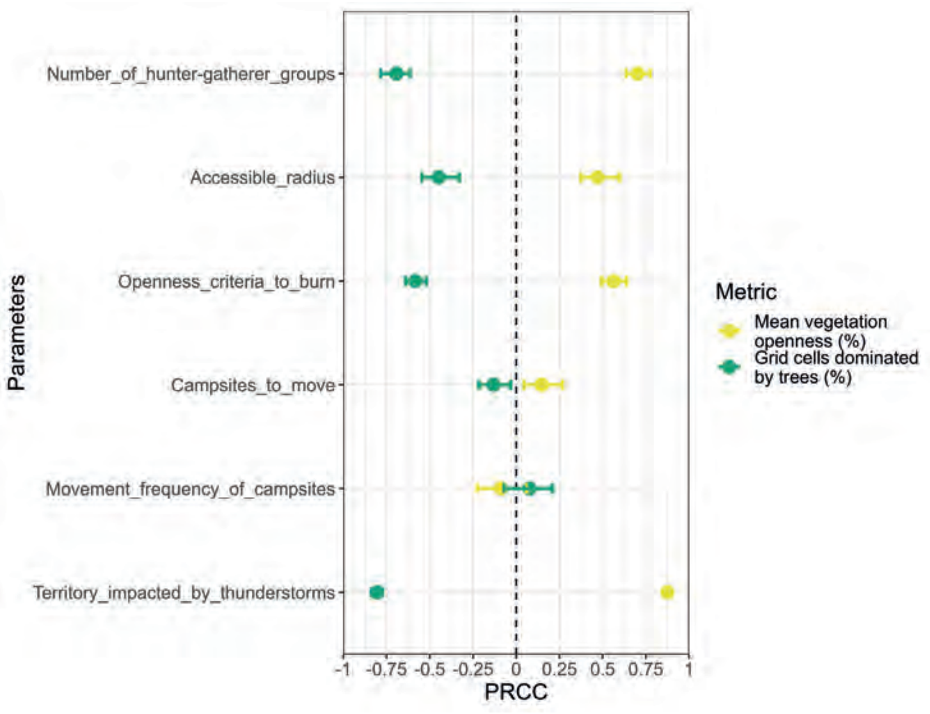


Figure 3.7 Results of LHS/PRCC sensitivity analysis with bars representing standard errors.

percentage). While these p-values > 0.05, it can still be concluded that its impact on the model output is relatively weaker. This is because the Movement_frequency_of_campsites parameter operates in conjunction with Campsites_to_move, and if it is set to 0%, the campsites will not be relocated regardless of their movement frequency.

3.4 Discussion

3.4.1 How much do pollen-based estimates correspond to climate-based vegetation cover?

Comparison of CARAIB and REVEALS datasets indicated a substantial difference between the two. Due to the low F1-score, they have poor agreement in terms of the first dominant PFTs distribution. Similar patterns came from the comparison of vegetation openness for these datasets. The results of the two-sample t-test showed that there is a substantial difference between them, and that the difference is unlikely to be due to random variation.

Since REVEALS and CARAIB are not “equal” models (i.e., REVEALS quantitatively reconstructs regional vegetation abundance from pollen assemblages and CARAIB is a dynamic vegetation model driven by climate forcings and assumptions about vegetation dynamics), the observed difference between REVEALS and CARAIB datasets can be partially explained by loss of information due to reclassification and resampling and the difference in the models themselves (Dallmeyer et al., 2023; Zapolska et al., 2023a). Discrepancies between CARAIB and REVEALS can be also partially explained by the different migration vegetation lags in different parts of Europe (Dallmeyer et al., 2022; Giesecke et al., 2017). However, quantifying the distinctions arising from variations in the models themselves and those resulting from plant migration remains challenging to quantify. The findings of Zapolska et al. (2023b) indicate that incorporating the CDF-t bias correction in the workflow significantly improves the overall reliability of CARAIB results when compared to independent reconstructions. Overall, given the spatio-temporal resolution and aggregated classification (Table 3.2), despite the acknowledged methodological biases we consider the provided datasets to be sufficiently reliable for the outlined research purposes of this study. CARAIB quantifies the amount of bare ground for each grid cell, unlike REVEALS. Therefore, estimates of bare ground can be used as a potential marker for the comparison results reliability (i.e., high fraction of bare ground indicates low reliability of comparison results) (Fig. AI.5 with bare ground fraction is available in Appendix I).

Comparing models like REVEALS and CARAIB would require modifying their initial results, as they produce different outputs. To address this issue, HUMLAND uses PFTs (Table 3.2) to combine CARAIB and REVEALS datasets in a continental-scale ABM. However, this approach may not be suitable for every biogeographical region in Europe, and regional differences between the models are not fully considered in the current study. Moreover, the current study's time constraints are based on REVEALS temporal resolution, which uses 500-year-long time windows to minimize standard errors and study vegetation transformations over millennia (Serge et al., 2023).

It is important to highlight that REVEALS was applied on pollen data from all sites (large lakes > 50 ha, and/or multiple sized lakes and bogs). Water bodies such as lakes tend to attract herbivores, and their activity can significantly alter ecosystems by reducing canopy height and structure, increasing in speed dispersal rates and trampling effects, and, therefore, changing plant species competition by promoting grazing-adapted species, transformation of carbon and nutrient cycles, increase in landscape heterogeneity, etc. (Bakker et al., 2016b). Hence, the difference between the REVEALS dataset and the CARAIB reconstruction in terms of higher vegetation openness could be attributed, at least in part, to local pollen counts influenced by the presence of megafauna near the sample sites. However, it is important to note that the vegetation reconstruction derived from REVEALS does not reflect the local conditions immediately around the water bodies where the samples were collected. Instead, it provides a broader perspective of regional and sub-continental vegetation coverage, and has been well validated using modern and historical data (Hellman et al., 2008; Marquer et al., 2020; Trondman et al., 2016). Therefore, the openness values obtained from REVEALS are likely not reflective of only the local impact of herbivores in the vicinity of the lakes.

Thus, it is crucial to emphasize that the CARAIB and REVEALS datasets exhibit substantial dissimilarities. We acknowledge that these disparities stem from factors such as inherent model differences, vegetation migration lags, variable sources of errors, etc. Despite these caveats, it is important to underline that the observed vegetation cover is not solely a product of climatic impact; other factors have also played a pivotal role in shaping vegetation in the study area.

3.4.2 What defines the intensity of anthropogenic impact?

Based on the results of LHS/PRCC, we can conclude that the impact of hunter-gatherer vegetation burning on continental-level is influenced by three key factors. Firstly, the intensity of these changes is contingent upon the number of hunter-gatherer groups inhabiting a given area, thereby establishing a link between population size and the strength of anthropogenic impact.

Secondly, the extent of human-induced vegetation change is determined by the natural vegetation openness around campsites. This factor might be connected to the preferences of the hunter-gatherers when selecting the location for their campsites. Numerous studies have been conducted on this topic, and among the predominant factors influencing the distribution of campsites are distance to water sources or to coasts, food resources and raw materials availability (Abe et al., 2016; Garcia, 2013; Zolnikov et al., 2013). The importance of these factors varies depending on the specific study area, period, and subsistence strategies of the hunter-gatherer groups. Other factors, such as surface area roughness or sun exposure, may also play a role (Zolnikov et al., 2013). Vegetation openness can be an additional factor that defines the spatial distribution of hunter-gatherer sites. Depending on the practices of specific hunter-gatherer groups and preferred openness, humans may initially choose naturally open areas that could contain the resources needed. In cases where such areas are not available, hunter-gatherer groups with knowledge of vegetation burning techniques could modify the surrounding environment to match their preferences and make specific areas suitable for their hunting activities and/or (re-)growth of consumed plants. Therefore, the openness of vegetation can be taken into consideration for hunter-gatherers when selecting campsite locations.

The parameters associated with the mobility of hunter-gatherers include Accessible_radius, Campsites_to_move, and Movement_frequency_of_campsites. Among these, Accessible_radius holds a greater influence on the model output compared to the latter two factors, which have minimal contributions to human-induced vegetation changes. This is because these parameters primarily allow the vegetation a chance to recover and return to its natural state in HUMLAND. On the other hand, the accessible radius, with higher values, creates a wider area around campsites that experiences constant anthropogenic impact without sufficient time for recovery. In other words, the movement frequency of campsites and number of campsites that relocate provide opportunities for vegetation to regenerate after anthropogenic impact, allowing these areas to revert to their initial condition. Conversely, a larger accessible radius extends the reach of human influence, creating a broader zone around campsites where vegetation is consistently impacted without adequate time for regrowth.

3.4.3 First insights into the role of hunter-gatherers and other agents in continental-level vegetation change

There are three types of impact which cause an increase of vegetation openness in this ABM: megafauna plant consumption, natural and human-induced fires. Before addressing the role of humans, it is important to clarify how two other forms of impact reshape the HUMLAND landscapes. While searching for initial potential scenarios to establish a context for human-induced modifications, we maintained parameter values related to the impact of megafauna and natural fires as constants.

The findings of this study reveal that the maximum potential consumption of vegetation by megafauna did not yield significant changes in vegetation (Fig. 3.4C and D). It is worth considering that our observations might be influenced by the different nature of anthropogenic and megafauna impacts on vegetation. Humans can impact both upper (trees) and lower (shrubs and herbs) levels of vegetation via fire use. In contrast, the influence of megafauna on these vegetation levels depends on the species present in a given area. If large and megaherbivores occupy an area, these animals employ diverse feeding strategies, enabling them to affect vegetation on multiple levels through plant consumption, as well as other forms of impact such as bark stripping and trampling (Beschta et al., 2020; Kowalczyk et al., 2021)–actions that likely reduced the abundance of woody plants (Bakker et al., 2016a; Pedersen et al., 2023). By the time of the Early Holocene, the decline in large animal populations must have lessened their impact on these plants, likely contributing to an increased frequency of fires and the spread of woody vegetation (Bakker et al., 2016a). Our study potentially aligns with this trajectory, as the megafauna impact within the HUMLAND did not diminish the proportion of cells dominated by trees throughout the studied one Early Holocene time window (Fig. 3.4C).

In HUMLAND simulations, we used estimates of potential maximal megafauna plant consumption. However, this level of consumption may not have been sustained at the same constant intensity level throughout every simulation step, particularly during phases of vegetation recovery after consumption or fires. If megafauna consumption is modelled at every simulation step with the same intensity as in the potential maximal consumption dataset, the HUMLAND output exhibits overestimation of vegetation openness relative to the REVEALS estimates, due to impediment of regrowth of woody vegetation across significant portions of the study area. In light of this, we deliberately excluded the interference of megafauna in the process of vegetation regrowth in HUMLAND. Hence, our modelling is likely to underestimate the effect of megafauna on the vegetation during its regeneration phase after disturbance, as herbivores often seek out such early-successional patches (due to accessibility of forage) and thereby may exert strong influence on tree regeneration (Kowalczyk et al., 2021). Additionally, the maximal extent of animal plant consumption might have been higher than indicated by the potential maximal megafauna plant consumption dataset due to underestimates of natural densities and overall biomasses caused by anthropogenic pressures across natural areas today (Robson et al., 2017).

Conversely, the HUMLAND model does not incorporate the hunting pressure that humans exerted on these animals and which may have decreased their impact.

Regarding natural fires, achieving the REVEALS estimates solely through the impact of thunderstorms is theoretically possible. However, it would require an unrealistic occurrence of thunderstorms affecting 4.7–7% of the study area every year (Fig. 3.4A and B), surpassing current estimates of thunderstorm frequency in Europe (see below). Consequently, to align with observed vegetation cover via REVEALS, the inclusion of human influence in our experiments becomes necessary.

To generate preliminary potential scenarios of modified vegetation, the most influential parameters associated with human activities were varied across their minimum, midpoint and maximal round values: Number_of_hunter-gatherer_groups (1, 2001, 4000), Accessible_radius (0, 3, 5), and Openness_criteria_to_burn (9, 55, 100). Campsites_to_move (50) and Movement_frequency_of_campsites (500) remained constant because they are less influential for the model output (sections 3.3.4 and 3.4.2).

LHS/PRCC results (Fig. 3.7) showed that the Territory_impacted_by_thunderstorms parameter has significant impact on the model output, but this parameter was constant during the generation of initial potential scenarios. Due to the absence of continental Early Holocene thunderstorm frequency estimates for Europe, we used decadal lightning observations for Europe during the period of 2008–2017 (Enno et al., 2020). In accordance with these estimates, the majority of Europe experiences 20−40 thunderstorm days per 1 km^2 annually (ibid.). Considering that thunderstorms in HUMLAND can only occur once on a grid cell per simulation step, it would mean that 0.02–0.04% of all grid cells would encounter the impact of thunderstorms every simulation step. Thus, the Territory_impacted_by_thunderstorms parameter had a constant value of 0.04 during these experiments.

If any variable is set to its minimum value, the model output significantly differs from REVEALS estimates, and they cannot be reached (Fig. 3.8). All variables should be between their maximal and midpoint values to obtain a scenario which matches REVEALS estimates. Consequently, hunter-gatherers practiced their activities and altered vegetation within a radius of 40−60 km around campsites (equivalent to 3 to 5 grid cells around a cell with a campsite on it in HUMLAND). Because the accessible radii in HUMLAND includes both foraging and logistical radii and varies between 0 and 5 grid cells (10−60 km including the grid cell with a campsite on it), the values of this parameter are expected to be more than 0 because this area only includes the foraging radii which is rarely beyond ~10 km (Binford, 1982). Within this range, only plant food, small game and aquatic

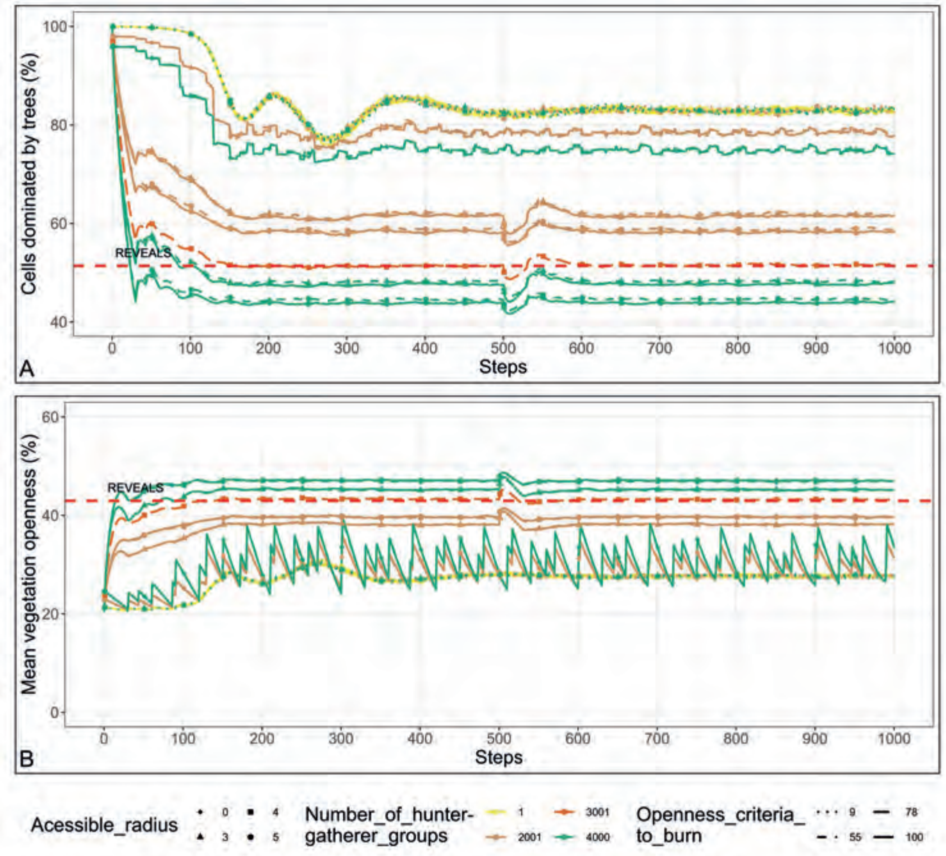


Figure 3.8 Percentage of grid cells dominated by trees (A) and mean vegetation openness (B) after combined impact of humans, climate, megafauna and natural fires. The following parameters were varied: number of hunter-gatherer groups, accessible radius and openness criteria to burn. Movement frequency of campsites (500), the number of them which move at specific time (50%), proportion of terrestrial cells with thunderstorms (0.04%) remained constant with fixed presence of megafauna plant consumption. Each line depicted on the experiment output graph represents the mean of 30 simulation runs. The horizontal dashed line indicates REVEALS estimates.

resources were available for hunter-gatherers. The importance of logistical radii increases with increasing dependence on large games (Kelly, 2013).

Presuming that the assumptions driving our modelling exercise are correct, our results indicate to what extent hunter-gatherer burning of landscapes could explain the landscape openness inferred from REVEALS. It is important to note that preferences for vegetation openness can vary among different hunter-gatherer groups, influenced by their specific adaptations, resource exploitation, and cultural practices. However, our results highlight a general trend of high-frequency human-induced fires. Repetitive small-scale fire use created mosaic environments with a diverse range of resources around their campsites, fostering variability and resource productivity (Bird et al., 2020; Nikulina et al., 2022; Scherjon et al., 2015).

Regarding the population size of hunter-gatherer groups, our results showed that the required number of groups to reach REVEALS estimates falls between 2001 and 4000 groups during the studied period (9200–8700 BP) (Fig. 3.8). Generally, historically documented hunter-gatherers exhibited significant variation in local group size, with an average of 25 (Kelly, 2013). Given the considerable variability in group size, estimating the population of Mesolithic humans using HUMLAND presents a challenge, and it should be noted that this was not the primary focus of this study. However, based on average estimates of group size, we can suggest that during 9200–8700 BP there were potentially around 50,000–100,000 people at least.

Comparing our estimates with other studies proves challenging due to the variability in already published data regarding hunter-gatherer population size. Some studies indicate that at approximately 13,000 BP, the human population size was estimated to already be around 410,000 individuals (Tallavaara et al., 2015). Conversely, other research suggests that, at 14,700 years BP, the population size was around 155, 000 individuals, which then decreased to approximately 143,000 individuals at 11,700 BP (Ordonez & Riede, 2022). The largest population size inferred was around 8000 BP of around 213,900 individuals, with a minimum estimate of around 52,000 individuals and a maximum estimate of approximately 1,111,000 individuals (ibid.). Finally, population size estimated in History database of the Global Environment (HYDE) 3.2. varies between 26,000 and 666,900 during 9000 BP, and between 46,420 and 881,890 during 8000 BP in Europe (Goldewijk et al., 2017). HUMLAND's population estimates are generally lower than other studies showed. This difference arises from HUMLAND's exclusive consideration of fire-utilizing populations, potentially underestimating the overall human population due to the omission of groups which did not practice landscape burning.

The currently obtained results for the three different parameters are still in a preliminary stage. As the first demonstration of the full potential of HUMLAND in identifying the most influential factor in continental-level vegetation change, we have produced one possible scenario which closely aligns with the results obtained through the REVEALS analysis (Fig. 3.8). In this scenario, we simulated 3001 hunter-gatherer groups that moved and burned areas where the vegetation openness was equal to or lower than 78% within a four-cell radius around their

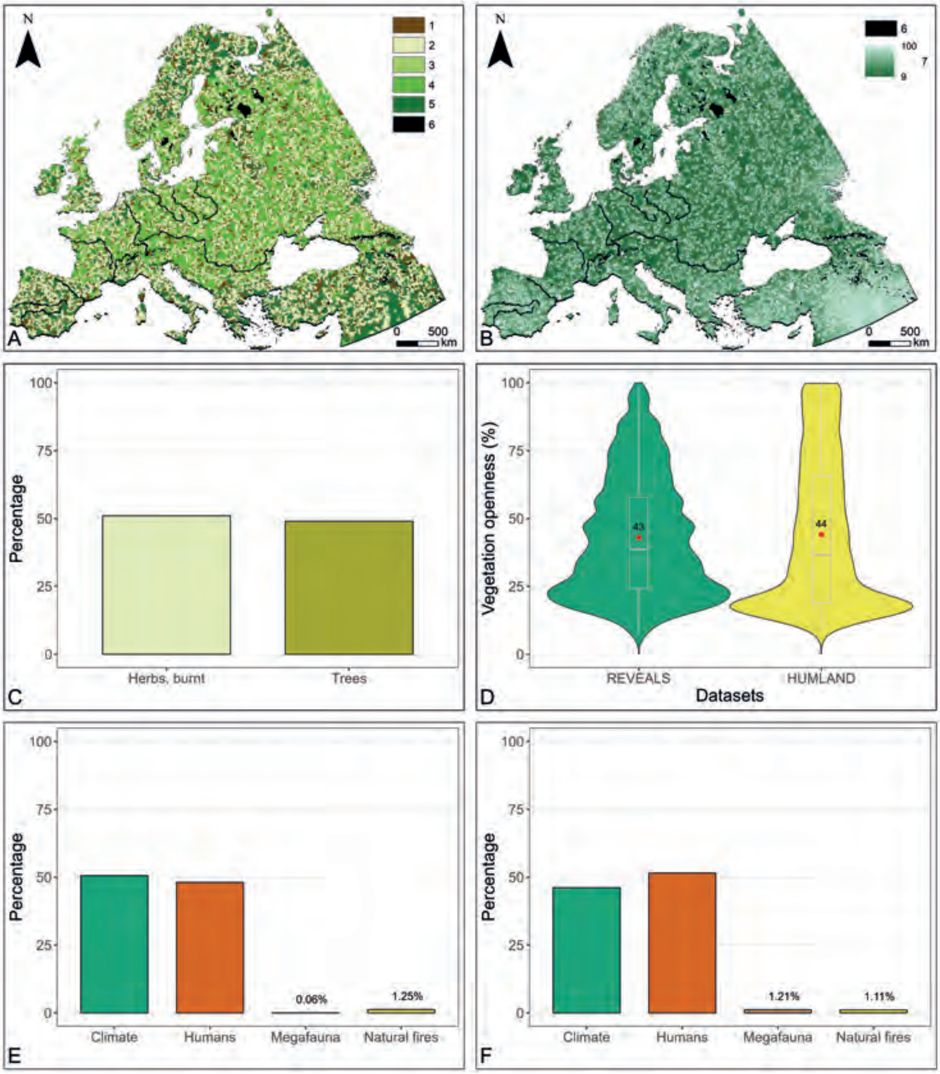


Figure 3.9 Possible scenario of modified first dominant PFTs (A), vegetation openness (B), bar graph of dominant PFT proportions (C), summary statistics of vegetation openness and their values' distribution (D; the dot indicates the mean value for each dataset) in the end of a HUMLAND run, and mean percentage of cells modified by different agents (impact on dominant PFTs (E) and vegetation openness (F) during equilibrium state). Dominant PFT proportions and summary statistics of vegetation openness were calculated for the cells with REVEALS and CARAIB estimates after excluding the grid cells where CARAIB predicts lower vegetation openness than the REVEALS results. Legend: 1–recently burnt areas; 2–herbs; 3–shrubs; 4–broadleaf trees; 5–needleleaf trees; 6–no data; 7–vegetation openness in percentages.

campsites. This scenario matches the REVEALS estimates, as the averaged ABM output of 30 runs after 450 steps exhibits a similar percentage of trees-dominated cells and mean vegetation openness to the REVEALS results (Fig. 3.8). The only deviation occurs at step 500 when the human agents relocate their campsites.

The obtained F1-score for this scenario is 0.50 with an accuracy of 0.51. In addition, we conducted a statistical analysis comparing 500 randomly selected grid cells from both the REVEALS and ABM output. The computed t-value was -2 (p-value = 0.03, df = 998). Thus, this scenario has stronger alignment with REVEALS, compared to CARAIB and REVEALS (Fig. 3.2, 3.3). Due to that, this scenario could serve as a possible representation of past modified landscapes Fig. 3.9).

Since this scenario matched the REVEALS data, we further examined the extent of modifications performed by each agent. Specifically, we averaged the observations of the number of grid cells modified by each agent from steps 450 to 1000 (Fig. 3.9E and F). Climate and humans were estimated as the factors responsible for the majority of changes, whereas megafauna and natural fires caused by thunderstorms in this ABM played a smaller role as evidenced by the mean number of grid cells modified by each agent during the equilibrium state. These findings suggest that humans and climate were the most influential factors in driving continental-level vegetation changes, while natural fires and megafauna activities in HUMLAND had less impact.

Increased burning during the Early Holocene has been previously identified in Europe on the basis of sedimentary charcoal records (Marlon et al., 2013). It was suggested that the impact of anthropogenic fire use was limited, mainly due to the relatively low population size (ibid.). High fire activity aligned with ecosystems reorganization as a result of deglaciation (ibid.). Our results suggest that early anthropogenic impact on the environment was the principal non-climate factor affecting landscapes during the early Holocene, in line with evidence obtained in other parts of the world (Ellis et al., 2021). It is important to highlight that our observations represent general patterns at the continental level. We acknowledge the possibility of regional variations, i.e., instances where humans may have had a smaller impact compared to climate, megafauna, and natural fires, and we also note the limitations to representation of some of these factors in the model.

3.5 Conclusion

We introduced the novel HUMLAND ABM application, capable of tracking and quantifying different types of impact on interglacial vegetation at the continental level. We compared the climate-based (CARAIB) and pollen reconstruction-based

(REVEALS) estimates for vegetation cover for a specific time window (9200–8700 BP), and our findings show a substantial disparity between the two datasets. We conclude that climate is just one of several factors contributing to the observed vegetation patterns, and other drivers also played an important role.

Our analysis showed that humans could constitute the primary non-climate drivers shaping European landscapes in the period analysed. The extent of anthropogenic vegetation modifications hinges primarily on three key parameters: the number of human groups, vegetation openness around campsites, and the size of an area impacted by humans. The first obtained scenario emphasized that humans had a strong impact on vegetation during the Early Holocene.

This study highlights the feasibility of creating a modelling approach suitable for tracking and quantifying the intensity of different impacts on interglacial landscapes at the continental level. Future work can focus on increasing the number of time steps to mitigate the differences between REVEALS and CARAIB datasets, and thus enhance our understanding of past processes by examining the temporal progression of our modelling exercises and their findings. In addition, more work is needed on how to represent the role of megafauna in vegetation dynamics and the potential role of hunting and other human activities therein.

Overall, this research contributes to our understanding of past human-environment interactions and demonstrates the potential of the HUMLAND ABM. The identified challenges and future directions highlight the need for continued interdisciplinary efforts and the acquisition of high-quality datasets to refine and expand the capabilities of ABM- based studies in studying anthropogenic impacts on landscapes.

3.6 Acknowledgements

This work was performed using compute resources from the Academic Leiden Interdisciplinary Cluster Environment (ALICE) provided by Leiden University. We would like to thank Prof. Jan Kolen (Leiden University, The Netherlands), Prof. Corrie Bakels (Leiden University, The Netherlands), Prof. Marie-Jose Gaillard-Lemdahl (Linnaeus University, Sweden), Dr. Tuna Kalayci (Leiden University, The Netherlands), Frank Arthur (University College of Southeast Norway, Norway), Prof. Hans Renssen (University College of Southeast Norway, Norway), Dr. Izabella Romanowska (Aarhus University, Denmark), Dr. Alex Brandsen (Leiden University, The Netherlands), Dr. Gabriela Florescu (Stefan cel Mare University, Suceava, Romania), Dr. Kim Cohen (Utrecht University, The Netherlands), Cyril Piou (CIRAD, France), Dr. Anneli Poska (Lund University, Sweden; Tallinn University of Technology, Estonia), Dr. Dennis

Braekmans (Leiden University, The Netherlands), Dr. Lucile Marescot (CIRAD, France), Agnes Schneider (Leiden University, The Netherlands), Femke Reidsma (Leiden University, The Netherlands), Dr. Andrew Sorensen (Leiden University, The Netherlands), Prof. Guido R. van der Werf (Vrije University, The Netherlands), Dr. Nicolas Viovy (Université Paris-Saclay, France), Julian Coupas (France), Dr. Wouter Verschoof-van der Vaart (Leiden University, The Netherlands), and Bjørn Peare Bartholdy (Leiden University, The Netherlands). We extend our gratitude to all the members of the Human Origins group at Leiden University (The Netherlands). The authors would also like to thank Prof. Louis M. François (University of Liège, Belgium) for providing the CARAIB global dynamic vegetation model and his help in running it.

CHAPTER 4

IMPACT OF NEANDERTHALS AND MESOLITHIC HUNTER-GATHERERS ON INTERGLACIAL VEGETATION IN EUROPE

Source

Nikulina, A., Zapolska, A., Serge, M. A., M. Roche, D., Mazier, F., Davoli, M., A. Pearce, E., Svenning, J. C., van Wees, D., Fyfe, R., MacDonald, K., Roebroeks W., & Scherjon, F. (in press). On the ecological impact of prehistoric hunter-gatherers in Europe: Early Holocene (Mesolithic) and Last Interglacial (Neanderthal) foragers compared. *PLOS One*

Supplementary material

Appendices III and IV

Data availability

The HUMLAND 2.0 code can be found in the repository at CoMSES library (https://doi.org/10.25937/qr4h-rt25). The generated scenarios have been submitted to the journal along with the article and will be available once the article is published.

Abstract

Recent studies have highlighted evidence of human impact on landscapes dating back to the Late Pleistocene–long before the advent of agriculture. Quantifying the extent of vegetation transformations by hunter-gatherers remains a major research challenge. We address this challenge by comparing climate-based potential natural vegetation cover with pollen-based vegetation reconstructions for the Last Interglacial and the Early Holocene. Differences between these datasets suggest that climate alone cannot fully explain the pollen-based vegetation patterns in Europe during these periods. To explore this issue, we used an upgraded version of the HUMan impact on LANDscapes (HUMLAND) agent-based model (ABM), combined with a genetic algorithm, to generate vegetation change scenarios. By comparing ABM outputs with pollen-based reconstructions, we aimed to identify parameter values that yield HUMLAND results closely matching the pollen-based vegetation cover. The updated ABM covers a broad temporal range, and incorporates the effects of hunting on herbivores and their influence on vegetation regeneration. The results show that the combined effects of megafauna, natural fires, and climatic fluctuations alone lead to vegetation cover estimates that are inconsistent with palaeoecological reconstructions. Instead, anthropogenic burning played a key role, with modelling results suggesting that European landscapes were already substantially modified by humans by the Early Holocene. In scenarios where human-induced burning was minimal or absent, foragers still shaped landscapes indirectly through hunting, which influenced herbivore densities and their impact on vegetation dynamics. Our study revealed that Neanderthals and Mesolithic humans influenced similar-sized areas around their campsites and shared comparable preferences for vegetation openness. Our results challenge the assumption that pre-agricultural humans had minimal ecological impact. Instead, this study provides strong evidence that both Neanderthals and Mesolithic foragers actively shaped European interglacial ecosystems, influencing vegetation dynamics long before agriculture.

4.1 Introduction

The past relationships between humans and their environment have been the subject of extensive research. While the emergence of agriculture is commonly regarded as the starting point for a strong anthropogenic influence on vegetation cover, recent studies have highlighted the substantial impact of hunter-gatherer communities on their environment through repetitive burning of vegetation (Bird et al., 2024; Innes & Blackford, 2023; Latalowa, 1992; Nikulina et al., 2022; Nikulina et al., 2024b; Poska et al., 2004; Rowley-Conwy, 2025; Rowley-Conwy & Layton, 2011; Scherjon et al., 2015; Smith, 2011; Wacnik, 2008; Zapolska et al., 2023a). It is important to recognize and assess the long-term effects of these early human activities preceding the emergence of agriculture (Zapolska et al., 2023a). Biodiversity conservation efforts often require a reference ecosystem or baseline (Burge et al., 2023), an inferred natural state before large-scale human exploitation of resources (Hildong-Rydevik et al., 2017). Identifying such baselines is challenging due to the complexities of past environmental processes (Schreve, 2019). Thus, studying the impact of early human activities on their environment is crucial not only for archaeology and related fields but also for informing ecosystem restoration projects aimed at a sustainable future.

In this study we focus on large-scale vegetation dynamics in Europe (Fig. 4.1) during the Last Interglacial (LIG, ~130,000–116,000 before present; all dates are given in calibrated years before present (hereafter abbreviated BP) (Fig. 4.1A) and the Early Holocene (~11,700–8000 BP, i.e., the period before the widespread adoption of agriculture in Europe) (Fig. 4.1B). We start with a comparison of potential natural (i.e., climate-driven) (Figs. 4.2A, 4.2B, 4.3A, 4.3B) and pollen-based (Figs. 4.2C, 4.2D, 4.3C, 4.3D) vegetation reconstructions, revealing substantial differences between the two datasets. We then assess these differences by implementing an agent-based model (ABM) to track and quantify various impacts on interglacial vegetation, with a particular focus on vegetation burning by hunter-gatherers (Fig. 4.4). It is important to emphasize that this study is primarily a modelling exercise based on currently available datasets from the broader body of research, which focuses on human-environment interactions at a continental scale (Arthur et al., 2023, 2025; Davoli et al., 2023; Lindholm et al., 2020; Pearce et al., 2024; Zapolska et al., 2023a).

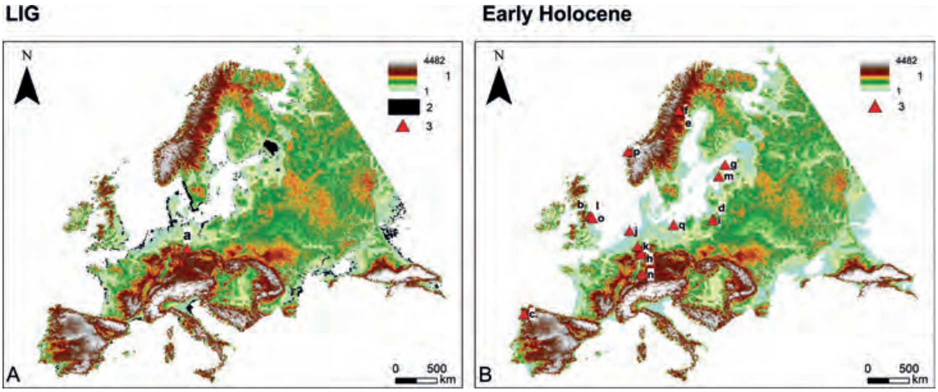


Figure 4.1 LIG (A) and Early Holocene (B) study area. Legend: 1–elevations (in meters above sea level, m a.s.l.); 2–no data; 3–case studies indicating possible vegetation burning by LIG and Early–Middle Holocene hunter–gatherers (Heidgen et al., 2022; Innes & Blackford, 2023; Latalowa, 1992; Nikulina et al., 2022; Poska et al., 2004; Sevink et al., 2023; Wacnik, 2008). List of case studies: a–Neumark-Nord; b–Bonfield Gill Head; c–Campo Lameiro; d–Dudka Island; e–Dumpokjauratj; f–Ipmatisjauratj; g–Kunda-Arusoo; h–Lahn valley complex; i–Lake Miłkowskie; j–-Meerstad; k–Mesolithic site at Soest; l–North Gill; m–Pulli; n–Rottenburg-Siebenlinden sites; o–Star Carr; p–Vingen sites; q–Wolin II.

Both study periods represent interglacial phases with broadly comparable vegetation dynamics (Kasse et al., 2022). The LIG has been proposed as a possible analogue for the Holocene and future environmental trends (Yin & Berger, 2015), hence the relevance of studying whether *Homo* played any role in the ecosystem dynamics of these times. In Europe, during both periods, humans subsisted as hunter-gatherers (foragers) who primarily relied on collection of wild resources (Ember, 2020) including plants, animals, and other natural resources. The absence of agriculture and domesticated animals during these periods may suggest that human impact on vegetation was minimal, with humans largely adapting to their natural environment rather than changing it. Ethnographic evidence (Nikulina et al., 2022; Rowley-Conwy & Layton, 2011; Scherjon et al., 2015; Smith, 2011) and a series of Early–Middle Holocene (~11,700–6000 BP) archaeological case studies (e.g., Heidgen et al., 2022; Nikulina et al., 2022; Sevink et al., 2023) (Fig. 4.1B) demonstrate that both past and recent hunter-gatherers used fire to alter vegetation for various purposes, including promoting useful plants, hunting, signalling, and clearing pathways (Kaplan et al., 2016; Nikulina et al., 2024b; Scherjon et al., 2015). Recently, evidence suggestive of such practices on a local scale has been published for the Neumark-Nord site in Germany, dating back to the LIG (Roebroeks et al., 2021) (Fig. 4.1A).

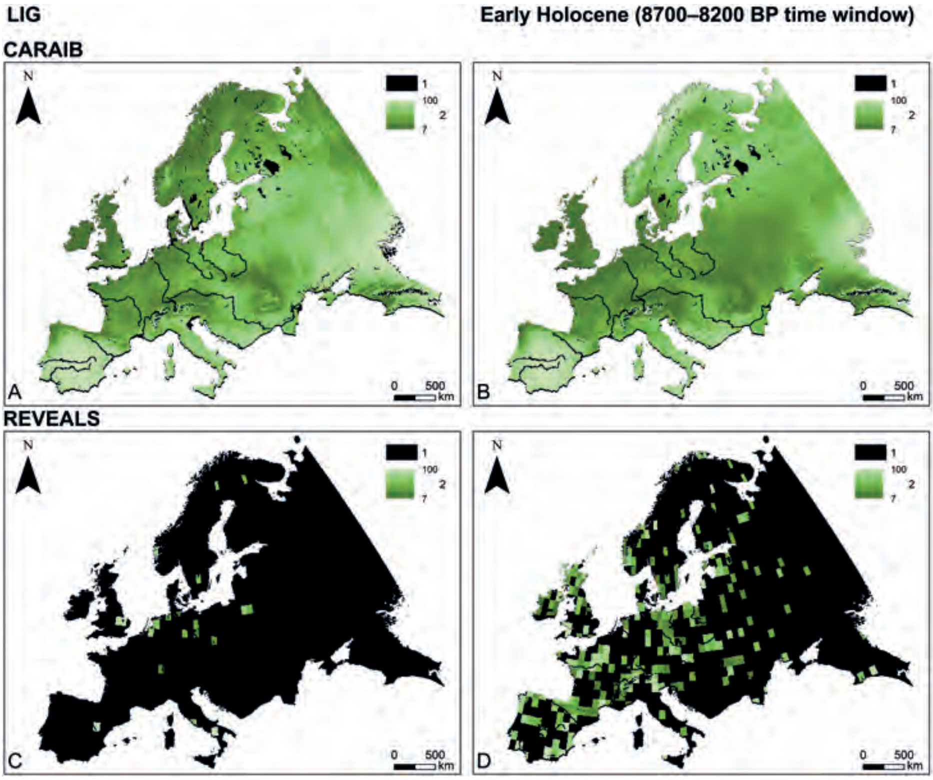


Figure 4.2 Vegetation openness: CARbon Assimilation In the Biosphere (CARAIB) LIG (A), CARAIB 8700–8200 BP (B); Regional Estimates of VEgetation Abundance from Large Sites (REVEALS) mesocratic I (C), REVEALS 8700–8200 BP. Vegetation openness for other time windows available in Appendix III (Figs. AIII.1 and AIII.2). Legend: 1–no data; 2–vegetation openness (%).

