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More than agriculture: analysing time-cumulative human impact on European land-cover of second half of the Holocene

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1	More than agriculture: analysing time-cumulative human impact on European land-
2	cover of second half of the Holocene
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20 Abstract:

Assessment of past anthropogenic modifications of land-cover dynamics is key to understanding the human role in the Earth system. Recent advances in palaeoenvironmental sciences allow us to assess the long-term impacts of anthropization on ecosystems, landscapes, and land-cover.

Our study aims to evaluate the role of human impact on European land-cover over the past 6000 years by comparing two independent datasets. First, we use a dynamic vegetation model forced by debiased climate model outputs. The climate model uses natural forcings only and therefore the computed vegetation distribution is interpreted as the potential natural vegetation. Second, we use pollen-based reconstructions, which intrinsically include anthropogenic influence. The discrepancies between the two datasets are attributed to human activity and quantified in a form of a human pressure index (HPI).

Patterns of spatio-temporal evolution of the HPI agree with previously published data about the spread of agriculture in Europe. In particular, both HPI and anthropogenic land-cover change (ALCC) scenarios indicate a rapid increase of the human pressure around 1200-1700 BP, and a significant increase of agriculture-related land-cover modifications by nearly 60% throughout the second half of the Holocene. However, initially high HPI values (up to 70%) at 5700-6200 BP, which correlate with population estimates (r = 0.75, p-value < 0.005), suggest high levels of anthropogenic land-cover transformations, introduced by earlier agricultural as well as non-agricultural activities.

37 The results of our study suggest that vegetation cover of the Mid-Holocene substantially differed from the state

of potential natural vegetation (PNV) due to cumulative effect of early human alterations on the land-cover.

39 This challenges the hypothesis that vegetation in the Mid-Holocene was in a relatively natural state and

40 contributes valuable insights to the onset of agriculture as the start of the Anthropocene.

42 Keywords: anthropogenic land-cover change; climate-forced vegetation modelling; pollen-based

43 reconstructions; Europe

- 44
- 45 Highlights:

10	-	This study	(au antifica	L uranaan	anthranaani	<u> </u>	aver abandaa	unding a huma	an nraadura inda	v /I IDI)
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- HPI shows 60% increase in anthropogenic land-cover modifications throughout the second half of the
 Holocene
- Population estimates correlate with HPI and agree with previously published data on land use
- High HPI values in the Mid-Holocene suggest significant impact of early agricultural and pre-agricultural
- 51 human practices
- 52

53 1. Introduction

Numerous scholars, particularly within the geological community, mark the start of the Anthropocene by the 54 transition to fossil fuel burning, artificial radionuclides spread by the thermonuclear bomb tests or rapid 55 changes in the biosphere, which typically begin between the Industrial Revolution (ca. AD 1800) and the early 56 1950s (Bauer et al., 2021; Crutzen, 2002; Head et al., 2022a; Steffen et al., 2011; Waters et al., 2016; 57 Zalasiewicz et al., 2021). However, in recent years researchers propose to account for the emergence of 58 humanity as a force on Earth's landscape. Scholars in archaeological and palaeoecological communities argue 59 that humans begun substantially impacting the environment several thousands of years earlier than previously 60 suggested (Braie and Erlandson, 2013b; Ellis et al., 2021; Erlandson and Braie, 2013; Lightfoot and Cuthrell, 61 2015; Nikulina et al., 2022; Smith and Zeder, 2013). It is thus debatable whether Anthropocene's "golden 62 spike" should be marked by the appearance of anthropogenic soils (Certini and Scalenghe, 2011), onset of 63 agriculture (Ruddiman, 2013), late Pleistocene megafaunal extinctions (Braje and Erlandson, 2013a), or 64 defining the "Anthropocene" term should be omitted altogether and used as a flexible term instead (Edgeworth 65 et al., 2015; Ruddiman, 2018; Rull, 2017; Swindles et al., 2023). Moreover, other terminology was proposed to 66 define early hominin impact on the environment, such as the Palaeoanthropocene (Foley et al., 2013). To 67 address the challenges associated with formalizing the Anthropocene as a distinct epoch (subdivision of the 68 Geological Time Scale), recent studies suggest to define the Anthropocene as an ongoing event (Edwards et 69 70 al., 2022; Gibbard et al., 2022; Bauer et al., 2021) or episode (Head et al., 2022b), rather than an epoch. In any case, in the light of the Anthropocene discussion, the history of anthropogenic impact on land-cover became a 71 key topic in palaeoenvironmental studies. 72

The role of land-cover modifications attributed to human activity over the Holocene is often quantified by 73 means of anthropogenic land-cover change (ALCC) models (HYDE 3.2: Goldewijk et al., 2017; KK10: Kaplan 74 et al., 2009; Pongratz et al., 2008). While their reliability is largely limited by a number of factors, such as not 75 explicitly accounting for effects of Holocene climate or geomorphic change and variability, and uncertainties in 76 the underlying data, ALCC models are currently the only available method to produce spatially- and temporally-77 continuous data of numerically expressed human-environment interactions (Kaplan et al., 2017). These models 78 79 are based on historical human population density estimates, the land needed to sustain that population, and its suitability, determined by climate and soil properties (Kaplan et al., 2009; Pirzamanbein and Lindström, 2022). 80

However, ALCC models, such as KK10 or HYDE 3.2, do not yet incorporate archaeological and 81 palaeoecological proxy data or historical descriptions of past land use (Trondman et al., 2015). Several 82 approaches have been developed to estimate past ALCCs to assess their possible effects on past land-cover 83 (Ramankutty and Foley, 1999; Olofsson and Hickler, 2008; Pongratz et al., 2008, 2010; Kaplan et al., 2009, 84 2011; Lemmen, 2009; Goldewijk et al., 2011). While existing ALCC scenarios (Goldewijk et al., 2017a; Kaplan 85 et al., 2009; Pongratz et al., 2008) significantly differ from each other (Gaillard et al., 2010; Kaplan et al., 2017), 86 they all tend to represent anthropogenic impact centred around agricultural activities. For example, multiple 87 studies focus on their representation of the onset and adoption of agriculture in different ALCC scenarios 88 (Smith et al., 2016; Stephens et al., 2019; Stocker et al., 2011; Vavrus et al., 2022), KK10 in particular. 89 features deforestation for crop cultivation and pastures to quantify human influence on land-cover (Kaplan et 90 al., 2009). However, deforestation by humans is not limited to agricultural purposes. Harrison et al. (2020), and 91 even Kaplan et al. (2017) themselves highlighted the need for inclusion of non-agricultural activities in the 92 analysis of spatial patterns of anthropogenic land use. 93

Furthermore, while human impact on the environment intensified with the introduction of agriculture, pre-94 95 agricultural landscapes were already far from "natural" or "intact" (Ellis et al., 2021). Humans have a long history of shaping their environments through niche construction activities (Nikulina et al., 2022), for example 96 97 through burning (Scherjon et al., 2015), and geographic range manipulations of plant and animal species (Finsinger et al., 2006; Rowley-Conwy and Layton, 2011), Such alterations had a smaller immediate effect on 98 the environment compared to agriculture, especially industrial practices, but niche-constructing activities 99 spanned many thousands of years, dating back as far as the Last Interglacial (Roebroeks et al., 2021), with 100 numerous studies reporting cases of land-cover modifications over late Pleistocene and early Holocene 101 (Archibald et al., 2012; Bos and Urz, 2003; Doughty, 2013; McWethy et al., 2010; Pinter et al., 2011; Roberts 102 et al., 2021). Therefore, the cumulative effect of the prehistory-long legacy of non-agricultural human practices 103 on land-cover remains poorly understood. 104

Quantitative reconstructions of past vegetation cover indicate that changes of vegetation in Europe reach
maximum complexity in terms of the rate of change during the second half of the Holocene (from 8200-4200
BP to present day; hereafter, dates are expressed as calibrated calendar years before AD 1950 and referred to
as BP) (Marguer et al., 2014; Mottl et al., 2021). In Europe this period is characterized by the adoption of

agriculture and intensification of human-induced land-cover change (Stephens et al., 2019; Morrison et al.,
2021; Harrison et al., 2020; Goldewijk et al., 2017a; Kaplan et al., 2011; Gronenborn and Horejs, 2021) as well
as by a substantially changing climate (Arthur et al., 2022; Zhang et al., 2017). Moreover, analysis of the
European Pollen Database indicated that anthropogenic land-cover change in pollen records becomes
detectable from 6000 BP (Fyfe et al., 2015). Hence, in this study we focus on quantifying the anthropogenic
impact on European land-cover over the period of the second half of the Holocene (6200 BP – AD 2015).