As a result of the inferred lower population sizes of foragers, researchers have characterized the LIG and the Early Holocene as periods with little to no human impact on landscapes compared to later phases. With fewer people interacting with the land, any ecological changes would have been relatively minor, particularly when compared to that of the larger agricultural populations with their different subsistence strategies. In addition, it is commonly assumed that human population size during the Mesolithic was larger than during the LIG (Pearce et al., 2023, 2024). As a result, only the activities of herbivores and/or natural fires are held responsible for transformations of natural vegetation cover during these periods, particularly during the LIG, and to have been mediated by climatic conditions (Feurdean et al., 2018; Mitchell, 2005; Pearce et al., 2023, 2024; Svenning, 2002; Vera, 2000).

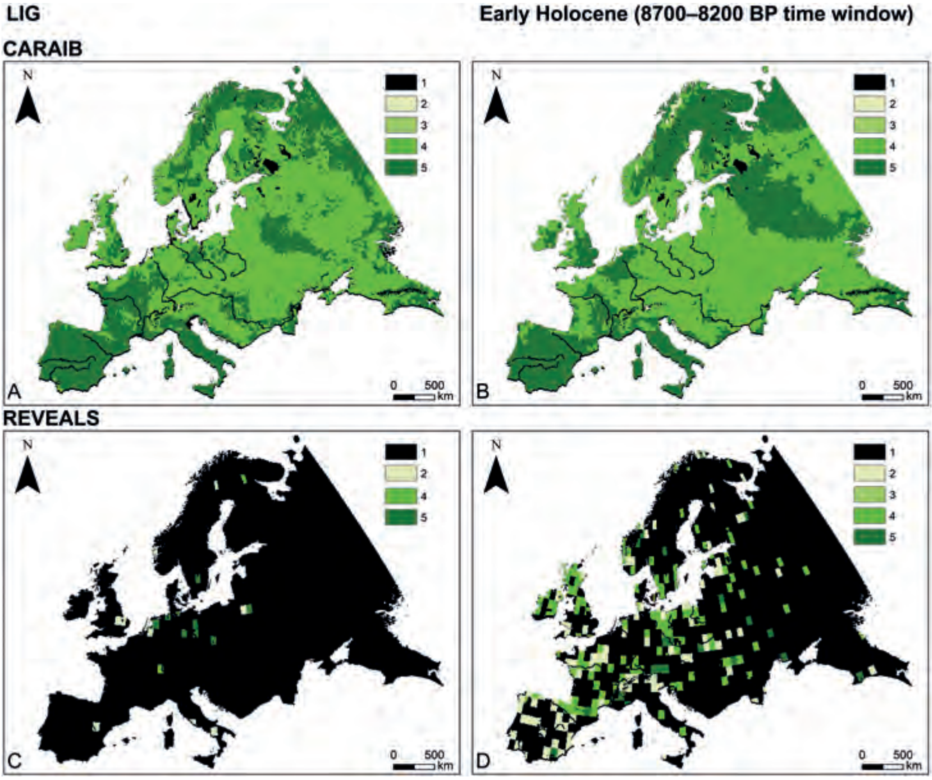


Figure 4.3 Distribution of dominant plant functional types (PFTs): CARAIB LIG (A), CARAIB 8700–8200 BP (B); REVEALS mesocratic I (C), REVEALS 8700–8200 BP. PFT distribution for other time windows available in Appendix III (Figs. AIII.3 and AIII.4). Legend: 1–no data; 2–herbs; 3–shrubs; 4–broadleaf trees; 5–needleleaf trees.

While there may have been substantial differences in *Homo* population sizes between the Early Holocene and the LIG, such inferred differences have largely been assumed rather than directly observed. For example, there exist no solid archaeological data allowing a straightforward comparison between census (actual) populations of the LIG and the Early Holocene. Specifically, a direct comparison between the archaeological record of the Early Holocene and the LIG is unwarranted: these periods are separated by a full glacial cycle with considerable impact on site preservation and distribution patterns, and differ dramatically in the way sites can be identified as “Last Interglacial” or “Mesolithic”, creating a very strong bias against the number of LIG sites (Roebroeks et al., 1992).

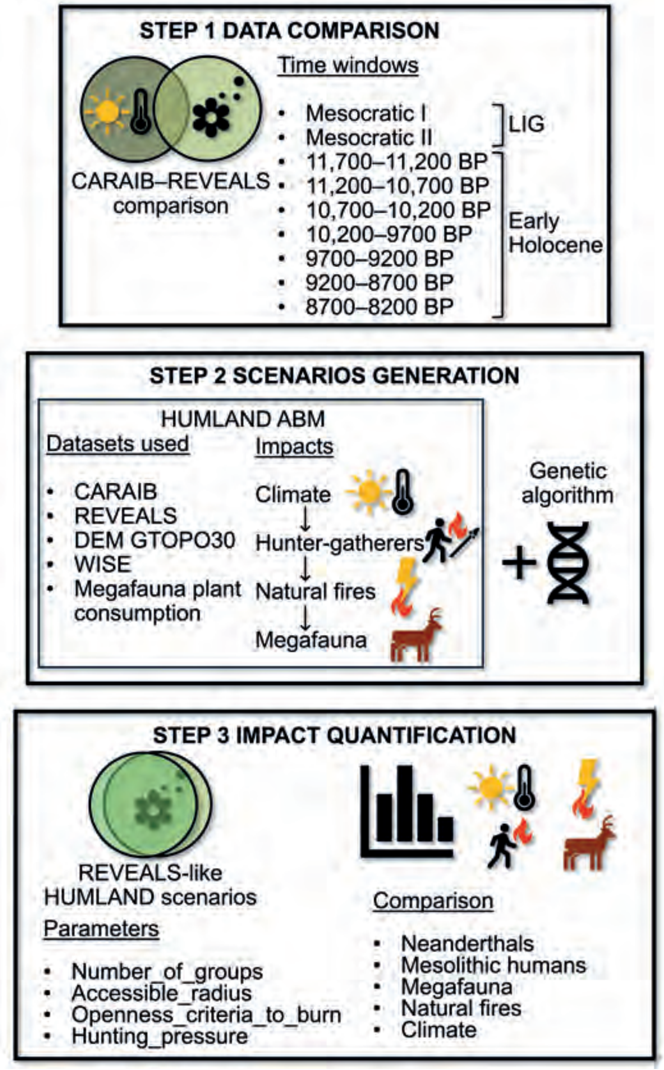


Figure 4.4 Overview of research steps including the comparison of CARAIB (climate-driven potential natural vegetation) and REVEALS (pollen-based vegetation reconstruction) data, the development and upgrade of the HUMLAND ABM, its integration with a genetic algorithm, and the generation of scenarios to quantify the impacts of Neanderthals, Mesolithic population, megafauna, natural fires, and climate on vegetation.

Demographic estimates usually rely on integrating multiple methods, scales, and proxies from archaeological sites (Schmidt et al., 2021), with genetic data playing an increasingly important role (Eller et al., 2009; Haber et al., 2016; Li et al., 2024; Sjödin et al., 2012). Solid data on Neanderthal population sizes during the LIG are not available. Although ancient DNA (aDNA) provides approximate effective population sizes–the number of reproductive individuals in an idealised population–for specific periods and regions occupied by Neanderthals (Li et al., 2024; Mellars & French, 2011; Rodríguez et al., 2022). A previous attempt to translate effective population sizes into census numbers yielded a broad estimate ranging from 5000 to 70,000 individuals, highlighting that these figures should be considered approximations rather than precise counts (Bocquet-Appel & Degioanni, 2013). Notably, this estimate lacks specificity regarding particular regions or timeframes within the extensive span of Neanderthal existence.

Challenges remain for the Early Holocene since available local aDNA estimates do not provide continental-scale census human population sizes for the Mesolithic (Allentoft et al., 2022, 2024; Günther et al., 2018; Li et al., 2024; Mattila et al., 2023; Miller et al., 2018). Other studies have used alternative methods and evidence to reconstruct Mesolithic demographic patterns within specific regions (Lundström et al., 2021; Schmidt et al., 2021; Van Maldegem et al., 2021). Continental-scale Early Holocene estimates relied on data and methods outside the scope of our research, including historical, ethnographic, and statistical modelling approaches (Goldewijk, 2024; Goldewijk et al., 2017; Ordonez & Riede, 2022). It is possible that actual human populations were higher during certain periods (Zilhao et al., 2024). Thus, comparing demographic patterns between the LIG and Early Holocene, and clearly relating them to hunter-gatherer impacts on landscapes, remains difficult.

The main research question addressed in this study is whether–and to which degree–hunter-gatherer activities could have impacted vegetation cover in Europe during the LIG and the Early Holocene. To address this question, we have set three primary objectives: 1) to evaluate the differences between potential natural vegetation (i.e., climate-based) as established via the CARAIB Dynamic Global Vegetation Model (DGVM) (François et al., 2011; Warnant et al., 1994; Zapolska et al., 2023a) and the reconstructed vegetation based on pollen obtained via the REVEALS model (Prentice & Webb, 1986; Serge et al., 2023; Sugita, 2007a) for the selected time windows (Fig. 4.4, step 1); 2) to generate potential scenarios of vegetation changes with outputs similar to REVEALS estimates due to megafauna plant consumption, anthropogenic and natural burning during the study periods (Fig. 4.4, steps 2 and 3); and 3) to track, quantify and compare the calculated impact of Neanderthals and Mesolithic humans on vegetation for the most frequently generated scenarios (Fig. 4.4, step 3).

To generate scenarios, we built upon a recently developed ABM called HUMan impact on LANDscapes (HUMLAND) (Nikulina et al., 2023, 2024a, 2024b), which was specifically adapted for the current study (Fig. 4.4). ABMs provide opportunities to examine interactions within complex systems, especially when real-time experiments are not feasible. By simulating multiple interacting factors, ABMs generate potential scenarios of system behaviour, which can then be compared to empirical data (Romanowska et al., 2019, 2021). This approach has been already widely used to study past human–environment interactions (Boogers & Daems, 2022; Lake, 2000; Riris, 2018; Sikk, 2023). HUMLAND was specifically designed to track and quantify different impacts on vegetation and to integrate various spatial datasets (Arthur et al., 2023, 2025; Davoli et al., 2023; Pearce et al., 2023; Serge et al., 2023; Zapolska et al., 2023a).

Building on insights gained from previous work (Nikulina et al., 2024b), the current study focuses on two LIG time windows (mesocratic I and mesocratic II) and seven 500-year time windows during the Early Holocene, spanning 11,700 to 8200 BP. This allows, for the first time, the quantification of Neanderthal impact on interglacial vegetation and enables a comparison with the prolonged impact of Mesolithic populations. Additionally, for this study, we enhanced HUMLAND by adding hunting pressure on herbivores and refining the representation of their impact on vegetation during regeneration after disturbances. This major update provides a more realistic depiction of the role of megafauna and allows for greater precision in quantification while distinguishing different impacts on vegetation.

For HUMLAND 2.0 we needed an approach that would enable systematic and computationally efficient exploration of a wide range of scenarios represented by different combinations of parameter values within this ABM. We implemented a genetic algorithm, an optimization technique inspired by natural selection (Katoch et al., 2021) for exploration of the parameter value space. Optimization involves testing various designs and adjusting model elements, such as agent behaviours and parameter values, to achieve a targeted outcome (Turgut & Bozdag, 2023). In our case, this outcome is a simulated vegetation cover that closely aligns with the past vegetation patterns (vegetation openness and distribution of dominant PFTs) represented by the REVEALS dataset. Genetic algorithms are widely recognized as a prominent approach for ABM optimization (Olsen et al., 2018; White et al., 2022), though application in archaeological research has been relatively limited (Scherjon, 2019). We present the first application of this algorithm to the HUMLAND ABM to identify combinations of parameter values that produce outputs similar to the REVEALS dataset. By using this innovative approach which integrates ABM, a genetic algorithm and various spatial datasets, we not only deepen our understanding of the history of human–environment interactions but also advance archaeological research by demonstrating the potential of genetic algorithms as an effective tool for optimizing complex multi-parameter models.

In this paper, our results are discussed in the context of broader questions about hunter-gatherer interactions with megafauna and demographic estimates for past populations, as detailed in the discussion section. The study represents a methodical effort to explore potential scenarios that depict the dynamics of past interglacial ecosystems in Europe where we observe a discrepancy between modelled environments from climate simulations and those reconstructed via proxies.

4.2 Materials and methods

Figure 4.4 provides an overview of our research steps. To achieve the first objective, CARAIB and REVEALS outputs were compared across all time windows. The CARAIB dataset represents theoretical potential natural vegetation (PNV) as shaped by climatic conditions (Figs. 4.2A, B; Figs. 4.3A, B; Figs. AIII.1 and AIII.3). This dataset is used as the starting point for every simulation run. The REVEALS dataset provides a reconstructed vegetation cover based on pollen data (Figs. 4.2C, D; Figs. 4.3C, D; Figs. AIII.2 and AIII.4), reflecting the result of the influence of various factors such as humans, megafauna, climate, and fires. In our ABM, the REVEALS data serves as a reference target vegetation cover for HUMLAND outputs.

CARAIB and REVEALS were compared for each time window in terms of two key aspects: the distribution of dominant PFTs and the vegetation openness across Europe (Nikulina et al., 2024b; Serge et al., 2023; Zapolska et al., 2023a). While these two aspects are related, they do not constitute directly comparable model outputs. The first output indicates the dominant PFT: the primary vegetation type (trees, herbs, or shrubs) within a grid cell. Vegetation openness represents the percentage of vegetation density within grid cells. There is no direct correspondence between specific openness values and the PFT presence.

We used the previously developed HUMLAND ABM 1.0 (Nikulina et al., 2023; Nikulina et al., 2024b) as the starting point for the major modifications needed to align this model with the scope of our current research. This led to the development and publication of the open-access HUMLAND 2.0 (Nikulina et al., 2024a), which integrates new datasets relevant to our specific temporal focus, and has a more realistic representation of herbivory impact. As a result, HUMLAND 2.0 enables the study of *Homo*'s influence on herbivores via hunting and the subsequent effects on vegetation, including during regeneration phases. A crucial new aspect of this study is the combination of HUMLAND 2.0 with a genetic algorithm to systematically generate and analyse a range of potential scenarios.

The HUMLAND ABM was also designed to quantify the extent of different types of impacts on interglacial vegetation at a continental level. To meet the third objective, we selected parameter values with the highest frequency in the generated scenarios where outputs closely matched REVEALS. For these scenarios, we quantified the impacts of climate, megafauna, natural and human-induced fires. As a result, this study represents the first attempt to distinguish different sources of impact for the study periods. More specifically our study provides the first quantification of Neanderthal vegetation impact at a continental scale, allowing for direct comparison with that of later Mesolithic populations.

4.2.1 HUMLAND ABM

In this study, we used as the base model the HUMLAND ABM 1.0 (Nikulina et al., 2023, 2024b) implemented in *NetLogo* 6.2.2 (Wilensky, 1999). This ABM explores vegetation dynamics, specifically PFT distribution and vegetation openness, in response to different factors, including climatic impact, human-induced and natural fires, and megafauna plant consumption. These factors are considered the most influential, widespread, and potentially observable at regional to sub-continental scales (Bond & van Wilgen, 1996; Feurdean et al., 2018; Mitchell, 2005; Nikulina et al., 2022, 2024b; Pearce et al., 2023, 2024; Pringle et al., 2023; Svenning, 2002; Whelan, 1995). We made major changes to the base model and developed HUMLAND 2.0 (Nikulina et al., 2024a). We added megafauna impact on vegetation regeneration (as detailed below). This included the introduction of hunting pressure, allowing for the exploration and quantification of the potential effects of Neanderthals and Mesolithic humans on herbivore populations.

HUMLAND 2.0 operates at a temporal resolution of one year and a spatial resolution of 10 km × 10 km, with each simulation running for a maximum of 1000 steps. We selected this spatial resolution as a compromise between the varying input data resolutions ranging from 1 km × 1 km to 100 km × 100 km, the localized yet varied scale of hunter-gatherer vegetation burning (estimated based on ethnographic evidence to range from several kilometres to 100 km^2), and the continental scope of the model (Nikulina et al., 2022, 2024b; Scherjon et al., 2015). A larger grid size could obscure the localized effects of foragers by blending them with other factors such as climatic changes. The number of steps (1000) was chosen to ensure that each simulation reaches an equilibrium state–where the key observations stabilize and do not substantially vary–usually occurring around step 450 (Nikulina et al., 2024b). For further analysis, primary HUMLAND output (mean vegetation openness and the mean number of grid cells dominated by herbs and trees) were recorded after step 450, when equilibrium is reliably reached. These outputs are collected only for grid cells that have both CARAIB and REVEALS values.

HUMLAND 2.0 is run separately for two discrete LIG time windows representing the period of maximum forest distribution in Europe and for four discrete Early Holocene 500-year time windows, covering the period from 10,200 to 8200 BP. Each simulation run is independent and does not overlap with others. The chosen time windows align with the temporal resolution of the datasets provided by REVEALS. The period between 11,200 and 10,200 BP was included in the CARAIB–REVEALS comparison but excluded from the simulations and the generation of potential scenarios via the genetic algorithm due to the difficulty of distinguishing human-induced changes from climatic changes during the glacial–interglacial transition at the onset of the Holocene (Dallmeyer et al., 2022; Seliger et al., 2021).

Here, we provide a brief introduction to HUMLAND 2.0. Further details can be found in Nikulina et al. (2024b) and in the Overview, Design concepts and Details (ODD) document for HUMLAND 2.0 (Nikulina et al., 2024a).

Each simulation step starts with a climatic impact affecting vegetation regrowth after fires or consumption by megafauna (Fig. 4.4). Since average recovery times (the number of years for vegetation to fully recover in accordance with a PNV PFT) were not available for the four PFT categories, we used estimates from the CARAIB model: herbs recover in seven years, needleleaf trees and shrubs in 43 years, and broadleaf trees in 30 years (Nikulina et al., 2024b). These specified recovery periods refer specifically to the point at which a PFT becomes the first dominant PFT following a disturbance. Generally, vegetation recovery depends on different factors including weather conditions, animal activity, season of disturbance, and even presence of specific nurse plants (Bashirzadeh et al., 2024; Kleynhans et al., 2021; Zwolinski, 1990). Various case studies report recovery times for vegetation cover ranging from several months to several years, depending on specific conditions; the recovery of plant community structure (e.g., species richness and dominance patterns) may take several decades (Bond & van Wilgen, 1996; Li & Guo, 2018; Masudi et al., 2024; Smith et al., 2016; Strand et al., 2019). In some cases, full ecosystem recovery can take more than seven years (Hao et al., 2022; Serra-Burriel et al., 2021).

These aspects to a certain degree are reflected in HUMLAND. When vegetation recovery begins following fire or vegetation consumption, vegetation openness decreases. This indicates that some vegetation cover reappears in HUMLAND within one year (one simulation step) after disturbance. In the following steps, vegetation progressively regains density until it reaches the PNV openness in accordance with the CARAIB data. This recovery process may be delayed if additional disturbances occur during the regeneration phase. The vegetation openness recovery rate is calculated by taking the difference between current vegetation openness (after disturbance) and the PNV openness, then dividing this difference by the average recovery time. During each simulation step, this recovery rate is subtracted from the current openness until it reaches the PNV openness.

PFT recovery follows a straightforward process in HUMLAND. Based on these the CARAIB estimates mentioned above, bare ground is replaced by herbs after seven simulation steps. Afterwards, herbs may be replaced by trees or shrubs after required number of steps, depending on the PNV PFT estimated by CARAIB.

HUMLAND 2.0 has adjustable parameter values for simulation runs (Table 4.1). The minimum and maximum values for most of these parameters were established previously (Nikulina et al., 2024b). HUMLAND includes several switches that allow for different combinations of impacts on vegetation, enabling their addition or removal as needed.

Natural ignition from thunderstorms is determined by the probability of ignition, which depends on the time elapsed since the last burning episode and the natural fire return intervals of the specific PNV PFT in that grid cell. Thus, the model accounts for the variations in the dominant PFT and probability of ignition and spread is different for needleleaf trees, broadleaf trees, shrubs and herbs. Fire return intervals were obtained via so-called “space-for-time” substitution, based on remote sensing data of fire activity (Archibald et al., 2013; Nikulina et al., 2024b).

Due to the continental scope of our study, we assumed that all fires replace the vegetation of a grid cell with bare ground in HUMLAND. However, observations from different regions indicate that fires do not always result in total vegetation loss; their impacts can range from minor fire scars to complete change of vegetation cover (Kleynhans et al., 2021). Predicting the exact consequences of fires on plant communities is challenging due to variations in fire size, frequency, and intensity (Johnson & Miyanishi, 2021; Zwolinski, 1990). While our assumption simplifies the modelling process, it may introduce some uncertainty into our results.

After anthropogenic and natural burning events, fires can spread to any of the eight neighbouring grid cells (Moore neighbourhood) based on their probability of ignition which depends on the PNV PFT. Fires cannot occur and spread on water bodies, bare ground and high mountains.

To more accurately depict the effects of megafauna on vegetation in HUMLAND 2.0 during the regeneration phase, and to explore scenarios where vegetation dynamics are not driven by anthropogenic fires, we implemented two key modifications in the initial model version: a reduction in the intensity of animal impact due to hunting pressure and due to the state of vegetation openness at the time of consumption.

Table 4.1 HUMLAND 2.0 parameter overview.

Parameters	Associated source of impact	Units/ Type	Values		Description
			Min	Max	
Territory_impacted_by_thunderstorms	Natural fires	%	0	100	Percentage of terrestrial grid cells impacted by thunderstorms per simulation step.
Natural_fires		Boolean	True/False		Indicates the presence or absence of thunderstorms during one simulation run.
Hunting_pressure	Hunter-gatherers, megafauna plant consumption	%	0	100	Reduces the estimated maximum potential megafauna plant consumption.
Megafauna_impact	Megafauna plant consumption	Boolean	True/False		Indicates the presence or absence of megafauna plant consumption during one simulation run.
Humans	Hunter-gatherers	Boolean	True/False		Indicates the presence or absence of anthropogenic impact during one simulation run.
Number_of_groups		Groups	0	4000	Specifies the number of human groups present in the study area during one simulation run.
Accessible_radius		Grid cells	0	5	Defines the territorial range within which humans move and set fires around their campsites.
Openness_criteria_to_burn		%	9	100	Specifies the threshold openness value below which humans set fires in grid cells dominated by trees or shrubs.
Movement_frequency_of_campsites		Steps	0	1000	Defines the frequency of campsite relocation by specifying the number of simulation steps after which relocation occurs.
Campsites_to_move		%	0	100	Percentage of campsites relocated at a given simulation step.

Humans are often mentioned as being responsible for the Quaternary megafauna extinction and further decline of functional diversity (Andermann et al., 2020; Bergman et al., 2023; Davoli et al., 2023; Sandom et al., 2014b; Smith et al., 2018; Svenning et al., 2024). In addition, the localized disruptions in herbivore populations preceded the widespread megafauna extinction, given the shared preferences for game species between Neanderthals and early modern humans in Eurasia (Dembitzer et al., 2022; Rosell et al., 2017; Staesche, 1983; Surovell et al., 2005;

Wißing et al., 2019). Given this, we introduced the Hunting_pressure parameter (Table 4.1), which reduces the estimated potential maximum plant consumption (as described in the "Datasets used in the HUMLAND ABM" section). This parameter affects megafauna plant consumption even when hunter-gatherers do not burn vegetation. In our model, this parameter does not impact LIG megafauna plant consumption on the British Isles because humans were not present or had sparse occupation there during this time (Lewis et al., 2011).

Besides hunting, the intensity of megafauna impact is determined by the state of vegetation openness. Many herbivores prefer areas with secondary vegetation and relatively open regrowth zones following disturbances such as fire (de la Torre et al., 2022; Gashchak & Paskevych, 2019; Girard et al., 2013; Popp & Scheibe, 2014; Zielke et al., 2019) because it increases the nutrition and palatability of new plants (Westlake et al., 2020). Consequently, fire attracts herbivores, which, in a reciprocal relationship, impact vegetation regeneration and fire behaviour (Bond & van Wilgen, 1996). Thus, areas with greater openness tend to experience more substantial herbivore impact. This serves as the second determinant of megafauna impact intensity within HUMLAND 2.0. Due to these two key modifications in megafauna plant consumption, animals now interact with grid cells at every simulation step, including those that are regenerating after fires.

Following the constraints imposed by hunting pressure, the resultant value of megafauna plant consumption of a grid cell after hunting (V_h) is further limited by the current vegetation openness (O_i) of the grid cell. This restriction yields the final estimate of megafauna NPP (Net primary productivity) metabolization (V_m) through formula 4.1:

$$V_m = \frac{O_i}{100} \times V_h \qquad (4.1).$$

Afterwards, the V_c value quantifies the percentage of vegetation consumed in each grid cell, excluding water bodies and high mountains, using formula 4.2:

$$V_c = \frac{V_m}{V_n} \times 100 \qquad (4.2)$$

V_n represents the current NPP of the consumed grid cell. The resulting V_c value is then combined with vegetation openness to reflect the impact of megafauna. In HUMLAND, megafauna can only consume vegetation in grid cells that are not completely open, meaning vegetation openness is less than 100%. After the megafauna plant consumption of a grid cell, the current NPP of this grid cell is reduced based on the calculated percentage of consumed vegetation (V_c).

In the beginning of each simulation run with human-induced fires, forager campsites are distributed randomly. During the LIG runs Neanderthals do not occupy or burn vegetation in the British Isles (Lewis et al., 2011), whereas Mesolithic hunter-gatherers are present in this region.

Regarding human-induced vegetation burning, three parameters influence its intensity as demonstrated by the sensitivity analysis of HUMLAND (Nikulina et al., 2024b): Number_of_hunter-gatherer_groups, Accessible_radius, and Openness_criteria_to_burn. Ethnographic evidence shows that hunter-gatherers burn vegetation for various reasons across different vegetation types (Mellars, 1976; Scherjon et al., 2015). The Openness_criteria_to_burn parameter partially reflects this variability. Higher values of this parameter result in more frequent burning by hunter-gatherers, targeting both relatively closed and open landscapes. In some cases, these landscapes may not have fully regenerated to their original vegetation openness level after previous disturbances such as fires or consumption. As a result, hunter-gatherers do not exclusively burn climax vegetation but may also target areas that have not fully recovered yet.

HUMLAND can store the last agent responsible for vegetation changes in grid cells at each simulation step. It is tracked through two grid cell variables: last_agent_impacted_pft and last_agent_impacted_openness. Updating the last_agent_impacted_pft variable requires an agent to replace the current dominant PFT with bare ground. This can occur through natural or anthropogenic fires, as every burning episode in HUMLAND results in vegetation being replaced by bare ground. Additionally, climate-induced changes can modify this parameter during the regeneration phase. It is important to note that megafauna can only update the last_agent_impacted_pft parameter when their impact is strong enough to transform vegetation by replacing a dominant PFT.

The last_agent_impacted_openness variable is updated when an agent induces a substantial transformation in the vegetation openness of a grid cell. This transformation is guaranteed in the case of a fire event, as it sets the vegetation openness of the burnt grid cell to 100% (bare ground). If, during vegetation regrowth, the vegetation openness of a grid cell closely aligns with CARAIB estimates (i.e., the difference between CARAIB and HUMLAND openness values is equal to or less than 10%), then last_agent_impacted_openness is modified due to climatic influence.

Given the relatively low-intensity impact of megafauna on all grid cells (i.e., V_c is below 1% per simulation step for most of grid cells), we assumed that for megafauna to be recognized as an agent responsible for changing vegetation openness of a grid cell, animals must effect a transformation to some extent comparable to that induced by fires and climate. Thus, if the vegetation openness of a grid cell deviates by more than 10% from CARAIB's openness estimates as a result of continuous and sustained megafauna impact over 10 simulation steps (equivalent to 10 years in HUMLAND), and in the absence of influence from other agents, megafauna can be identified as the agent responsible for the transformation in vegetation openness for that specific grid cell.

4.2.2 Datasets used in the HUMLAND ABM

We used the Spatial Analyst and Data Management toolboxes in *ArcMap* 10.6.1 to standardize the spatial extent and resolution (10 km × 10 km) of the datasets used in this study (Table AIII.2). The datasets, along with their original grid cell sizes, are listed below. Each newly generated 10 km × 10 km grid cell was assigned values from larger grid cells in the original datasets. Additionally, certain datasets were reclassified as detailed below. For this study, we incorporated input datasets covering two LIG time windows, corresponding to the period of maximum biomass development in Europe, and seven Early Holocene time windows.

To ensure consistency in our analysis, we excluded Anatolia, Cyprus, and the Balkans from all time windows considered in this study (Fig. 4.1). These regions have the earliest evidence of agriculture in Europe (Hamon & Manen, 2021; Milisauskas, 2002). By excluding them, we can focus on the impact of hunter-gatherer vegetation burning while minimizing potential factors related to agricultural activities during the Holocene.

The initial landscape is reconstructed via the DEM Global Topography 30 Arc-Second (~1 km) elevation dataset (GTOPO30) (www.usgs.gov; Danielson & Gesch, 2011; Gesch et al., 1999), Water Information System for Europe (WISE) (https://water.europa.eu/) and CARAIB outputs which are used as a starting point for all simulation runs (Hubert et al., 1998; Laurent et al., 2008; Otto et al., 2002; Warnant et al., 1994). Details on the CARAIB model setup can be found in Appendix III.

CARAIB outputs used in this ABM include distribution of fractions of 26 PFTs (PNV distribution), PNV vegetation openness, and potential natural NPP per 26 km × 26 km grid cell (Zapolska et al., 2023a, 2023b). CARAIB simulations are based on climate simulations performed with the iLOVECLIM climate model. It includes the VECODE reduced-form vegetation model (Brovkin et al., 1997), which computes plant and soil behaviours necessary for simulating first-order vegetation-climate feedback in climate models (Zapolska et al., 2023a). In turn, CARAIB is a more comprehensive mechanistic vegetation model that simulates vegetation dynamics based on interactions with climatic and soil conditions. It also models heterotrophic respiration and litter/soil carbon dynamics (Warnant et al., 1994).

To simulate Holocene climate evolution, we applied iLOVECLIM in a transient run (where the climate model runs continuously over a specified period). The outputs were resampled (averaged over the years) to match 500-year-long REVEALS time windows, ensuring alignment between CARAIB and REVEALS datasets for comparative analysis.

In contrast to the Holocene, aligning CARAIB and REVEALS outputs is challenging for the LIG. This difficulty arises from the fact that this stage was identified based on pollen assemblages. LIG stages were identified based on pollen assemblages, and the timing and duration of the LIG varied across different regions in Europe (Kasse et al., 2022; Sier et al., 2015). As a result, the exact start and end points of this period remain unclear. In our research, precisely aligning REVEALS time windows with corresponding CARAIB outputs is critical. While achieving a perfect match may not currently be possible for the LIG, we have chosen to focus on the REVEALS mesocratic I (*Quercus* zone) and II (*Carpinus* zone) time windows corresponding to the maximum biomass development (Birks & Birks, 2004; Lang, 1994).

To select CARAIB output for the time slice with maximum forest fraction during the LIG, we conducted a series of transient climate simulations (Arthur et al., 2025), followed by cross-validation through equilibrium simulations (climate model is run under fixed forcing conditions until it reaches a state of equilibrium) for three specific time slices characterized by high forest fractions in the transient runs: 120,000 years BP, 124,000 years BP, and 128,000 years BP. Our tests (not shown) determined that 128,000 years BP represents the peak of forest fraction during the LIG within our modelling setup. The corresponding CARAIB output was used as the starting point for two LIG time windows during LIG HUMLAND 2.0 runs. While we acknowledge that using this LIG CARAIB output may contribute to discrepancies between this dataset and REVEALS estimates, and that this can be considered a limitation of our study, it currently remains the only viable approach for running HUMLAND simulations for the LIG.

Before running HUMLAND simulations, CARAIB outputs were transformed and compared against pollen-based estimates of plant cover initially reconstructed for 1° × 1° (~100 km × 100 km) grid cells for each time window. These estimates were obtained from the REVEALS model which is based on pollen records from multiple-sized lakes and bogs and/or large lakes (>50–100 ha) (Pearce et al., 2023; Prentice & Webb, 1986; Serge et al., 2023; Sugita, 2007a). The REVEALS dataset also serves as the optimization target for genetic algorithm experiments. We compared CARAIB and REVEALS following the approach used in HUMLAND (Nikulina et al., 2024b). Both CARAIB and REVEALS PFTs were included in the current simulations and analysed within four PFT categories: needleleaf and broadleaf trees, shrubs and herbs (Fig. 4.3). The corresponding table between CARAIB PFTs and REVEALS plant taxa and morphological types is available in Appendix III (Table AIII.1). 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.

The results from REVEALS are influenced by several input parameters, including original pollen counts, relative pollen productivity (RPPs) and their standard deviations, fall speed of pollen, basin type (lake or bog), size (radius, m), maximum extent of the regional vegetation (km), wind speed ($m.s^{-1}$), and atmospheric conditions (Serge et al., 2023). For our study, we used REVEALS reconstructions for the Holocene, based on 31 plant taxa (ibid.), and for the LIG, based on 30 plant taxa (Pearce et al., 2023). Some taxa from the original pollen diagrams are absent from our pollen-based reconstructions, as pollen productivity estimates are not available. While pollen productivity estimates are available for many taxa, previous studies have stressed the importance of minimizing the inclusion of strict entomophilous taxa in REVEALS reconstructions to improve accuracy (Mazier et al., 2012; Serge et al., 2023). As a result, some categories may be over- or underestimated depending on the taxa available within each category. In our study, we used REVEALS reconstructions for the LIG and the Early Holocene based on the work of Pearce et al. and Serge et al., with details on the applied protocols available in the respective studies (Pearce et al., 2023, 2024; Serge et al., 2023).

The REVEALS model estimates vegetation cover based on pollen data but does not account for the presence of bare soil. To address this limitation, some studies have improved land-cover reconstructions by incorporating bare ground fractions derived from dynamic vegetation model outputs such as the Lund–Potsdam–Jena General Ecosystem Simulator (LPJ-GUESS), or by considering the spatial extent of glaciers (Githumbi et al., 2022; Strandberg et al., 2022).

Besides dominant PFTs, we used potential natural (CARAIB) and pollen-based (REVEALS) vegetation openness in percentages (Fig. 4.2). REVEALS estimates for vegetation openness include the percentage of all herbs and *Calluna vulgaris* for each grid cell (Nikulina et al., 2024b; Serge et al., 2023; Trondman et al., 2015). In contrast to REVEALS, CARAIB estimates vegetation openness for two vertical levels: lower (herbs, shrubs and bare ground) and upper (trees). We classified bare ground and herbs as indicators of open areas, while trees and shrubs were classified as closed areas. For each vertical CARAIB level, the maximum possible openness value is 100%, representing the percentage of an area not covered by shrubs or trees. Consequently, the highest combined openness value for a grid cell is 200%, indicating a completely open area containing only bare ground and/

or herbs. To align CARAIB with REVEALS in terms of vegetation openness, we assigned a single openness value per grid cell in the CARAIB dataset, using the smaller value between the two levels to represent the fraction of the area without trees or shrubs. By applying this transformation, both REVEALS and CARAIB datasets were adjusted to represent comparable distributions of dominant PFTs and vegetation openness.

We combined CARAIB NPP with potential maximal megafauna plant consumption (i.e., metabolization of NPP by wild terrestrial mammals ≥ 10 Kg) to estimate the percentage of vegetation consumed by megafauna (see section HUMLAND ABM). Since body mass is a key functional trait influencing animal impact, we adopted the 10 kg threshold, a widely used benchmark in ecological studies (Davoli et al., 2023, 2024; Moleón et al., 2020; Svenning et al., 2024). The potential maximal vegetation consumption of wild herbivore communities was first calculated across the continent prior to the extensive influence of humans on landscapes in the form of consumed kg/km^2 per year per 30 km × 30 km grid cell (Davoli et al., 2023). We used the obtained dataset for the LIG runs as the maximal possible megafauna plant consumption during this time. From this dataset we excluded the species absent from the Holocene fossil record, including straight-tusked elephants (*Palaeoloxodon antiquus)* (Crees et al., 2016; Davoli et al., 2024; Sommer, 2020). As a result, the obtained dataset reflects maximal possible megafauna plant consumption during the Early Holocene because it considers all areas of the continent that could have been frequented by the species based on climatic suitability, when the actual range of these species had been already substantially reduced due to human impact in the Late Pleistocene (Davoli et al., 2023, 2024). Given the absence or sparse presence of Neanderthals in the British Isles during the LIG (Lewis et al., 2011), we added an additional spatial layer to HUMLAND 2.0. This layer defines areas with no hunter-gatherer impact on megafauna plant consumption, and where hunter-gatherers were absent in the LIG ABM runs.

To incorporate LIG sea level differences in HUMLAND, we used available reconstructions and estimates of past sea levels. Specifically, for Northwest Europe, we utilized coastline reconstructions based on the work of Cohen et al. (Cohen et al., 2022). However, similarly detailed reconstructions were unavailable for other European regions. Consequently, we applied a uniform sea level rise of 6 m for the remainder of Europe during the LIG. This value is derived from global high-stand estimates, which indicate multiple peaks ranging from 2–3 m to 5.5–9 m a.s.l. (Dutton & Lambeck, 2012; Hearty et al., 2007). With these considerations, we defined the study area for the LIG datasets by excluding regions falling within the reconstructed North European LIG sea levels and currently situated below

6 m a.s.l. (Fig. 4.1A). Because no comprehensive reconstructions exist for the distribution of major rivers and lakes in Europe during the LIG, we adopted their modern distributions based on the WISE dataset.