Estimation of the magnitude of human-induced changes in land-cover is often performed through analysis of 115 palaeoecological data acquired from pollen-based reconstructions (Bartlein et al., 2011; Dallmeyer et al., 2019; 116 Marguer et al., 2017; Prentice et al., 1998; Strandberg et al., 2022). One of such reconstructions, the Regional 117 Estimates of VEgetation Abundance from Large Sites (REVEALS) model (Sugita, 2007a), was used to create 118 gridded pollen-based estimates of Holocene plant cover for NW-central Europe north of the Alps (five time 119 windows of the Holocene) (Trondman et al., 2015) and more recently for all of Europe through the Holocene 120 (11,700 BP to present) (Githumbi et al., 2022). The REVEALS reconstructions from Marguer et al., (2017) have 121 been used in the recent study of Dallmeyer et al. (2023), who applied an approach based on the comparison 122 between REVEALS-based reconstructions and land use forced vegetation model outputs for northern and 123 central Europe. Their study concluded that anthropogenic land use was the main driver of the decrease in 124 forest cover in Europe during mid- and late-Holocene (100 – 8000 BP). To further this analysis, we simulate 125 vegetation for the second half of the Holocene (6200 BP - AD 2015) and compare the results with an extended 126 version of the REVEALS-based reconstructions (Serge et al., 2023). Serge et al. (2023) used the same 127 protocol as described in Githumbi et al (2022) to produce the most spatially extensive and temporally 128 continuous pollen-based reconstructions of plant cover in Europe (at a spatial resolution of 1° × 1° for 30°-71° 129 N. 20° W-47° E; spatial distribution is shown in Figure 2) over the Holocene at a temporal resolution of 500 130 years between 11,700 and 700 BP. For the most recent period, Serge et al. (2023) allocated smaller time 131 windows with a higher temporal resolution: 700-350 BP, 350-100 BP, and 100 BP-present (where the present 132 is the year of coring). 133

While indicating the significance of land use as a key factor in driving past land-cover change in Europe,
Dallmeyer et al. (2023) highlighted several challenges that arise when comparing pollen-based quantitative
vegetation reconstructions with outputs from vegetation models. In our current study, we address two of these

challenges: biases in simulated climate and distinction between anthropogenic and non-anthropogenic drivers 137 of land-cover change. To overcome these challenges, we propose a method that compares pollen-based 138 reconstructions with a theoretical state of vegetation cover - potential natural vegetation (PNV), which 139 represents climate-forced vegetation without human intervention or management (Hengl et al., 2018). 140 In this study, by analysing relationships between simulated PNV and pollen-based estimates of regional 141 vegetation abundance, we aim to (1) evaluate how far from natural conditions our REVEALS-based vegetation 142 is, by comparison with modelled potential natural vegetation, (2) quantify time-cumulative impact of human 143 modifications of European land-cover (accumulated impacts of human activity on natural ecosystems through 144 time) over the second half of the Holocene (6200 BP - AD 2015) including both agricultural and non-145 agricultural human activities, and (3) assess the performance of the developed methodology through 146 comparison with existing ALCC scenarios KK10 and HYDE 3.2. 147

148 2. Methodology

149 2.1. Study design

In this study, we address the challenge of distinguishing between anthropogenic and non-anthropogenic 150 drivers of land-cover change. Pollen-based land-cover reconstructions allow the identification of phases of 151 vegetation compositional change comparable with periods of climate change, derived from independent 152 climate reconstructions to account for the importance of climate-driven vegetation change (Seddon et al., 153 2014). However, the interaction of natural forces with anthropogenic influences induces complex processes 154 with profound effects on the environmental system (Kalis et al., 2003). It is thus not always easy to attribute 155 temporal changes in vegetation composition to a certain impact factor. The complex nature of interactions 156 between different impact factors often makes it difficult to distinguish between climatic and anthropogenic 157 origin of changes in vegetation patterns. Anthropogenic impact on vegetation composition is often derived from 158 pollen-based reconstructions using cultural indicators (e.g. Deza-Araujo et al., 2020; Behre, 1981). The 159 applicability of these indicators has been limited to regional studies due to regional variations in cultural 160 practices and vegetation dynamics. Recently, Deza-Araujo et al. (2022) suggested the use of agricultural land 161 use probability (LUP) index based on existing cultural indicators. This approach allows the use of the method 162 beyond the specific regions where the cultural indicators were developed. However, while promising, its 163

application to continental scales has not been explored. The relative importance of different impact factors for 164 various regions and time periods is, therefore, still a matter of debate (Marguer et al., 2017; Dallmeyer et al., 165 2023). Moreover, quantifying the effect of early non-agricultural human practices (such as burning, wood 166 harvesting for different purposes, settlement activities, and geographic range manipulations of species) on 167 land-cover remains a challenging task, since these practices cannot be retrieved using cultural indicatorsthat 168 target agricultural land use through the presence of representative taxa in pollen records, i.e. Cerealia type (t.) 169 (e.g. Githumbi et al., 2022; Gaillard, 2007). To tackle these challenges, analysis of pollen-based reconstructions 170 would benefit from comparison to a reference state that would represent vegetation over the studied time 171 period without anthropogenic changes of vegetation. Thus, in order to evaluate the extent of human-induced 172 land-cover change in Europe during the second half of the Holocene (6200 BP - AD 2015), we applied a 173 method that compares vegetation cover obtained through REVEALS-based reconstructions with an alternative 174 description of past vegetation cover - potential natural vegetation (PNV). The concept of PNV has been the 175 subject of past debate (e.g. Loidi et al., 2010; Jackson, 2013; Hengl et al., 2018; Somodi et al., 2012; Farris et 176 al., 2010). We consider that PNV describes a theoretical state of vegetation cover that would exist under the 177 assumption that the vegetation is in balance with environmental controls, such as climatic conditions and 178 disturbances, without any human intervention or management (Hengl et al., 2018). In a palaeoenvironmental 179 modelling context, PNV is often referred to an artificial construct simulated by a dynamic vegetation model 180 (DVM) without prescribed land use forcing, that represents climate-forced potential vegetation in the absence 181 of human-induced vegetation changes and other disturbances (e.g. wildfire, megafauna) (Trondman et al., 182 2015). PNVs are routinely used in various modelling exercises, such as to evaluate vegetation naturalness 183 (Strona et al., 2016), analyse response of vegetation to climate change (Ren et al., 2021), or evaluate 184 reconstructions of past regional vegetation patterns (Cruz-Silva et al., 2022). A PNV distribution is often 185 simulated by vegetation models, which are based on modern empirical relationships between vegetation and 186 climate (Levavasseur et al., 2013). Taking advantage of the PNV concept as best available description of the 187 plausible vegetation of an area, we simulated PNV for the second half of the Holocene (6200 BP – AD 2015) 188 using the CARbon Assimilation In the Biosphere (CARAIB) dynamical vegetation model (Dury et al., 2011; 189 François et al., 2011; Laurent et al., 2008; Otto et al., 2002; Warnant et al., 1994), forced by downscaled bias-190 corrected climate simulated by the iLOVECLIM model (Zapolska et al., 2023). 191

192 2.2. Design of the climate simulations

The climate simulations were performed with the iLOVECLIM model, version 1.1.5 (revision 1512). This model 193 is a code fork of the original LOVECLIM 1.2 model (Goosse et al., 2010), revised by Roche (2013) and further 194 expanded by Quiquet et al. (2018). In this study we used the online interactive downscaling method embedded 195 in iLOVECLIM, first described by Quiquet et al. (2018). Our version of iLOVECLIM includes the following 196 components: the atmospheric model, ECBilt (Opsteegh et al., 1998), the sea-ice ocean component, CLIO 197 (Goosse and Fichefet, 1999), and the reduced-form dynamic global vegetation model, VECODE (Brovkin et al., 198 1997). We refer the reader to the reference articles for a complete description of the iLOVECLIM model 199 (Roche, 2013) and downscaling method (Quiquet et al., 2018; Arthur et al., 2022). 200

Vegetation is an important component of climate dynamics, which impacts climate via physiological, 201 biogeophysical and biogeochemical processes. It is, therefore, necessary to simulate vegetation cover to 202 accurately simulate climate. This is why our climate simulations were performed with the VECODE reduced-203 form vegetation model (Brovkin et al., 1997) which computes plant and soil behaviours necessary to simulate 204 the first order vegetation-climate feedback in climate models. Being a reduced-form DGVM, VECODE only 205 computes 2 vegetation types: trees and grass (and bare ground as a dummy type). This is enough for the first 206 order feedback to the atmospheric model, since it encompasses the three main classes affecting the albedo, 207 the surface roughness and the link to the water cycle. However, it is far from being sufficient to reflect 208 vegetation changes at the level of complexity needed for our main intercomparison with the REVEALS output. 209 as described further in this study. This is why the resulting climatic evolution was then bias-corrected and used 210 as an input to a much more complex vegetation model which has the necessary complexity to see the fine-211 scale structures we are concentrating on. The input was provided as climatologies (climatological means) of 212 daily values for each time window (TW) (Supplementary table 1) without transient change in climate input 213 (equilibrium simulations). 214

To summarise, the use of VECODE in the initial computation affected the large-scale climate providing the first-order response of dynamical vegetation coupled to climate at large scales, such as desertification (complete change from trees to grass or bare ground, and vice versa) or large shifts from forests to grassland. Fine-scale changes were then computed using the more complex (and more computationally intensive) CARAIB DGVM, so as to look into changes that are usually attributed to human impact on vegetation, such as changes in vegetation composition which are far beyond the reach of the reduced-form VECODE model. The
 coherency of the large-scale changes of the two vegetation models has been checked through the
 intercomparison between the results of the two models, and the results showed that they are consistent in
 patterns of large-scale vegetation response to climatic factors (not shown).

We applied iLOVECLIM to simulate the transient evolution of the climate during the Holocene. The 224 experiments were first initialised with a state derived from a 3,000 year long equilibrium simulation at 11,700 225 226 BP. Subsequently, we performed a full transient simulation from 11,700 BP up to present. Owing to the large time scale response of the ocean and furthermore to the fact that the climate system is never in equilibrium 227 with forcing boundary conditions, we only considered the part 6,000 BP to present in our analysis, using the 228 section 11.700 BP to 6,000 BP as a further adaptation of climate to transient boundary conditions. For both 229 equilibrium and transient simulations, we used boundary conditions evolving as closely as possible to the state 230 of knowledge. Namely, we used astronomical parameters from Berger (1978), greenhouse gas levels (Schilt et 231 al., 2010: Raynaud et al., 2000), ice sheets from the GLAC-1D reconstruction (Tarasov et al., 2012: Tarasov 232 and Peltier, 2002) as well as evolving bathymetry and land-ocean mask coherent with those ice-sheet 233 geometries (with the same methodology as Bouttes et al., 2023). Between the year 6200 BP and the year 700 234 BP time windows (TWs) (Supplementary table 1) were assigned at 500 years temporal resolution, and the 235 lengths of the three most recent time windows were fixed to 350(700 - 350 BP), 250(350 - 100 BP), and 165236 (AD 2015 - 1850). 237

The use of the model results for the intercomparison with pollen data in the context of the current study could be considered indicative under assumption of minimal model biases. To correct biases of iLOVECLIM modelled results, we applied the CDF-t bias correction technique (Vrac et al., 2012). CDF-t was previously reported to yield significantly stronger agreement between the simulated results and pollen-based climate and biome reconstructions, compared to modelled results without CDF-t application (Zapolska et al., 2023). A full procedure of the bias correction methodology and its limitations can be found in Zapolska et al. (2023).

The observational reference dataset used for bias correction is the EWEMBI dataset (EartH2Observe, WATCH Forcing Data (WFDEI), and ERA-Interim reanalysis data merged and bias-corrected for the InterSectoral Impact Model Intercomparison Project) (Lange, 2016). The EWEMBI data covers 38 years from 1979 to 2016. To match to the length of the observation dataset (which is required for the CDF-t methodology), we extracted 38 median years of 14 TWs (Supplementary table 1), consistent with the TWs of the REVEALS pollen-based
land-cover reconstruction dataset for further analysis. Following the bias correction, each of 14 sets of climatic
parameters was averaged to get daily mean climate characteristics of TWs.

The reliability of the described modelling workflow and the comparison of simulated climate and vegetation with available proxy data were evaluated in previous studies. Arthur et al. (2022) assessed the downscaled iLOVECLIM simulation for the Holocene before the application of CDF-t, while Zapolska et al. (2023) evaluated the downscaled iLOVECLIM and CARAIB performance for periods characterized by different climatic conditions with the CDF-t application.

256 2.3. Modelled potential natural vegetation

Potential natural vegetation was simulated using the CARbon Assimilation In the Biosphere (CARAIB) model 257 (Otto et al., 2002; Laurent et al., 2008; Warnant et al., 1994; François et al., 2011; Dury et al., 2011) forced 258 with 14 sets of climates simulated by the iLOVECLIM model (bias-corrected and averaged over TWs, as 259 described above). The CARAIB model is composed of five modules describing respectively (1) the hydrological 260 budget, (2) canopy photosynthesis and stomatal regulation, (3) carbon allocation and plant growth, (4) 261 heterotrophic respiration and litter/soil carbon dynamics, and (5) plant competition and biogeography (Francois 262 et al., 2011). In this study, we did not include the fire module in the simulations, and the fire regime was 263 calibrated based on modern times. Water and carbon reservoirs in CARAIB are updated with a daily timestep, 264 while photosynthesis and plant respiration are calculated every two hours to account for non-linear effects 265 associated with the variation of photosynthetic/respiration fluxes over the day. The model simulates a given set 266 of plant functional types (PFTs), which can coexist on the same grid cell. Trees are assumed to grow above 267 herbs and shrubs (or bare ground), creating two vegetation levels with maximum coverage up to 1 at each 268 level. Thus, the maximum vegetation fraction of a grid cell is 2, provided that both upper (trees) and lower 269 (grass and shrubs) levels are fully vegetated. Vegetation cover output is updated every month for herbaceous 270 PFTs and yearly for arboreal PFTs (François et al., 2011; Henrot et al., 2017). For a more detailed description 271 of the CARAIB model we refer the reader to Otto et al (2002), Laurent et al (2008), Warnant et al (1994), 272 François et al (2011), Dury et al (2011). 273

The input climatic fields used to run the CARAIB vegetation model were daily values of: (1) the mean near-274 surface air temperature, (2) the daily amplitude of air temperature change, (3) precipitation, (4) air relative 275 humidity, (5) percentage of sunshine hours and (6) wind speed. In the current study, daily temperature 276 amplitudes and wind speed were taken from observations (Daily temperature amplitudes: Climatic Research 277 Unit (CRU) data, mean over 1901-2015; wind speed: EWEMBI dataset) and kept constant for all time periods. 278 279 Surface temperature, precipitation, relative humidity, and sunshine hours were derived from iLOVECLIM. Biases in temperature, precipitation and relative humidity were corrected using the CDF-t approach (Vrac et 280 al., 2012). These sets of bias-corrected climate data were used to perform snapshot simulations with CARAIB 281 run until equilibrium (200 years), to obtain characteristic PNV patterns for the specified TWs. 282