In HUMLAND, areas with closed vegetation can only transition to more open vegetation after fires or plant consumption. Our ABM can only create a match with REVEALS estimates if the initial CARAIB vegetation openness (climax vegetation) is equal to or less than pollen-based estimates (i.e., more closed vegetation can open further) or where shrubs or trees can transition to bare ground and herbs. Consequently, all grid cells that did not meet these criteria were excluded from the CARAIB–REVEALS comparison and from the genetic algorithm experiments.

4.2.3 Genetic algorithm

We used the genetic algorithm optimization technique to generate potential scenarios and determine the parameter values for HUMLAND 2.0 that are needed to produce ABM outputs closely aligned with the REVEALS data (Fig. 4.4). This technique was originally developed in the 1960s–1970s by John Holland and his collaborators (Holland, 1975; Yang & He, 2019). A genetic algorithm encodes an objective function as arrays of bits or character strings, representing chromosomes, and employs genetic operators to manipulate these strings. Solutions are selected based on fitness, enabling the algorithm to converge toward an optimal solution to a problem in hand (Yang & He, 2019). This process involves the following steps: 1) encoding solutions into strings; 2) defining a fitness function and selection criterion; 3) creating a population of individuals and evaluating their fitness; 4) evolving the population by generating new solutions through crossover, mutation, and fitness-proportionate reproduction; 5) selecting new solutions based on their fitness and replacing the old population with better individuals; and 6) decoding the results into the solution(s) to the problem (ibid.).

We implemented the genetic algorithm and subsequent analysis of the modelling results using *R* (RStudio Version 1.3.1093, R Core Team, 2020). We used the *nlrx* package which explores various model parameters within predefined ranges to minimize a fitness criterion (Salecker et al., 2019). Our optimization goal was to minimize two differences: 1) the discrepancy between mean vegetation openness obtained from REVEALS (O_r) and HUMLAND (O_h), and 2) the difference in the mean percentage of grid cells dominated by trees from REVEALS (T_t) and HUMLAND (T_h). Thus, we used two following fitness functions (formulas 4.3 and 4.4):

$$f(O) = \frac{|O_r - O_h|}{100} \tag{4.3}$$

and

$$f(O) = \frac{|T_t - T_h|}{100} \tag{4.4}$$

O is mean vegetation openness, and T is the mean percentage of grid cells dominated by trees. These values were calculated only for grid cells that contained both REVEALS and CARAIB estimates. As a result, we conducted two main groups of genetic algorithm experiments. The first group focused on minimizing the difference in mean vegetation openness obtained via REVEALS and HUMLAND. The second group aimed to minimize the REVEALS–HUMLAND difference in the percentages of grid cells dominated by trees. For each fitness function per time window, we conducted 60 separate genetic algorithm experiments using different random seeds for the following three subsets 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. Consequently, we obtained a total of 360 genetic algorithm results per time window, and 2160 results in total for all time windows.

As we had already identified the most influential parameters for human-induced vegetation changes and their minimum and maximum values in HUMLAND (Nikulina et al., 2024b) (Table 4.1), we used these values for only those specific parameters (Table 4.2). In the genetic algorithm experiments we also incorporated the Hunting_pressure parameter which is estimated as a percentage ranging from 0% to 100%. The Territory_impacted_by_thunderstorms had a constant 0.04% value in accordance with the decadal lightning observations for Europe (Enno et al., 2020). For this parameter we used modern estimates due to the absence of continental LIG and Early Holocene thunderstorm frequency values.

The genetic algorithm was configured with a population size (popSize) of 30 and a total of 20 iterations (iters). The fitness function output measurements were recorded after step 450 when HUMLAND reaches its equilibrium (Nikulina et al., 2024b).

To assess the effectiveness of the genetic algorithm results, we first calculated the percentage of HUMLAND scenarios that produced outputs comparable to REVEALS estimates. Specifically, we determined the proportion of scenarios where (1) the mean vegetation openness differs from REVEALS by 10% or less, and (2) the percentage of grid cells dominated by trees differs from REVEALS by 10% or less. This calculation provided a quantitative measure of the overall success of each experimental subset.

Afterwards, for the successful scenarios, we computed Pearson correlation coefficients (PCC). These correlations were then visualized as a correlation matrix using the *corrr* and *ggcorrplot* packages (Kassambara, 2023; Kuhn et al., 2022). Additionally, we performed principal component analysis (PCA) utilizing the *FactoMineR* package (Lê et al., 2008). To explore the parameter values for generated

Table 4.2 Genetic algorithm setup details. A black dot indicates that a variable was optimized within its specified minimum and maximum values (as outlined in Table 4.1), whereas a white dot signifies that the variable remained constant. The experiment subsets are categorized as follows: 1) megafauna impact; 2) megafauna impact combined with natural fires; and 3) megafauna impact, natural fires, and human-induced fires.

Parameter	Experiment subset 1	Experiment subset 2	Experiment subset 3
Territory_impacted_by_thunderstorms	0.04	0.04	0.04
Megafauna_impact	True	True	True
Natural_fires	False	True	True
Humans	False	False	True
Number_of_hunter-gatherer_groups	○	○	●
Accessible_radius	○	○	●
Openness_criteria_to_burn	○	○	●
Hunting_pressure	●	●	●
Campsites_to_move	0	0	0
Movement_frequency_of_campsites	0	0	0

scenarios similar to REVEALS and to identify the most frequently occurring value ranges, we used box and violin plots created via the *ggplot* package (Wickham, 2016) and measures from descriptive statistics (mean, standard deviation and mode).

To evaluate the visibility of each agent's impact on vegetation at the continental level, we calculated the mode (the most frequent value in a data set) for the scenarios that led to the similar output with REVEALS. We calculated the mode values for each generated parameter value distributions separately within each time window. Subsequently, we selected combinations of the generated parameter values that closely matched these separate mode values. In cases where parameter value distributions had several modes, we selected multiple combinations. Using the selected parameter combinations, we conducted additional HUMLAND simulation runs (Table AIII.6). Throughout these runs, HUMLAND tracked for each grid cell (excluding water bodies and high mountains) the last agent that influenced the vegetation openness of the grid cell and modified the first dominant PFT of that grid cell. The obtained observations were averaged and presented in bar charts for LIG and the Early Holocene separately.

4.3 Results

4.3.1 Comparison of REVEALS and CARAIB datasets

The results of the CARAIB–REVEALS comparison for all time windows are shown in Figure 4.5. The comparative outcomes for the two LIG time windows are derived from a notably smaller set of 10 km × 10 km grid cells (1211 and 1277) than for the Early Holocene, where a substantially larger number of grid cells was considered in our study, ranging between 14,703 and 16,478 depending on the specific time window. The REVEALS grid cells included in the analysis are shown in Figures 4.2C, 4.2D, 4.3C, and 4.3D for two specific time windows. The other time windows are presented in Figures AIII.2 and AIII.4.

Across all time windows CARAIB consistently exhibits substantially higher mean percentages of grid cells dominated by trees compared to REVEALS (Fig. 4.5, shown in green). Additionally, a consistent trend is observed in mean vegetation openness estimates, with CARAIB showing substantially lower estimates than

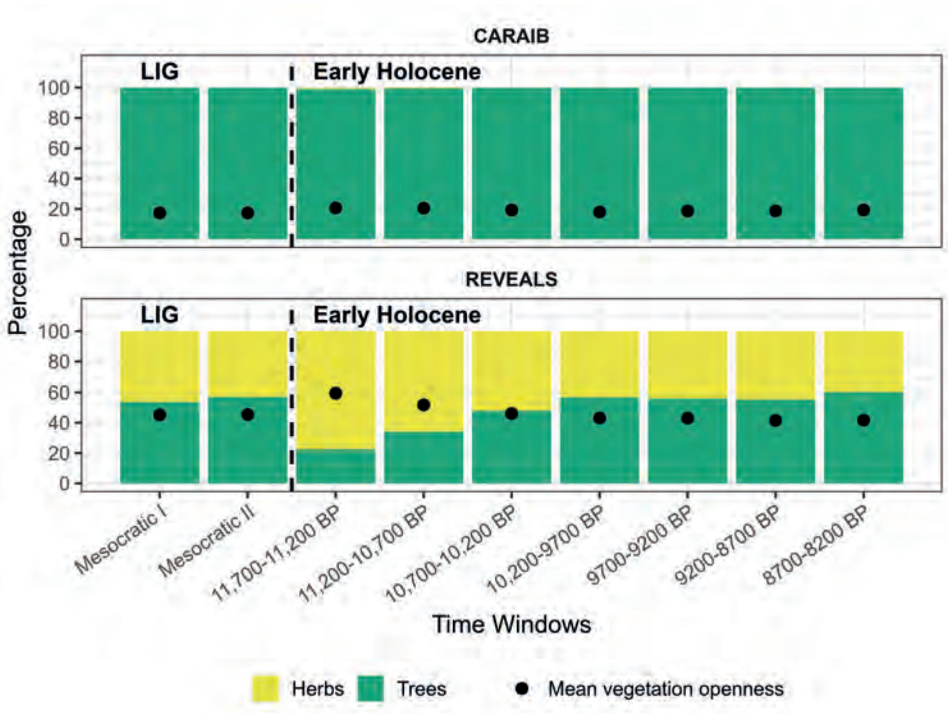


Figure 4.5 CARAIB–REVEALS comparison of mean vegetation openness (black dots) and the mean percentage of grid cells dominated by herbs (yellow) and trees (green) for the LIG and the Early Holocene.

REVEALS (Fig. 4.5, shown by dots). The mean percentage of grid cells dominated by herbs follows a similar pattern (Fig. 4.5, shown in yellow). Thus, pollen-based reconstructions indicate a more open environment than CARAIB.

Intriguingly, our results reveal a noteworthy inversion in the mean percentage of grid cells with herbs and trees in the REVEALS estimates (Fig. 4.5, bottom figure) between 10,700–9700 BP. In the initial phases of the Early Holocene (11,700–10,200 BP), REVEALS reconstructions show that herb-dominated grid cells outnumbered those dominated by trees. However, from 10,200 to 8200 BP, there is a shift toward the predominance of tree-dominated grid cells. This pattern remains relatively stable, with a slight increase occurring at 8700–8200 BP. The LIG time windows show a comparable pattern, with notably similar variations in the proportions of grid cells dominated by herbaceous and arboreal vegetation. Based on the results of this CARAIB–REVEALS comparison we selected the time windows for HUMLAND runs: two LIG and four Early Holocene (10,200–8200 BP) time windows (Fig. 4.5).

4.3.2 Vegetation dynamics without human-induced burning: megafauna plant consumption, hunting, and natural fires

There are two experimental subsets that excluded human-induced fires: 1) megafauna impact, where fires were completely absent, and 2) megafauna impact with natural fires (Table 4.2). In both subsets, animal hunting was present, meaning the potential maximum megafauna plant consumption was reduced according to the values specified by Hunting_pressure.

The instances where ABM results align with the REVEALS estimates, particularly concerning the PFT distribution, are rare (Table 4.3). Thus, our results show that it is almost impossible to produce scenarios similar to the pollen estimates without fires and specifically without burning by foragers.

Table 4.3 Percentage of possible scenarios with output similar to REVEALS without anthropogenic fires. In these scenarios humans do not engage in vegetation burning, but they exert hunting pressure on herbivores.

Time windows	No fire events		Natural fires only	
	PFT distribution	Mean vegetation openness	PFT distribution	Mean vegetation openness
Mesocratic I	0%	66%	0%	65%
Mesocratic II	0%	69%	23%	71%
10,200–9700 BP	0%	0%	0%	63%
9700–9200 BP	0%	0%	0%	82%
9200–8700 BP	0%	0%	0%	90%
8700–8200 BP	0%	0%	0%	100%

In HUMLAND scenarios without anthropogenic fires but producing vegetation openness outputs consistent with the REVEALS data, humans would have needed to reduce megafauna pressure through hunting. During the LIG, this would require decreasing megafauna plant consumption by 20–25% to match the openness levels shown in the REVEALS estimates (Fig. 4.6). In contrast, during the Early Holocene, achieving the openness levels shown by REVEALS data would require a much greater impact on megafauna, with 80–90% of the animal population removed via hunting (Fig. 4.6). In other words, without hunting, megafauna impact would have resulted in landscapes different than those reconstructed by REVEALS.

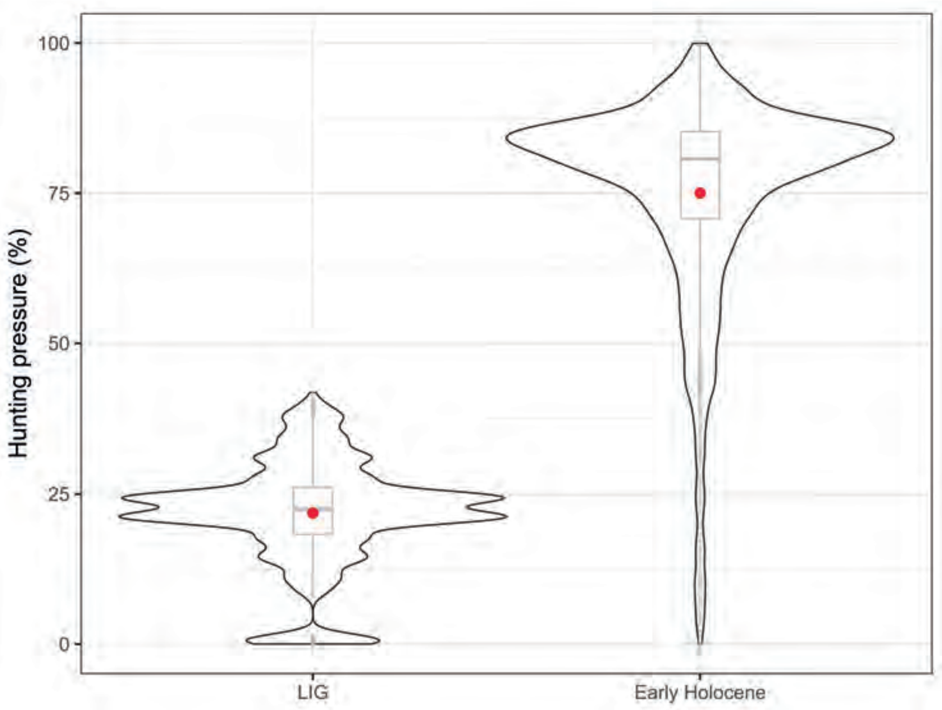


Figure 4.6 Summary statistics and values' distribution of the Hunting_pressure parameter values required to generate HUMLAND scenarios with output similar to REVEALS without anthropogenic fires. Humans do not engage in vegetation burning, but they exert hunting pressure on herbivores. The dot indicates the mean value for each dataset. For the LIG, most simulations matching REVEALS outputs have Hunting_pressure values around 20–25%, whereas for the Early Holocene, they typically cluster around 80–90%.

4.3.3 Vegetation dynamics with human-induced burning: megafauna plant consumption, hunting, natural and anthropogenic fires

Human-induced burning is incorporated into the third experimental subset, alongside natural fires and megafauna impact (Table 4.2). In these experiments, HUMLAND parameters were adjusted using a genetic algorithm within their predefined ranges (Table 4.1) to generate outputs closely matching REVEALS data. As a result, the majority of generated scenarios had results that matched REVEALS estimates (Table 4.4). Further analyses, including PCA (Tables AIII.3 and AIII.4) and PCC (Fig. AIII.5), were performed only on scenarios closely matching the REVEALS data.

Table 4.4 Percentage of possible scenarios with output similar to REVEALS with anthropogenic fires. These scenarios include the combined direct impact of all agents on vegetation: human induced and natural fires, and megafauna plant consumption.

Time windows	PFT distribution	Mean vegetation openness
Mesocratic I	89%	98%
Mesocratic II	94%	99%
10,200–9700 BP	98%	100%
9700–9200 BP	98%	100%
9200–8700 BP	98%	100%
8700–8200 BP	98%	100%

PCC showed that the variables within the LIG dataset have both positive (i.e., when one increases, the other also increases) and negative correlations, while in the Early Holocene results, correlations are exclusively negative (i.e., an increase in one factor coincides with a decrease in another) (Fig. AIII.5). The magnitudes of the correlation coefficients between parameters are generally absent, low or modest for both periods. PCA results show that contribution of some variables to principal components (i.e., new variables that are derived from an original set of variables to reduce the dimensionality of data) varies over time and across genetic algorithm experiment groups (Tables AIII.3 and AIII.4). Consequently, it is difficult to identify a single parameter or specific combination of parameters that consistently has the greatest influence on model outputs. A distinct result is that the absolute loadings (i.e., how much a variable contributes to the component) of the Hunting_pressure parameter are overall lower for LIG results compared to the Holocene runs.

The range of parameter values required to produce scenarios comparable to REVEALS outputs varies across time periods and experiments (Fig. 4.7). A consistent observation is that higher values for the Openness_criteria_to_burn are necessary to produce PFT distribution scenarios (with means of 77% for the LIG and 71% for the Early Holocene) compared to vegetation openness scenarios (with means of 49% for the LIG and 60% for the Early Holocene) (Figs. 4.7A, B). A similar trend is noted for the Number_of_groups parameter (Figs. 4.7C, D), where the mean values for tree distribution scenarios are 3266 for the LIG and 2895 for the Early Holocene, while for vegetation openness scenarios, the means are 1936 for the LIG and 2243 for the Mesolithic. Overall, within each group of genetic algorithm experiments, the values of these parameters for the Neanderthal and Mesolithic periods are similar, showing minimal differences between the LIG and Early Holocene ranges.

The accessible radius values for the PFT scenarios are consistent, with a mean around three and the most frequent values at three and four grid cells around campsites across most time windows (Fig. 4.7E). In the vegetation openness scenarios, the Neanderthal mean radius is around two. However, the area impacted by Mesolithic humans shows a reduction from three grid cells during 10,200–9700 BP to an average of two grid cells between 8700–8200 BP, with most values at one during this time window (Fig. 4.7F).

The results indicate significant variability in potential hunting pressure across different study periods within the PFT scenarios: an average decrease of 24% in megafauna plant consumption is needed during the LIG, compared to 48% during the Early Holocene (Fig. 4.7G). Conversely, the vegetation openness scenarios show similar average hunting pressures for both time periods, around 34% (Fig. 4.7H). However, the most frequent values differ between the periods. For the LIG, vegetation openness scenarios typically require a reduction in plant consumption by megafauna ranging from 21% to 39%, whereas for the Early Holocene, the range is much broader, from 1% to 82%. The PFT scenarios generally indicate hunting pressure of 0% to 4% for the LIG, and 0% to 67% for the Mesolithic. Similarly, the vegetation openness scenarios reveal that the most common values for the Openness_criteria_to_burn vary between periods: ranging from 23% to 48% for the LIG and from 36% to 69% for the Early Holocene (Fig. 4.7B). For the PFT scenarios, the most common values for this parameter remain relatively close across the periods (Fig. 4.7A).

4.3.4 Continental scale visibility of different types of impact

To evaluate the role, visibility and impact of hunter-gatherers' fires on vegetation, we quantified the number of grid cells affected by each agent across the most frequent scenarios. The parameter values, selected based on the mode of the generated parameter distributions for each time window (Fig. 4.8), are detailed in Table AIII.6.

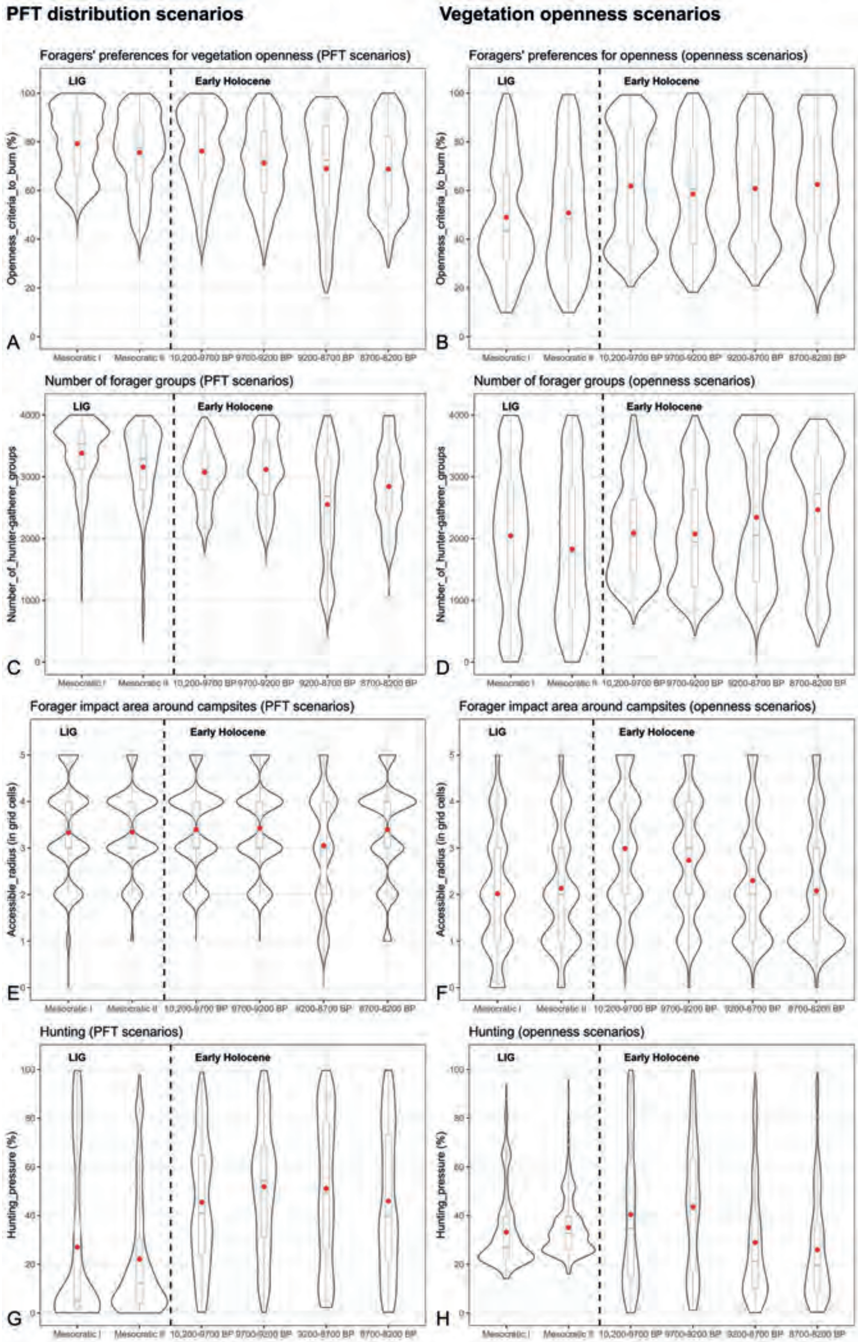


Figure 4.7 Summary statistics and distribution of the parameters' values required to generate scenarios with output similar to REVEALS for PFT distribution (A, C, E, G) and vegetation openness (B, D, F, H) with hunting and anthropogenic fires. The dot indicates the mean value for each dataset.

The mean number of modifications by climate, megafauna, natural and human-induced fires is shown in Figure 4.8. Climate had a greater influence on PFT distribution (on average 62% of grid cells during the LIG and 72% of grid cells during the Early Holocene) compared to its impact on vegetation openness (9% during the LIG, 35% during the Early Holocene). A consistent trend from the LIG to the Early Holocene is the declining role of megafauna plant consumption, although it remained a significant factor for vegetation openness (77% during the LIG, and 57% during the Early Holocene), but less so for PFT distribution (31% during the LIG and 1% during the Early Holocene). Meanwhile, the visibility of human impact increased. Neanderthals initiated visible changes on a continental scale, though these modifications were minimal during the LIG: Neanderthals impacted PFTs in 6% of grid cells and vegetation openness in 14% grid cells. The Neanderthal impact may have been overwritten by climatic fluctuations and megafauna effects, particularly during the LIG simulation runs. During the Early Holocene, vegetation burning by hunter-gatherers then became the second most influential agent for PFT distribution after climate, affecting an average of 26% of European landscapes, with a maximum of 47% of grid cells.

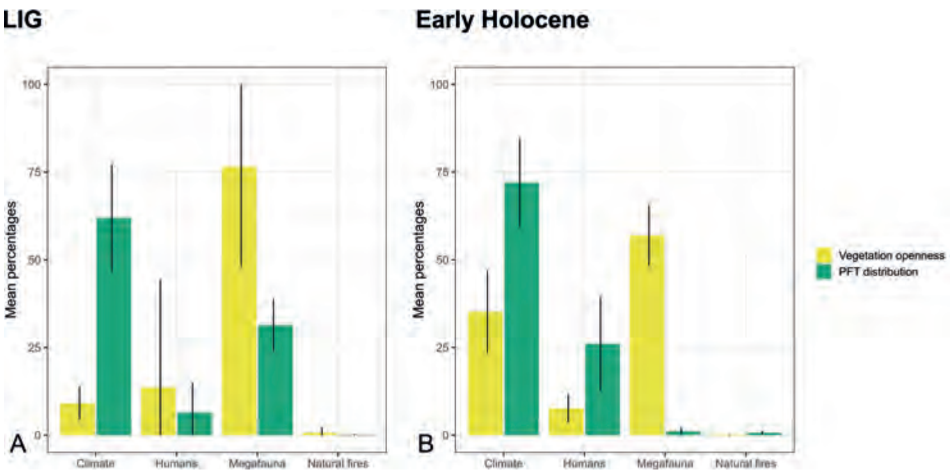


Figure 4.8 Mean percentages of grid cells modified by different agents during the HUMLAND equilibrium state: A–LIG most frequent scenarios; B–Early Holocene most frequent scenarios.

4.4 Discussion

4.4.1 Temporal vegetation dynamics: CARAIB vs REVEALS

It is important to emphasize that CARAIB and REVEALS reconstruct regional vegetation in different ways, which naturally leads to some divergence in output (Nikulina et al., 2024b). CARAIB is driven by climate forcing and modelled vegetation dynamics. REVEALS is based on transformation of pollen count data into quantitative estimates of regional vegetation cover. Moreover, differences in pollen data availability across grid cells between time periods make direct comparisons challenging. REVEALS reconstructions for the Holocene benefit from broader spatial coverage, whereas estimates for the LIG are largely restricted to regions that were glaciated during the late Saalian (MIS 6) (Figs. AIII.2 and AIII.4) (Roebroeks et al., 2024). Moreover, aligning REVEALS LIG time windows with specific CARAIB outputs is challenging (Kasse et al., 2022; Sier et al., 2015). The parameter values for foragers' impact area and preferences for vegetation openness around campsites during the LIG (Fig. 4.7A, E), obtained via the genetic algorithm, are largely applicable to Central Europe, where most REVEALS estimates are concentrated. As a result, continental-scale CARAIB–REVEALS comparisons for the LIG, as well as extrapolation of LIG HUMLAND results to the entire continent, should be done with caution.

It is important to highlight that different areas across Europe have varying post-depositional processes, preservation conditions, and research histories which introduce additional uncertainty when attempting to generalize conclusions at continental scale (Roebroeks et al., 2024). Despite these challenges, our study advances our understanding of the potential dynamics of interglacial landscapes and the role of *Homo* within them, particularly during the Early Holocene, where we obtained more robust results due to the relatively extensive REVEALS coverage (Figs. 4.2, 4.3, AIII.2 and AIII.4). Additionally, this study represents the first attempt to integrate these and other datasets into a single ABM spanning such an extensive period.

A comprehensive comparison between CARAIB and other climate-based vegetation models lies beyond the scope of this study. A recent comparison of CARAIB, Spatially Explicit Individual Based DGVM (SEIB-DGVM), and ORCHIDEE-DGVM against REVEALS data showed statistically similar results compared to REVEALS on the continental scale (Bertrix et al., 2025). Thus, using only CARAIB in our continental-scale study should not be viewed as a limitation. We emphasize that CARAIB is an established and widely used model in paleoclimatic research (François et al., 2011; Warnant et al., 1994; Zapolska et al., 2023a).

While testing the impact of different input parameters on the REVEALS output is beyond the scope of our research, it is important to note that the assumptions of the REVEALS model are explicitly defined, ensuring transparency in the interpretation and evaluation of our results. Several of these assumptions have been tested and validated, and the REVEALS model itself has undergone extensive evaluation across multiple areas across Europe (Hellman et al., 2008; Mazier et al., 2012; Soepboer et al., 2010), North America (Sugita et al., 2010), and on a continental scale (Serge et al., 2023), defining a European scale protocol (ibid., Mazier et al., 2012). Thus, we believe our findings provide a reliable basis for addressing the research questions of this study.

The differences between the CARAIB and REVEALS datasets remain consistent between the LIG and Early Holocene, except for 11,700–10,200 BP (Fig. 4.5). This exception may be partly attributed to the glacial/interglacial cycle affecting the late arrival of some trees (Giesecke et al., 2017; Svenning & Skov, 2004). Because of this, distinguishing climate influences on vegetation from other processes is particularly challenging for 11,700–10,200 BP. Therefore, we did not conduct HUMLAND runs for this period (refer to Appendices for further clarifications).

The overall similarity in the degree of difference between CARAIB and REVEALS for the Early Holocene and the LIG likely reflects their comparable vegetation development and similar or slightly higher annual LIG temperatures relative to the present interglacial (Kasse et al., 2022). However, ecosystem dynamics and role of different factors in it varied between these periods, as shown by HUMLAND's impact quantifications (Fig. 4.8). These differences may be due to discrepancies between the LIG and the Holocene: LIG higher eustatic sea level, variations in insolation (ibid.), shifts in megafauna composition (Davoli et al., 2023), and differences in *Homo* populations.

4.4.2 HUMLAND scenarios with and without human-induced vegetation burning

Without fires, including natural ones, it is nearly impossible to produce HUMLAND scenarios with vegetation outcomes similar to REVEALS (Table 4.3). While HUMLAND outputs similar to pollen-based estimates can be generated using natural fires alone, without anthropogenic burning, the likelihood of such scenarios is low (Table 4.3).

These results indicate that the inclusion of fires set by hunter-gatherers is necessary to consistently generate outputs comparable to REVEALS. Thus, megafauna and climate alone were likely not the only factors shaping vegetation dynamics in Europe, not just during the Early Holocene–as indicated by the first HUMLAND results (Nikulina et al., 2024b)–but also during the LIG. When fires, particularly human-induced burning, are included in our genetic algorithm experiments, most of the generated outputs align with REVEALS (Table 4.4), suggesting that fires and particularly anthropogenic fires could have played an important role in European interglacial ecosystems.

The identified importance of fires during the Holocene aligns with findings from other studies, which show an increase in biomass burning in the Early Holocene (Marlon et al., 2013; Pearce et al., 2024). However, reconstructing the dynamics of fire on a continental scale for the LIG and comparing it to the Early Holocene is challenging due to the limited availability of LIG proxy data (Daniau et al., 2010). Current estimates indicate that biomass burning was generally more widespread during interglacial phases compared to glacial periods, highlighting the importance of fires in shaping interglacial landscapes–a finding consistent with our results (ibid., Lawson et al., 2013). Fire-related patterns during both periods can exhibit similarities due to overall similar vegetation dynamics between the LIG and the Holocene (Davoli et al., 2023; Kasse et al., 2022). On the other hand, some studies suggest that fire activity may have been more widespread during the Early Holocene than in the LIG (Lawson et al., 2013; Pearce et al., 2024), whereas other regions experienced higher fire frequencies during the LIG (Margerum et al., 2024). In addition, archaeological evidence points to the importance of fire in locations occupied by LIG Neanderthals (Pop & Bakels, 2015; Roebroeks et al., 2021).

The PCA and PCC results indicate that each HUMLAND parameter uniquely contributes to scenarios involving anthropogenic fires (Fig. AIII.5; Tables AIII.3 and AIII.4), making it difficult to identify the most influential parameters or their combinations for overall ecosystem functioning. At the same time, these results showed that the Hunting_pressure parameter had a smaller impact during the LIG compared to the Early Holocene (Tables AIII.3 and AIII.4). The following section examines how Neanderthals and Mesolithic humans impacted herbivore plant consumption via assessment of the generated values for this parameter.

4.4.3 Human-megafauna interaction

To reach REVEALS estimates without anthropogenic burning, HUMLAND 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). Experiments with anthropogenic fires showed that humans could reduce megafauna plant consumption by 0–39% during the LIG, and by 0–82% during the Early Holocene (Fig. 4.7G, H). Without reducing animal impact through hunting, the simulated vegetation openness would be different from what is shown in the REVEALS data.

Despite lower hunting pressure values in the LIG compared to the Early Holocene, hunting during the LIG was likely important, given the larger megafauna population size before 100,000 BP (Bergman et al., 2023) and emerging evidence for early pre-sapiens megafauna extinctions (Svenning et al., 2024). In addition, solid evidence suggests that Neanderthals were top carnivores, obtaining protein and fat from terrestrial animals, though not exclusively (Gaudzinski-Windheuser & Roebroeks, 2014; Roebroeks & Soressi, 2016). Neanderthals hunted various animals, including reindeer (*Rangifer tarandus*), horses (*Equus*), larger species such as bovids (Bovidae) and rhinoceros (*Stephanorhinus*) (Gaudzinski-Windheuser & Roebroeks, 2014; Roebroeks & Soressi, 2016). Recent studies have confirmed that Neanderthals also hunted the largest Pleistocene mammals, straight-tusked elephants, and possibly engaged in large-scale collective subsistence activities (Gaudzinski-Windheuser et al., 2023). This aligns with growing evidence that the largest herbivores were generally preferred (Dembitzer et al., 2022; Moclán et al., 2021). Additionally, it is suggested that Neanderthals exhibited animal exploitation practices comparable to those of (sub-)recent foragers (Bar-Yosef, 2004; Gaudzinski & Roebroeks, 2000; Roebroeks & Soressi, 2016; Wißing et al., 2019). In some cases, local–regional reduction or extinction of animal populations appears to have occurred before the widespread presence of *Homo sapiens* (Dembitzer et al., 2022; Speth & Clark, 2006; Surovell et al., 2005).

HUMLAND scenarios indicate that even in absence of anthropogenic burning, foragers still played a crucial role in vegetation change, albeit indirectly through hunting, which led to a decline in megafauna plant consumption. Thus, interglacial landscapes could have been indirectly affected by *Homo* even without or with reduced anthropogenic burning. However, scenarios without human-induced fires are probably less likely, as suggested by archaeological evidence for fire use from Neanderthal and Mesolithic contexts (Nikulina et al., 2022).

4.4.4 Neanderthal and Mesolithic human impacts on vegetation

By integrating the genetic algorithm in our study, we substantially expanded our ability to generate and explore a diverse range of HUMLAND scenarios. This approach allowed us to efficiently navigate through potential outcomes, providing insights into the complex interactions between humans and the environment. As shown in Table 4.3, even with relatively good Holocene REVEALS coverage (Figs. 4.2D, 4.3D), most of the HUMLAND scenarios without human-induced fires fail to produce outputs comparable to REVEALS estimates, particularly for the distribution of dominant PFTs. This result underscores the importance of anthropogenic activities, particularly burning by foragers, for European vegetation dynamics.

4.4.4.1 Preferences for vegetation openness around campsites

The relevance of human-induced fires for both study periods is further supported by the values derived for the Openness_criteria_to_burn parameter which determines the decision-making process of hunter-gatherer groups regarding vegetation burning in a grid cell (Figs. 4.7A, B). These results showed that Neanderthals and Mesolithic humans had similarities in preferences for vegetation openness around their campsites and for starting fires based on surrounding vegetation density. In PFT distribution scenarios both LIG and Early Holocene foragers often burnt areas which were 45–78% open. This suggests that both groups engaged in fire practices across a diverse range of landscapes, including areas that were already relatively open (up to 78%).

On the other hand, scenarios generated for vegetation openness showed clear differences between Mesolithic and Middle Palaeolithic strategies. Our results indicate that in most cases Mesolithic humans engaged in burning activities across a broad range of vegetation openness (36–69%). This suggests that these groups may have implemented burning practices across both relatively open and closed areas. Conversely, Neanderthals, in the majority of vegetation openness scenarios, engaged in burning of primarily relatively dense areas (23–48% open).

The observed differences in parameter values for vegetation openness scenarios may be attributed to variations in megafauna influence on vegetation during the study periods. Given the stronger impact of herbivory on vegetation–especially on openness (Fig. 4.8)–during the LIG compared to the Holocene, resulting from larger megafauna populations and differences in community composition, Neanderthals likely needed fewer burning events to achieve vegetation openness around their campsites similar to that preferred by Mesolithic populations. Based on this interpretation of the modelling results, both Mesolithic hunter-gatherers and Neanderthals must have had the ability to alter the vegetation around their campsites, and both groups could burn landscapes relatively often if necessary. The extent of this modification likely depended on their specific subsistence activities, and the initial vegetation openness within the occupied area.

4.4.4.2 Vegetation burning range size around campsites

Modelling results indicate that the size of the area impacted by foragers remained relatively consistent (~30–40 km around campsites) across both periods for tree dominance scenarios (Fig. 4.7E). For vegetation openness scenarios matching REVEALS data, Neanderthals influenced slightly smaller areas (~20 km), while Mesolithic humans impacted larger areas (~20–30 km) at the beginning of the

Holocene, with their influence becoming more localized (~10 km) by the end of the Early Holocene (Fig. 4.7F).

Thus, both Neanderthal and Mesolithic populations showed similarities in their spatial impact patterns in the tree dominance scenarios. Openness scenarios revealed both differences and similarities: Mesolithic humans demonstrated flexible spatial strategies, typically impacting smaller areas (~10 km) but also influencing areas comparable in size to those affected by Neanderthals.

4.4.4.3 Potential minimal population size estimates

Although estimating *Homo* population sizes is beyond the scope of the current ABM (Nikulina et al., 2024b), our modelling results may inform on minimal population sizes of European hunter-gatherers. This is because HUMLAND only includes groups that use fire, and not the entire population.