283

284 2.4. The REVEALS Pollen-Based Land-cover Reconstructions

For comparison with the modelled PNV, we used a part of the last set of gridded pollen-based REVEALS plant-285 cover estimates for 31 taxa at a spatial scale of 1° × 1° across 30°–71° N, 20° W–47° E (north-western, central 286 Europe, Mediterranean area, and part of the East until 47° E) for 14 contiguous time slices of 100-500 years 287 covering second half of the Holocene (Serge et al., 2023). Previous grid-based estimates (Githumbi et al., 288 2022; Trondman et al., 2015) were designed for the purpose of conducting studies on the impact of land cover 289 on climate using climate models and DGVMs (Strandberg et al., 2022). The REVEALS dataset is the only 290 current land-cover reconstruction approach based on pollen data to quantify past regional cover of individual 291 plant taxa. It effectively accounts for intertaxonomic differences in pollen productivity and dispersal properties 292 as well as the size and type of sedimentary basins. It combined 1607 pollen records and benefited from earlier 293 efforts and projects (Landclim I and II) in collecting pollen dataset (Githumbi et al., 2022; Trondman et al., 294 2015) obtained from databases and individual data contributors. There are many areas of Europe where 295 environments that preserve pollen (i.e. lakes, bogs, forest hollows) are sparse, therefore the geographic 296 distribution of pollen-based reconstruction is uneven. 297

REVEALS transforms pollen assemblages in large lakes to abundance of individual plant taxa in the
 surrounding vegetation at a large spatial scale (ca. 100 km × 100 km; Hellman et al., 2008a, b) using a
 mechanistic modelling approach that uses an empirical understanding of relative pollen production between

pollen morphological types, and pollen dispersal mechanisms. It was developed for pollen records from large 301 lakes (> 50-100 ha), but extensive simulation and empirical studies showed that multiple small-sized sites can 302 be used when large lakes are not available in a region, although it generally results in larger standard errors on 303 the estimates of plant cover (Sugita, 2007; Fyfe et al., 2013; Mazier et al., 2012; Trondman et al., 2015). As 304 previous studies (Mazier et al., 2012; Trondman et al., 2015; Githumbi et al., 2022), Serge et al., (2023) used a 305 1° resolution grid and applied REVEALS on all available pollen records in each grid cell to produce an estimate 306 of plant taxa abundance per grid cell through time. The estimates obtained for 31 individual taxa were later 307 summed to produce estimates of the area occupied by plant functional types according to Table 1. Estimating 308 the proportion of bare ground using pollen reconstructions is challenging due to the inherent limitations of the 309 data. Hence, in REVEALS data, the total cover of plant taxa within a grid cell is always 100%. 310

All gridded REVEALS reconstructions for Europe follow the same protocol and criteria as published in Mazier 311 et al. (2012) and Trondman et al. (2015), and lately by Githumbi et al. (2022). Gridded REVEALS estimates are 312 influenced by the quality of individual records used (pollen count size, taxonomic resolution, and chronological 313 uncertainty), basin size, and type of sites (lakes or bogs), the number of pollen records used in each grid cell, 314 and the reliability of the relative pollen productivities (RPPs) used (Githumbi et al., 2022; Trondman et al., 315 2015; Serge et al., 2023). The precision of gridded REVEALS estimates is indicated by their standard errors. 316 Caution should be applied when using REVEALS estimates from unreliable grid cells, and when standard 317 errors of the gridded REVEALS estimates are equal or greater than REVEALS estimates (Serge et al., 2023). 318 Hence, the number of available REVEALS grid cells for analysis varies depending on the availability of reliable 319 pollen data for each TW. Across the 14 TWs studied here, the number of grid cells ranged from 456 to 363. 320 This range reflects variations in quantity and quality of the pollen data available for analysis during each time 321 window. 322

323

324 2.5. Classification of plant functional types

To reconstruct vegetation patterns and their changes throughout the Holocene we applied the concept of plant functional types (PFTs). Plants were classified into PFTs based on their physical, phylogenetic and phenological characteristics, as well as their bioclimatic and functional features. PFTs included in the CARAIB model are described in François et al. (1998). In this study, each selected plant taxon was assigned to a

specific unique PFT (Table 1) based on previously published classification used for model-data comparison in
 palaeovegetation studies (François et al., 2011; Henrot et al., 2017; Popova et al., 2013). Standard errors of

the REVEALS dataset (Serge, 2023) were calculated for each PFT according to the delta method (Stuart and
 Ord, 1994).

CARAIB PFT	Short	Plant taxa/pollen-morphological types (31 taxa)
	name	
Herbs (C3 herbs "humid",	Н	Amaranthaceae /Chenopodiaceae, Artemisia, Cerealia t.,
C3 herbs "dry", C4 herbs)		Cyperaceae, Filipendula, Plantago lanceolata, Poaceae, Rumex
		acetosa t., Secale cereale
Broadleaved evergreen	BEBTS	Calluna vulgaris, Ericaceae
boreal/temp cold shrubs		
Broadleaved evergreen	BETWS	Buxus sempervirens
temperate warm shrubs		
Needleleeved everyneen	NDTT	Abiaa Juninarua Riaga Rinua
Needleleaved evergreen		Ables, Juniperus, Picea, Pinus
boreal/temp cold trees		
Broadleaved evergreen	ВЕММТ	Phillvrea, evergreen Quercus t.
masa maditarrangan troos		
meso-mediterranean trees		
Broadleaved evergreen	BETMT	Pistacia
thermo-mediterranean		
trees		
1003		
Broadleaved summergreen	BSBTT	Alnus, Betula, Corylus avellana, Salix
boreal/temp cold trees		
Broadleaved summergreen	BSTCT	Carpinus betulus, Fagus, Fraxinus, deciduous Quercus t., Tilia,
temperate cool trees		Ulmus

Broadleaved summergreen	BSTWT	Castanea sativa, Carpinus orientalis /Ostrya t.
temperate warm trees		
temperate warm trees		

Table 1. Plant-functional types and corresponding plant taxa according to previously published classification used for model–data comparison in palaeovegetation studies (François et al., 2011; Henrot et al., 2017; Popova et al., 2013).

In CARAIB, plant growth in northern Europe is hindered by frigid climatic conditions of polar tundra, which 336 prevents vegetation from populating the grid cells. Therefore, high latitudes in CARAIB are composed of bare 337 ground with a few herbs (Supplementary Fig. 7). Pollen-based reconstructions, however, reflected presence of 338 Betula, Ericaceae, Cyperaceae, Pinus and Poaceae in those areas across all studied TWs. A recent study of 339 Sun et al. (2022) demonstrated the impact of the lack of representation of bare ground in REVEALS-based 340 estimates. Hence, to eliminate some of the potential biases related to this issue, we chose to exclude high 341 latitudes (70-71°N) from the intercomparison. With this we aimed to prevent the negative bias due to low 342 agreement between the studied datasets over these zones, dictated by their technical characteristics. 343 Furthermore, it is important for readers to exercise caution when interpreting regions with a high fraction of 344 bare ground in the CARAIB model outputs (e.g., certain parts of the Iberian Peninsula) (Supplementary Fig. 7). 345 The differences in the representation of bare ground across the studied datasets may increase the uncertainty 346 of the analysis in these areas. 347

348 2.6. Comparison between REVEALS estimates and CARAIB simulations

Comparison of the CARAIB simulations with the REVEALS estimates required a transformation of the spatial and temporal resolution of the CARAIB model output. We aggregated the PNV simulated by CARAIB to the same grid resolution as the REVEALS estimates (1°x1° grid cells) and extracted only those grid cells where the pollen data were available (ranging from 456 to 363 grid cells for the analyzed TWs). CARAIB vegetation is represented by two vertical layers that were adjusted to match a resolution of 1°, used by the REVEALS method.