To produce possible scenarios with output similar to the pollen-based vegetation cover, the mean estimated number is 1936–3266 groups for the LIG and 2243–2895 groups for the Early Holocene (Fig. 4.7C, D). Drawing upon the average documented group size of 25 among historical hunter-gatherer societies (Kelly, 2013), our modelling suggests that during the Early Holocene, Europe may have had a minimum population ranging from 56,000 to 72,000 individuals between 10,200 and 8200 BP. These estimates are consistent with the outcomes of the first HUMLAND application (Nikulina et al., 2024b). Regarding the LIG minimal population size estimates, HUMLAND indicates that 48,000–82,000 individuals were required to match REVEALS.

It is challenging to compare our minimal population size estimates with other existing data or to directly evaluate the HUMLAND results from both periods. Since HUMLAND can only estimate potential minimal population size, our Early Holocene estimates are generally lower than the currently available continental-scale estimates, which range from approximately 80,000 to 180,000 (Goldewijk, 2024; Goldewijk et al., 2017) and 52,000 to 1,111,000 (Ordonez & Riede, 2022). Our minimum estimate of 56,000 is consistent with the lower bound of the latter range.

The HUMLAND minimum population size estimates for the LIG are comparable to those for the Early Holocene. Our LIG values generally align with and slightly exceed the only available census estimates for Neanderthals, which suggest a broad range of 5000 to 70,000 individuals without specifying particular geographic regions or temporal intervals within Neanderthal history (Bocquet-Appel & Degioanni, 2013). It has been suggested that the Neanderthal population may have increased during some phases (Zilhao et al., 2024), such as the LIG, due to higher ungulate populations and an abundance of plant resources under favourable interglacial conditions (Bocquet-Appel & Degioanni, 2013). Therefore, it is difficult to support the widely-held assumption that the overall hunter-gatherer population size during the Early Holocene exceeded that of the LIG–an assumption often interpreted as implying a greater impact on vegetation by Holocene foragers (Pearce et al., 2023; Svenning, 2002). The available distribution patterns of LIG archaeological sites are likely incomplete, determined by large-scale geomorphological processes and research bias, rendering LIG sediments difficult to access (Nielsen et al., 2017; Roebroeks et al., 1992, 2024). Unlike Mesolithic sites, the LIG archaeological evidence has undergone a complete glacial–interglacial cycle, which rendered most surviving sites inaccessible due to the deposition of covering layers (Roebroeks et al., 1992). Furthermore, most of the Mesolithic evidence consists of (surface) flint scatters that can be attributed to this phase based on typological characteristics alone (ibid.). Conversely, there are no distinctive stone tools produced by Neanderthals that can be attributed specifically to the LIG. Instead, site identification relies on a combination of stratigraphic data and multiple paleoenvironmental proxies, hence requiring a taphonomic setting that is only rarely encountered (ibid.).

Thus, our modelling exercise suggests that the number of groups required to align the HUMLAND output with REVEALS is comparable for both the LIG and the Mesolithic. As we can only provide minimum estimates for both populations, this finding does not exclude the possibility that the census size of the two populations did differ, potentially being higher in one of the study periods. However, we currently lack sufficient data to determine this definitively.

An additional complexity in assessing the HUMLAND population size estimates and the vegetation openness preference values is the absence of thunderstorm frequency data for the study periods. Instead, we used modern values (Enno et al., 2020), which may not accurately reflect past environments. Distinguishing between natural fires and human-induced burning is often challenging in paleoenvironmental proxies (Nikulina et al., 2022). This uncertainty suggests that the obtained minimal population estimates and vegetation openness degree to start fires should, to some extent, be adjusted, if thunderstorm frequency was different during the LIG and the Early Holocene than today. While lightning is the main source of natural fires (Janssen et al., 2023; Whelan, 1995), the occurrence and spread of fire also depend on additional factors (e.g., fuel accumulation and moisture, weather and seasonal changes). HUMLAND incorporates these aspects to some extent: different PFTs have varying probabilities of fire ignition, and megafaunal activity and fires reduce available fuel. Some important variables such as wind patterns and seasonal climate variability are outside the temporal and spatial focus of our study. Nevertheless, any increase in the contribution of natural fires to vegetation changes would likely be limited, given the overall comparable climatic conditions between the Holocene and the LIG.

4.4.4.4 Visibility of anthropogenic burning on continental level

To properly interpret the calculated extent of modifications done by each agent (Fig. 4.8), it is crucial to consider that HUMLAND records only the last agent responsible for the final vegetation change. Within a single simulation step, the model initiates impacts on vegetation in the following order: anthropogenic vegetation burning, natural fires, megafauna plant consumption, and in the subsequent step, vegetation regeneration due to climatic effects for grid cells previously affected by fires or animals (Fig. 4.4). This ordering means that anthropogenic impacts (earlier in the sequence) may be overwritten by subsequent events. While the model effectively captures human-induced fire effects (Nikulina et al., 2024b), human impacts can be masked by later processes, leading the model to reflect only the minimal detectable human influence, rather than the full extent of anthropogenic impacts on vegetation.

The percentages of grid cell modifications by each agent (Fig. 4.8) demonstrate that megafauna influences vegetation openness across numerous grid cells within HUMLAND. It is important to emphasize that, at each simulation step, herbivores do not reduce vegetation by more than 1% on any given grid cell. This calculation is based on the combination of CARAIB NPP and the potential maximum megafauna plant consumption (for further details see the Materials and Methods section). Despite this modest per-step reduction, herbivory affects a substantial number of grid cells at the continental scale, and through its cumulative effect, replaces the first dominant PFT in approximately 30% of grid cells during the LIG and in 1% during the Early Holocene, reflecting differences in megafauna populations between these periods. Overall, the quantitative impact of herbivory remains lower than that of a fire event in a single simulation step, as fire immediately diminishes all vegetation within the affected grid cells in HUMLAND.

The HUMLAND results show the megafauna's influence on the overall vegetation structure during the LIG combined with climatic effects playing a key role in transforming European vegetation (Fig. 4.8A). 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. This underscores the role of both Neanderthals and Mesolithic humans in shaping interglacial vegetation dynamics. The mean percentage of grid cells modified by Neanderthals is relatively low: on average 6% for PFT distribution and 14% for vegetation openness (Fig. 4.8A). Nonetheless, Neanderthal impact remains detectable and represents an important component of overall interglacial ecosystem dynamics. By initiating vegetation changes that made certain areas more appealing to animals, Neanderthals may have enhanced herbivore impacts in recently burnt regions. However, the visibility of Neanderthal impacts may be obscured by climatic fluctuations and subsequent megafauna activity.

During the Early Holocene, megafauna continued to be a key driver of vegetation openness (Fig. 4.8B). Despite this significant influence, herbivores had minimal impact on PFT distribution (only 1% on average, Fig. 4.8B). Mesolithic humans were the second most influential factor after climate in shaping PFT distribution through fire use, consistent with earlier HUMLAND findings (Nikulina et al., 2024b), even with the improved representation of megafauna plant consumption in HUMLAND 2.0. HUMLAND results showed that, unlike megafauna, Mesolithic humans could open up vegetation and even completely replace shrubs and trees with bare ground, where herbs regrew. This ability allowed Mesolithic humans to transform approximately 26% of grid cells on average, reaching a maximum of 47% in PFT distribution, and to alter vegetation openness in 8% of grid cells on average, with a maximum of 14%. These findings indicate that human agency played a substantial role in shaping European landscapes, already before the emergence of agriculture (Fig. 4.8B; Tables 4.3 and 4.4).

4.5 Conclusion

By combining the spatially explicit HUMLAND ABM with a genetic algorithm to manipulate parameter values we were able to generate scenarios of early human-induced vegetation changes that match pollen reconstructions during the LIG and the Early Holocene in Europe. Our findings suggest that hunter-gatherers had a substantial impact on interglacial vegetation through the use of fire. The simulation outcomes suggest that human activities may have affected approximately 26% of PFT distributions, with a potential maximum of 47%, and on average, 8% of the vegetation openness, with a maximum of 14%, across the European landscape before the emergence of agriculture. HUMLAND outputs showed that megafauna, natural fires, and climatic fluctuations alone were insufficient to produce the pollen-based vegetation reconstructions, highlighting the importance of human agency in altering vegetation cover. These findings align with existing ethnographic studies on hunter-gatherer impact on landscapes, as well as archaeological evidence from Neanderthal and Mesolithic case studies.

Our results demonstrate that climate and especially megafauna played an impotant role in vegetation transformation during both the LIG and the Mesolithic, with a stronger effect of megafauna in the LIG. At the same time, foragers in both periods contributed to vegetation changes through fire use. In scenarios where human-induced burning was minimal or absent, both Neanderthals and Mesolithic humans still shaped landscapes indirectly by hunting large herbivores, thereby reducing their browsing and grazing pressure on vegetation. Without hunting pressure, vegetation in HUMLAND would be different (likely more open during the LIG) from pollen-based estimates suggest.

Our modelling exercise suggested that Neanderthals and Mesolithic humans shared similarities in their impact. Scenarios generated using the genetic algorithm showed that both groups influenced similarly sized areas around their campsites, had similar preferences for vegetation openness, and a comparable number of groups was requred to align HUMLAND model outputs with REVEALS data.

Future research should address gaps in the archaeological and paleoecological record identified by our study and expand our approach to other time periods and continents by incorporating more CARAIB–REVEALS comparisons in the HUMLAND ABM. The American continent is of particular interest, as the late arrival of *Homo sapiens* there allows for comparisons between landscapes with and without human impact. To enhance the precision and reliability of future modelling exercises on early human impact on landscapes via improving the quantity of proxy-based reconstructions, such as REVEALS, necessitates an expansion in the geographic coverage and density of sites from which proxies are obtained. Furthermore, modelling approaches and setups used in generating datasets that could be included in models like HUMLAND require refinements to minimize inherent biases and limitations (e.g., vegetation response to deglaciation within dynamic vegetation models). Local-scale research holds high relevance for studying past human-environment interactions to test whether patterns observed at the continental level are also visible at finer scales.

4.6 Acknowledgements

This work was performed using compute resources from the Academic Leiden Interdisciplinary Cluster Environment (ALICE) provided by Leiden University. We would like to thank Prof. Jan Kolen (Leiden University, The Netherlands), Prof. Corrie Bakels (Leiden University, The Netherlands), Dr. Tuna Kalayci (Leiden University, The Netherlands), Dr. Frank Arthur (University College of Southeast Norway, Norway), Prof. Hans Renssen (University College of Southeast Norway, Norway), Dr. Kim Cohen (Utrecht University, The Netherlands), Prof. Guido R. van der Werf (Vrije University, The Netherlands), Prof. Amanda Henry (Leiden University, The Netherlands), Oda Nuij (Leiden University, The Netherlands), and Isabeau Aurore Bertrix (Université Paris Saclay, France). We extend our gratitude to all the members of the Human Origins group at Leiden University (The Netherlands) for inspiring discussions. The authors would also like to thank Prof. Louis M. François (University of Liège, Belgium) for providing the CARAIB global dynamic vegetation model and his help in running it.

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.

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B

APPENDICES

Appendix I
Supplementary data to Nikulina et al. (2024b)

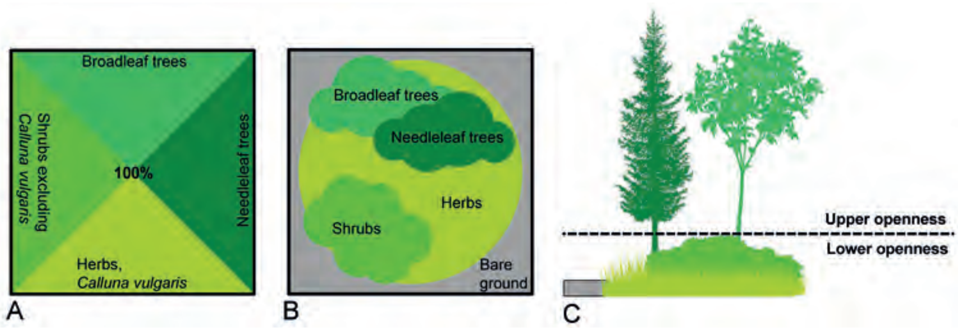

Figure AI.1 Vegetation openness representation in REVEALS (A) and in CARAIB (B, C).

Table AI.1 CARAIB and REVEALS conflicting grid cells excluded from the analysis.

CARAIB	REVEALS	Reason
PNV openness is higher than observed vegetation openness	Maximal observed vegetation openness (i.e., estimated vegetation openness + standard error) is lower than PNV openness.	In the current ABM PNV openness cannot be higher than pollen-based vegetation openness.
First dominant PFT: herbs/shrubs	First dominant PFT: trees	In the current ABM trees cannot dominate if climatic conditions only allow dominance of herbs or shrubs.
First dominant PFT: trees/herbs	First dominant PFT: shrubs	In the current ABM shrubs cannot dominate if climatic conditions only allow dominance of trees or herbs.

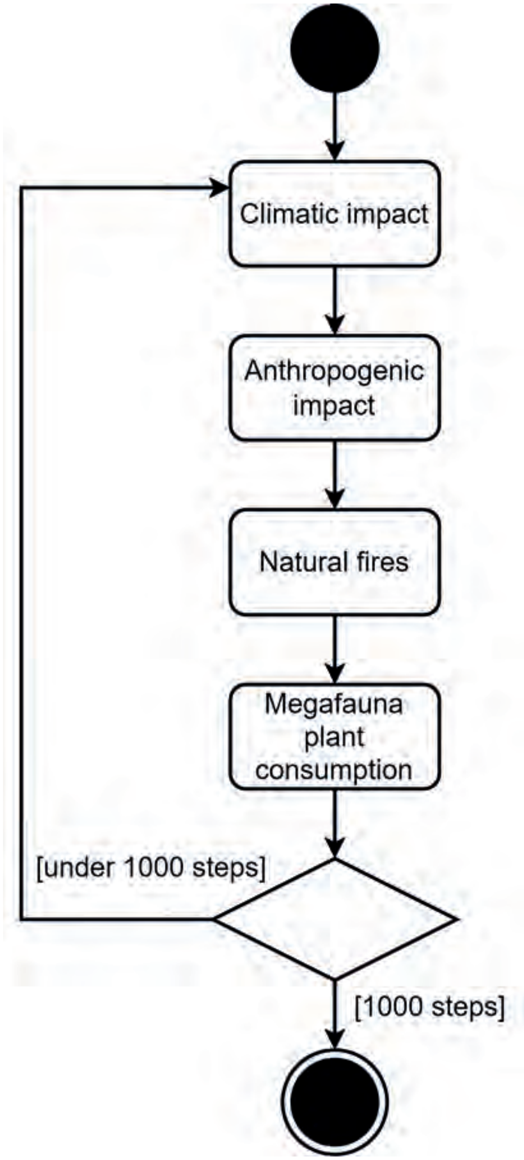

Figure AI.2 HUMLAND activity diagram.

Table AI.2 Existing estimates of FRI / fire frequency from sediment sites dated to the Early–Middle Holocene in Europe.

Region	Vegetation	Dates	FRI/fire activity	Reference
60 km northeast of city of Tampere (southern boreal vegetation zone)	The establishment of Picea in the area dated to 5290 BP	5290–1700 BP	Fire frequency was 60–90 years or probably 130–180 years (natural fire regime)	Pitkänen et al., 2001
Mediterranean basin	Open landscape that developed into rather closed forests	11,700–10,400 BP	High IFF (inferred fire frequency) (FRI: 50–350; fire frequency 2,5–4,8 episodes per 500 years)	Vannière et al., 2008
	Deciduous forests	10,400–8600 BP	Even more frequent fires (FRI: 50–350; fire frequency 2–5 episodes per 500 years)	
Lowlands of the Transylvanian Plain	Less open deciduous woodland	7100–4700 BP	317-year mFRI and a maximum FF of 3 fires/1000 years (gradual increase of anthropogenic impact)	Feurdean et al., 2013
Eastern Latvia	Open landscape (dominance of grass)	11,700–9500 BP	1–4 fires per 1,000 years	Feurdean et al., 2017
	Boreal forest	9500–7500 BP	Shorter FRI (200 years)	
Balkan Peninsula	Boreal forest	8050–4000 BP	Low-to-moderate CHAR values, a 300-year mFRI (200–400 years) and 12 charcoal peaks for this time interval. Other mountain boreal forests: FRI of 50–100 (Bulgaria), 60–250 (Carpathians and Bohemia), 80–100 (Mediterranean) years	Feurdean et al., 2019
Central part of the East European Plain	Series of consecutive phases of birch and birch-pine forests with an admixture of broadleaved trees	6850–5600 BP	100 years and was frequently in the range of 10–20 years (presence of anthropogenic impact)	Novenko et al., 2018
	After 5000 BP the expansion of woodland coverage (to 60–70%), the increase in the proportion of broadleaved trees and the appearance of spruce (mixed forest)	5600–3000 BP	Fire frequency is 300–500 years (presence of anthropogenic impact)	

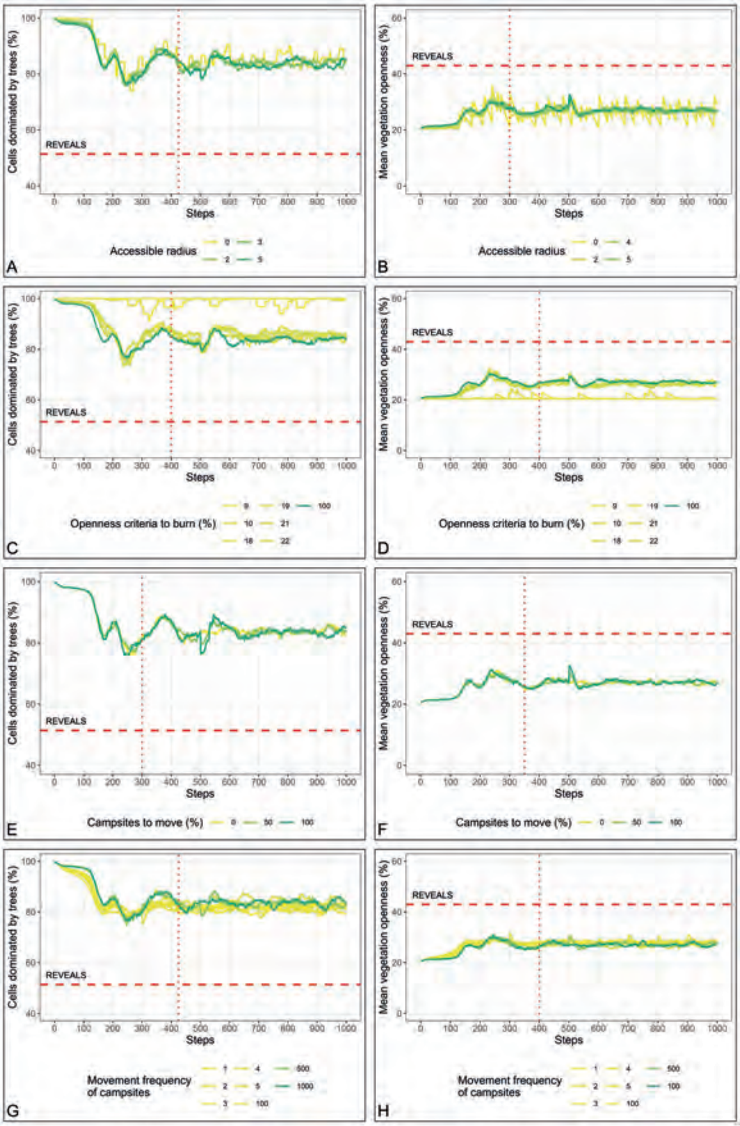

Figure AI.3 Results of experiments conducted for 100 hunter-gatherer groups: A–percentage of grid cells dominated by trees after the accessible radius was varied; B–mean vegetation openness after the accessible radius was varied; C–percentage of grid cells dominated by trees after the openness criteria to burn was varied; D–mean vegetation openness after the openness criteria to burn was varied; E–percentage of grid cells dominated by trees after the percentage of moving campsites was varied; F–mean vegetation openness after the percentage of moving campsites was varied; G–percentage of grid cells dominated by trees after the movement frequency was varied; H–mean vegetation openness after the movement frequency was varied. Each line depicted on the experiment output graph represents the mean of 30 simulation runs. The horizontal dashed line indicates REVEALS estimates, and the vertical dotted line shows the step when simulations reach equilibrium.

Table AI.3 Experiment results for human-induced vegetation changes caused by 100 groups with different other parameter values. Equilibrium indicates the step when the simulation output does not vary dramatically. Minimum varied parameter values show the starting impact of the agent, and maximum varied parameter values define the maximal possible impact of an agent (i.e., when REVEALS estimates are reached).

Sources of impact	Varied parameters	Constants		Equilibrium reached (steps)		Minimum varied parameter values and mean of standard deviation	Maximum varied parameter values and mean of standard deviation	
		Parameters	**Value**	**Trees**	**Openness**		**Trees**	**Openness**
Humans	Accessible_radius	Territory_impacted_by_thunderstorms	False	425	300	0 (5.8*; 2.7**)	3 (5.3*)	2 (2.7**)
		Megafauna	False					
		Openness_criteria_to_burn	50					
		Campsites_to_move	50					
		Movement_frequency_of_campsites	500					
	Openness_criteria_to_burn	Territory_impacted_by_thunderstorms	False	400	400	9 (0*; 0**)	21 (6.2*)	19 (3**)
		Megafauna	False					
		Accessible_radius	5					
		Campsites_to_move	50					
		Movement_frequency_of_campsites	500					
	Campsites_to_move	Territory_impacted_by_thunderstorms	False	300	350	0 (5*; 2.5**)	0 (5*)	0 (2.5**)
		Megafauna	False					
		Accessible_radius	5					
		Openness_criteria_to_burn	50					
		Movement_frequency_of_campsites	500					
	Movement_frequency_of_campsites	Territory_impacted_by_thunderstorms	False	425	400	3; 4*** (3.6*; 1.8**)	1 (2.7*)	1 (1.4**)
		Megafauna	False					
		Accessible_radius	5					
		Openness_criteria_to_burn	50					
		Campsites_to_move	50					

*this value represents the mean standard deviation calculated for the proportion of grid cells dominated by trees between steps 450 to 1000
**this value represents the mean standard deviation calculated for the mean vegetation openness between steps 450 to 1000
***the first value indicates minimal impact for the percentage of grid cells dominated by trees; the second number indicates minimal impact for the mean vegetation openness

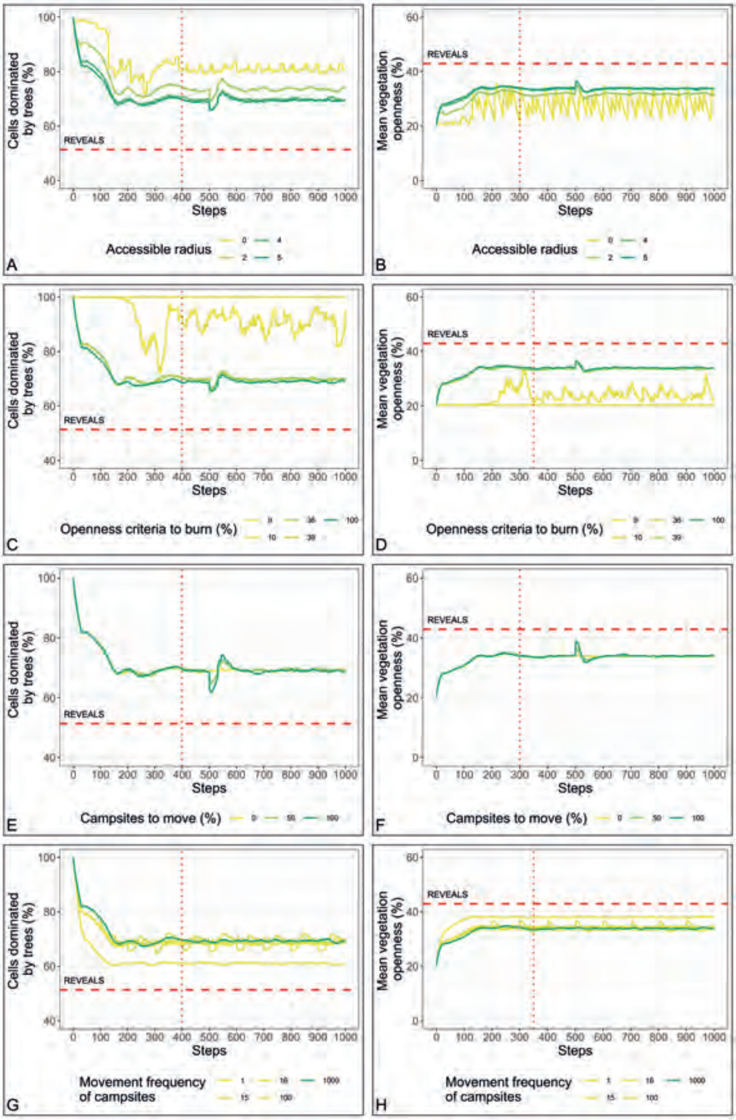

Figure AI.4 Results of experiments conducted for 1000 hunter-gatherer groups: A–percentage of grid cells dominated by trees after the accessible radius was varied; B–mean vegetation openness after the accessible radius was varied; C–percentage of grid cells dominated by trees after the openness criteria to burn was varied; D–mean vegetation openness after the openness criteria to burn was varied; E–percentage of grid cells dominated by trees after the percentage of moving campsites was varied; F–mean vegetation openness after the percentage of moving campsites was varied; G–percentage of grid cells dominated by trees after the movement frequency was varied; H–mean vegetation openness after the movement frequency was varied. Each line depicted on the experiment output graph represents the mean of 30 simulation runs. The horizontal dashed line indicates REVEALS estimates, and the vertical dotted line shows the step when simulations reach equilibrium.

Table AI.4 Experiment results for human-induced vegetation changes caused by 1000 groups with different other parameter values. Equilibrium indicates the step when the simulation output does not vary dramatically. Minimum varied parameter values show the starting impact of the agent, and maximum varied parameter values define the maximal possible impact of an agent (i.e., when REVEALS estimates are reached).

Sources of impact	Varied parameters	Constants		Equilibrium reached (steps)		Minimum varied parameter values and mean of standard deviation	Maximum varied parameter values and mean of standard deviation	
		Parameters	Value	Trees	Openness		Trees	Openness
Humans	Accessible_radius	Territory_impacted_by_thunderstorms	False	400	300	0 (2.4*; 1.1**)	4 (1.7*)	4 (0.8**)
		Megafauna	False					
		Openness_criteria_to_burn	50					
		Campsites_to_move	50					
		Movement_frequency_of_campsites	500					
	Openness_criteria_to_burn	Natural_fires	False	400	350	9 (0*; 0**)	39 (1.7*)	36 (0.8)
		Megafauna	False					
		Accessible_radius	5					
		Campsites_to_move	50					
		Movement_frequency_of_campsites	500					
	Campsites_to_move	Territory_impacted_by_thunderstorms	False	400	300	0 (1.6*; 0.8**)	0 (1.6*)	0 (0.8**)
		Megafauna	False					
		Accessible_radius	5					
		Openness_criteria_to_burn	50					
		Movement_frequency_of_campsites	500					
	Movement_frequency_of_campsites	Territory_impacted_by_thunderstorms	False	400	350	15; 16*** (1.4*; 0.6**)	1 (1*)	1 (0.5**)
		Megafauna	False					
		Accessible_radius	5					
		Openness_criteria_to_burn	50					
		Campsites_to_move	50					

*this value represents the mean standard deviation calculated for the proportion of grid cells dominated by trees between steps 450 to 1000

**this value represents the mean standard deviation calculated for the mean vegetation openness between steps 450 to 1000

***the first number indicates minimal impact for the percentage of grid cells dominated by trees; the second number indicates minimal impact for the mean vegetation openness

Table AI.5 Experiment results for human-induced vegetation changes caused by 4000 groups with different other parameter values. Equilibrium indicates the step when the simulation output does not vary dramatically. Minimum varied parameter values show the starting impact of the agent, and maximum varied parameter values define the maximal possible impact of an agent (i.e., when REVEALS estimates are reached).

Sources of impact	Varied parameters	Constants		Equilibrium reached (steps)		Minimum varied parameter values and mean of standard deviation	Maximum varied parameter values and mean of standard deviation	
		Parameters	Value	Trees	Openness		Trees	Openness
Humans	Accessible_ radius	Natural_fires	False	300	200	0 (1.3*; 0.6**)	5 (0.9*)	4 (0.5**)
		Megafauna	False					
		Openness_criteria_to_burn	50					
		Campsites_to_move	50					
		Movement_frequency_of_campsites	500					
	Openness_ criteria_to_ burn	Natural_fires	False	325	300	9 (0*; 0**)	58 (0.8*)	46 (0.5*)
		Megafauna	False					
		Accessible_radius	5					
		Campsites_to_move	50					
		Movement_frequency_of_campsites	500					
	Campsites_ to_move	Natural_fires	False	200	200	0 (0.9*; 0.4*)	0 (0.9*)	0 (0.4*)
		Megafauna	False					
		Accessible_radius	5					
		Openness_criteria_to_burn	50					
		Movement_frequency_of_campsites	500					
	Movement_ frequency_ of_campsites	Natural_fires	False	200	300	21; 19*** (1*;0.5**)	1 (0.7*)	1 (0.4*)
		Megafauna	False					
		Accessible_radius	5					
		Openness_criteria_to_burn	50					
		Campsites_to_move	50					

*this value represents the mean standard deviation calculated for the proportion of grid cells dominated by trees between steps 450 to 1000
**this value represents the mean standard deviation calculated for the mean vegetation openness between steps 450 to 1000
***the first number indicates minimal impact for the percentage of grid cells dominated by trees; the second number indicates minimal impact for the mean vegetation openness

A1

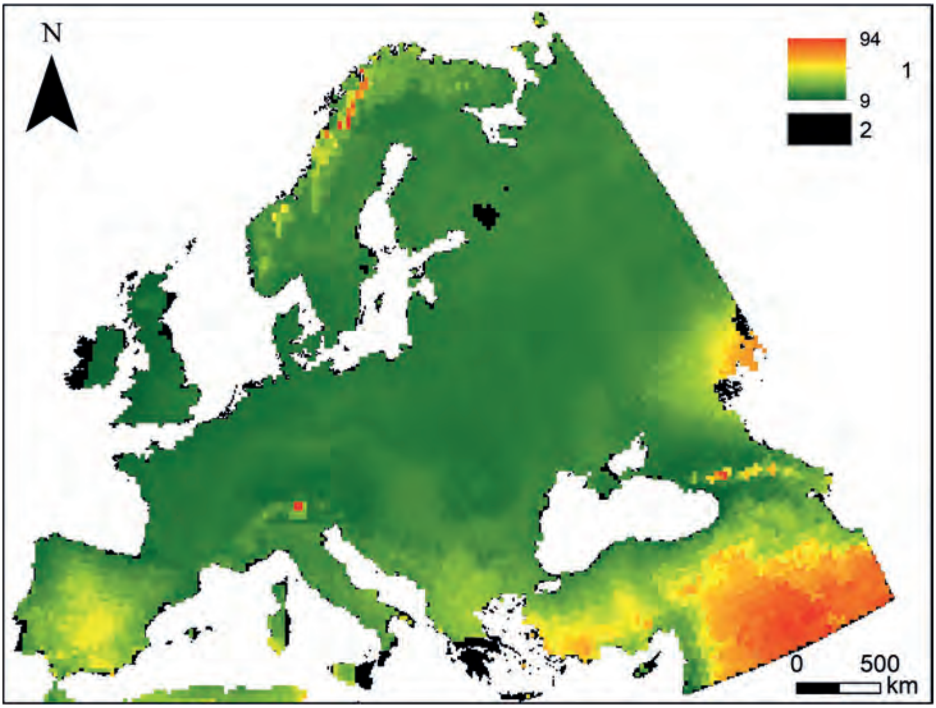

Figure AI.5 CARAIB bare ground. Legend: 1–fraction of bare ground in percentages; 2–no data.

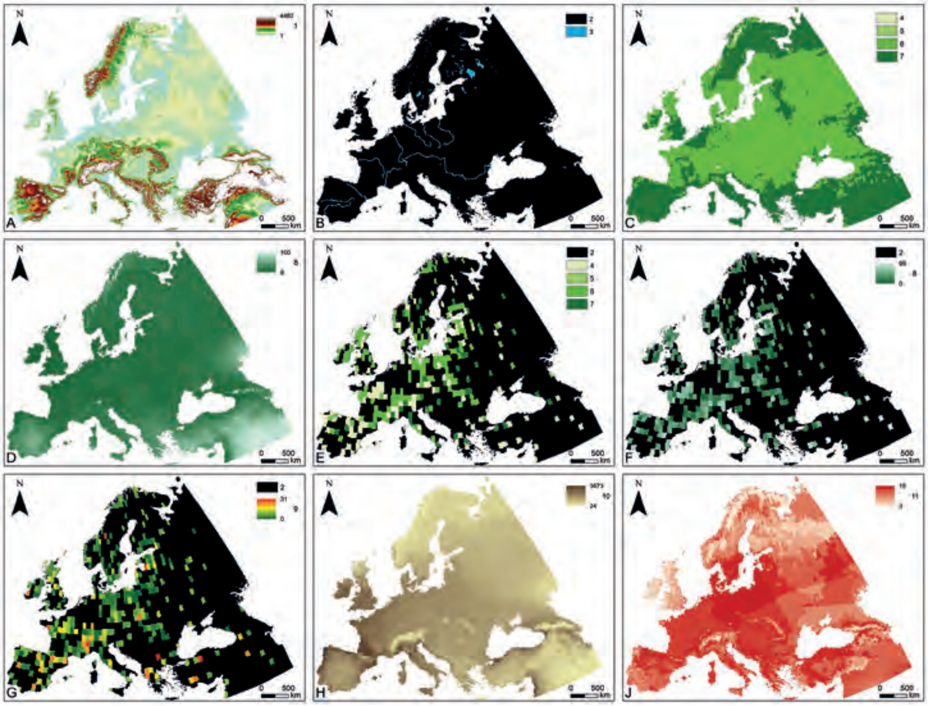

Figure AI.6 Datasets used in the current ABM: DEM (A), major rivers and lakes (B), CARAIB distribution of first dominant PFTs (C) and vegetation openness (D), REVEALS distribution of first dominant PFTs (E) and vegetation openness (F) and its standard errors (G), CARAIB NPP (H), megafauna vegetation consumption (I). Legend: 1–elevation (m); 2–no data; 3–major rivers and lakes; 4–herbs; 5–shrubs; 6–broadleaf trees; 7–needleleaf trees; 8–vegetation openness in percentages; 9–standard errors for REVEALS vegetation openness; 10–CARAIB NPP (g/m^3); 11–megafauna vegetation consumption (g/m^3).

Table AI.6 Confusion matrix for CARAIB and REVEALS PFT comparison.

	Predicted Positive	**Predicted Negative**
Actual Positive	5	0
Actual Negative	7776	8225

Table AI.7 Experiment results for megafauna, thunderstorm and climatic impact on vegetation. Equilibrium indicates step at which the simulation output reaches a stable state. Minimum varied parameter values show the starting impact of the agent, and maximum varied parameter values define the maximal possible impact of an agent (i.e., when REVEALS estimates are reached).

Sources of impact	Varied parameters	Constants		Equilibrium reached (steps)		Minimum varied parameter values and mean of standard deviation	Maximum varied parameter values and mean of standard deviation	
		Parameters	Value	Trees	Openness		Trees	Openness
Thunderstorms	Territory_impacted_by_thunderstorms	Humans	False	450	450	0.1 (1.5*; 0.8**)	7 (0.5*)	4.7 (0.3**)
		Megafauna	False					
Thunderstorms, megafauna	Territory_impacted_by_thunderstorms	Humans	False	375	375	0.1 (1.4*; 0.7**)	7 (0.5*)	4.7 (0.3**)
		Megafauna	True					

*this value represents the mean standard deviation calculated for the proportion of grid cells dominated by trees between steps 450 to 1000
**this value represents the mean standard deviation calculated for the mean vegetation openness between steps 450 to 1000

Table AI.8 Experiment results for human-induced vegetation changes caused by different group numbers. Equilibrium indicates the step at which the simulation output reaches a stable state. Minimum varied parameter values show the starting impact of the agent, and maximum varied parameter values define the maximal possible impact of an agent (i.e., when REVEALS estimates are reached).

Sources of impact	Varied parameters	Constants		Equilibrium reached (steps)		Minimum varied parameter values and mean of standard deviation	Maximum varied parameter values and mean of standard deviation	
		Parameters	Value	Trees	Openness		Trees	Openness
Humans	Number_of_hunter-gatherer_groups	Territory_impacted_by_thunderstorms	False	325	230	1 (20.8*; 9.6**)	3167 (1.1*)	3128 (0.5**)
		Megafauna	False					
		Accessible_radius	5					
		Openness_criteria_to_burn	50					
		Campsites_to_move	50					
		Movement_frequency_of_campsites	500					

*this value represents the mean standard deviation calculated for the proportion of grid cells dominated by trees between steps 450 to 1000
**this value represents the mean standard deviation calculated for the mean vegetation openness between steps 450 to 1000

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Table AI.9 Confusion matrix for HUMLAND and REVEALS PFT comparison.

	Predicted Positive	**Predicted Negative**
Actual Positive	3925	3854
Actual Negative	3856	4371

Appendix II
HUMLAND ABM 1.0 Overview, design concepts and details (ODD) protocol

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AII.1 Purpose

Humans started transforming their environment long before the emergence of agriculture and industrialization. Foraging societies conduct niche construction activities including vegetation burning which significantly modifies the occupation area of hunter-gatherers. Currently available evidence suggests that both Neanderthals and Mesolithic humans practiced vegetation burning. Due to the scarcity of evidence and the absence of a common research protocol to study the anthropogenic impact on landscapes, there are gaps in research about the dynamics of interglacial environments and the role of hominins in landscape changes. Particularly, the extent of vegetation burning organized by hunter-gatherers is still a focal point of research.