Then, relationship between REVEALS and CARAIB was analysed by computing a weighted matching ratio between PFT fractions of both models, using the following formulas:

359
$$WMR = \sum_{PFT=1}^{Nb.PFT} frac_{PFT,reveals} \times MR_{PFT} ,$$

and

where Nb.PFT – maximum number of PFTs, frac PFT, reveals – fraction of a PFT in REVEALS dataset, frac PFT, caraib
 – fraction of corresponding PFT in CARAIB dataset, MRPFT – matching ratio per PFT, WMR – weighted
 matching ratio of REVEALS and CARAIB.

Similarity between CARAIB and REVEALS estimates per PFT was expressed in matching ratio (MR) values. 363 Considering that the two datasets are independent and of a different nature, the use of absolute values of MRs 364 for the intercomparison could have been challenging due to limitations and biases of the methodology. Such 365 biases remain in all TWs (assuming their stationarity), but MRs may not be constant through time. In this study 366 it is assumed that this variation occurs due to human impact, which is the factor that is not stationary in time 367 throughout our study period. Therefore, we focused on temporal changes within PFTs rather than absolute 368 differences between the datasets to minimize the impact of such biases on our results. To this end, we have 369 chosen to analyze the relative change in the MR values between each TW and the TW calculated in the most 370 recent period (TW1). 371

WMR was calculated to ensure that more weights are given to the PFTs that are more abundant within a grid cell. Under an assumption that WMR represents percentage of vegetation unaltered by anthropogenic activity, by reversing it we calculate a human pressure index (HPI):

375 $HPI = (100 - WMR) \div 100.$

Then, a mean HPI over each 1°-wide latitudinal zone was calculated for each TW.

377 Translating the discrepancies between the two studied datasets into the HPI was made under the assumption

that changes in relationship between the two datasets at the second half of the Holocene are mainly caused by

anthropogenic activity. This assumption is supported by a growing body of evidence, including

palaeoenvironmental reconstructions, that suggests a significant and widespread impact of human activities on

European land-cover during this period (Roberts et al., 2019, 2018; Ruddiman and Ellis, 2009; Nielsen et al.,

2012; Kaplan et al., 2009; Ellis et al., 2013; Strandberg et al., 2022). While megafauna presence is also not simulated by PNV models, the extinction of many megafaunal species during the late Pleistocene and the Holocene in Europe (Mann et al., 2019; Sandom et al., 2014; Stewart et al., 2021; Koch and Barnosky, 2006) decreases their potential role in large-scale changes in vegetation patterns over the second half of the Holocene. Taken together, these lines of evidence support our assumption that anthropogenic activity is the main driver of changes in the relationship between the datasets during the second half of the Holocene.

388

389 2.7. Correlation with ALCC scenarios

In order to compare our results with existing literature on anthropogenic impact on European land-cover, we 390 used two most commonly used in landscape research ALCC scenarios. KK10 and HYDE 3.2. ALCCs offer the 391 advantage over other datasets as they provide datasets that are continuous in space and time, whilst other 392 approaches (for example, demographic proxies such as archaeological dates (e.g. Shennan et al., 2013), or 393 human impact indicators from pollen data) have discontinuous coverage, and are not necessarily linearly 394 related to land cover changes (Hiscock and Attenbrow, 2016). KK10 and HYDE 3.2 differ in the way they 395 estimate and represent land-cover change. KK10 consists of data expressed in a form of a deforestation index 396 at annual resolution, which, in this study, was averaged over the years within each of the REVEALS time 397 windows (Supplementary Table 1). HYDE 3.2 estimates are presented in a form of simulated land use. In this 398 study, to represent anthropogenic land use for agricultural purposes we analysed HYDE 3.2 data on croplands 399 and grazing. HYDE 3.2 data is irregularly spaced in time over the Holocene: from 100 years temporal 400 resolution in the Late Holocene to 1000 years in the early and Mid-Holocene. We used linear interpolation to 401 obtain the data for the studied time windows. We also performed transformations of spatial resolution of both 402 ALCC scenarios by aggregating the grid cells to the 1°x1° REVEALS grid, and extracted data only for the grid 403 cells that have available data in REVEALS. 404

For comparison between HPI and KK10 and HYDE, we assumed that extracted land use from the ALCC scenarios should be roughly equivalent to human impact on land-cover. We then analysed correlation between these three datasets to investigate if they represent human-induced land-cover changes in a similar manner. Additionally, we evaluated the relationship between HPI values and HYDE 3.2 population density estimates to

- 409 understand if presence of humans spatially correlates with changes in HPI. HYDE 3.2 population density is
- 410 primarily based on demographers' estimates for the last 3000 years (McEvedy and Jones, 1978), with earlier
- 411 population sizes being estimated using back extrapolation (Goldewijk et al., 2010).
- 412
- 413
- 414

416 3. Results

417 We have analysed palaeovegetation data expressed in fractions of PFTs for 14 TWs throughout the second

418 half of the Holocene (6200 BP – AD 2015) from CARAIB simulations (representing PNV) and REVEALS

- estimates (representing pollen-based regional vegetation abundance). The definitions of TWs are summarised
- 420 in Supplementary Table 1.
- 421 The analysis of the relationship between simulated PNV and pollen-based regional estimates of vegetation
- 422 abundance is based on the evolution of discrepancies in the two datasets and expressed as relative change in
- 423 the MR values between each TW and the TW calculated in the most recent period (TW1) (Fig.1). Throughout
- 424 the studied time period, we observe decreases in MR of herbs (H), broadleaved summergreen
- 425 boreal/temperate cold trees (BSBTT) and broadleaved summergreen temperate cool trees (BSTCT). MR of
- 426 broadleaved evergreen boreal/temperate cold shrubs (BEBTS) increases, and MR of broadleaved evergreen
- 427 temperate warm shrubs follows a non-linear trend.



- 428
- Figure 1. Temporal evolution of agreement per PFT between the CARAIB simulations and the
- 430 REVEALS estimates expressed as difference in matching ratio (MR) from MR at TW1 (present 100
- 431 BP).

- Figure 1 shows that different PFTs had different levels of dissimilarities and evolved differently through time.
- Therefore, to analyse anthropogenic impact on vegetation dynamics that would account for all the changes
- 434 within PFTs we introduce a human pressure index (HPI). HPI is calculated based on matching ratios of
- individual PFTs for each grid cell, and the weight of the variables is determined by the abundance of each PFT
- 436 in the REVEALS estimates.
- 437



Figure 2. Human pressure index per grid cell in Europe from TW14 (5700 - 6200 BP) to TW1 (present - 100
BP). 1-highest human pressure; and 0-lowest human pressure value.

We observe high HPI values at 5700-6200 BP (TW14) across the Mediterranean region and eastern Europe (Fig. 2). Throughout the Holocene HPI values become progressively higher in central, western and northern Europe, with the majority of the grid cells having extremely high HPI values at modern time (TW1) across the continent. During the whole studied period high HPI is observed in northern Europe (Scandinavia), which is an artefact of intrinsic biases of two datasets compared (Section 4.4). Hence, the high latitudal zones (70-71°N) are not included in the subsequent analyses.

In Figure 3, we subdivide our study area into latitudinal zones of 1 degree, corresponding to the size of grid 447 cells used for our analysis. This division allows us to display latitudinal trends of HPI changes through the 448 second half of the Holocene in Europe. We chose to present the dynamic per latitudinal zone based on the 449 historical context of our study period in Europe, which corresponds to the transition and establishment of 450 agriculture (Stephens et al., 2019; Morrison et al., 2021; Harrison et al., 2020; Goldewijk et al., 2017a; Kaplan 451 et al., 2011; Gronenborn and Horejs, 2021). Archaeological sources (e.g. Gronenborn and Horejs, 2021; 452 Stephens et al., 2019) provide evidence that this agricultural transition followed a south-to-north trend, with 453 agriculture being established first in the Mediterranean region, and gradually expanding northward. While we 454 acknowledge that this is an oversimplified description of the complex dynamics of the processes involved, by 455 presenting the data in this manner, we visualize the general temporal trend of HPI increase, potentially largely 456 affected by the agricultural expansion. 457

Vegetation of mid-latitudes resulted to be relatively preserved at earlier times. Contrastingly, Southern latitudes (37.5 °N to 41.5 °N) have relatively high HPI throughout the studied period. 42.5 °N to 54.5 °N are the areas where the changes are the largest within the studied timeframe, demonstrating a northward direction of HPI increase in time through the second half of the Holocene.