Landscape dynamics are complex and include variable components such as climatic fluctuations, megafauna impact, natural fires, and anthropogenic activities. Thus, there is a need for further research which can allow us to assess different possible scenarios for anthropogenic impact which play a role in landscape change. Therefore, the purpose of this model is to track and quantify the intensity of different impacts on landscapes on the continental level and to determine the most influential factor in transformation of interglacial vegetation with specific focus on burning organized by hunter-gatherers. This model accumulates different types of spatial datasets (Section AII.6) which are used as input and target for ABM results. Additionally, the study incorporates recently obtained specifically for this research continental-scale estimates of fire return intervals (FRI) and speed of vegetation regrowth in the current simulation. The obtained results include maps of possible scenarios of modified landscapes in the past and quantification of input of each agent (climate, humans, megafauna and natural fires). The model has been implemented in *NetLogo* (version 6.2.2) and is accessible via the CoMSES model depository (https://www.comses.net/, search for HUMLAND; DOI: 10.25937/fxdq-fn86).

AII.2 Entities, state variables, and scales

The following entities are included in the model: agents representing hominin groups (one agent is one group, Table AII.1), campsites (turtles, have only one static variable my_hominin which indicates the group occupying this campsite) and grid cells (patches, Table AII.2).

Table AII.1 Hominin state variables.

Variable name	Variable type and units	Meaning
my_home	Dynamic, patch	A patch where a campsite is located (home patch of a group)
my_campsite	Dynamic, turtle	Campsite is the home of a hominin group

Table AII.2 Grid cells state variables.

Variable name	Variable type and units	Meaning
patch_elevation	Static, float, meters	Absolute elevation (a.s.l.)
patch_natural_pft	Static, integer	CARAIB (CARbon Assimilation In the Biosphere) first dominant PFT: 1–herbs, 2–shrubs, 3–needleleaf trees, 4–broadleaf trees, -1–no data
patch_pollen_pft	Static, integer	REVEALS (Regional Estimates of VEgetation Abundance from Large Sites) first dominant PFT: 1–herbs, 2–shrubs, 3–needleleaf trees, 4–broadleaf trees, -1–no data
patch_pft_updating	Dynamic, integer	Current dominant PFT: 1–herbs, 2–shrubs, 3–needleleaf trees, 4–broadleaf trees, -1–no data, 0–burnt/fully consumed area
patch_natural_openness	Static, float, percentage	CARAIB vegetation openness: 0–minimal value (0%, totally closed), 100–maximal value (100%, totally open), -1–no data
patch_pollen_openness	Static, float, percentage	REVEALS vegetation openness: 0–minimal value (0%, totally closed), 99–maximal value (99%, totally open), -1–no data
patch_pollen_openness_se	Static, float	REVEALS vegetation openness standard error (se)
patch_pollen_openness_max	Static, float, percentage	Maximal possible REVEALS openness: patch_pollen_openness + patch_pollen_openness_se
patch_openness_updating	Dynamic, integer, percentage	Current vegetation openness: 0–minimal value (0%, totally closed), 100–maximal value (100%, totally open), -1–no data
rivers_lakes	Static, integer	Presence of big rivers and lakes: 0–no rivers/lakes, 1–presence of rivers/lakes, -1–no data
fri	Static, integer, years	FRI values for each PFT
patch_natural_npp	Static, float, g/m^2	CARAIB NPP
megafauna_npp_consumption	Static, float, g/m^2	Megafauna carbon consumption
fire_delay_after_consumption	Dynamic, integer	Delay in the frequency of natural fires after partial megafauna consumption of vegetation
openness_regrowth_rate	Dynamic, float	Openness regrowth speed per step after impact

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Variable name	Variable type and units	Meaning
last_burning_episode	Dynamic, integer	Simulation step of the last fire episode of a patch
next_burning_episode	Dynamic, integer	Possible next natural fire event when probability of ignition is 100%.
last_partial_consumption_episode	Dynamic, integer	Step of the last partial consumption episode of a patch
last_agent_impacted_pft	Dynamic, integer	Last agent that changed a dominant PFT of a patch: 1–humans, 2–natural fires, 3–climate, 4–megafauna
last_agent_impacted_openness	Dynamic, integer	Last agent that impacted a patch: 1–humans, 2–natural fires, 3–climate, 4–megafauna
herbs_regeneration_step	Dynamic, integer	Step when herbs will regrow after vegetation burning or consumption
shrubs_regeneration_step	Dynamic, integer	Step when shrubs will regrow after vegetation burning or consumption
needleleaf_trees_regeneration_step	Dynamic, integer	Step when needleleaf trees will regrow after vegetation burning or consumption
broadleaf_trees_regeneration_step	Dynamic, integer	Step when broadleaf trees will regrow after vegetation burning or consumption
agent_that_could_impact_neigbouring_pathes	Dynamic, integer	Agent that can potentially cause burning on neighbouring patches: 1–humans, 2–natural fires, 3–climate, 4–megafauna
hominin_accessible_area	Dynamic, integer	Defines if the patch is within accessible area for humans: 1–within the area, 0–not accessible for humans
raster_layer	Dynamic, integer/float	Used to create an ASCII file with modelling results

The model is two-dimensional, and its spatial extent is a rectangle with 544 x 430 patches. Each cell of input raster datasets (Section AII.6, Table AII.6) is resampled (i.e., spatial resolution was changed) to 10 km × 10 km in size. The world wraps horizontally and vertically. The current version of the model imports all spatial datasets for one time window (9200–8700 BP). One simulation step equals one year, and the current simulation does not account for seasonal variability. One run is 1000 time steps.

AII.3 Process overview and scheduling

Simulation starts with setup when input datasets are imported, entities are created, their state variables are set, and the conflicting cells are removed. In HUMLAND, more closed vegetation can only switch to more open vegetation after a disturbance event (fire, grazing). In our data comparison, where CARAIB shows a greater degree of openness in vegetation than REVEALS, we exclude these locations:

the ABM will not be able to generate vegetation that is comparable to REVEALS as it is constrained by the CARAIB-prescribed PNV. As a result, the similarity between ABM output and REVEALS datasets can only be improved for grid cells where initial vegetation openness is equal to or lower than observed estimates. These are the conflicting grid cells which are not taken into account when the primary observations (mean vegetation openness and percentage of dominant PFTs for cells with both REVEALS and CARAIB data) during the simulation runs are taken.

The process overview of simulation runs is shown in Figure AII.1. Plots update at each step, and the simulation stops after 1000 steps. Each of them starts with vegetation regeneration. This submodel (Section AII.7) executes only for patches which were previously (i.e., during the earlier step) burnt or consumed.

Hominins are the first agent that reduces vegetation cover. The anthropogenic fire submodel (Section AII.7) is executed via three phases. During the first phase, hominins randomly move towards one of neighbouring patches within the area defined by accessible radius around their campsites. When a hominin reaches a patch with trees or shrubs as a dominant PFT and vegetation openness smaller or equal to a number defined via the Openness_criteria_to_burn variable, this patch is burnt. During the second phase, fire spread is initiated. Finally, the current vegetation openness of burnt patches and dominant PFT are compared with REVEALS data.

The natural fires submodel (Section AII.7) is initiated after hominin impact. During the setup the number of patches, that will be hit by thunderstorms per step, is calculated based on a value of the Territory_impacted_by_thunderstorms variable. Every simulation step random patches are chosen and impacted by thunderstorms. Thunderstorms can occur in high mountains, lakes and rivers, but these episodes never lead to ignition. Depending on the probability of ignition of a patch which are not water bodies or high mountains, patches can be burnt after thunderstorms. Similarly to anthropogenic burning, thunderstorms can cause fire spread. Finally, the current vegetation openness of burnt patches and dominant PFT are compared with REVEALS data.

Only grid cells with fully recovered vegetation can be consumed by megafauna. This assumption arises from our use of estimates for potential maximal megafauna plant consumption and the absence of data regarding partial consumption during the vegetation regrowth phase. After plant consumption, vegetation openness increases depending on the CARAIB NPP values and the maximal megafauna plant consumption estimates. Regarding megafauna impact on PFTs, it is assumed that megafauna equally consumes all PFTs present on a grid cell, i.e., besides the first dominant PFT megafauna consumes second, third and fourth dominant PFTs in equal proportions. That is why, the first dominant PFT is replaced, only if the vegetation was entirely consumed by megafauna, and vegetation openness value after consumption is 100%. In this case, the first dominant PFT would be replaced by bare ground

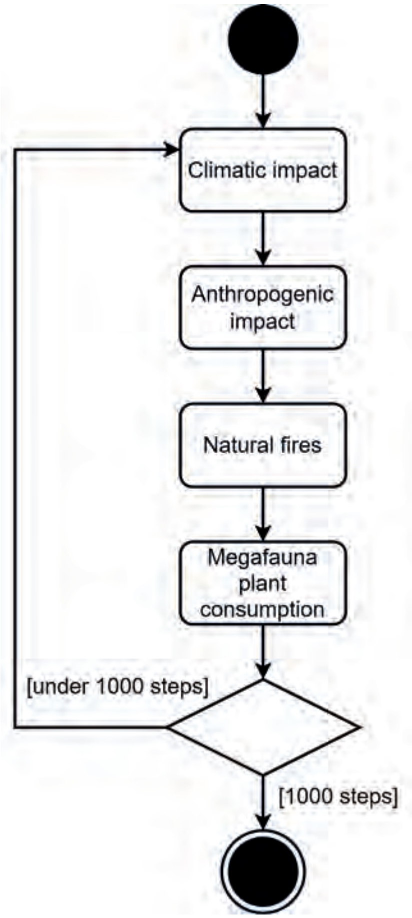

Figure AII.1 Activity diagram of process overview.

AII.4 Design concepts (after Nikulina et al., 2024b)

AII.4.1 Basic principles

The history of anthropogenic impacts on the environment spans over many years, with humans already engaging in landscape transformations before the emergence of agriculture. Ethnographic observations show that hunter-gatherers or foragers (i.e., groups that mainly depended on food collection or foraging of wild resources) influence their surroundings in several ways including modification of vegetation communities via burning. This practice was identified for all vegetation types except tundra at different spatial scales and for diverse objectives including driving game, stimulating the growth of edible plants, and clearing pathway.

Besides ethnographic data, evidence from archaeological contexts show that fire use was an important part of the technological repertoire of the *Homo* lineage since at least the second half of the Middle Pleistocene. Human-induced vegetation burning during the Late Pleistocene has been proposed as a potential factor in several case studies spanning various continents. Notably, the earliest evidence of such activities on a local scale was identified at the Neumark-Nord site in Germany, dated to the Last Interglacial (Eemian, ~130,000–116,000 BP). In addition, fire-using foragers were suggested as one of the primary drivers of vegetation openness in Europe during the Last Glacial Maximum, i.e., possibly constituting one of the earliest large-scale anthropogenic modifications of system earth.

While these Pleistocene cases are still subject to debate, human-induced vegetation burning conducted by hunter-gatherers during the Early–Middle Holocene (~11,700–6000 BP) is generally accepted, even though the quality of the data is not necessarily that different. However, the number of case studies is higher for the Early–Middle Holocene than for the Pleistocene. Most of the Early–Middle Holocene evidence comes from the European context.

Despite the presence of case studies for anthropogenic burning (intentional or not) of past landscapes by hunter-gatherers, it is still difficult to establish whether these local-scale impacts caused changes at the regional and (sub-)continental scales. Furthermore, overall landscape dynamics do not only depend on humans, and rather represent the complex interplay of natural and cultural processes at different spatio-temporal scales. Landscapes are thus complex systems where heterogeneous components interact to impact on ecological processes, and might demonstrate non-linear dynamics and emergence. Therefore, it is often challenging to distinguish different impacts on landscapes using proxy-based reconstructions (e.g., palynological datasets).

Modelling approaches offer excellent opportunities to explore how complex components of systems might interact, particularly when real-time experiments are not possible. Spatially-explicit agent-based modelling (ABM) is commonly used to explore complex systems where multiple factors intertwine and to propose possible scenarios of system functioning, and the outcomes of ABMs can be compared to empirical data. This approach has been applied in various contexts to study past human-environment interactions and land use/land cover changes. There are examples of such models for past societies that practiced agriculture and animal husbandry, and for hunter-gatherer groups. In the case of ABM developed to study foragers, the use of fire by hunter-gatherers to transform foragers' surroundings and the landscape consequences of these practices are usually not discussed.

This model includes four types of impact on vegetation: climatic impact, anthropogenic fires, thunderstorms, and megafauna plant consumption. Thunderstorms were included because lightning is one of the most general and widespread triggers of natural fire. Another source of impact is climate, and it is included as a crucial element for vegetation regeneration after fires or vegetation consumption. Finally, megafauna are also a part of the current ABM, because the herbivory activity impacts litter accumulation, and high levels of megafauna plant consumption reduce fire occurrence in many areas.

AII.4.2 Emergence

The model's key results are increase of average vegetation openness and decrease of the percentage of cells dominated by trees. These results emerge from joint (i.e., several agents together) and separate (i.e., only one agent) impacts of different agents (hominins, thunderstorms and megafauna) on vegetation. The increase of vegetation openness and change of PFT's distribution are driven by a specific combination of agents and values of variables that influence their behaviour.

AII.4.3 Adaptation

There is no adaptation in the model.

AII.4.4 Objectives

Vegetation burning is an objective for hominins. Each step hominins move randomly to one of the neighbouring patches. If it covered by shrubs or trees and its vegetation openness is equal or lower than the Openness_criteria_to_burn value, then the fire will be set. Otherwise, humans do not impact this patch. Megafauna and thunderstorms do not have objectives.

AII.4.5 Learning

Agents do not learn.

AII.4.6 Prediction

Agents do not predict.

AII.4.7 Sensing

Humans are assumed able to sense dominant PFT and vegetation openness of a grid cell where humans are located. Hominins can sense if their campsites and home patches are beyond accessible radius. It is useful in cases when two campsites are located nearby, and their accessible areas overlap. If a hominin is far from his campsite (does not sense his campsite anymore i.e., it is beyond accessible radius), this hominin automatically comes back to its campsite.

AII.4.8 Interaction

Hominins directly affect patches. If a hominin decides to burn a patch, its state variables are modified.

AII.4.9 Stochasticity

Stochasticity is used in initializing the model when random distribution of hominins within the study is set. Additionally, hominins randomly choose one of neighbouring patches on which hominins move around campsites. Finally, humans randomly choose patches when the campsites will be moved during simulation runs. This happens with a specific frequency defined via the Movement_frequency_of_campsites variable.

Thunderstorm impact also includes stochasticity. The number of patches are defined via the Territory_impacted_by_thunderstorms parameter. Several random inland patches are selected every simulation step to potentially have natural fire. The actual natural vegetation burning depends on a probability of ignition P(I) (AII.1):

$$P(I) = \frac{T - B}{F} \qquad \text{(AII.1)},$$

where B is the step when the last burning episode occurred, F–FRI, and T–the number of simulation steps (ticks) since the beginning of the simulation. Once P(I) is calculated, a random float number between 0 and 1 is chosen. If $R \leq P(I)$, this patch will be burnt. Similarly to ignition caused by natural fires, fire can spread on neighbouring patches after natural and human-induced fires. For the neighbouring patches the P(I) is calculated, and the fire event can occur depending on the obtained P(I) and random a random float number.

AII.4.10 Collectives

There are no collectives in the model.

AII.4.11 Observation

The primary model observations are distribution of dominant PFT (percentage of patches covered by each PFT) and mean vegetation openness for patches which have both REVEALS estimates and CARAIB values (i.e., not all patches are considered). These values are provided via plots on the model interface and extracted tables. The ABM output is considered similar to REVEALS data if the simulation produced the same percentage of first dominant PFTs and mean vegetation openness values or if the difference between ABM output and REVEALS data varies within ±5% (the range of change is 10%). Additionally, the different types of impact (i.e., the number of grid cells modified by each type of impact) are tracked via recording which impact caused openness and PFT changes.

AII.5 Initialization (after Nikulina et al., 2024b)

First, the environment is created during the initialization. Patch state variables at the end of the initialization step are described in Table AII.3. In HUMLAND, more closed vegetation can only switch to more open vegetation after a disturbance event (fire, grazing). In our data comparison, where CARAIB shows a greater degree of openness in vegetation than REVEALS, we exclude these locations: the ABM will not be able to generate vegetation that is comparable to REVEALS as it is constrained by the CARAIB-prescribed PNV. As a result, the similarity between ABM output and REVEALS datasets can only be improved for grid cells where initial vegetation openness is equal to or lower than observed estimates. Secondly, there are several grid cells where climatic conditions only favour dominance of herbs or shrubs, but observed vegetation indicates dominance of trees. Besides that, shrubs cannot dominate grid cells where climatic conditions favour trees or herbs in HUMLAND. Such cases do not improve similarity between ABM output and REVEALS data, and, therefore, these grid cells were also excluded (Table AII.5).

Table AII.3 Patch state variables and their values at the end of the initialization stage.

Variable name	Value	Explanation
patch_elevation	In accordance with GTOPO30	Value is set depending on GTOPO30 dataset
patch_natural_pft	In accordance with CARAIB first dominant PFT	Value is set between 1 and 4 depending on CARAIB dataset
patch_pollen_pft	In accordance with REVEALS first dominant PFT	Value is set between 1 and 4 depending on CARAIB dataset
patch_pft_updating	patch_pft_updating = patch_natural_pft	Variable has the same value as theoretical potential natural vegetation provided by CARAIB
patch_natural_openness	In accordance with CARAIB vegetation openness	Value is set between 9 and 100 depending on CARAIB dataset
patch_pollen_openness	In accordance with REVEALS vegetation openness	Value is set between 0 and 99 depending on REVEALS dataset
patch_pollen_openness_se	In accordance with REVEALS standard errors	Value is set depending on REVEALS dataset
patch_pollen_openness_max	patch_pollen_openness + patch_pollen_openness_se	Maximal possible REVEALS vegetation openness
patch_openness_updating	patch_natural_openness = patch_openness_updating	Variable has the same value as theoretical potential natural vegetation provided by CARAIB
rivers_lakes	0 or 1	Value depends on WISE dataset
fri	246, 426, 286 or 293	The value depends on CARAIB first dominant PFT (Table AII.4)
patch_natural_npp	In accordance with CARAIB NPP	Value is set depending on CARAIB dataset
megafauna_npp_consumption	In accordance with megafauna vegetation consumption dataset	Value is set depending on megafauna vegetation consumption data
fire_delay_after_consumption	-1	Before megafauna consumption of a patch this variable is set to -1
openness_regrowth_rate	0	Before simulation runs this value is set to 0
last_burning_episode	0	Before simulation runs this value is set to 0
next_burning_episode	last_burning_episode + fri	Defines the step when this patch has 100% chances to be burnt
last_partial_consumption_episode	-1	Before megafauna consumption of a patch this variable is set to -1
last_agent_impacted_pft	3	Before simulation starts the vegetation cover is created by climate only. Thus, all patches have value 3
last_agent_impacted_openness	3	Before simulation starts the vegetation cover is created by climate only. Thus, all patches have value 3

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Variable name	Value	Explanation
herbs_regeneration_step	0	Before agent's impact all patches do not require regeneration step
shrubs_regeneration_step	0	Before agent's impact all patches do not require regeneration step
needleleaf_trees_regeneration_step	0	Before agent's impact all patches do not require regeneration step
broadleaf_trees_regeneration_step	0	Before agent's impact all patches do not require regeneration step
agent_that_could_impact_neigbouring_pathes	0	This value is 0 prior to simulation runs, because there was no impact yet
hominin_accessible_area	0 or 1	If the patch is within accessible area, the value is set to 1. Otherwise, this variable equals 0
raster_layer	-	Used to create .asc file. This variable can have any value depending on chosen patch variable

Table AII.4 Mean FRI for each dominant PFT.

PFT	Mean FRI estimated via MODIS
Needleleaf trees	246
Broadleaf trees	426
Shrubs	286
Herbs	293

Table AII.5 CARAIB and REVEALS conflicting cells excluded from the analysis during initiation stage.

CARAIB	REVEALS	Reason
Possible natural (CARAIB) vegetation openness is higher than observed vegetation openness	Maximal observed (REVEALS) vegetation openness (i.e., estimated vegetation openness + standard error) is lower than possible natural (CARAIB) vegetation openness.	In the current ABM possible natural vegetation openness cannot be higher than pollen-based vegetation openness.
First dominant PFT: herbs/ shrubs	First dominant PFT: trees	In the current ABM trees cannot dominate if climatic conditions only allow dominance of herbs or shrubs.
First dominant PFT: trees/ herbs	First dominant PFT: shrubs	In the current ABM shrubs cannot dominate if climatic conditions only allow dominance of trees or herbs.

Once the environment is created, hominins and their campsites are randomly distributed on surfaces with vegetation. The number of campsites and hominins is defined via the Number_of_groups parameter. Patches around campsites are defined as accessible areas. The Accessible_radius parameter defines the size of this area in the number of grid cells around campsites, and the hominin_accessible_area state variable equals 1 for patches within the accessible area. Hominins cannot move beyond their foraging areas, on water bodies (sea, big lakes, and main rivers) high mountains. These are the patches with absolute elevations more than 2500 m. Water bodies and the most elevated areas do not have vegetation cover, and, therefore, cannot be burnt or consumed. Except for the patch_elevation and rivers_lakes, patches with high mountains and water bodies have -1 for their state variables.

AII.6 Input data (after Nikulina et al., 2024b)

The simulation uses several datasets (Table AII.6). To standardize their spatial extent and resolution Spatial Analysts and Data management *ArcMap* 10.6.1 toolboxes were used. Grid cell sizes of the datasets were resampled to 10 km × 10 km.

The initial landscape before simulation runs were reconstructed via the following datasets: GTOPO30, Water Information System for Europe (WISE) and three outputs of a dynamic vegetation model CARbon Assimilation In the Biosphere (CARAIB). GTOPO30 is a digital elevation model (DEM) derived from several raster and vector sources of topographic information. We used this DEM to represent elevation data in the ABM. WISE dataset is based on the information from the Water Framework Directive database, and we used WISE to define the distribution of major rivers and lakes (natural barriers for fire spread) in the model.

In the context of this research, the CARAIB dataset represents theoretical potential natural vegetation (PNV) distribution driven by climatic conditions only. As an input climate we used climatic variables simulated by the iLOVECLIM model with embedded online interactive downscaling. The iLOVECLIM-simulated climatic variables were bias-corrected using the CDF-t bias correction technique and averaged over the studied period to get daily mean climate characteristics of our period of interest. A full description of the modelling setup and the application of the CDF-t technique within this setup is described and tested.

CARAIB outputs used in this study include distribution of fractions of 26 plant functional types (PNV PFTs), vegetation openness (PNV openness), leaf area index (LAI) and net primary productivity (PNV NPP) for the period 9200–8700 BP. Before being imported to the ABM, the mentioned CARAIB outputs were transformed. As the CARAIB dataset here represents climate-only forced vegetation, it is used in

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the current ABM as the starting point (i.e., before impact of humans, natural fires and megafauna) of each simulation and as target for vegetation regrowth after impacts.

Table AII.6 Input datasets to the simulation environment (after Nikulina et al., 2024b).

Dataset	Initial data type	Initial spatial resolution/scale	Meaning, units
GTOPO30	Raster	1 km	Digital elevation model, m
WISE	Vector	1:10000000	Distribution of large rivers and lakes
CARAIB first dominant PFT	Raster	~26 km (0.25°)	Potential natural (climate-based) first dominant PFT
CARAIB vegetation openness			Potential natural (climate-based) vegetation openness, in percentage
NPP			Potential net primary carbon productivity (excluding carbon used for respiration), g/m^2
Megafauna vegetation consumption	Raster	30 km	Potential maximal megafauna vegetation consumption (i.e., metabolization of NPP), kg/km^2 (converted to g/m^2)
REVEALS first dominant PFT	Vector	~100 km (1°)	Observed past first dominant PFT
REVEALS vegetation openness			Observed past vegetation openness, in percentage
REVEALS vegetation openness standard errors			Standard errors for estimates of observed past vegetation openness.

AII.7 Submodels (after Nikulina et al., 2024b)

AII.7.1 Climatic impact

The vegetation regrowth after the impact of thunderstorms, megafauna, and/or humans is determined by the climatic conditions. Therefore, this submodel only modifies grid cells that were previously burned or consumed, and during the first simulation step, it does not alter vegetation openness and PFT of patches.

The grid cells' patch_openness_updating and patch_pft_updating (Figs. AII.2 and AII.3) are changed in response to the climatic impact until they match the values of patch_natural_openness and patch_natural_pft, respectively. If the difference between patch_natural_openness and patch_openness_updating is equal to or less than 10%, the grid cell is considered to have recovered naturally, and the last agent that impacted this patch is assumed to be the climate (last_agent_impacted_openness = 3). Similarly, if patch_natural_pft is equal to patch_pft_updating, the last agent that impacted the PFT of this grid cell is climate (last_agent_impacted_pft = 3).

We used the CARAIB mean number of years to recover (Table AII.7) to calculate the vegetation openness recovery rate and to define the step when natural PFT would reestablish on the grid cell after vegetation burning and/or consumption. PFT recovery on all impacted patches always begins with herbs, which replace bare ground after seven simulation steps. Subsequently, depending on the initial dominant PFT estimated by CARAIB after the required number of years since fire or complete consumption (Table AII.7), the herbs may be replaced by trees or shrubland.

After megafauna plant consumption, natural and anthropogenic fires the rate of vegetation openness recovery (V_{or}) is calculated via the following formula (AII.2):

$$V_{or} = \frac{O_i - O_c}{\mu} \tag{AII.2}$$

O_i represents the vegetation openness after the impact caused by fire or megafauna, O_c refers to the CARAIB estimates of vegetation openness, and μ – the mean number of years required for recovery of the initial vegetation openness prior to the fire event or plant consumption (Table AII.7). During each simulation step, V_{or} is subtracted from the current simulation openness until it reaches the CARAIB estimates of vegetation openness.

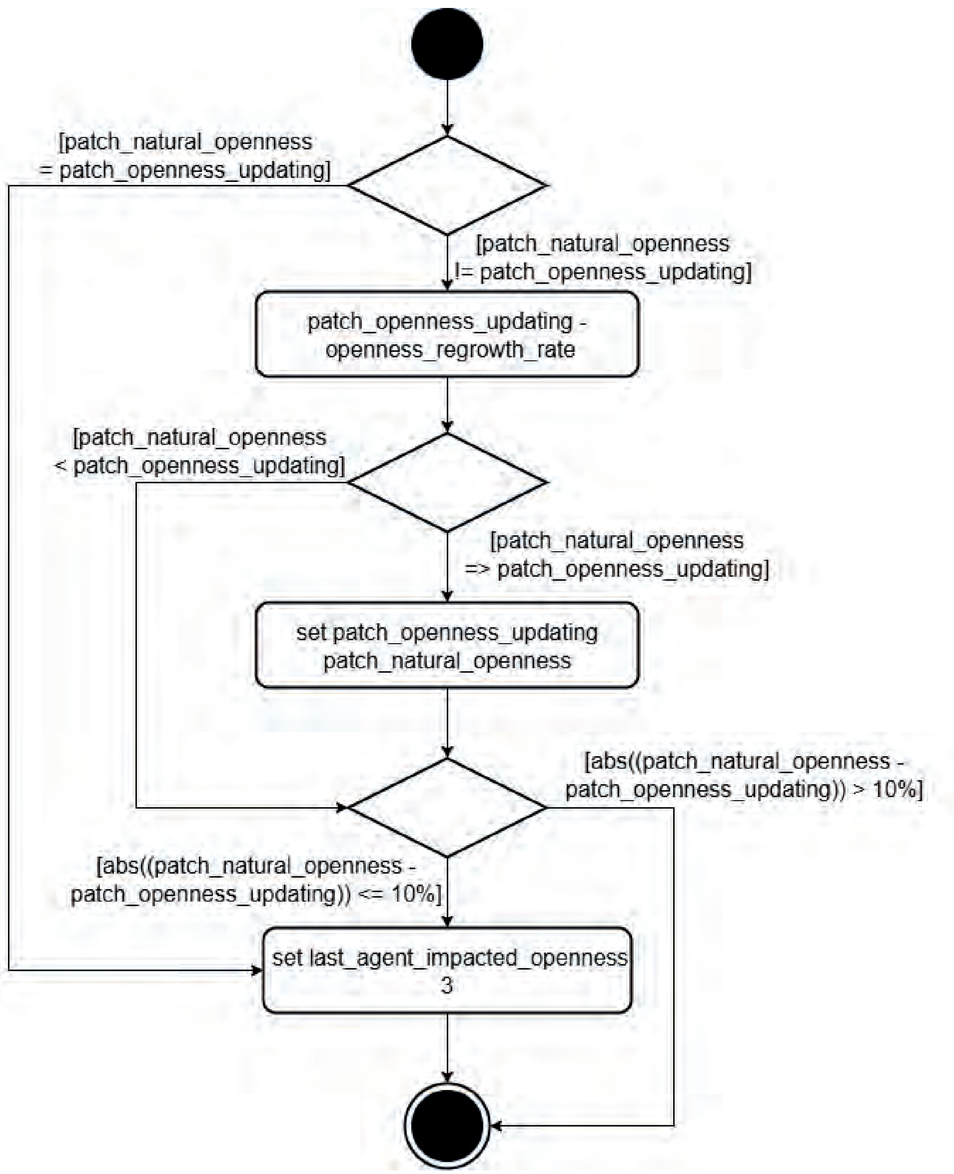

Figure AII.2 Activity diagram for climatic impact on vegetation openness.

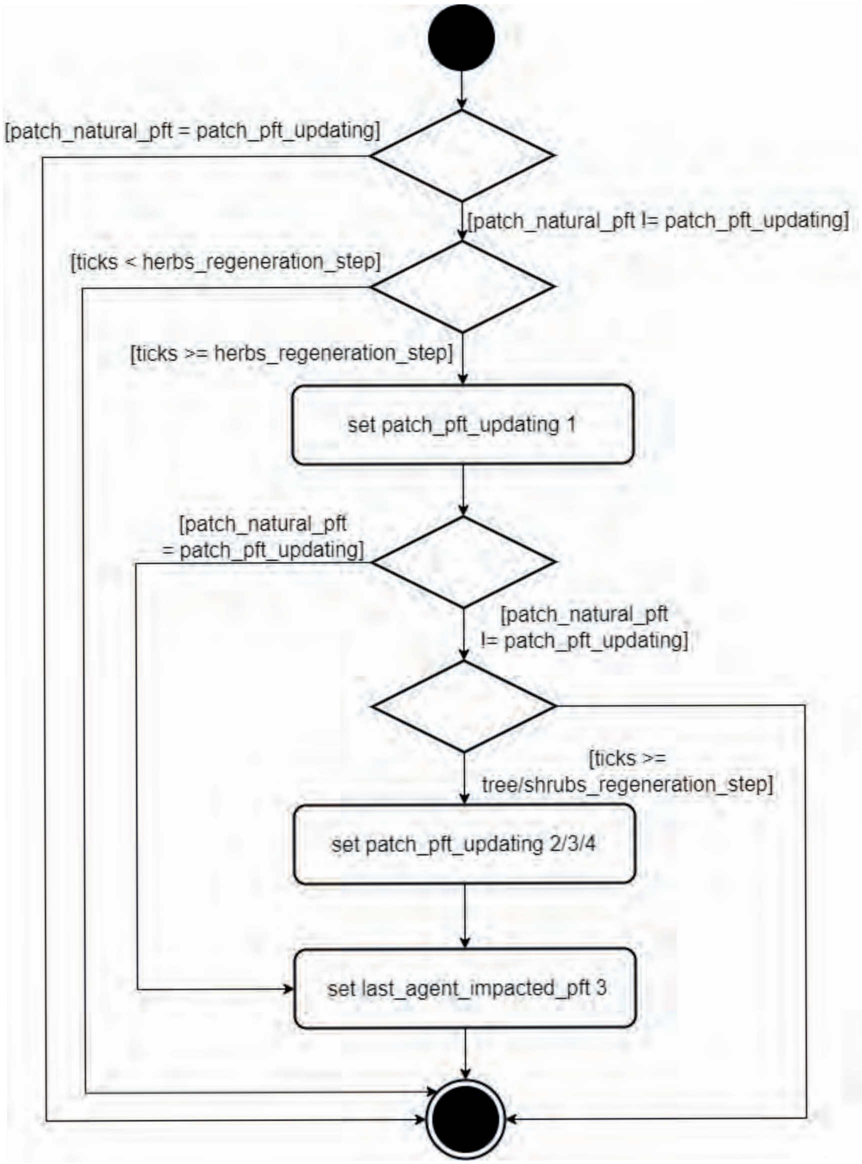

Figure AII.3 Activity diagram for climatic impact on distribution of dominant PFTs.

A2

Table AII.7 Mean number of years to recover for each dominant PFT (after Nikulina et al., 2024b).

PFT	Number of years
Needleleaf trees	43
Broadleaf trees	30
Shrubs	43
Herbs	7

AII.7.2 Anthropogenic impact

This submodel introduces changes to the vegetation through human-induced fires. There are five parameters which define human behaviour and intensity of their impact: Number_of_groups, Accessible_radius, Campsites_to_move, Movement_frequency_of_campsites, and Openness_criteria_to_burn.

The first parameter defines the number of hunter-gatherer groups present at the study area during one simulation run, and, therefore, this parameter is associated with human population size. The accessible radius parameter defines the territory within which humans move and set fires around campsites.

Due to the importance of mobility for hunter-gatherer lifestyle, there are two parameters associated with movements of foragers: Movement_frequency_of_campsites (the number of simulation steps after which a group can relocate their campsite) and Campsites_to_move (the percentage of groups that relocate a campsite at certain step defined by movement frequency). Due to the temporal resolution of the current simulation, hunter-gatherers' highest possible frequency of camp movements is every step (i.e., once per year). The search radius for the new grid cell to establish a site is twice bigger than the accessible radius. Any grid cell can be chosen for the new site, except the previously occupied grid cell. The newly established accessible area can overlap with the previous one.

Since hunter-gatherers have different reasons to burn landscapes, and that this practice was documented in almost all vegetation types with more cases for foragers occupying shrublands and forests, the openness criteria to burn was introduced. In the current simulation, humans only burn grid cells dominated by trees or shrubs with vegetation openness lower or equal to this criterion. A low value minimizes the number of positive decisions to start a fire, and higher values increase human-induced fires, because even relatively open areas can be burnt by people in this case.

Humans randomly move between adjacent patches within a defined area determined by the Accessible_radius (the number of grid cells) around campsites. When a human is present on a patch with vegetation openness that is equal to

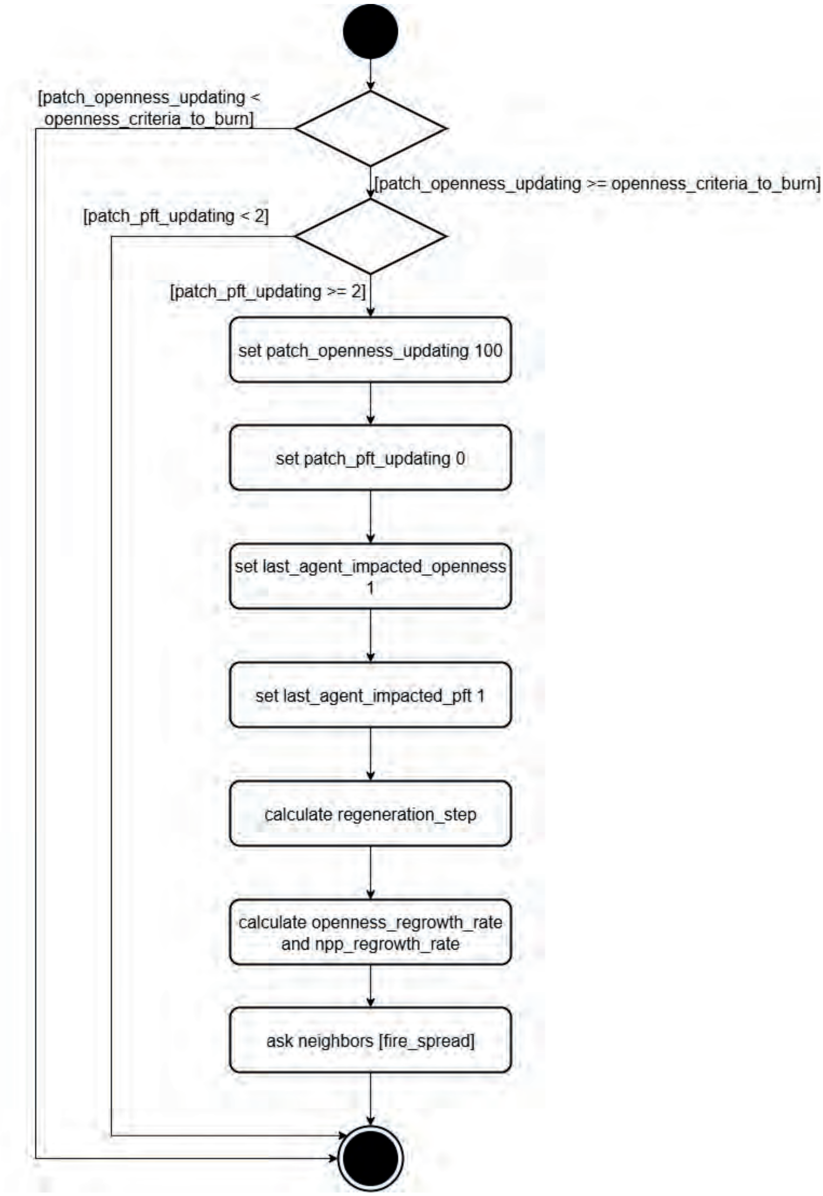

Figure AII.4 Activity diagram for anthropogenic impact.

A2

or lower than the prescribed criteria for burning and contains shrubs or trees (patch_pft_updating >= 2), this human sets fire on that patch. Consequently, the openness of the patch is updated to 100% (completely open), and its PFT (patch_pft_updating) is set to 0, indicating a burnt area. In this scenario, the variables last_agent_impacted_openness and last_agent_impacted_pft are assigned a value of 1 to denote anthropogenic impact. The time step at which this burning event occurs is recorded as last_burning_episode, and next_burning_episode is updated based on the dominant natural PFT (Table AII.4). Subsequently, after calculating the regeneration steps (ticks + number of years from Table AII.4) and openness regrowth rates (Section AII.7.1), the spread of vegetation to neighbouring patches is initiated (Section AII.7.4).