Although there are limitations to the methodology used in our study that affect the robustness of our results in northern latitudes, we observe a clear and gradual increase in HPI over time at latitudes south of 54.5°N (Fig. 3), which covers a large part of continental Europe. This enables us to track the long-term dynamics of human activity on land-cover across both time and space for a significant portion of the continent, which is where the majority of vegetation changes have occurred.

62.5	0.71	0.61	0.62	0.64	0.71	0.71	0.73	0.71	0.72	0.75	0.73	0.73	0.76	0.85	11
61.5	0.59	0.61	0.60	0.60	0.61	0.63	0.67	0.66	0.67	0.71	0.74	0.71	0.75	0.78	14
60.5	0.69	0.72	0.70	0.68	0.69	0.70	0.65	0.66	0.71	0.74	0.77	0.83	0.83	0.82	17
59.5	0.53	0.53	0.52	0.58	0.58	0.60	0.61	0.64	0.63	0.69	0.70	0.74	0.77	0.77	11
58.5	0.55	0.59	0.56	0.58	0.58	0.60	0.56	0.58	0.57	0.61	0.68	0.71	0.72	0.77	18
57.5	0.61	0.57	0.58	0.62	0.64	0.62	0.62	0.67	0.65	0.67	0.72	0.74	0.75	0.75	20
56.5	0.57	0.54	0.56	0.61	0.65	0.63	0.66	0.64	0.71	0.74	0.79	0.80	0.81	0.82	22
55.5	0.69	0.72	0.74	0.73	0.74	0.69	0.73	0.68	0.73	0.69	0.71	0.79	0.81	0.85	20
54.5	0.57	0.60	0.56	0.57	0.58	0.56	0.59	0.60	0.63	0.63	0.67	0.68	0.78	0.82	26
53.5	0.56	0.56	0.57	0.61	0.62	0.66	0.66	0.70	0.72	0.70	0.75	0.82	0.86	0.92	26
52.5	0.60	0.61	0.66	0.66	0.67	0.68	0.72	0.68	0.68	0.70	0.81	0.83	0.90	0.89	22 4
51.5	0.71	0.70	0.71	0.75	0.73	0.73	0.76	0.74	0.77	0.82	0.81	0.80	0.93	0.91	16 9
50.5 ہے	0.65	0.65	0.66	0.68	0.79	0.78	0.80	0.83	0.83	0.85	0.86	0.89	0.92	0.92	19 ဋ
49.5	0.75	0.73	0.78	0.77	0.83	0.81	0.86	0.89	0.88	0.87	0.89	0.90	0.90	0.92	22 a
48.5	0.78	0.81	0.83	0.83	0.80	0.79	0.79	0.82	0.84	0.80	0.84	0.89	0.90	0.89	18 8
47.5	0.68	0.72	0.72	0.73	0.73	0.75	0.77	0.80	0.82	0.83	0.85	0.84	0.87	0.90	23 5
46.5	0.76	0.75	0.77	0.81	0.78	0.77	0.78	0.79	0.77	0.76	0.78	0.78	0.80	0.80	19
45.5	0.70	0.71	0.70	0.71	0.73	0.75	0.79	0.79	0.79	0.75	0.83	0.80	0.86	0.83	16
44.5	0.79	0.81	0.81	0.81	0.83	0.84	0.83	0.86	0.84	0.85	0.86	0.87	0.94	0.90	10
43.5	0.78	0.78	0.76	0.75	0.75	0.73	0.76	0.71	0.74	0.76	0.79	0.82	0.89	0.90	22
42.5	0.78	0.79	0.80	0.81	0.80	0.82	0.83	0.83	0.84	0.84	0.85	0.88	0.91	0.88	22
41.5	0.87	0.86	0.87	0.88	0.85	0.86	0.88	0.87	0.85	0.88	0.85	0.85	0.86	0.86	19
40.5	0.92	0.89	0.88	0.87	0.87	0.84	0.80	0.82	0.85	0.85	0.88	0.88	0.92	0.95	19
39.5	0.89	0.86	0.88	0.90	0.93	0.92	0.93	0.93	0.95	0.94	0.94	0.93	0.95	0.95	11
38.5	0.95	0.93	0.93	0.94	0.94	0.94	0.94	0.94	0.92	0.91	0.96	0.95	0.96	0.96	11
37.5	0.94	0.92	0.93	0.91	0.92	0.92	0.93	0.95	0.92	0.92	0.97	0.97	0.95	0.95	17
	TW14	TW13	TW12	TW11	TW10	TW9	TW8	TW7	TW6	TW5	TW4	TW3	TW2	TW1	
	5700-	5200-	4700-	4200-	3700-	3200-	2700-	1700-	1700-	1200-	700-	350-	100-	AD 2015-	
	6200 BP	5700 BP	5200 BP	4700 BP	4200 BP	3700 BP	3200 BP	2200 BP	2200 BP	1700 BP	1200 BP	700 BP	350 BP	1850	
							tir	me							

Figure 3. Human pressure index (HPI) over latitudinal zones in Europe from TW14 (5700 - 6200 BP) to

469 TW1 (present - 100 BP). 1-highest human pressure; and 0-lowest human pressure value. Zones with

470 less than 10 grid cells are not shown.

471 To determine statistical significance of our results, and their evolution in comparison to present day, we

472 calculate the percentage of grid cells with HPI values significantly different from the modern time TW1 at the

473 0.05 level (paired Student's t-tests). Figure 4 illustrates that the percentage of grid cells with values that

474 indicate significantly lower human pressure compared to modern values (N-S) decreases as we move from

early time to modern time, indicating that roughly 60% of grid cells had significantly lower HPI (are significantly

less impacted by human activity) at 5700-6200 BP, compared to modern values.



478	Figure 4. Percentage of grid cells with indicated difference in HPI between the TW1 (AD 2015-1850)
479	and each consequent TW. P: positive slope (the most recent time window has lower human pressure
480	index); N: negative slope (the most recent time window has higher human pressure index); S:
481	significant; NS: non-significant at the 0.05 level (paired Student's t-tests). For example, for the
482	difference between TW14 and TW1, the dark brown part of the bar shows that 60% had a statistically
483	significant negative slope, indicating that TW1 had a significantly higher HPI value than TW14. For the
484	maps of the differences in HPI please refer to the Supplementary Fig. 1, 2.
485	Overall, across Europe our results indicate a gradual increase of HPI throughout the second half of the
486	Holocene (Fig.5), which escalated after TW5 (1200-1700 BP). Moreover, at the beginning of our simulation
487	(TW14) we observe an average HPI of 0.72, which suggests that vegetation cover in Europe at 5700-6200 BP
488	corresponded to modelled potential natural state of vegetation only for nearly 30%.



490 Figure 5. Human pressure index (HPI) in Europe from TW14 (5700 - 6200 BP) to TW1 (present - 100
491 BP).

Re-analysis of the KK10 and HYDE 3.2 estimates at REVEALS spatio-temporal resolution reveals that HYDE
3.2 cropland and grazing area increase (Fig.6, left), and KK10 deforestation for agriculture rise (Fig.6, right)
follow similar patterns to HPI increase (Figure 5). However, the initial HPI values at TW14 are significantly
higher than anthropogenic land use change compared to the rates of spread of agricultural practices
(Supplementary Fig. 3,4).



498 Figure 6. HYDE 3.2 simulated land use, expressed as fraction of croplands and grazing per grid cell 499 (left panel), and KK10 simulated land use, expressed as deforestation index (right panel).