AII.7.3 Natural fires

Based on the value of the parameter Territory_impacted_by_thunderstorms, the number of grid cells experiencing thunderstorms per simulation step is determined. This parameter is expressed as a percentage, and based on its value, the calculation determines how many grid cells will be affected by thunderstorms. These thunderstorms randomly occur on different grid cells within the study area. It is important to note that thunderstorms can occur over rivers, lakes, and high mountains, but these areas are not susceptible to burning.

Following the occurrence of thunderstorms, fires may initiate fire spread depending on the probability of ignition for the affected grid cells (Fig. AII.5). The spread of fire (Section AII.7.4) to neighbouring grid cells can occur after both human-induced and natural fires. Thunderstorms do not always result in vegetation burning, and the ignition of fire does not always lead to its propagation after natural or human-induced ignitions.

The probability of ignition P(I) is determined based on the time elapsed since the last burning episode (B) and the FRI (F), obtained from the MODIS dataset (Table AII.4) (AII.3):

$$P(I) = \frac{T - B}{F} \tag{AII.3}$$

Here, T represents the number of simulation steps (ticks) since the beginning of the simulation. If the probability of ignition is equal to or higher than a randomly chosen number (ignt, as shown in Fig. AII.5), the corresponding patch will be burnt. The consumption of patches by megafauna impacts the probability of ignition. Depending on the percentage of vegetation consumed (as described in Section AII.7.5), the occurrence of the next burning episode can be delayed. To calculate the probability of delayed ignition, the same formula is used, but

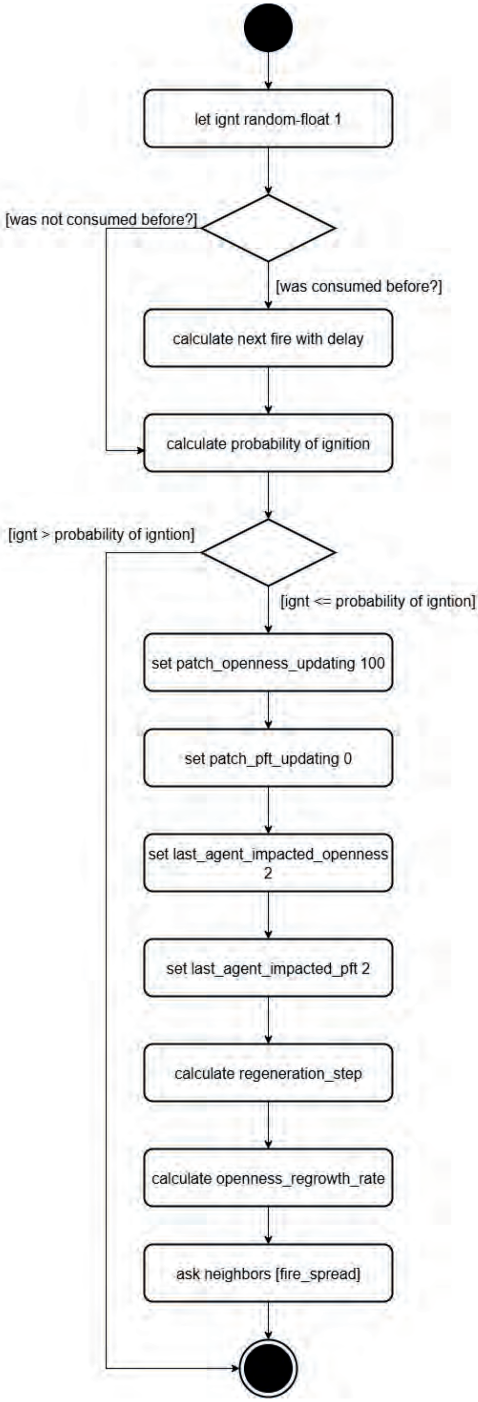

Figure AII.5 Activity diagram for thunderstorm impact.

A2

with a modification: instead of using the current number of ticks (T), we use the sum of T and fire_delay_after_consumption. This patch state variable represents the number of years by which the next burning episode was postponed due to megafauna vegetation consumption (Section AII.7.5). The value of B is also updated as a result of megafauna impact (details provided below).

Once a patch is burned (indicated by patch_pft_updating = 0 and patch_openness_updating = 100), the regrowth rate of openness (Section AII.7.1) and the steps for PFT regeneration (ticks + number of years from Table AII.5) are determined. Additionally, the information of the last agent that impacted the patch is updated Section AII.7.1). Subsequently, the neighbouring patches are prompted to spread the fire as explained in Section AII.7.4.

AII.7.4 Fire spread

Following natural and anthropogenic burning, fire has the potential to spread to neighbouring patches. However, the actual ignition of these patches depends on the probability of ignition, which is calculated using the same method described for natural fires in Section AII.7.3. If a patch is burnt because of fire spread, it will inherit the same values for last_agent_impacted_pft and last_agent_impacted_openness as the patch from which the fire spread originated.

AII.7.5 Megafauna consumption

Megafauna is the final agent responsible for vegetation transformation in the model (Fig. AII.6). Only grid cells with fully recovered vegetation are susceptible to consumption by megafauna. Following plant consumption, the vegetation openness increases based on CARAIB NPP values and estimates of maximal megafauna plant consumption.

Regarding the impact of megafauna on PFTs, it is assumed that megafauna consumes all PFTs present on a grid cell in equal proportions, besides the first dominant PFT. Therefore, if the vegetation is entirely consumed by megafauna and the vegetation openness reaches 100%, the first dominant PFT is replaced with bare ground. In such cases, both last_agent_impacted_pft and last_agent_impacted_openness are assigned a value of 4, indicating that the impact was caused by megafauna. However, if the dominant PFT remains unchanged after megafauna consumption, only last_agent_impacted_openness is updated.

The percentage of vegetation consumed (V_c) is calculated for each grid cell, excluding water bodies and high mountains, using the following formula (AII.4):

$$V_c = \frac{V_m}{V_n} \times 100 \qquad \text{(AII.4)}$$

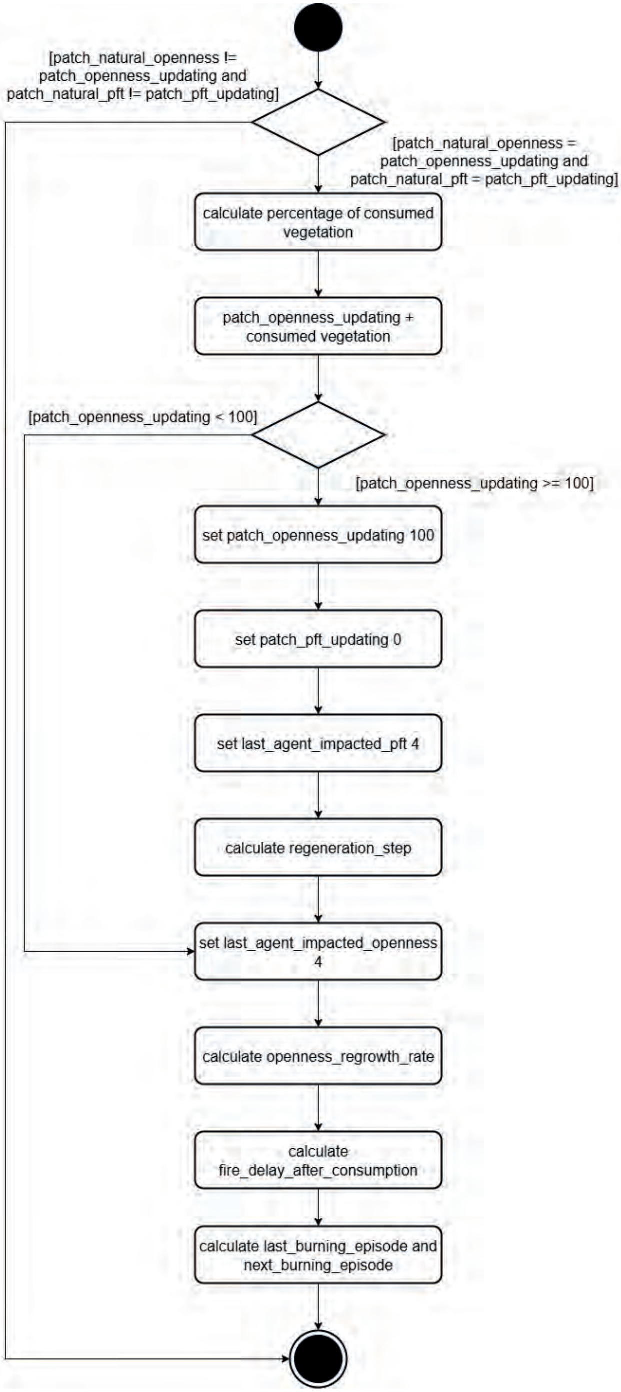

Figure AII.6 Activity diagram for megafauna impact.

V_m represents the grid cell value for potential maximal megafauna metabolization of NPP, and V_n corresponds to the CARAIB NPP. Once the percentage of consumed vegetation is calculated for a grid cell, this value is added to the existing vegetation openness to increase it after the impact of megafauna. Furthermore, the first dominant PFT is updated based on the resulting vegetation openness after vegetation consumption.

When there is partial consumption of vegetation by megafauna (i.e., when the first dominant PFT remains unchanged), it leads to delays in fire activity because time is required to accumulate plant material that can be burnt. The number of years by which fire activity is delayed is calculated by multiplying with the FRI of the respective PFT at the patch (Table AII.4). Consequently, depending on the percentage of vegetation consumed, the time step at which the vegetation has a 100% probability of being burnt in the presence of an ignition source is postponed.

Appendix III
Supplementary data to Nikulina et al. (in press)

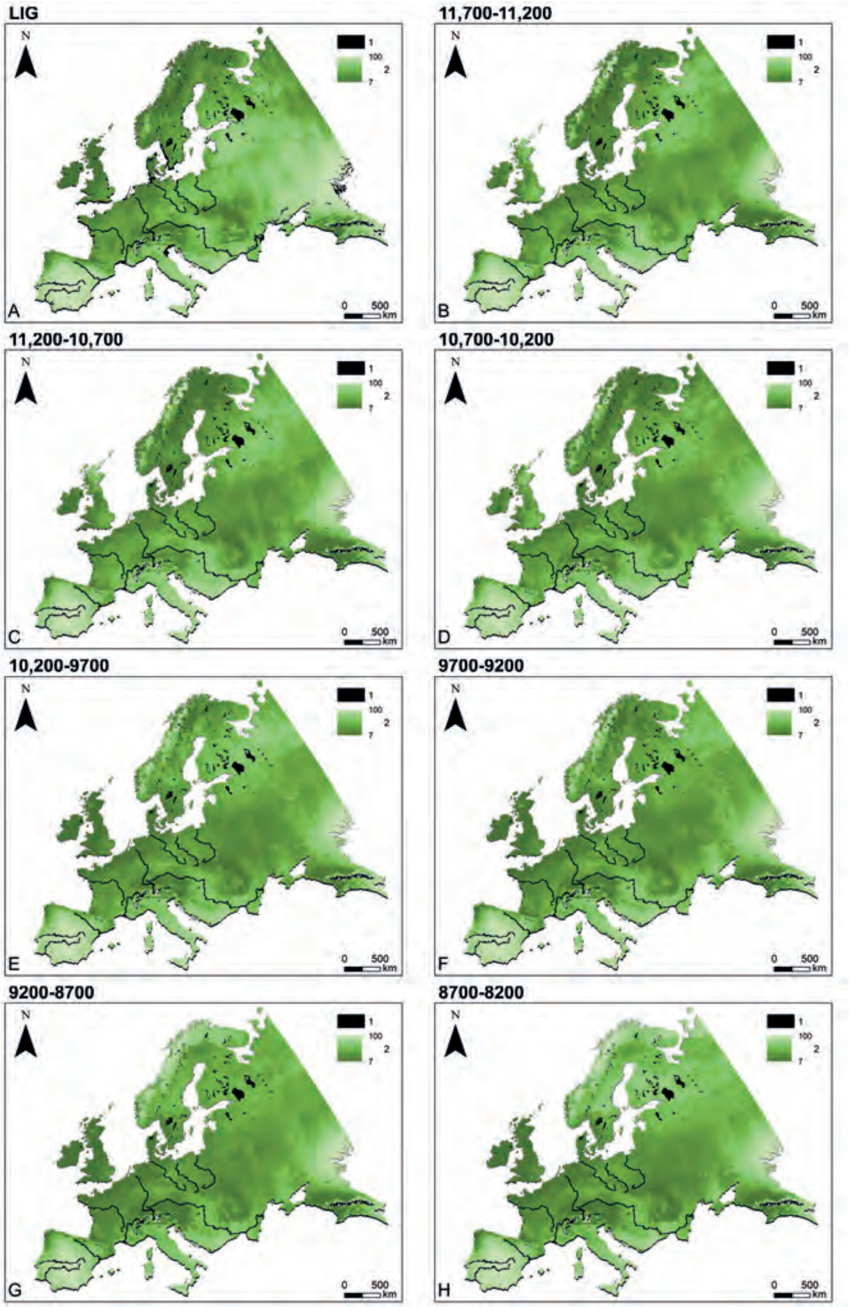

Figure AIII.1 CARAIB vegetation openness for the Last Interglacial (A), 11,700–11,200 BP (B), 11,200–10,700 (C), 10,700–10,200 (D), 10,200–9700 (E), 9700–9200 (F), 9200–8700 (G), 8700–8200 BP (H). Legend: 1–no data, 2–vegetation openness (in %).

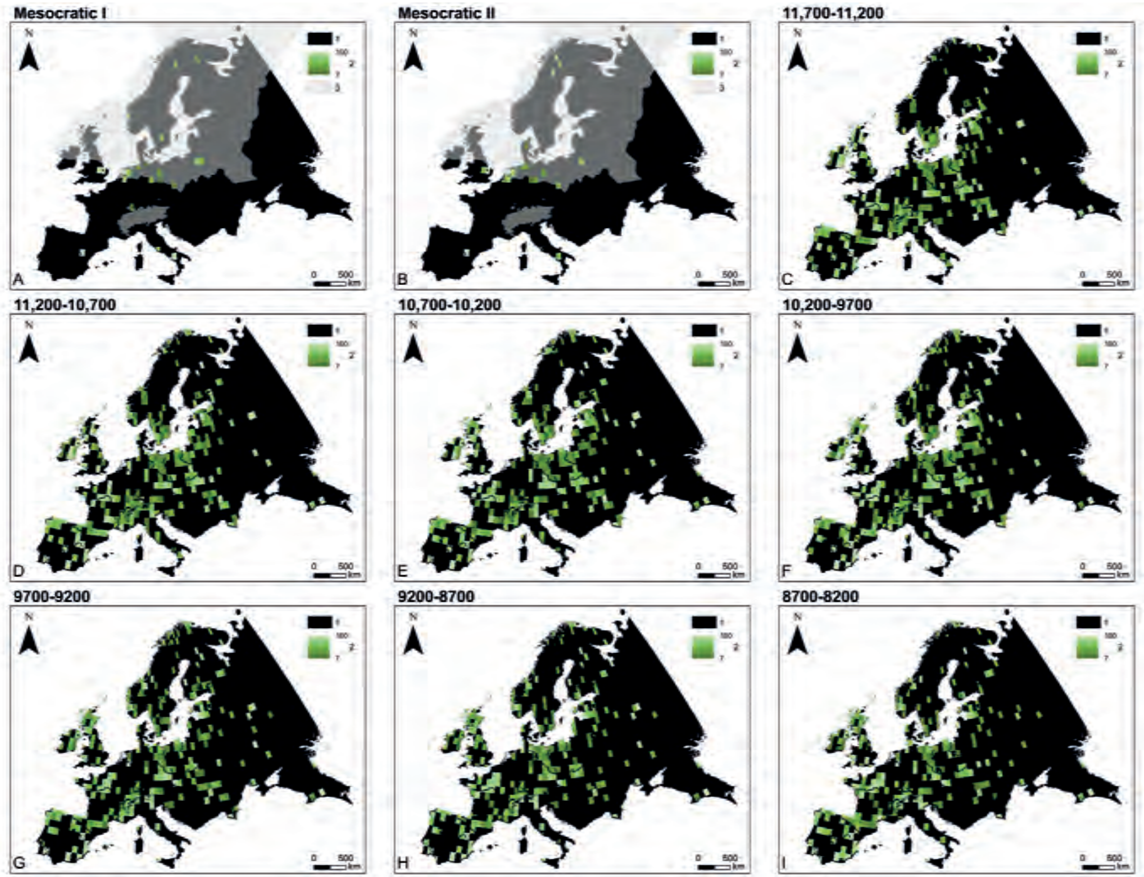

Figure AIII.2 REVEALS vegetation openness for Mesocratic I (A), Mesocratic II (B), 11,700–11,200 BP (C), 11,200–10,700 (D), 10,700–10,200 (E), 10,200–9700 (F), 9700–9200 (G), 9200–8700 (H), 8700–8200 BP (I). Legend: 1–no data, 2–vegetation openness (in %); 3–The northern European and Alpine Saalian glaciation (Lehmkuhl et al., 2021; Svendsen et al., 2004).

A3

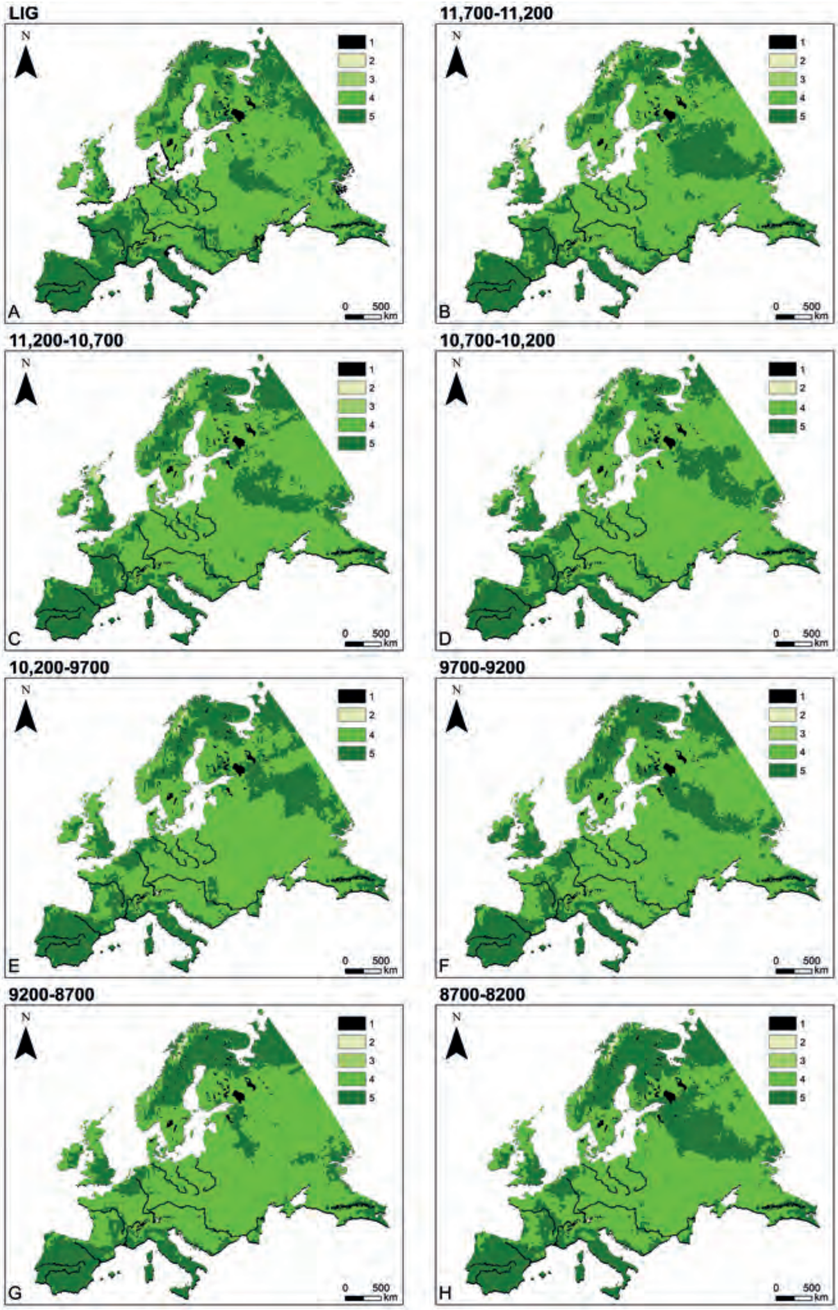

Figure AIII.3 CARAIB distribution of the first dominant PFTs for the Last Interglacial (A), 11,700–11,200 BP (B), 11,200–10,700 (C), 10,700–10,200 (D), 10,200–9700 (E), 9700–9200 (F), 9200–8700 (G), 8700–8200 BP (H). Legend: 1–no data, 2–herbs, 3–shrubs; 4–broadleaf trees; 5–needleleaf trees.

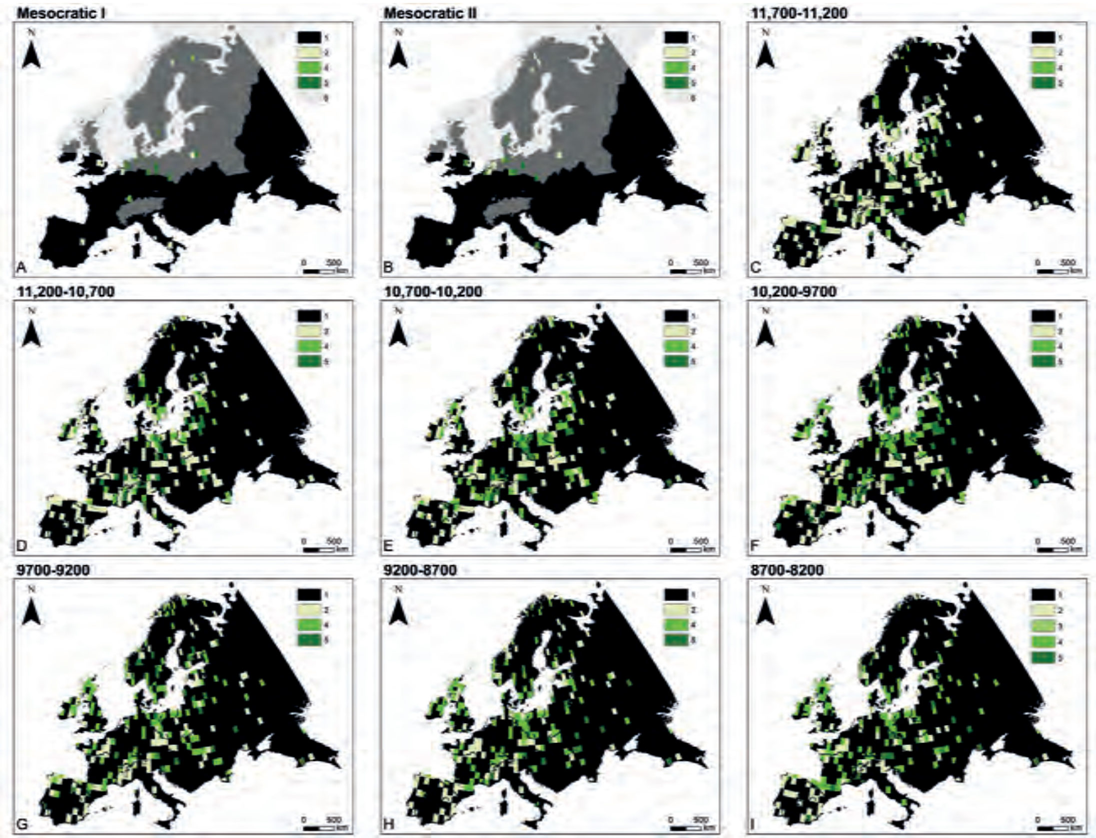

Figure AIII.4 REVEALS distribution of the first dominant PFTs for Mesocratic I (A), Mesocratic II (B), 11,700–11,200 BP (C), 11,200–10,700 (D), 10,700–10,200 (E), 10,200–9700 (F), 9700–9200 (G), 9200–8700 (H), 8700–8200 BP (I). Legend: 1–no data, 2–herbs, 3–broadleaf trees; 4–needleleaf trees, 5–the northern European and Alpine Saalian glaciation (Lehmkuhl et al., 2021; Svendsen et al., 2004).

A3

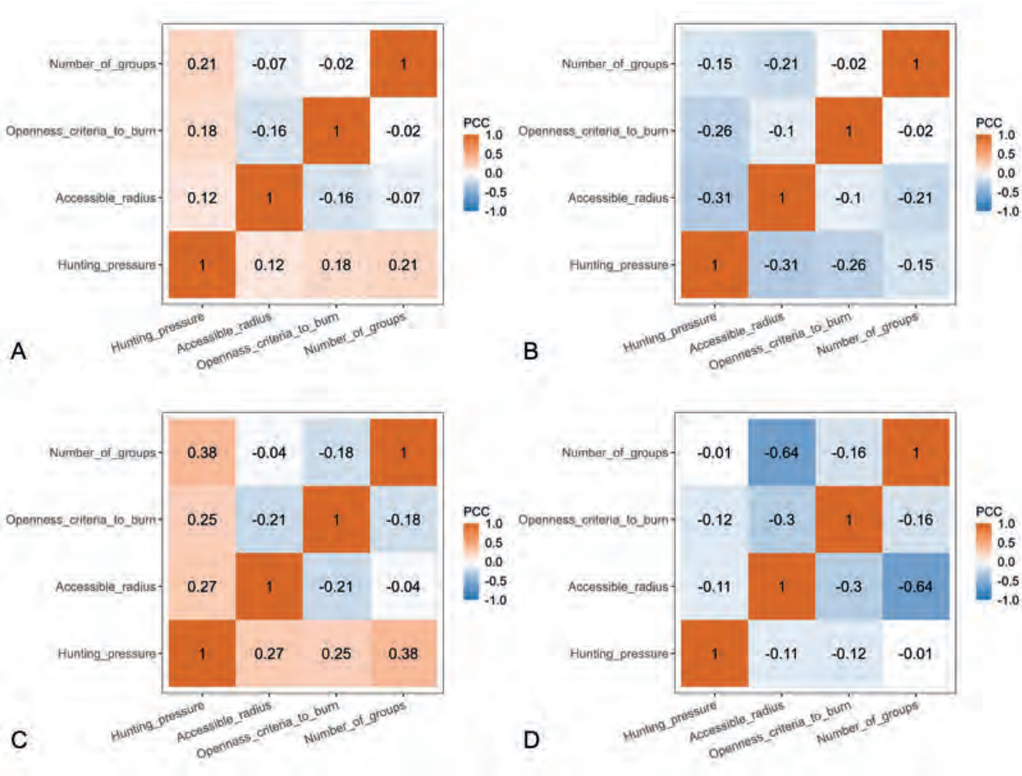

Figure AIII.5 Correlation matrices and Pearson correlation coefficients (PCC) between variables of the possible scenarios for LIG (A) and Early Holocene (B) tree distribution scenarios; LIG (C) and Early Holocene (D) vegetation openness scenarios. The experiments include the combined direct impact of all agents on vegetation: anthropogenic and natural fires, climatic impact and megafauna plant consumption. The darkest blue indicates the strongest negative correlation between the Number_of_groups and Accessible_radius parameters within the Early Holocene vegetation openness scenarios. Lighter colours represent either absent/low or modest correlations for the other parameters.

Table AIII.1 PFTs used in ABM (HUMLAND PFTs) and correspondence between CARAIB PFTs and REVEALS plant taxa (after Nikulina et al., 2024b).

CARAIB PFTs	Plant taxon / pollen morphological types	HUMLAND PFTs
Needle-leaved evergreen boreal/ temp cold trees Needle-leaved evergreen meso mediterranean trees Needle-leaved evergreen subtropical trees Needle-leaved evergreen supra mediterranean trees Needle-leaved evergreen temperate cool trees Needle-leaved summergreen boreal/temp cold trees Needle-leaved summergreen subtropical swamp trees	*Abies* *Picea* *Pinus* *Juniperus*	Needleleaf trees
Broadleaved evergreen meso mediterranean trees Broadleaved evergreen subtropical trees Broadleaved evergreen thermo mediterranean trees Broadleaved evergreen tropical trees Broadleaved raingreen tropical trees Broadleaved summergreen boreal/temp cold trees Broadleaved summergreen temperate cool trees Broadleaved summergreen temperate warm trees	*Alnus* *Betula* *Carpinus betulus* *Carpinus orientalis* *Castanea sativa* *Corylus avellana* *Fagus* *Fraxinus* *Phillyrea* *Pistacia* deciduous *Quercus* t. evergreen *Quercus* t. *Salix* *Tilia* *Ulmus*	Broadleaf trees
Broadleaved evergreen boreal/ temp cold shrubs Broadleaved evergreen temperate warm shrubs Broadleaved evergreen xeric shrubs Broadleaved summergreen arctic shrubs Broadleaved summergreen boreal/temp cold shrubs Broadleaved summergreen temperate warm shrubs Subdesertic shrubs Tropical shrubs	*Buxus sempervirens* *Calluna vulgaris* Ericaceae	Shrubs
C3 herbs ("dry") C3 herbs ("humid") C4 herbs	Amaranthaceae/Chenopodiaceae *Artemisia* Cerealia t. Cyperaceae *Filipendula* *Plantago lanceolata* Poaceae *Rumex acetosa* t. *Secale cereale*	Herbs

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Table AIII.2 Datasets used in HUMLAND (after Nikulina et al., 2024b)

Dataset	Initial data type	Initial spatial resolution/scale	Meaning, units	Source
GTOPO30	Raster	1 km	Digital elevation model, m	https://www.usgs.gov/
WISE	Vector	1:10,000,000	Distribution of large rivers and lakes	https://water.europa.eu/
CARAIB first dominant PFT	Raster	~26 km (0.25°)	PNV: first dominant PFT	http://www.umccb.ulg.ac.be/Sci/m_car_e.html
CARAIB vegetation openness			PNV: vegetation openness (%)	
NPP			PNV NPP (excluding carbon used for respiration), g/m2	
Megafauna vegetation consumption	Raster	30 km	Potential maximal megafauna vegetation consumption (i.e., metabolization of NPP), kg/km^2 (converted to g/m^2)	Davoli et al., 2023, 2024
REVEALS first dominant PFT	Vector	~100 km (1°)	Pollen-based first dominant PFT	Serge et al., 2023
REVEALS vegetation openness			Pollen-based past vegetation openness (relative %)	
REVEALS vegetation openness standard errors			Standard errors for estimates of pollen-based past vegetation openness	

Table AIII.3 PCA results for the successful genetic algorithm outputs aiming to minimize the HUMLAND–REVEALS difference in mean percentage of grid cells dominated by trees. The experiments include the combined impact of all agents on vegetation: anthropogenic and natural fires, hunting, climatic impact and megafauna plant consumption.

Variables / Time windows		Openness_criteria_to_burn	Hunting_pressure	Number_of_groups	Accessible_radius
Mesocratic I	Comp. 1 (54.2%)	0.54	0.07	0.36	-0.74
	Comp. 2 (26.1%)	-0.63	0.24	0.72	-0.08
Mesocratic II	Comp. 1 (46.7%)	0.78	0.04	-0.44	-0.42
	Comp. 2 (36.5%)	0	0.06	0.69	-0.71
10,200–9700 BP	Comp. 1 (44.7%)	-0.31	0.17	-0.67	-0.63
	Comp. 2 (36%)	-0.18	0.82	-0.17	-0.5
9700–9200 BP	Comp. 1 (48.3%)	-0.31	0.48	-0.68	0.44
	Comp. 2 (30.4%)	-0.01	0.69	0.02	-0.72
9200–8700 BP	Comp. 1 (51.2%)	-0.51	0.65	0.33	-0.43
	Comp. 2 (28%)	-0.66	0	-0.05	0.74
8700–8200 BP	Comp. 1 (47.8%)	-0.27	0.58	0.31	0.69
	Comp. 2 (33.9%)	-0.38	0.53	-0.69	0.29

Table AIII.4 PCA results for the successful genetic algorithm outputs aiming to minimize the HUMLAND–REVEALS difference in mean vegetation openness. The experiments include the combined impact of all agents on vegetation: anthropogenic and natural fires, hunting, climatic impact and megafauna plant consumption.

Variables / **Time windows**		**Openness_ criteria_to_burn**	**Hunting_ pressure**	**Number_ of_groups**	**Accessible_ radius**
Mesocratic I	Comp. 1 (58.8%)	-0.74	0.09	0.40	0.51
	Comp. 2 (29.4%)	-0.02	0.11	-0.75	-0.65
Mesocratic II	Comp. 1 (45.1%)	0.77	0.01	-0.17	-0.61
	Comp. 2 (43.7%)	-0.22	0.24	-0.79	-0.51
10,200–9700 BP	Comp. 1 (59.9%)	0.16	0.25	0.63	-0.71
	Comp. 2 (27%)	-0.84	0.44	0.24	0.17
9700–9200 BP	Comp. 1 (50.3%)	-0.16	0.39	0.64	-0.62
	Comp. 2 (33.8%)	-0.83	0.1	0.2	0.49
9200–8700 BP	Comp. 1 (61.7%)	-0.14	0.09	0.67	-0.72
	Comp. 2 (21.4%)	-0.85	0.47	0.19	0.06
8700–8200 BP	Comp. 1 (56%)	0.12	0.05	0.67	-0.72
	Comp. 2 (27.8%)	-0.81	0.52	0.22	0.1

Table AIII.5 Mean, mode and standard deviation (SD) for parameter values obtained via the genetic algorithm with outputs similar to REVEALS. The distribution of parameter values is in Fig. 4.7 of the main body of the article.

Time windows	Parameters and experiment types																							
	Openness_to_burn						Hunting_pressure						Number_of_groups						Accessible_radius					
	Trees			Openness			Trees			Openness			Trees			Openness			Trees			Openness		
	Mean	SD	Mode	Mean	SD	Mode	Mean	SD	Mode	Mean	SD	Mode	Mean	SD	Mode	Mean	SD	Mode	Mean	SD	Mode	Mean	SD	Mode
LIG	77	14	55 77 78	49	23	48	24	29	4	34	13	21 22 23 24 25 27 31 39	3266	591	3323	1936	1136	563	3	1	3	2	1	1
Mesocratic I	79	13	78	48	22	23	27	33	4	33	15	21 22 23	3381	488	3323	2044	1122	139 1087 2017 2515	3	1	3	2	1	2
Mesocratic II	75	15	55 77	50	24	48	22	25	0 1	35	11	24 27 31 39	3156	657	2943	1830	1140	563	3	1	3	2	1	1

A3

Time windows	Parameters and experiment types																							
	Openness_to_burn						Hunting_pressure						Number_of_groups						Accessible_radius					
	Trees			Openness			Trees			Openness			Trees			Openness			Trees			Openness		
	Mean	SD	Mode	Mean	SD	Mode	Mean	SD	Mode	Mean	SD	Mode	Mean	SD	Mode	Mean	SD	Mode	Mean	SD	Mode	Mean	SD	Mode
Early Holocene	71	17	45, 47, 57, 59, 69	60	22	36, 38, 42, 62, 69	48	27	31	34	26	4	2895	691	3575	2243	957	1089	3	1	4	3	1	1
10,200–9700 BP	76	15	57	61	23	36, 62	45	25	31	40	29	1, 6, 10, 44, 74, 82	3071	462	3161	2090	759	1329	3	1	4	3	1	2
9700–9200 BP	71	15	65	58	22	38	51	25	24, 30, 45, 60, 67	43	26	35, 43, 57	3117	543	3115	2074	897	1188, 3453	3	1	4	2	1	3
9200–8700 BP	68	20	45, 59	60	21	38	51	29	43	28	23	4	2550	911	3453	2342	1085	1627	3	1	4	2	1	1
8700–8200 BP	68	17	47	62	23	42, 69	45	29	0, 3, 38	25	21	21	2843	608	2490	2466	998	1079, 1460, 2901, 3315, 3336	3	1	4	2	1	1

Table AIII.6 Details of HUMLAND runs conducted to track the extent and visibility of modifications done by each agent.

Time windows	Parameter values							
	Openness_to_burn		Hunting_pressure		Number_of_groups		Accessible_radius	
	Trees	Openness	Trees	Openness	Trees	Openness	Trees	Openness
Mesocratic I	81	29	0	21	3323	139	3	4
		29		23		1091		2
		37		26		2017		1
		28		21		2497		3
Mesocratic II	92	33	10	30	2943	563	4	4
10,200–9700 BP	87	47	42	11	3161	1329	4	5
9700–9200 BP	74	72	52	42	3123	1191	4	4
		80		74		3375		1
9200–8700 BP	81	41	75	6	3450	1627	2	1
8700–8200 BP	71	77	14	16	2488	1079	5	3
		72		9		1460		2
		92		10		2901		1
		62		7		3315		1

A3

AIII.1 paleoenvironmental modelling setup

The potential natural vegetation (PNV) simulations in this study were conducted using a modelling framework that combines iLOVECLIM climate model, and VECODE and CARAIB vegetation models. Below, we detail the configurations and roles of each model.

AIII.1.1 ILOVECLIM: paleoclimate simulation

Climate simulations were performed with the iLOVECLIM Earth System model of intermediate complexity (Goosse et al., 2010), revised by Roche (Roche, 2013) and further expanded by Quiquet et al. (Quiquet et al., 2018). The applied version of iLOVECLIM includes the following: the atmospheric model, ECBilt (Opsteegh et al., 1998), the sea-ice ocean component, CLIO (Goosse & Fichefet, 1999), and the reduced-form dynamic global vegetation model (DGVM), VECODE (Brovkin et al., 1997). These components are used to simulate climate.

ILOVECLIM operates on a relatively low spatial resolution T21 grid (5.625° latitude/longitude), which in the current study is increased to 0.25° latitude/longitude through the use of the online interactive downscaling method embedded in iLOVECLIM, first described by Quiquet et al. (Quiquet et al., 2018) and tested within the current modelling setup by Zapolska et al. (Zapolska et al., 2023a).

We applied iLOVECLIM to simulate evolution of the climate during the Holocene and LIG through a set of transient runs. Holocene transient run was resampled to a time step that correspond to REVEALS time windows (TWs): time windows between the year 6200 BP and the year 700 BP were assigned at 500 years temporal resolution, following by fixed time windows at 350 (700–350 BP), 250 (350–100 BP), and 165 (2015 CE–1850). To simulate climate during the Last Interglacial (LIG) we first performed a transient iLOVECLIM run over the whole LIG and identified periods with high forest fraction in VECODE outputs: 120,000 BP, 124,000 BP, and 128,000 BP. For these three periods we performed equilibrium climate simulations, which were used to drive the CARAIB model. The transient experiments were initialised with states derived from 3000-year long equilibrium simulations at 11,700 BP (early Holocene) and 129,000 BP (early LIG).

For all simulations, we used the following boundary conditions: standardised boundary conditions for palaeoclimate simulations, provided by the Palaeoclimate Modelling Intercomparison Project Phase 4 (PMIP-4) (Kageyama et al., 2017), astronomical parameters from Berger (Berger, 1978), greenhouse gas levels (Raynaud et al., 2000; Schilt et al., 2010), ice sheets from the GLAC-1D reconstruction (Tarasov et al., 2012; Tarasov & Peltier, 2002) as well as evolving bathymetry and land-ocean mask coherent with those ice-sheet geometries (with the same methodology as Bouttes et al., 2022).

To further improve reliability of the modelled results in context of intercomparison with pollen data, we applied the CDF-t bias correction technique (Vrac et al., 2012) to correct biases of iLOVECLIM modelled results (Zapolska et al., 2023b).

AIII.1.2 VECODE: dynamic vegetation modelling

To provide a necessary climate-biomass feedback loop for the climate simulations we used a reduced-form DGVM VECODE (Brovkin et al., 1997). VECODE simulates eco-physiological characteristics of vegetation and soil dynamics in a manner necessary for climate models of intermediate complexity. Vegetation in VECODE DGVM is described using two plant functional types (PFTs): trees and grass (with bare ground as a dummy type).

VECODE dynamics is coupled with atmospheric and oceanic modules of iLOVECLIM at an annual timestep, which simulates plant and soil behaviours necessary for accurately simulating the first-order vegetation-climate feedback in iLOVECLIM. However, its level of complexity is not enough to reflect fine-scale changes that are typically attributed to human impact on vegetation. Thus, iLOVECLIM-simulated bias corrected climate was used as an input for CARAIB, a more complex vegetation model.

AIII.1.3 CARAIB: high-resolution vegetation modelling

CARAIB (CARbon Assimilation In the Biosphere) is a grid-point process-based dynamic vegetation model that operates at a grid size of the provided input data (here 0.25° latitude/longitude). CARAIB is a comprehensive and mechanistic vegetation model that simulates the vegetation dynamics based on its relationship with climatic and soil conditions.

It combines several modules: hydrological budget (Hubert et al., 1998), canopy photosynthesis and stomatal regulation, carbon allocation and plant growth (Otto et al., 2002), heterotrophic respiration and litter/soil carbon dynamics, plant competition and biogeography. CARAIB outputs used in this ABM include distribution of fractions of 26 PFTs (PNV distribution), PNV vegetation openness, and potential natural NPP per 26 km × 26 km grid cell.

To simulate the potential natural vegetation during the Holocene we conducted a series of equilibrium runs with the same boundary conditions and spatio-temporal resolution as iLOVECLIM, using its simulated climate as input and obtaining CARAIB-simulated PNV.

REVEALS estimates for LIG provide data for the highest forested period during the LIG without specifying time bounds of such period. Hence, to represent the peak of forest fraction in LIG we performed three equilibrium CARAIB simulations at 120,000 BP, 124,000 BP, and 128,000 BP. These three periods were selected due to their high forested fraction in VECODE outputs (integrated vegetation module within iLOVECLIM climate model). These simulations (not shown) determined that 128,000 BP had the highest forest fraction during the LIG within our setup. The corresponding CARAIB output for this period was thus used in the HUMLAND 2.0 LIG simulations.

AIII.2 Pearson correlation coefficients and principal component analysis

In Figure AIII.5, the variables within the LIG dataset have both positive and negative correlations, while in the Early Holocene results, correlations are exclusively negative (blue). The magnitudes of the correlation coefficients between parameters are generally modest or low/absent for both LIG (-0.21–0.38) and the Early Holocene (-0.3–0) experiments. Relatively strong correlation (-0.64) is identified between the Number_of_groups and Accessible_area parameters within the vegetation openness experiments (Figure AIII.5D).

PCA results show that contribution of some variables to principal components (i.e., new variables that are derived from an original set of variables to reduce the dimensionality of data) vary through time and genetic algorithm experiment groups (i.e., minimization of the difference in mean vegetation openness or in percentage of grid cells dominated by trees). The distinct result is that the absolute loadings (i.e., how much a variable contributes to the component) of the Hunting_pressure parameter are overall lower for LIG results than for the Holocene runs (Tables AIII.3 and AIII.4). The absolute loadings of the Openness_criteria_to_burn parameter are relatively high for the LIG results regarding PFT distribution (Table AIII.4). The absolute loadings of this parameter slightly decrease for the dominance of trees experiments in the earlier part of the Early Holocene, and increase again during 9200–8700 BP (Table AIII.4). The absolute loadings for the Number_of_groups and the Accessible_radius parameter are relatively high for all time periods (Tables AIII.3 and AIII.4).

AIII.3 CARAIB–REVEALS comparison for 11,700–10,200 BP

REVEALS showed higher percentages of herbs in comparison with the percentage of trees during 11,700–10,200 BP and the inversion of these values between 10,200–9200 BP (Fig. 4.5, bottom figure). These observations might be partially explained by the position of these periods within the glacial/interglacial cycle which could entail a late arrival of some tree types (Giesecke et al., 2017; Svenning & Skov, 2004). The duration of postglacial migration lags is unclear. There are suggestions for both relatively short lags of maximally 1500 years, and substantially longer ones including estimates that many plant species have not reached equilibrium with climate even nowadays (Birks & Birks, 2008; Dallmeyer et al., 2022; Seliger et al., 2021; Svenning & Sandel, 2013). It is also unclear whether the observed species-level lags impact continental-scale distribution of forests (Dallmeyer et al., 2022). Due to that, distinguishing between the potential influences of human activities and climate could be challenging in this context for the 11,700–10,200 BP. In addition, the CARAIB vegetation model used in this study is driven by outputs from an equilibrium iLOVECLIM climate model. In the present setup, both the vegetation and climate models are in equilibrium, and hence do not capture transient changes. ILOVECLIM uses ice sheet data, which then remain static throughout the equilibrium-based simulation. This setup inherently limits representation of several aspects of the Early Holocene, including the transition to warmer conditions in the beginning of the Holocene and the associated soil changes due to deglaciation (transient change in soil composition, texture, and nutrient availability). Thus, we made a deliberate decision not to conduct HUMLAND simulations for 11,700–10,200 BP. We have directed our focus on 10,200–8200 BP and two LIG time windows.

Appendix IV
HUMLAND ABM 2.0 Overview, design concepts and details (ODD) protocol

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This document provides a comprehensive overview, design concepts, and detailed descriptions of the HUMLAND ABM 2.0. This model was developed to track and quantify the intensity of different impacts on vegetation on the continental scale and to determine the most influential factor in transformation of interglacial vegetation with specific focus on burning organized by hunter-gatherers. This document follows the Overview, Design concepts, and Details (ODD) protocol to ensure clarity and consistency in model documentation.

The model is accessible via the CoMSES library (search for HUMLAND). HUMLAND 2.0 and all associated data and scripts are licensed under the MIT License.

When referencing HUMLAND 2.0, please cite both the model and the associated publication.

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AIV.1 Purpose

Humans started transforming their environment long before the emergence of agriculture and industrialization. Foraging societies conduct niche construction activities including vegetation burning which substantially modifies hunter-gatherers' surroundings. Currently available ethnographic and archaeological evidence suggests that both Neanderthals and Mesolithic humans practiced vegetation burning during the Last Interglacial (LIG; ~130,000–116,000 BP) and the Early Holocene (~11,700–8000 BP). Due to the scarcity of evidence and the absence of a common research protocol to study the anthropogenic impact on landscapes, there are gaps in research about the dynamics of interglacial environments and the role of *Homo* in landscape changes. Particularly, the extent and visibility of vegetation burning organized by hunter-gatherers is still a focal point of research.

Landscape dynamics are complex and include variable components such as climatic fluctuations, megafauna impact, natural fires, and anthropogenic activities. Thus, there is a need for further research which can allow us to assess different possible scenarios for anthropogenic impact in landscape changes. Therefore, the purpose of this model is to track and quantify the intensity of different impacts on vegetation on the continental level and to determine the most influential factor in transformation of interglacial vegetation with specific focus on burning organized by hunter-gatherers. This model accumulates different types of spatial datasets (Section AIV.6) which are used as input and target for ABM runs. Additionally, the study incorporates recently obtained specifically for this research continental-scale estimates of fire return intervals (FRI) and speed of vegetation regrowth. The obtained results include possible scenarios (combinations of HUMLAND parameter values) with maps of modified vegetation in the past and quantification of changes done by of each source of impact (climate, humans, megafauna and natural fires). The model has been implemented in *NetLogo* (version 6.2.2). HUMLAND 1.0 and 2.0 are accessible via the CoMSES model depository (https://www.comses.net/, search for HUMLAND).

AIV.2 Entities, state variables, and scales

The following entities are included in the model: agents representing hominin groups (one agent is one group, Table AIV.1), campsites (turtles, have only one static variable my_hominin which indicates the group occupying this campsite) and grid cells (patches, Table AIV.2).

Table AIV.1 Hominin state variables.

Variable name	Variable type and units	Meaning
my_home	Dynamic, patch	A patch where a campsite is located (home patch of a group).
my_campsite	Dynamic, turtle	A campsite which is the home of a hominin group.

Table AIV.2 Grid cells state variables.

Variable name	Variable type and units	Meaning
patch_elevation	Static, float, meters	Absolute elevation (a.s.l.)
patch_natural_pft	Static, integer	CARAIB (CARbon Assimilation In the Biosphere) first dominant PFT: 1–herbs, 2–shrubs, 3–needleleaf trees, 4–broadleaf trees, -1–no data
patch_pollen_pft	Static, integer	REVEALS (Regional Estimates of VEgetation Abundance from Large Sites) first dominant PFT: 1–herbs, 2–shrubs, 3–needleleaf trees, 4–broadleaf trees, -1–no data
patch_pft_updating	Dynamic, integer	Current dominant PFT: 1 herbs, 2–shrubs, 3–needleleaf trees, 4–broadleaf trees, -1–no data, 0–burnt/fully consumed area
patch_natural_openness	Static, float, percentage	CARAIB vegetation openness: 0 – minimal value (0%, totally closed), 100–maximal value (100%, totally open), -1–no data
patch_pollen_openness	Static, float, percentage	REVEALS vegetation openness: 0–minimal value (0%, totally closed), 100–maximal value (100%, totally open), -1–no data
patch_pollen_openness_se	Static, float	REVEALS vegetation openness standard error (se)

Variable name	Variable type and units	Meaning
patch_pollen_openness_max	Static, float, percentage	Maximal possible REVEALS openness: patch_pollen_openness + patch_pollen_openness_se
patch_openness_updating	Dynamic, integer, percentage	Current vegetation openness: 0–minimal value (0%, totally closed), 100–maximal value (100%, totally open), -1–no data
rivers_lakes	Static, integer	Presence of big rivers and lakes: 0–no rivers/lakes, 1–presence of rivers/lakes, -1–no data
fri	Static, integer, years	FRI values for each PFT
patch_natural_npp	Static, float, g/m^2	CARAIB NPP
patch_npp_updating	Dynamic, integer	Current patch npp which can be changed due to different types of impact during runs
npp_regrowth_rate	Dynamic, float	NPP regrowth speed per step after impact
megafauna_npp_consumption	Static, float, g/m^2	Megafauna carbon consumption
megafauna_max_consumption_restricted_hunting	Static, float	Potential maximal megafauna plant consumption restricted by hunting
continuous_consumption	Dynamic, integer	Counts the number of ticks (steps) during which megafauna continuously consumed this patch
fire_delay_after_consumption	Dynamic, integer	Delay in the frequency of natural fires after partial megafauna consumption of vegetation
openness_regrowth_rate	Dynamic, float	Openness regrowth speed per step after impact
last_burning_episode	Dynamic, integer	Simulation step of the last fire episode of a patch
next_burning_episode	Dynamic, integer	Possible next natural fire event when probability of ignition is 100%
last_partial_consumption_episode	Dynamic, integer	Step of the last partial consumption episode of a patch
last_agent_impacted_pft	Dynamic, integer	Last agent that changed a dominant PFT of a patch: 1–humans, 2–natural fires, 3–climate, 4–megafauna
last_agent_impacted_openness	Dynamic, integer	Last agent that impacted a patch: 1–humans, 2–natural fires, 3–climate, 4–megafauna.
herbs_regeneration_step	Dynamic, integer	Step when herbs will regrow after vegetation burning or consumption
shrubs_regeneration_step	Dynamic, integer	Step when shrubs will regrow after vegetation burning or consumption
needleleaf_trees_regeneration_step	Dynamic, integer	Step when needleleaf trees will regrow after vegetation burning or consumption
broadleaf_trees_regeneration_step	Dynamic, integer	Step when broadleaf trees will regrow after vegetation burning or consumption
agent_that_could_impact_neigbouring_pathes	Dynamic, integer	Agent that can potentially cause burning on neighbouring patches: 1–humans, 2–natural fires, 3–climate, 4–megafauna.
hominin_accessible_area	Dynamic, integer	Defines if the patch is within accessible area for humans: 1–within the area, 0–not accessible for humans

Variable name	Variable type and units	Meaning
occupation	Static, integer	Stores -1 for the British Isles patches for the LIG runs because this region was not occupied by hominins
raster_layer	Dynamic, integer/float	Used to create an ASCII file with modelling results

The model is two-dimensional, and its spatial extent is a rectangle with 544 x 430 patches (grid cells). Each grid cell of input raster datasets (Section AIV.6, Table AIV.6) is resampled (i.e., spatial resolution was changed) to 10 km × 10 km in size. The world wraps horizontally and vertically. The current version of the model imports all spatial datasets for two LIG and seven Early Holocene time windows. One simulation step equals one year, and the current simulation does not account for seasonal variability. One run is 1000 time steps.

AIV.3 Process overview and scheduling

Simulation starts with setup when input datasets are imported, entities are created, their state variables are set, and the conflicting grid cells are removed. In HUMLAND, more closed vegetation can only switch to more open vegetation after a disturbance event (e.g., fire, grazing). In our data comparison, where CARAIB shows a greater degree of openness in vegetation than REVEALS (maximum pollen-based estimates, which represent the sum of estimated REVEALS openness and the standard error), we exclude these locations. This decision is taken because HUMLAND will not be able to generate vegetation that is comparable to REVEALS as it is constrained by the CARAIB-prescribed theoretical potential natural vegetation (PNV). As a result, the similarity between ABM output and REVEALS datasets can only be improved for grid cells where initial vegetation openness is equal to or lower than observed pollen-based maximum estimates.

The process overview of simulation runs is shown in Figure AIV.1. Each of them starts with vegetation regeneration. This submodel (Section AIV.7) executes only for patches which were previously (i.e., during the earlier step) burnt or consumed.

Hominins are the first agent that reduces vegetation cover. The anthropogenic fire submodel (Section AIV.7) is executed via three phases. During the first phase, hominins randomly move towards one of the eight neighbouring patches within the area defined by accessible radius around their campsites. When a hominin reaches a patch with trees or shrubs as a dominant PFT and vegetation openness smaller or equal to a number defined via the Openness_criteria_to_burn variable, this patch is burnt. During the second phase, fire spread is initiated.

The natural fires submodel (Section AIV.7) is initiated after hominin impact. During the setup the number of patches, that will be hit by thunderstorms per

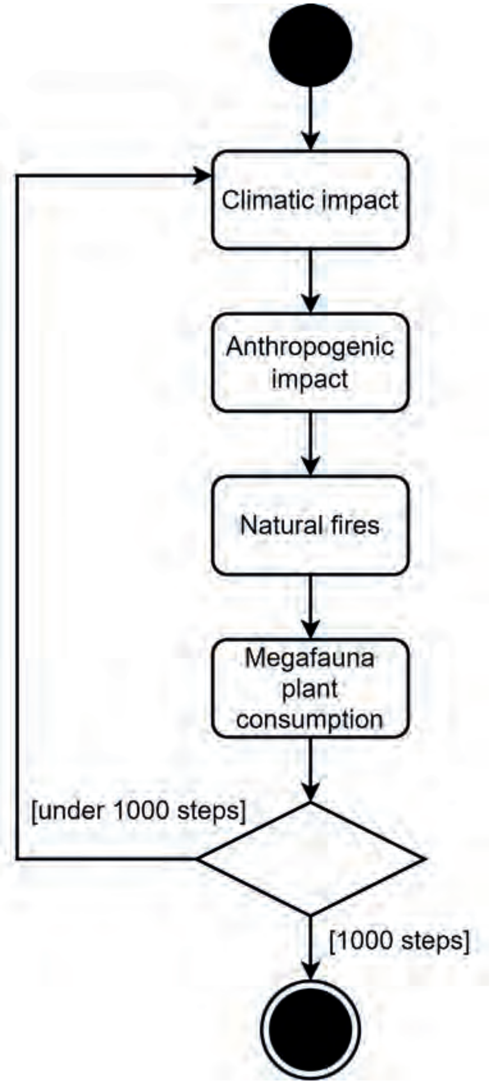

Figure AIV.1 Activity diagram of process overview.

step, is calculated based on a value of the Territory_impacted_by_thunderstorms variable. Every simulation step random patches are chosen and impacted by thunderstorms. Thunderstorms can occur in high mountains, lakes and rivers, but these episodes never lead to ignition. Depending on the probability of ignition of a patches which are not water bodies or high mountains can be burnt after thunderstorms. Similarly to anthropogenic burning, thunderstorms can cause fire spread.

In HUMLAND 1.0 only grid cells with fully recovered vegetation can be consumed by megafauna. In HUMLAND 2.0, both fully recovered and regenerating grid cells can be affected by megafauna. Many herbivores exhibit a preference for areas characterized by secondary vegetation and relatively open regrowth locations following disturbances such as fire because of increased nutrition and palatability of new plants. After plant consumption, vegetation openness increases depending on the CARAIB NPP, current vegetation openness of a patch and hunting pressure. Regarding megafauna impact on PFTs, it is assumed that megafauna equally consumes all PFTs present on a grid cell, i.e., besides the first dominant PFT megafauna consumes second, third and fourth dominant PFTs in equal proportions. That is why, the first dominant PFT is replaced, only if the vegetation was entirely consumed by megafauna, and vegetation openness value after consumption is 100%. In this case, the first dominant PFT would be replaced by bare ground.

Once all sources of impact have affected the study area, the current mean vegetation openness and the distribution of dominant PFTs are compared with REVEALS data. Plots are updated at each step, and the simulation stops after 1000 steps.

AIV.4 Design concepts (after Nikulina et al., 2024b, in press)

AIV.4.1 Basic principles

The history of anthropogenic impacts on the environment spans over many years, with humans already engaging in landscape transformations before the emergence of agriculture. Ethnographic observations show that hunter-gatherers or foragers (i.e., groups that mainly depended on food collection or foraging of wild resources) influence their surroundings in several ways including modification of vegetation communities via burning. This practice was identified for all vegetation types except tundra at different spatial scales and for diverse objectives including driving game, stimulating the growth of edible plants, and clearing pathway.

Besides ethnographic data, evidence from archaeological contexts show that fire use was an important part of the technological repertoire of the *Homo* lineage since at least the second half of the Middle Pleistocene. Human-induced vegetation burning during the Late Pleistocene has been proposed as a potential factor in several case studies spanning various continents. Notably, the earliest evidence of such activities on a local scale was identified at the Neumark-Nord site in Germany, dated to LIG. In addition, fire-using foragers were suggested as one of the primary drivers of vegetation openness in Europe during the Last Glacial

Maximum, i.e., possibly constituting one of the earliest large-scale anthropogenic modifications of system earth.

While these Pleistocene cases are still subject to debate, human-induced vegetation burning conducted by hunter-gatherers during the Early–Middle Holocene (~11,700–6000 BP) is generally accepted, even though the quality of the data is not necessarily that different. However, the number of case studies is higher for the Early–Middle Holocene than for the Pleistocene. Most of the Early to Middle Holocene evidence originates from Europe, with some additional evidence from Australia.

Despite the presence of case studies for anthropogenic burning (intentional or not) of past landscapes by hunter-gatherers, it is still difficult to establish whether these local-scale impacts caused changes at the regional and (sub-)continental scales. Furthermore, overall landscape dynamics do not only depend on humans, and rather represent the complex interplay of natural and cultural processes at different spatio-temporal scales. Landscapes are thus complex systems where heterogeneous components interact to impact on ecological processes, and might demonstrate non-linear dynamics and emergence. Therefore, it is often challenging to distinguish different impacts on landscapes using proxy-based reconstructions (e.g., palynological datasets).

Modelling approaches offer excellent opportunities to explore how complex components of systems might interact, particularly when real-time experiments are not possible. Spatially-explicit agent-based modelling (ABM) is commonly used to explore complex systems where multiple factors intertwine and to propose possible scenarios of system functioning, and the outcomes of ABMs can be compared to empirical data. This approach has been applied in various contexts to study past human-environment interactions and land use/land cover changes. There are examples of such models for past societies that practiced agriculture, animal husbandry, and for hunter-gatherer groups. In the case of ABM developed to study foragers, the use of fire by hunter-gatherers to transform foragers' surroundings and the landscape consequences of these practices are usually not discussed.

This model includes four types of impact on vegetation: climatic impact, anthropogenic fires, thunderstorms, and megafauna plant consumption. Thunderstorms were included because lightning is one of the most general and widespread triggers of natural fires. Another source of impact is climate, and it is included as a crucial element for vegetation regeneration after fires or vegetation consumption. Finally, megafauna are also a part of the current ABM, because the herbivory activity impacts litter accumulation, and high levels of megafauna plant consumption reduce fire occurrence in many areas.

AIV.4.2 Emergence

The model's key results are increase of average vegetation openness and decrease of the percentage of grid cells dominated by trees and shrubs. These results emerge from joint (i.e., several agents together) and separate (i.e., only one agent) impacts of different agents and processes (hominins, thunderstorms and megafauna plant consumption) on vegetation. The increase of vegetation openness and change of PFT's distribution are driven by a specific combination of agents and values of variables that influence their behaviour.

AIV.4.3 Adaptation

There is no adaptation in the model.

AIV.4.4 Objectives

Vegetation burning is an objective for hominins. Each step hominins move randomly to one of the neighbouring patches. If it covered by shrubs or trees and its vegetation openness is equal or lower than the Openness_criteria_to_burn value, then the fire will be set. Otherwise, humans do not impact this patch. Megafauna and thunderstorms do not have objectives.

AIV.4.5 Learning

Agents do not learn.

AIV.4.6 Prediction

Agents do not predict.

AIV.4.7 Sensing

Humans are assumed able to sense dominant PFT and vegetation openness of a grid cell where humans are located. Hominins can sense if their campsites and home patches are beyond accessible radius. It is useful in cases when two campsites are located nearby, and their accessible areas overlap. If a hominin is far from its campsite (does not sense this campsite anymore i.e., it is beyond accessible radius), this hominin automatically comes back to the campsite.

AIV.4.8 Interaction

Hominins directly affect patches. If a hominin decides to burn a patch, its state variables are modified.

AIV.4.9 Stochasticity

Stochasticity is used in initializing the model when random distribution of hominins within the study is set. Additionally, hominins randomly choose one of the eight neighbouring patches to which hominins move around campsites. Finally, humans randomly choose patches when the campsites will be relocated during simulation runs. This happens with a specific frequency defined via the Movement_frequency_of_campsites variable. The parameter Campsites_to_move defines the percentage of campsites that will be relocated. Campsites for this action are chosen randomly.

Thunderstorm impact also includes stochasticity. The number of patches are defined via the Territory_impacted_by_thunderstorms parameter. Several random inland patches are selected every simulation step to potentially have natural fire. The actual natural vegetation burning depends on a probability of ignition P(I) (AIV.1):

$$P(I) = \frac{T - B}{F} \qquad \text{(AIV.1),}$$

where B is the step when the last burning episode occurred, F–FRI, and T–the number of simulation steps (ticks) since the beginning of the simulation. Once P(I) is calculated, a random float number between 0 and 1 is chosen. If $R \leq P(I)$, this patch will be burnt. Similarly to ignition caused by natural fires, fire can spread on neighbouring patches after natural and human-induced fires. For the neighbouring patches the P(I) is calculated, and the fire event can occur depending on the obtained P(I) and random a random float number.

AIV.4.10 Collectives

There are no collectives in the model.

AIV.4.11 Observation

The primary model observations are distribution of dominant PFTs (percentage of patches covered by each PFT) and mean vegetation openness for patches which have both REVEALS estimates and CARAIB values (i.e., not all inland patches are considered). These values are provided via plots on the model interface and extracted tables. The ABM output is considered similar to REVEALS data if a simulation produced the same percentage of first dominant PFTs and mean vegetation openness values or if the difference between ABM output and REVEALS data varies within 10%. Additionally, the different types of impact (i.e., the number of grid cells modified by each type of impact) are tracked via recording which impact caused openness and PFT changes.

AIV.5 Initialization (after Nikulina et al., 2024b, in press)

First, the environment is created during the initialization. Patch state variables at the end of the initialization step are described in Table AIV.3. In HUMLAND, more closed vegetation can only switch to more open vegetation after a disturbance event (fire, grazing). In our data comparison, where CARAIB shows a greater degree of openness in vegetation than maximum REVEALS estimates, we exclude these locations: the ABM will not be able to generate vegetation that is comparable to REVEALS as it is constrained by the CARAIB-prescribed PNV. Secondly, there are several grid cells where climatic conditions only favour dominance of herbs or shrubs, but observed vegetation indicates dominance of trees. Besides that, shrubs cannot dominate grid cells where climatic conditions favour trees or herbs in HUMLAND. Such cases do not improve similarity between ABM output and REVEALS data, and, therefore, these grid cells were also excluded (Table AIV.5).

Table AIV.3 Patch state variables and their values at the end of the initialization stage.

Variable name	Value	Explanation
patch_elevation	In accordance with GTOPO30	Value is set depending on GTOPO30 dataset
patch_natural_pft	In accordance with CARAIB first dominant PFT	Value is set between 1 and 4 depending on CARAIB dataset
patch_pollen_pft	In accordance with REVEALS first dominant PFT	Value is set between 1 and 4 depending on CARAIB dataset
patch_pft_updating	patch_pft_updating = patch_natural_pft	Variable has the same value as theoretical potential natural vegetation provided by CARAIB.
patch_natural_openness	In accordance with CARAIB vegetation openness	Value is set between 9 and 100 depending on CARAIB dataset
patch_pollen_openness	In accordance with REVEALS vegetation openness	Value is set between 0 and 99 depending on REVEALS dataset
patch_pollen_openness_se	In accordance with REVEALS standard errors	Value is set depending on REVEALS dataset
patch_pollen_openness_max	patch_pollen_openness + patch_pollen_openness_se	Maximal possible REVEALS vegetation openness
patch_openness_updating	patch_natural_openness = patch_openness_updating	Variable has the same value as theoretical potential natural vegetation provided by CARAIB.
rivers_lakes	0 or 1	Value depends on WISE dataset
fri	246, 426, 286 or 293	The value depends on CARAIB first dominant PFT (Table AIV.4)
patch_natural_npp	In accordance with CARAIB NPP	Value is set depending on CARAIB dataset

A4

Variable name	Value	Explanation
patch_npp_updating	In accordance with CARAIB NPP	Value is set depending on CARAIB dataset. During simulation runs this value is updated
npp_regrowth_rate	-1	No regrowth rate is calculated before impact during simulation runs
megafauna_npp_ consumption	In accordance with megafauna vegetation consumption dataset	Value is set depending on megafauna vegetation consumption data
megafauna_max_ consumption_ restricted_hunting	Calculated depending on megafauna vegetation consumption dataset andthe Hunting_pressure value	Potential maximal megafauna plant consumption after hunting pressure
continuous_ consumption	0	Before megafauna started consumption this value is set to 0
fire_delay_after_ consumption	-1	Before megafauna consumption of a patch this variable is set to -1
openness_regrowth_ rate	0	Before simulation runs this value is set to 0
last_burning_episode	0	Before simulation runs this value is set to 0
next_burning_ episode	last_burning_episode + fri	Defines the step when this patch has 100% chances to be burnt
last_partial_ consumption_ episode	-1	Before megafauna consumption of a patch this variable is set to -1
last_agent_ impacted_pft	3	Before simulation starts the vegetation cover is created by climate only. Thus, all patches have value 3
last_agent_ impacted_openness	3	Before simulation starts the vegetation cover is created by climate only. Thus, all patches have value 3
herbs_regeneration_ step	0	Before agent's impact all patches do not require regeneration step
shrubs_ regeneration_step	0	Before agent's impact all patches do not require regeneration step
needleleaf_trees_ regeneration_step	0	Before agent's impact all patches do not require regeneration step
broadleaf_trees_ regeneration_step	0	Before agent's impact all patches do not require regeneration step
agent_that_could_ impact_neigbouring_ pathes	0	This value is 0 prior to simulation runs, because there was no impact yet
hominin_accessible_ area	0 or 1	If the patch is within accessible area, the value is set to 1.Otherwise, this variable equals 0
occupation	0 or -1	If 0 can be occupied and burnt by humans. If -1 cannot be occupied or burnt by humans

Variable name	Value	Explanation
raster_layer	-	Used to create .asc file. This variable can have any value depending on chosen patch variable

Table AIV.4 Mean FRI for each dominant PFT.

PFT	Mean FRI estimated via MODIS
Needleleaf trees	246
Broadleaf trees	426
Shrubs	286
Herbs	293

Table AIV.5 CARAIB and REVEALS conflicting cells excluded from the analysis during initiation stage.

CARAIB	REVEALS	Reason
Possible natural (CARAIB) vegetation openness is higher than observed vegetation openness	Maximal observed (REVEALS) vegetation openness (i.e., estimated vegetation openness + standard error) is lower than possible natural (CARAIB) vegetation openness.	In the current ABM possible natural vegetation openness cannot be higher than pollen-based vegetation openness.
First dominant PFT: herbs/shrubs	First dominant PFT: trees	In the current ABM trees cannot dominate if climatic conditions only allow dominance of herbs or shrubs.
First dominant PFT: trees/herbs	First dominant PFT: shrubs	In the current ABM shrubs cannot dominate if climatic conditions only allow dominance of trees or herbs.

Once the environment is created, hominins and their campsites are randomly distributed on surfaces with vegetation. The number of campsites and hominin groups is defined via the Number_of_groups parameter. Patches around campsites are defined as accessible areas. The Accessible_radius parameter defines the size of this area in the number of grid cells around campsites, and the hominin_accessible_area state variable equals 1 for patches within the accessible area. Hominins cannot move beyond their foraging areas, on water bodies (sea, big lakes, and main rivers) and high mountains. These are the patches with absolute elevations more than 2500 m. Water bodies and the most elevated areas do not have vegetation cover, and, therefore, cannot be burnt or consumed. Except for the patch_elevation and rivers_lakes, patches with high mountains and water bodies have -1 for other state variables.

AIV.6 Input data (after Nikulina et al., 2024b, in press)

The simulation uses several datasets (Table AIV.6). To standardize their spatial extent and resolution Spatial Analysts and Data management *ArcMap* 10.6.1 toolboxes were used. Grid cell sizes of the datasets were resampled to 10 km × 10 km. To ensure consistency in our analysis, we made the decision to exclude specific regions, namely Anatolia, Cyprus, and the Balkans, from all time windows considered in this study. The rationale behind this exclusion is that these regions have the earliest evidence of agriculture in Europe. To account for the differences in sea levels during the LIG compared to the present, we used available reconstructions and estimates of sea level. Specifically, we utilized coastlines reconstructed for Northwest Europe. However, such detailed reconstructions were not available for the rest of Europe. Consequently, we assigned a uniform value of 6 m for the rest of Europe during the LIG. During the LIG runs, Neanderthals do not occupy or burn vegetation in the British Isles due to the absence or very sparse presence of people during this period. To ensure this region remains unoccupied, we created a specific spatial layer. Consequently, each LIG time window requires 10 spatial layers, while Early Holocene time windows require nine. For both LIG time windows, we used the same spatial layers from CARAIB, corresponding to the maximal biomass development in Europe. In total, 57 spatial layers are stored in the input data folder for HUMLAND 2.0.

The initial landscape before simulation runs were reconstructed via the following datasets: GTOPO30, Water Information System for Europe (WISE) and outputs of a dynamic vegetation model CARbon Assimilation In the Biosphere (CARAIB). GTOPO30 is a digital elevation model (DEM) derived from several raster and vector sources of topographic information. We used this DEM to represent elevation data in the ABM. WISE dataset is based on the information from the Water Framework Directive database, and we used WISE to define the distribution of major rivers and lakes (natural barriers for fire spread) in the model.

In the context of this research, the CARAIB dataset represents PNV distribution driven by climatic conditions only. As an input climate we used climatic variables simulated by the iLOVECLIM model with embedded online interactive downscaling. The iLOVECLIM-simulated climatic variables were bias-corrected using the CDF-t bias correction technique and averaged over the studied period to get daily mean climate characteristics of our period of interest. A full description of the modelling setup and the application of the CDF-t technique within this setup is described and tested.

CARAIB outputs used in this study include distribution of fractions of 26 plant functional types (PNV PFTs), vegetation openness (PNV openness), and net primary productivity (PNV NPP). Before being imported to the ABM, the mentioned CARAIB outputs were transformed. As the CARAIB dataset here represents climate-only forced vegetation, it is used in the current ABM as the starting point (i.e., before impact of humans, natural fires and megafauna) of each simulation and as target for vegetation regrowth after impacts.

Table AIV.6 Input datasets to the simulation environment (after Nikulina et al., 2024b).

<table>
<tr><th>Dataset</th><th>Initial data type</th><th>Initial spatial resolution/scale</th><th>Meaning, units</th></tr>
<tr><td>GTOPO30</td><td>Raster</td><td>1 km</td><td>Digital elevation model, m</td></tr>
<tr><td>WISE</td><td>Vector</td><td>1:10000000</td><td>Distribution of large rivers and lakes</td></tr>
<tr><td>CARAIB first dominant PFT</td><td rowspan="3">Raster</td><td rowspan="3">~26 km (0.25°)</td><td>Potential natural (climate-based) first dominant PFT</td></tr>
<tr><td>CARAIB vegetation openness</td><td>Potential natural (climate-based) vegetation openness, in percentage</td></tr>
<tr><td>NPP</td><td>Potential net primary carbon productivity (excluding carbon used for respiration), g/m^2</td></tr>
<tr><td>Megafauna vegetation consumption</td><td>Raster</td><td>30 km</td><td>Potential maximal megafauna vegetation consumption (i.e., metabolization of NPP), kg/km^2 (converted to g/m^2)</td></tr>
<tr><td>REVEALS first dominant PFT</td><td rowspan="3">Vector</td><td rowspan="3">~100 km (1°)</td><td>Observed past first dominant PFT</td></tr>
<tr><td>REVEALS vegetation openness</td><td>Observed past vegetation openness, in percentage</td></tr>
<tr><td>REVEALS vegetation openness standard errors</td><td>Standard errors for estimates of observed past vegetation openness</td></tr>
</table>

A4

AIV.7 Submodels (after Nikulina et al., 2024b, in press)

AIV.7.1 Climatic impact

The vegetation regrowth after the impact of thunderstorms, megafauna, and/or humans is determined by the climatic conditions. Therefore, this submodel only modifies grid cells that were previously burned or consumed.

The grid cells' patch_openness_updating and patch_pft_updating (Figs. AIV.2 and AIV.3) are changed in response to the climatic impact until they match the values of patch_natural_openness and patch_natural_pft, respectively. If the difference between patch_natural_openness and patch_openness_updating is equal to or less than 10%, this grid cell is considered to have recovered naturally, and the last agent that impacted this patch is assumed to be climate (last_agent_impacted_openness = 3). Similarly, if patch_natural_pft is equal to patch_pft_updating, the last agent that impacted the PFT of this grid cell is climate (last_agent_impacted_pft = 3).

We used the CARAIB mean number of years to recover (Table AIV.7) to calculate the vegetation openness recovery rate and to define the step when natural PFT would reestablish on the grid cell after vegetation burning and/or consumption. PFT recovery on all impacted patches always begins with herbs, which replace bare ground after seven simulation steps. Subsequently, depending on the PNV PFT estimated by CARAIB after the required number of years since fire or complete consumption (Table AIV.7), the herbs may be replaced by trees or shrubs.

After consumption or fires the rate of vegetation openness recovery (V_{or}) is calculated via the following formula (AIV.2):

$$V_{or} = \frac{O_i - O_c}{\mu} \quad \text{(AIV.2)}$$

O_i represents the vegetation openness after the impact caused by fire and/or megafauna, O_c refers to the CARAIB estimates of vegetation openness, and μ – the mean number of years required for recovery of the initial vegetation openness prior to the fire event or plant consumption (Table AIV.7). NPP recovery is calculated similarly, but instead of using the O_c, model utilizes CARAIB NPP. Instead of the O_i, HUMLAND uses the current carbon content following fire and/or megafauna plant consumption. During each simulation step, V_{or} is subtracted from the current simulation openness until it reaches the CARAIB estimates of vegetation openness. Similarly, the calculated NPP recovery rate is summarised with the current carbon content until the current NPP is the same as PNV NPP.

Table AIV.7 Mean number of years to recover for each dominant PFT (after Nikulina et al., 2024b).