To further investigate the relationship between HPI and agriculture, we analyse the onset of agriculture in 500 REVEALS vegetation reconstructions, marked by first appearance of Cerealia t. and Secale cereale pollen in 501 the dataset. We assume that the agricultural onset is represented as a year of the earliest (within the time 502 bounds of our study) appearance of the aforementioned agricultural taxa in REVEALS at each grid cell 503 (Supplementary Fig. 6). However, the identification of the onset of agriculture based on agricultural PFT in 504 505 REVEALS is constrained by the limitations of this approach, described by Trondman et al. (2015). We, therefore, do not identify patterns similar to the onset of agriculture in Europe described by the existing 506 anthropogenic land-cover change (ALCC) scenarios. 507

Additionally, we explore the correlation between HPI and ALCC simulated agricultural practices. Although we observe a weak correlation between the two variables (Supplementary Fig. 3-4), the HPI index at 5700-6200 BP is significantly correlated with HYDE 3.2 population density estimates (Fig.7), thus reflecting human presence in landscapes.



512

513 Figure 7. Correlation between human pressure index (HPI) versus HYDE 3.2 population density 514 estimates over latitudinal zones in Europe for TW14 (5700-6200 BP).

515

517 4. Discussion

Analysing land-cover change in Europe using REVEALS estimates and independent climatic and land use 518 data, Marguer et al. (2017) suggested that climate is a major driver of vegetation change during the Holocene 519 as a whole and at the sub-continental scale, stating that the land use impact increase gradually after 7000 BP 520 while identifying four critical phases of land use effects on vegetation. Our methodology compared REVEALS 521 estimates with simulated climate-only-driven potential natural vegetation (PNV) over the studied period to 522 discount from the analysis changes in vegetation that were predominantly caused by changing climate. 523 Previous studies suggest that climate change and anthropogenic activity are assumed to be the main driving 524 factors of land-cover change in Europe over the second half of the Holocene (Marguer et al., 2017; Strandberg 525 et al., 2022; O'Dwyer et al., 2021; Kuosmanen et al., 2018; Poska et al., 2022; Roberts et al., 2019, 2018). 526 527 Thus, the difference between the two types of vegetation was introduced as a human pressure index (HPI). This index represents how different reconstructed vegetation is from a natural state, and thus includes both 528 direct (*i.e.* deforestation and plant cultivation) and indirect (through biogeochemical feedbacks) anthropogenic 529 changes in vegetation composition. These changes reflect continuous and prolonged human impact on 530 European land-cover through various practices, which accumulated their consequence over time, building up a 531 cumulative human pressure. 532

533 4.1. Fire regime

In this study, CARAIB simulations did not include the fire module, and thus, the potential impact of wildfires 534 could contribute to dissimilarities between PNV and vegetation reconstructions. The studied period in Europe is 535 covering a transition from hunter-gatherer to agricultural societies (Stephens et al., 2019; Gronenborn and 536 Horeis, 2021). Human induced biomass burning was previously linked to both agricultural (*i.e.* slash-and-burn) 537 (Vannière et al., 2016) and non-agricultural practices (*i.e.* initiating selectively support food growth, tool in 538 social interactions, or keeping away predators) (Scherjon et al., 2015). Thus, fires throughout the studied 539 period were expected to have predominantly anthropogenic origin, which reflects human pressure on land-540 cover, and thus contributes to increase in HPI. Previously, sedimentary charcoal composites analysis revealed 541 that humans have significantly influenced fire activity throughout the Holocene in Europe (Dietze et al., 2018; 542 Connor et al., 2019; Vannière et al., 2016; Carracedo et al., 2018), and outlined that human impact on fire 543 regime could be both direct (via its use as a land management tool) and indirect (via affecting biogeochemical 544

545 cycles and increase landscape flammability) (Dietze et al., 2018; Connor et al., 2019). Thus, the wildfire regime 546 of the studied period was also altered by human activities, which brings additional challenges to making a clear 547 distinction between "natural" and "anthropogenic" fires (e.g. Vanniere et al., 2015; Power et al., 2008). Due to 548 not having available methods to separate natural from human-induced fires, and assuming minor role of 549 natural fires in the analysis compared to anthropogenic impact on land-cover change, wildfires were not 550 explicitly included in our analysis.

4.2. Insight from REVEALS dataset analysis - comparison with previous studies

Previously, land-cover naturalness and anthropogenic impact on vegetation were assessed through analysing 552 changes in forested areas (Strona et al., 2016; Kaplan et al., 2017; Pirzamanbein and Lindström, 2022; 553 Woodbridge et al., 2018) and via cultural indicator-types in pollen sequences (Deza-Araujo et al., 2022, 2020; 554 Behre, 1981; Mercuri et al., 2013; Gaillard, 2013; Mazier et al., 2006, 2009). Apart from known cultivars, many 555 cultural indicator pollen types are components of natural vegetation, characteristic of open conditions, natural 556 grazing dynamics or disturbed soils, particularly in southern Europe (Fyfe et al., 2019; Roberts et al., 2019) and 557 thus require careful interpretation. Within the framework of the LANDCLIM project (Gaillard et al., 2010) 558 anthropogenic land-cover changes were commonly expressed as vegetation openness indicated in the 559 REVEALS model results (Trondman et al., 2015). 560

Recently, REVEALS estimates were compared with DVM-simulated vegetation with a goal of assessing land-561 cover change in Europe and analysing underlying processes behind the observed changes (Dallmever et al., 562 2023). Similar to our study, Dallmeyer et al. (2023) attributed varying discrepancy over time between the two 563 datasets to human activity. Here we applied a more complex approach that takes into account vegetation 564 composition in the form of fractions of plant functional types (PFTs) and their evolution through time, and used 565 more spatially explicit REVEALS estimates. We identified that in addition to vegetation openness (expressed 566 as fraction of herbaceous cover), anthropogenic changes affected distribution of other PFTs, such as 567 broadleaved summergreen boreal/temperate cold trees (BSBTT), broadleaved summergreen temperate cool 568 trees (BSTCT), broadleaved evergreen boreal/temperate cold shrubs (BEBTS), and broadleaved evergreen 569 temperate warm shrubs (BETWS) (Fig.1). Lechterbeck et al. (2014) also found that early agriculture resulted in 570 compositional changes in forests in southern Germany, rather than increased openness. 571

Analysing the REVEALS dataset. Marguer et al. (2017) indicated a decrease of broadleaved forest and an 572 expansion of coniferous woodland during the Mid-Holocene. Our findings support the hypothesis about the 573 anthropogenic nature of changes in broadleaved summergreen PFTs (BSBTT and BSTCT) (Fig. 1). However, 574 contrastingly to Marguer et al. (2017), we observed no significant variation in MR of needleleaved evergreen 575 plant group (NBTT), which suggests that the coniferous woodland expansion reported by Marguer et al. (2017) 576 is likely driven by climatic factors. In addition to changes in vegetation openness and herbs (such as 577 Filipendula, Artemisia, Plantago and Rumex acetosa t.) (Gaillard, 2007), anthropogenic activity in REVEALS 578 estimates were previously attributed to changes in agricultural taxa (Cerealia t. and Secale cereale) (Trondman 579 et al., 2015). Our results supported the hypothesis about anthropogenic nature of changes in openness. 580 represented by the fraction of herbs. However, we observed the absence of statistically significant difference in 581 582 HPI values between grid cells with and without the presence of agricultural taxa in REVEALS (Supplementary Fig. 5). The observed results may be attributed to the representation of agricultural land in REVEALS 583 reconstructions. For example, the classification does not include other cultivated plants, such as Fagopyrum 584 (buckwheat), Linum usitatissimum (common flax) and Juglans regia (walnut) (Trondman et al., 2015). This 585 suggests that the HPI reflects human pressure on vegetation in a more broad sense than just Cerealia t. and 586 Secale cereale crop cultivation. 587