PFT	Number of years

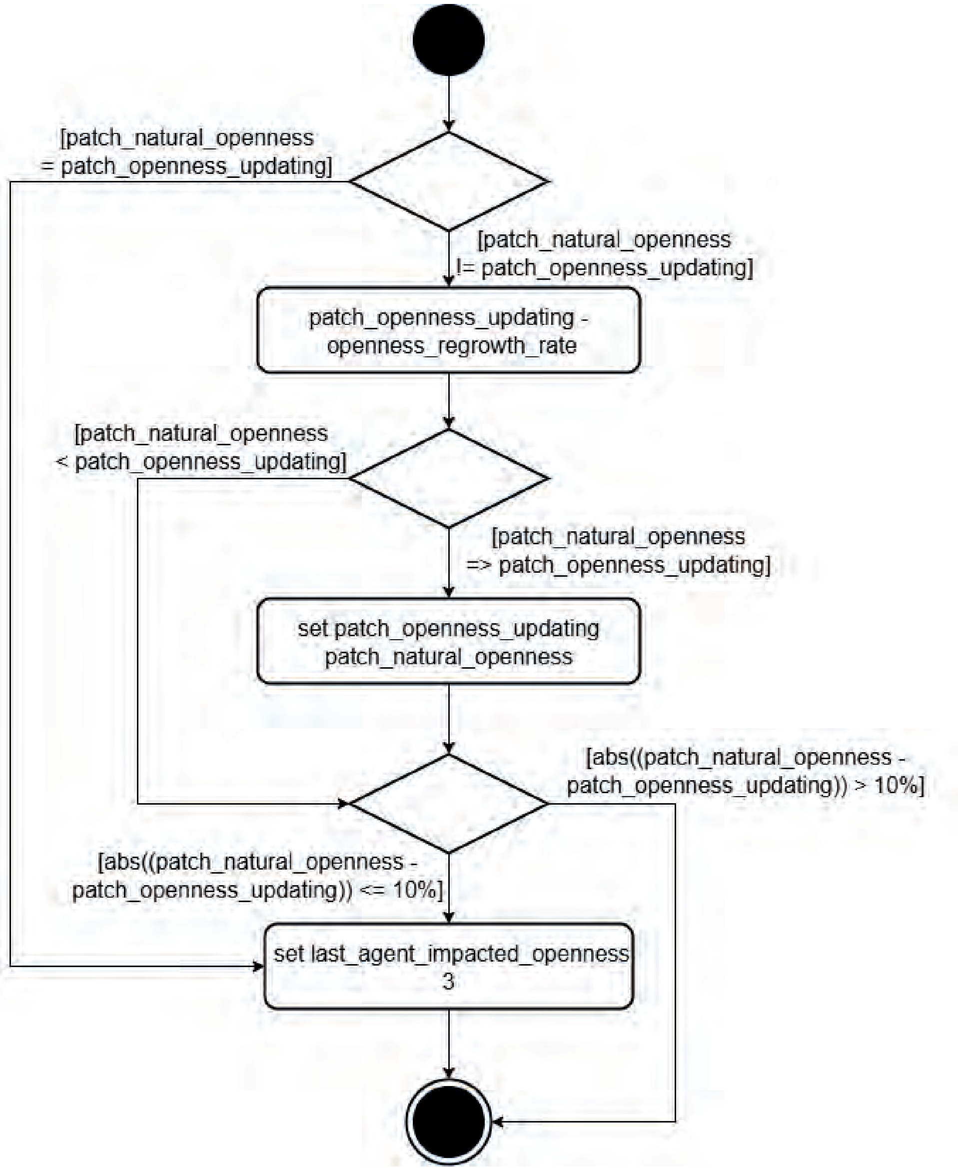

Figure AIV.2 Activity diagram for climatic impact on vegetation openness.

A4

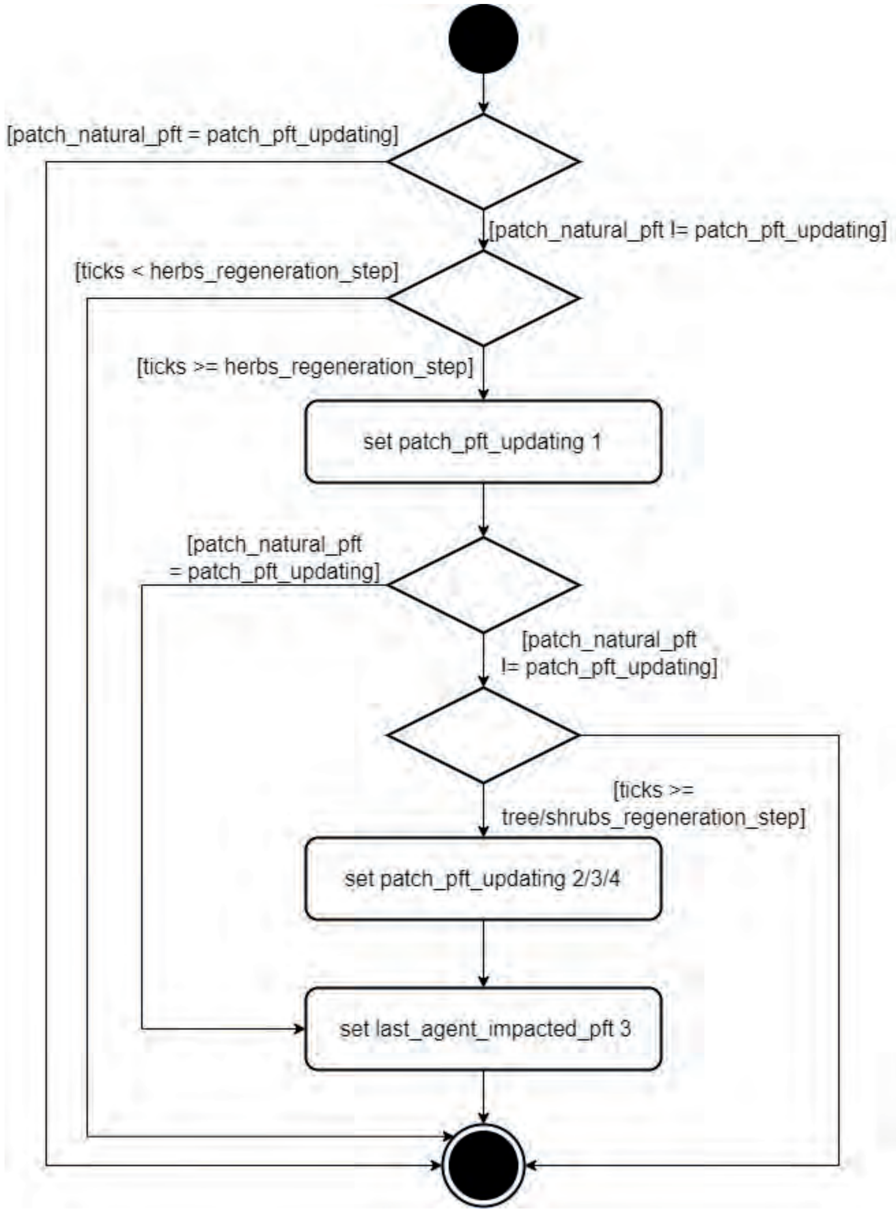

Figure AIV.3 Activity diagram for climatic impact on distribution of dominant PFTs.

Needleleaf trees	43
Broadleaf trees	30
Shrubs	43
Herbs	7

AIV.7.2 Anthropogenic impact

This submodel introduces changes to the vegetation through human-induced fires. There are five parameters which define human behaviour and intensity of their impact: Number_of_groups, Accessible_radius, Campsites_to_move, Movement_frequency_of_campsites, and Openness_criteria_to_burn. An additional parameter, Hunting_pressure, is introduced in HUMLAND 2.0.

The first parameter defines the number of hunter-gatherer groups present at the study area during one simulation run. Therefore, this parameter is associated with human population size. The accessible radius parameter defines the territory within which humans move and set fires around campsites.

There are two parameters associated with movements of foragers' campsites: Movement_frequency_of_campsites (the number of simulation steps after which a group can relocate their campsite) and Campsites_to_move (the percentage of groups that relocate a campsite at certain step defined by movement frequency). Due to the temporal resolution of the current simulation, hunter-gatherers' highest possible frequency of camp movements is every step (i.e., once per year). The search radius for the new grid cell to establish a site is twice bigger than the accessible radius. Any grid cell can be chosen for the new site, except the previously occupied grid cell, high mountains and water bodies. The newly established accessible area can overlap with the previous one.

A4

Since hunter-gatherers have different reasons to burn landscapes, and that this practice was documented in almost all vegetation types with more cases for foragers occupying shrublands and forests, the openness criteria to burn was introduced. In the current simulation, humans only burn grid cells dominated by trees or shrubs with vegetation openness lower or equal to this criterion. A low value minimizes the number of positive decisions to start a fire, and higher values increase human-induced fires, because even relatively open areas can be burnt by people in this case.

Humans randomly move between adjacent patches within a defined area determined by the Accessible_radius (the number of grid cells) around campsites. When a human is present on a patch with vegetation openness that is equal to or lower than the prescribed criteria for burning and contains shrubs or trees (patch_pft_updating >= 2), this human group sets fire on that patch. Consequently, the openness of the patch is set to 100% (completely open), and its PFT (patch_pft_

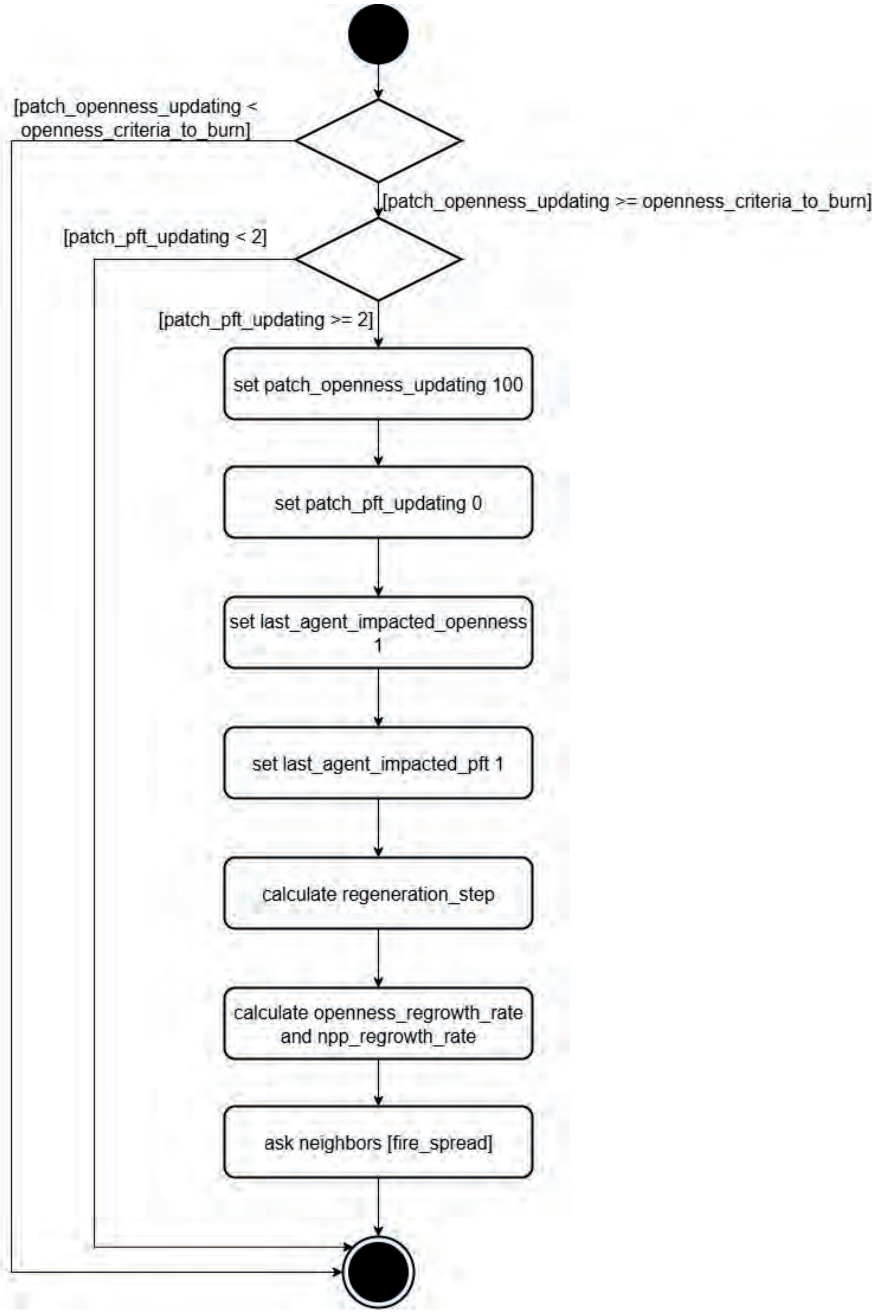

Figure AIV.4 Activity diagram for anthropogenic impact.

updating) is set to 0, indicating a burnt area. In this case, the variables last_agent_impacted_openness and last_agent_impacted_pft are assigned a value of 1 to denote anthropogenic impact. The time step at which this burning event occurs is recorded as last_burning_episode, and next_burning_episode is updated based on the dominant natural PFT. Subsequently, after calculating the regeneration steps (ticks + number of years from Table AIV.4) and openness regrowth rates (Section AIV.7.1), the spread of vegetation to neighbouring patches is initiated (Section AIV.7.4).

The Hunting_pressure parameter defines the percentage reduction in the potential maximum megafauna plant consumption. More details on these calculations can be found in section AIV.7.5.

AIV.7.3 Natural fires

Based on the value of the parameter Territory_impacted_by_thunderstorms, the number of grid cells experiencing thunderstorms per simulation step is determined. This parameter is expressed as a percentage, and based on its value, the calculation determines how many grid cells will be affected by thunderstorms. These thunderstorms randomly occur on different grid cells within the study area. It is important to note that thunderstorms can occur over rivers, lakes, and high mountains, but these areas are not susceptible to burning.

Following the occurrence of thunderstorms, fires may initiate fire spread depending on the probability of ignition for the affected grid cells (Fig. AIV.5). The spread of fire (Section AIV.7.4) to neighbouring grid cells can occur after both human-induced and natural fires. Thunderstorms do not always result in vegetation burning, and the ignition of fire does not always lead to its spread after natural or human-induced ignitions.

The probability of ignition P(I) is determined based on the time elapsed since the last burning episode (B) and the FRI (F), obtained from the MODIS dataset (Table AIV.4) (AIV.3):

$$P(I) = \frac{T - B}{F} \qquad \text{(AIV.3)}$$

Here, T represents the number of simulation steps (ticks) since the beginning of the simulation. If the probability of ignition is equal to or higher than a randomly chosen number (ignt, as shown in Fig. AIV.5), the corresponding patch will be burnt. The consumption of patches by megafauna impacts the probability of ignition. Depending on the percentage of vegetation consumed (as described in Section AIV.7.5), the occurrence of the next burning episode can be delayed. To calculate the probability of delayed ignition, the same formula is used, but with a

A4

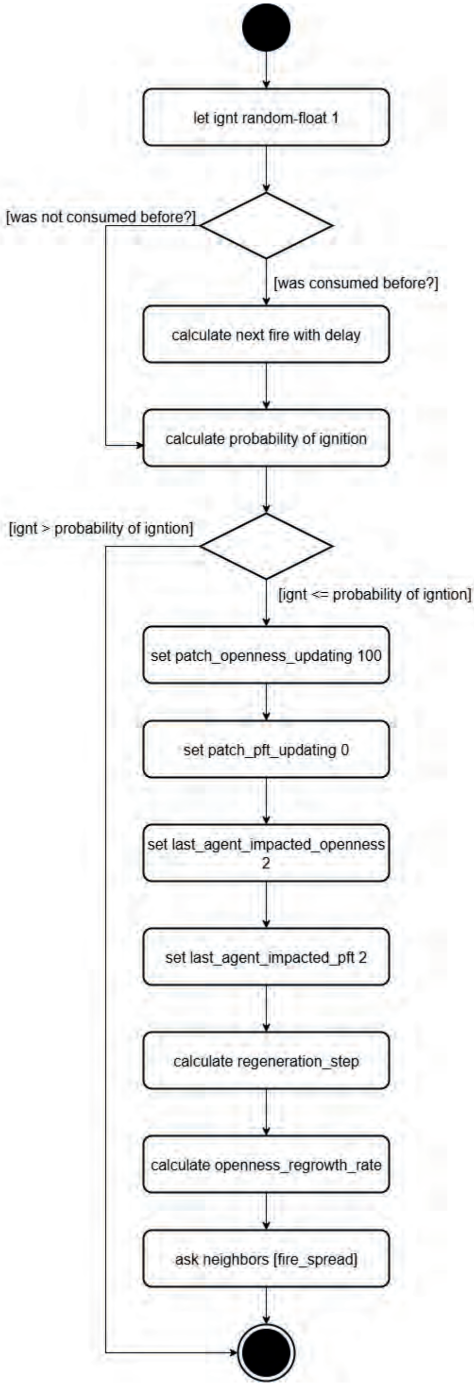

Figure AIV.5 Activity diagram for thunderstorm impact.

modification: instead of using the current number of ticks (T), we use the sum of T and fire_delay_after_consumption. This patch state variable represents the number of years by which the next burning episode was postponed due to megafauna vegetation consumption (section AIV.7.5). The value of B is also updated as a result of megafauna impact (details provided below).

Once a patch is burned (indicated by patch_pft_updating = 0 and patch_openness_updating = 100), the regrowth rate of openness (Section AIV.7.1) and the steps for PFT regeneration (ticks + number of years from Table AIV.7) are determined. Additionally, the information of the last agent that impacted the patch is updated Section AIV.7.1). Subsequently, the neighbouring patches are prompted to spread the fire as explained in Section AIV.7.4.

AIV.7.4 Fire spread

Following natural and anthropogenic burning, fire has the potential to spread to neighbouring patches. However, the actual ignition of these patches depends on the probability of ignition, which is calculated using the same method described for natural fires in Section AIV.7.3. If a patch is burnt because of fire spread, it will inherit the same values for last_agent_impacted_pft and last_agent_impacted_openness as the patch from which the fire spread originated.

AIV.7.5 Megafauna consumption

Megafauna is the final agent responsible for vegetation transformation in the model (Fig. AIV.6). Compared to the previous version of HUMLAND, in this version, megafauna consumes both fully and partially recovered areas. Following plant consumption, the vegetation openness increases based on CARAIB NPP, current NPP, and estimates of maximal megafauna plant consumption.

We introduced the Hunting_pressure parameter which decreases the estimated potential maximal plant consumption (Table AIV.6) within a range spanning from 0% to 100%. This parameter does not impact LIG megafauna plant consumption in the British Isles because Neanderthals were not present or had very sparse occupation there during this time. Besides hunting, the intensity of megafauna impact is determined by the state of vegetation openness. Areas with greater openness tend to experience more substantial herbivore impact compared to relatively closed locations. This serves as the second determinant of megafauna impact intensity within HUMLAND 2.0. Due to the two modifications made to megafauna plant consumption in this model, megafauna affect grid cells at every simulation step in HUMLAND 2.0.

First, the potential maximal megafauna plant consumption is restricted (V_h) by the Hunting_pressure (H_p) percentage for each grid cell (AIV.4):

A4

$$V_h = V_i \times \frac{H_p}{100\%} \tag{AIV.4}$$

V_i is the initial potential maximal megafauna plant consumption obtained from the imported dataset (Table AIV.6). Once V_h is calculated it does not change during one simulation run. For each grid cell this value is stored as megafauna_max_consumption_restricted_hunting.

Following the constraints imposed by hunting pressure, the resultant value of megafauna plant consumption of a grid cell after hunting (V_h) undergoes further restriction based on the current vegetation openness (O_i) of the grid cell. This restriction yields the final estimate (V_m) of megafauna impact through the following formula (AIV.5):

$$V_m = V_h \times \frac{O_i}{100} \tag{AIV.5}$$

Afterwards, the V_c value quantifies the percentage of vegetation consumed in each grid cell, excluding water bodies and high mountains (AIV.6):

$$V_c = 100 \times \frac{V_m}{V_n} \tag{AIV.6}$$

V_n corresponds to the current NPP of the consumed grid cell. The resulting V_c value is then summarized with the current vegetation openness to reflect the impact of megafauna. Megafauna only impact grid cells with vegetation openness lower than 100%, i.e., there is no herbivory consumption of grid cells without vegetation. Subsequently, after the megafauna plant consumption of a grid cell, the current NPP of this grid cell is reduced based on the calculated percentage of consumed vegetation (V_c).

Regarding the impact of megafauna on PFTs, it is assumed that megafauna consumes all PFTs present on a grid cell in equal proportions, besides the first dominant PFT. Therefore, if the vegetation is entirely consumed by megafauna and the vegetation openness reaches 100%, the first dominant PFT is replaced with bare ground. In such cases, last_agent_impacted_pft and last_agent_impacted_openness is assigned to a value of 4, indicating that the impact was caused by megafauna.

However, if the dominant PFT remains unchanged after megafauna consumption, the last_agent_impacted_openness is updated after the patch has experienced 10 consecutive ticks of megafauna impact (continuous_consumption = 10) and if the difference between CARAIB and current vegetation openness is more than 10%. This decision was taken considering the relatively low-intensity impact of megafauna on all grid cells (i.e., most of the time megafauna reduces not

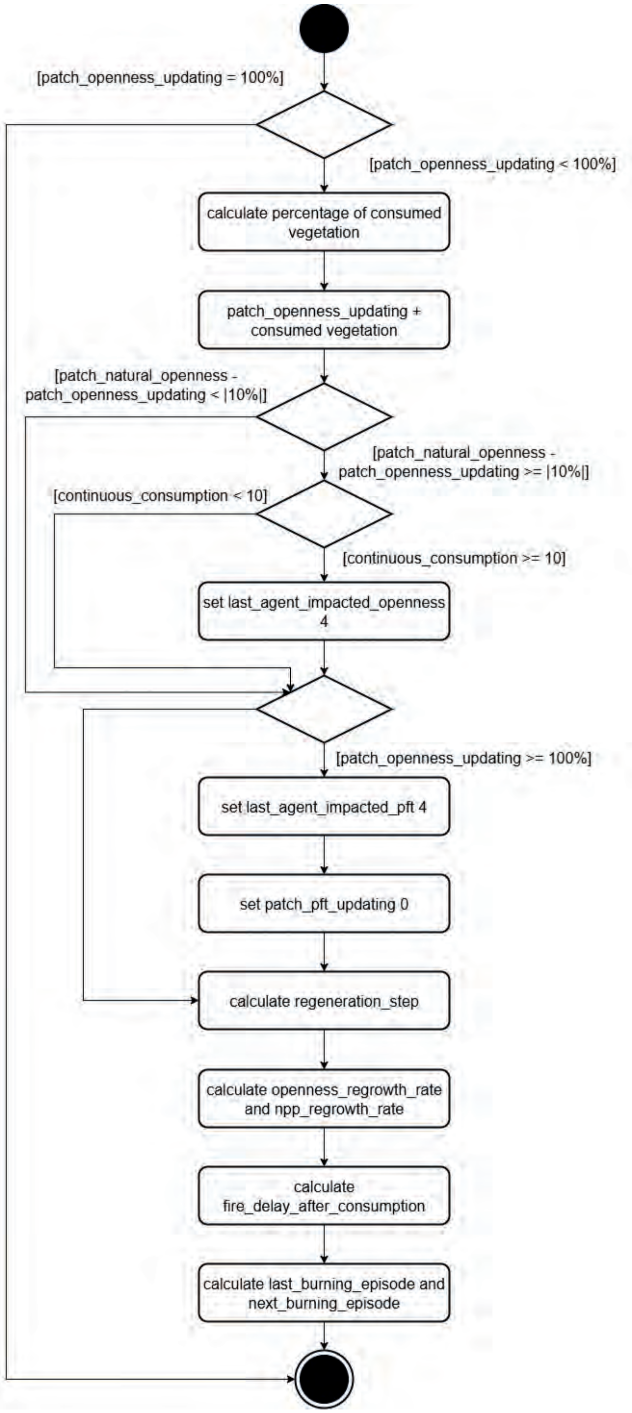

Figure AIV.6 Activity diagram for megafauna impact.

A4

more than V_m = 1% vegetation on each grid cell per simulation step). We assumed that for megafauna to be recognized as an agent responsible for changing vegetation openness of a grid cell, herbivores must effect a transformation to some extent comparable to that induced by fires and climate per simulation step.

When there is partial consumption of vegetation by megafauna (i.e., when the first dominant PFT remains unchanged), it leads to delays in fire activity because time is required to accumulate plant material that can be burnt. The number of years by which fire activity is delayed is calculated by multiplying with the FRI of the respective PFT at the patch (Table AIV.4). Consequently, depending on the percentage of vegetation consumed, the time step at which the vegetation has a 100% probability of being burnt in the presence of an ignition source is postponed.

GLOSSARY

A

a.s.l. Above Sea Level. 93, 122, 138, 237, 281

ABM Agent-based modelling. Modelling approach used to study complex systems. In ABM heterogeneous individuals act and interact between each other and with their environment. As a result, population-level structures, patterns, and properties can emerge from this interaction. 21, 23, 25, 28, 34–39, 79–80, 82–88, 90–92, 94, 96, 107–108, 114–115, 120–121, 125, 127–129, 133, 135, 138–139, 143, 149, 154, 157–158, 162, 166–168, 170, 172–173, 175–179, 198, 203, 207–209, 214, 220, 229, 235–236, 239, 242, 244, 246–247, 267, 275, 279–280, 283, 286–289, 291–293, 315

aDNA Ancient DNA. 55, 126, 163–165, 170, 176, 179

AP/NAP Ratio of arboreal and non-arboreal pollen taxa percentages. 50–51, 53, 60, 62

B

Black carbon Fire residue produced by incomplete combustion of organic matter. 50, 56, 163, 186, 196, 206

C

CARAIB CARbon Assimilation In the Biosphere. Dynamic vegetation model which calculates carbon and water fluxes between the atmosphere and the terrestrial biosphere. CARAIB simulates the major processes of the plant development (establishment, growth, decease) as well as their geographic distributions (Plant Functional Types or species) in response to climate change. 21, 23–26, 28–29, 35–38, 83–92, 95–99, 102, 106–107, 113–116, 123–126, 128, 130–131, 134–140, 142–143, 149–150, 156, 158–159, 162, 166–171, 177, 179, 190, 215, 220, 229, 237–239, 244–249, 256, 258, 262, 264, 267–268, 274–277, 281–283, 285, 288–294, 301, 304

D

DGVM Dynamic Global Vegetation Model. 126, 149, 274–275

F

F1-score A measure of a test's accuracy in binary classification, which considers both the precision and the recall of the test to compute the score. The F1 score ranges from 0 to 1, with 1 being the best possible score, indicating perfect precision and recall. 88, 90, 97, 106, 114

Foragers (Hunter-gatherers) Populations that mainly depend on food collection or foraging of wild resources. 21, 33–34, 44, 48–50, 53, 56, 58, 76–77, 81–82, 93, 119–120, 122–123, 129, 134, 140, 143, 149, 152–153, 155, 158, 163–164, 166, 169–170, 172–177, 184–185, 187, 203–204, 241–242, 252, 285–286, 297

FRI Fire Return Intervals. The average period between fires under the presumed historical fire regime. 83, 94, 171, 222, 236–237, 243, 246, 254, 258, 281–282, 288, 291, 299, 304

G

Genetic algorithm An optimization technique inspired by the principles of natural selection. This technique is used to explore the space of possible solutions. 21, 38–39, 120, 125, 127, 129–130, 136, 139–141, 145–146, 149, 151–152, 157–158, 162, 168, 173–174, 176–178, 197, 204, 215, 269–271, 276

GIS Geographic Information System. 5, 168, 190, 314

GTOPO30 A global digital elevation model with a horizontal grid spacing of 30 arc seconds (approximately 1 kilometre). 83–84, 135, 245, 247–248, 268, 289, 292–293

H

HUMLAND HUMan impact on LANDscapes. 21–26, 28–29, 34, 36–39, 79–80, 82–84, 86–88, 90–95, 97–98, 104, 107–110, 112–115, 119–120, 125, 127–136, 138–141, 143–145, 148–152, 154–158, 162, 167–179, 203, 221, 232, 235–236, 238, 244, 267–270, 273, 276–277, 279–281, 283, 285, 289, 292, 294, 297, 301

Hunter-Gatherers (Foragers) Populations that mainly depend on food collection or foraging of wild resources. 1, 3, 21–22, 33–37, 39, 41–42, 44–58, 60, 62–63, 66, 69, 71, 73–76, 80–83, 91–93, 101–102, 104–105, 107–108, 110–112, 119–122, 126, 128–129, 133–135, 138, 141, 148, 150–151, 153–155, 157, 162–165, 166–167, 169–170, 172, 174–175, 177–179, 212, 223, 225, 231, 236, 241–242, 252, 280, 285–286, 297

I

iLOVECLIM Intermediate Level Ocean-Atmosphere-Vegetation Integrated Model. An intermediate complexity fully coupled climate Earth system model that aims at computation and understanding of the climate system on a millennial timescale. 84, 135–136, 169, 183, 206–207, 247, 274–277, 292

L

Levoglucosan A degradation product obtained from cellulose burning at temperatures more than 300°C. 50, 57, 163, 197, 209

LHS Latin Hypercube Sampling. A statistical method for generating a near-random sample of parameter values from a multidimensional distribution. It is used to perform uncertainty and sensitivity analysis on numerical models. 97, 105, 107, 110, 172

LPJ-GUESS Lund–Potsdam–Jena General Ecosystem Simulator. 137

LRA Landscape Reconstruction Algorithm. A framework of vegetation reconstruction that includes REVEALS as the first step, and LOVE (LOcal Vegetation Estimates)–as the second step. 53

N

Niche Construction The process whereby organisms, through their metabolism, their activities and their choices, modify their own and/or other species niches. 32, 36, 39, 42–44, 46–50, 62, 73–76, 163–165, 184–185, 202, 204, 208, 211, 213, 236, 280

Non-pollen palynomorphs Remains of organisms within the size range of pollen grains (c. 10–250 µm) (e.g., fungi, zoological remains, plant fragments, algae). 50–52, 54, 60–62, 72–73, 163–164, 183

NPP Net Primary Productivity. It is the difference between Gross Primary Productivity (total amount of energy captured by photosynthesis in an ecosystem) and the energy used in respiration (NPP = GPP - R). NPP represents the energy available for growth and reproduction of plants and for consumption by herbivores and decomposers. 83, 85, 87, 95–96, 133, 135, 138, 156, 170, 229, 237, 239, 245, 247–248, 256, 258, 268, 275, 282, 285, 290, 293–294, 301–302

P

PAHs Polycyclic Aromatic Hydrocarbons. A group of organic compounds composed of multiple aromatic rings. They are environmental pollutants formed primarily during the incomplete combustion of organic materials such as coal, oil, gas, wood, and garbage. 50, 56, 188

Parenchyma A part of plant tissue found in most non-woody plants. 51, 58, 75, 165, 179, 206

PFT Plant Functional Type. A set of species that share similar characteristics. 36–38, 83–92, 94–96, 98, 100, 106–107, 113, 124, 127–131, 134–137, 141, 143, 145–146, 148, 153, 155–157, 166, 168, 170–172, 176, 220, 229, 232, 237–239, 242–249, 251–252, 254, 256, 258, 264–265, 267–268, 275–276, 281–283, 285, 287–291, 293–294, 296–297, 299, 301–302, 304

Phytoliths Rigid, microscopic structures made of silica, present in some plant tissues and persisting after the decay of the plant. 50–52, 55–56, 58–59, 75–76, 165, 179, 182, 189, 205, 208, 212, 214, 217

PNV Potential natural vegetation. 83–85, 87, 89–90, 128, 130–131, 135, 220, 239, 244, 247, 268, 274–275, 283, 289, 292–294

PRCC Partial Rank Correlation Coefficient. A statistical method used to measure the strength and direction of association between an input variable and an output variable, while controlling for the effects of other input variables. The PRCC value ranges from -1 to 1, and values near 0 indicating weak or no correlation. 97, 105, 107, 110, 172

R

REVEALS Regional Estimates of Vegetation Abundance from Large Sites. A method to reconstruct plant cover at a regional spatial scale of ca. 100 km × 100 km via transforming pollen data from large lakes and multiple small-sized sites. 21, 23–26, 28–29, 35–38, 83, 86–90, 96–102, 104, 106–107, 109–115, 123–130, 136–137, 139–146, 149–152, 154–156, 158, 162, 166–171, 173–177, 179, 220, 223–227, 229–232, 237–239, 244–246, 248, 263, 265, 267–271, 274, 276–277, 281–283, 285, 288–289, 291, 293

S

SEIB-DGVM Spatially Explicit Individual Based DGVM. 149

Simulation A dynamic model that incorporates changes over time. 21, 28, 37, 79, 83–85, 87–88, 90–96, 100–102, 104–105, 109–111, 128–136, 141, 144, 148, 156–157, 162, 166, 169–171, 176, 178, 183, 186, 194, 212, 215, 223–227, 230–231, 236, 238–239, 243–249, 252, 254, 274–277, 282–285, 288, 290, 292–294, 297, 299, 302, 304

T

t-value A measure used to assess whether the difference between the means of two groups is significant or if it could have happened by random chance. 90, 97, 114

V

VECODE VEgetation COntinuous DEscription model. 135, 274, 275, 276

Vegetation openness In the context of this research, vegetation openness is broadly defined as vegetation density. 22, 37–38, 45, 52–53, 56, 65–66, 80–81, 83–85, 87–90, 92–93, 95–102, 105–109, 111–113, 115, 120, 128–129, 131, 133–135, 137, 139–143, 145–146, 148, 152–153, 155–158, 166, 168, 170–174, 176–177, 220, 223–226, 229–231, 237, 239, 241–250, 252, 256, 258, 262–263, 266, 268, 270, 275–276, 281–283, 285–289, 291, 293–295, 297, 301–302, 304

W

WISE Water Information System for Europe. 37, 83–84, 135, 139, 245, 247–248, 268, 289, 292–293

G

CURRICULUM VITAE

Anastasia Nikulina was born on February 13, 1993, in Novosibirsk, Russia. Upon graduating from Gymnasium 1 in Novosibirsk in 2011, she began her undergraduate studies at Novosibirsk State University (Novosibirsk, Russia). In the summer of 2015, she graduated with a Bachelor's degree in History. She then pursued her Master's degree in Archaeology of North and Central Asia at the same university, graduating with honours in 2017. Since the beginning of her studies, Anastasia has participated in archaeological excavations in Russia, including Denisova Cave (Altai Krai), Afontova Gora-2 (Krasnoyarsk Krai), Tartas-1 (Novosibirsk Oblast), and Ust-Voikar (Yamalo-Nenets Autonomous Okrug), and in France at Fourneau-du-Diable (Dordogne). Anastasia has seven years of fieldwork experience on archaeological sites dating from the Palaeolithic to the Middle Ages.

During the second year of her Bachelor's program, Anastasia selected specialization in GIS for archaeological studies. She became a member of an interdisciplinary research team studying human–environment interactions in Western Siberia, with projects supported by the Russian Foundation for Basic Research (now the Russian Centre for Science Information), the Russian Science Foundation, and the Ministry of Science and Higher Education of the Russian Federation. After completing her Master's program, Anastasia was involved in the French–Russian International Associated Laboratory ARTEMIR. During this time, she expanded her expertise and applied 3D modelling in her work.

In 2019, Anastasia became a PhD candidate at Leiden University (The Netherlands) as part of the Terranova project supported by the European Union's Horizon 2020 program and recognized as a Marie Skłodowska-Curie Actions Innovative Training Network. Anastasia's research focused on the earliest human impacts on interglacial landscapes in Europe. Besides conducting research, Anastasia's involvement in Terranova included public outreach activities, including blogging about her research, and engaging in public events. Additionally, she was one of the main coordinators for the development of Terranova's massive open online course (MOOC), which is available free of charge. Furthermore, Anastasia contributed to the Terranova digital atlas, a comprehensive tool mapping landscape evolution across Europe, which is currently available to the scientific community upon request.

After completing her PhD, Anastasia joined the European Research Council (ERC) SSE1K project "Science, Society and Environmental Change in the First Millennium CE" as a postdoctoral researcher. The project focuses on human–environment interactions in the Mediterranean during the first millennium CE and is interdisciplinary, bringing together researchers from Ca' Foscari University (Venice, Italy), the University of Basel (Basel, Switzerland), and Durham University (Durham, UK). Anastasia is based at Durham University, where she is working on ABM as part of the project.

Anastasia's involvement in various projects has led her to present at 14 international conferences, including the INQUA Congress in 2023 (Rome, Italy) and the Computer Applications and Quantitative Methods in Archaeology (CAA) conference in 2021–2023 (online; Oxford, UK; Amsterdam, The Netherlands). In 2021, Anastasia's presentation at the CAA conference was honoured with the Nick Ryan Bursary Award for the best talk. Additionally, Anastasia was an invited speaker at several events, including the Hortus Talks podcast series organized by the Botanical Garden in Amsterdam (The Netherlands), the Computational and Digital Archaeology Laboratory Series at the University of Cambridge (UK), the workshop "Advances in Modelling Past Human Ecosystems" at Cologne University (Germany), the symposium on "Fire in Human Evolution" at Leiden University (The Netherlands), and the graduate conference "Humans and the Landscape(s): An Everlasting Story of Mutual Interactions" at University of Basel (Switzerland).

Anastasia has also participated in various international schools and training programs, including Neural Networks for Archaeologists with Python at Pisa University (Italy). She has contributed to several multi-author, peer-reviewed papers, serving as the lead author in six instances. In addition, she has published developed ABMs after peer review in an open-access model library.

```
;;;;;;;;
;; Go ;;
;;;;;;;;

to go
  color_vegetation

  vegetation_regeneration

  if humans = true [
    if round Movement_frequency_of_campsites > 0 [
      if ticks >= step_to_move_campsites and Campsites_to_move
      round Movement_frequency_of_campsites != 1200 [
        move_campsites
        set step_to_move_campsites (ticks +
          ( round Movement_frequency_of_campsites) )
      ]
    ]

    walk_humans
  ]

  if Natural_fires = true [
    thunderstorm_burning
  ]

  if megafauna_impact = true [
    megafauna_vegetation_consumption
  ]

  ;;;;;;;;;;;;;;;;;;;;;;
  ;; Updates globals ;;
  ;;;;;;;;;;;;;;;;;;;;;;

  let average_sum sum [
    patch_openness_updating
  ] of patches with [
    PATCH_POLLEN_OPENNESS >= 0
  ]
  set current_average_openness
  (average_sum / ALL_PATCHES_WITH_POLLEN_OPENNESS)
```