588 4.3. Consistency of our findings with ALCC scenarios

Contrastingly, the evolution of HPI patterns through the studied period generally coincide in time and location 589 with previously simulated by ALCC human induced vegetation changes. Anthropogenic impact on land-cover 590 was previously reported to shift north throughout the second half of the Holocene (Goldewijk et al., 2017; 591 Kaplan and Krumhardt. 2011: Stephens et al., 2019), which is reflected in HPI values, which rise following 592 similar trajectory (Fig. 3). Moreover, at 6000 BP our results present a general agreement in patterns of HPI 593 with the KK10 ALCC scenario (Kaplan and Krumhardt, 2011). Both indicate anthropogenic land-cover 594 modifications across Mediterranean Europe and partial modifications in central and northern Europe (Figure 2. 595 Supplementary Fig. 1). The areas of high human pressure index coincide with the spread of agriculture. 596 indicated in the HYDE 3.2 ALCC (Goldewijk et al., 2017a). However, HPI indicated higher anthropogenic land-597 cover change at 6000 BP than KK10 and HYDE 3.2 in eastern Europe, which is not reflected in either of the 598 two ALCC. It should be noted that both ALCC scenarios are derived from GIS models that are primarily based 599

on population estimates and geographic information (Marguer et al., 2017; Kaplan et al., 2009; Goldewijk et al., 600 2017a). Therefore, they are constrained by various methodology limitations and do not always agree with 601 archaeological records. For example, findings of KK10 and HYDE 3.2 scenarios for eastern Europe differ from 602 conclusions of the ArchaeoGLOBE project, an empirical global assessment initiative of land use based on 603 archaeological knowledge (Stephens et al., 2019). ArchaeoGLOBE results suggested that the onset of 604 intensive (in the case of HYDE 3.2) and widespread agriculture (in the case of both KK10 and HYDE 3.2) in the 605 region was significantly underestimated (for up to 7500 years) in both ALCC scenarios. According to 606 ArchaeoGLOBE estimates, common levels of intensive agriculture onset in the region were present at 6000 BP 607 (Stephens et al., 2019), which supported our results, indicating relatively high HPI values over the region in the 608 Mid-Holocene (Fig. 2). 609

In our findings, we observed nearly 60% of grid cells to have a significant increase in HPI values at TW1 (AD 610 1850 – 2005), compared to TW14 (5700-6200 BP) (Fig. 4). Since this period is characterised by the onset and 611 spread of agriculture over the study region (Stephens et al., 2019; Kaplan and Krumhardt, 2011; Goldewijk et 612 al., 2017a), we assumed this value to be largely attributed to agricultural activity. Reported increase in HPI 613 agrees with the ALCC estimates and FAO land use statistics (FAO, 2022), which reports that 52.3% of the 614 area of European Union was 1961 classified as agricultural. Similarly, the ALCC scenarios suggest that for the 615 study area at TW1 (modern time) nearly 56% of land-cover was transformed by anthropogenic activity 616 accordingly to KK10, and HYDE 3.2 estimates suggested nearly 45% of land-cover to be impacted by 617 agriculture (18% grazing and 27% cropland) (Fig.6). ALCC estimates agree with the FAO land use statistics 618 (FAO, 2022), since they are partially based on FAO statistics (in case of HYDE 3.2). In this study we analysed 619 data for continental Europe, contrastingly to FAO land use statistics, which is constrained by the EU borders. 620 Additionally, the REVEALS dataset is not spatially continuous. Thus, the values in Figure 6 are not directly 621 comparable to FAO statistics. However, the ALCC land use indices at TW1 have similar levels of magnitude to 622 extent of agricultural land reported by FAO, confirming that both KK10 and HYDE 3.2 mainly represent land-623 cover change for agricultural purposes, and indicating that the HPI detected land-cover change for agricultural 624 purposes in a similar manner to analysed ALCC scenarios. 625

626 We note that agriculture appeared in Europe as early as ca. 8000 – 9000 BP (Stephens et al., 2019;

Gronenborn and Horejs, 2021), and by the earliest TW covered in this study (5700-6200 BP), it had become

widespread in some European regions (Stephens et al., 2019). Consequently, high HPI values at that period 628 are to a degree attributed to early agricultural practices, particularly in the Mediterranean region and Southern 629 Europe (Fig. 2.3). However, HPI shows a significantly larger anthropogenic land-cover change at TW14 (5700-630 6200 BP) than the two considered ALCCs (Fig. 5.6 Supplementary Fig. 3.4). Considering the fact that land-631 cover changes in KK10 and HYDE 3.2 reflect the establishment of the first agricultural societies (Goldewijk et 632 al., 2017b; Kaplan et al., 2009), and show 17% and 0% of agriculture-driven landscape changes at TW14 633 correspondingly (Fig. 6), we suggest that high HPI values at TW14 (Fig. 3.5) are partially attributed to pre-634 agricultural anthropogenic land-cover modifications that accumulated throughout the history of human-635 environment interactions in Europe and led to high levels of vegetation divergence from potential natural state. 636 These findings emphasize the importance of accounting for early anthropogenic landscape impact, reported in 637 previous studies (Archibald et al., 2012; Bos and Urz, 2003; Doughty, 2013; McWethy et al., 2010; Pinter et al., 638 2011; Roberts et al., 2021; Ellis et al., 2021; Nikulina et al., 2022). 639

640 4.4. Methodological limitations

It should be noted that the overestimation in HPI could be partially attributed to methodology limitations. Such 641 limitations were caused by data availability in the REVEALS dataset, as well as by unequal reliability of the 642 REVEALS grid cells (Serge et al., 2023). The intercomparison between reconstructed and modelled vegetation 643 was also previously reported to be challenging (Dallmever et al., 2023). In addition, to correct biases of the 644 used climate model we used the CDF-t approach (Vrac, 2018; Zapolska et al., 2023), but no bias correction 645 was performed for the vegetation model (CARAIB). For the intercomparison PNV data was resampled and 646 reclassified to be compatible with the REVEALS dataset, which in turn led to simplifications and resampling 647 biases. For example, as in this work we assigned each taxon to a unique PFT category, the taxon Ericaceae 648 was only included in broadleaved evergreen boreal/temperate cold shrubs (BEBTS) PFT (Table 1). However 649 the Ericaceae family includes species that live both in the north and at high elevations (herbs and low shrubs, 650 i.e. Vaccinium, Arctostaphylos uva-ursi), and in the South (trees, i.e. Arbutus unedo, Erica arborea) (Serge et 651 al., 2023). 652

We hypothesise that the descending temporal trend and high HPI values in northern latitudes were mainly caused by the aforementioned methodology biases, such as PFT classification limitations and differences in representation of bare ground in studied datasets. Moreover, the trees at high latitudes might be confined in small topographic depressions that induce a local micro-climate that we cannot reproduce at our spatial scale.
However, the rising HPI values through the studied period in most of continental Europe (south of 54.5°N) were
mainly associated with human activity, which was previously reported to shift north throughout the second half
of the Holocene (Goldewijk et al., 2017a; Kaplan and Krumhardt, 2011; Stephens et al., 2019).

660 4.5. Quantifying uncertainties

It should be noted that the absolute HPI values (Fig. 2, 3, 5) should be treated with caution, as they are 661 affected by various methodology biases discussed in this study. To our knowledge, there is no approach to 662 quantify given uncertainties. However, the study of Zapolska et. al (2023) estimated methodological 663 uncertainties of the used approach by comparing PNV simulations from bias-corrected CARAIB and 664 statistically modelled PNV distribution of Levavasseur et al., (2012), based on BIOME6000 pollen 665 reconstructions. Their findings indicate that methodological biases can constitute up to nearly 50% when 666 analysing matching ratios between PNV datasets of a different origin, which would place a lower boundary on 667 the HPI absolute value at 6000 BP (Fig.5) at about 30%, but likely more if median taken. To eliminate the 668 impact of these biases on our conclusions, we emphasise the importance of changes from one TW to another, 669 rather than absolute differences between the datasets, as the impact of methodology biases remains constant 670 in all TWs (assuming their stationarity). Hence, our conclusions are largely based on the analysis of temporal 671 changes in HPI values and trends that appear in these changes. 672

To verify our findings, further studies aimed at evaluation of human pressure on land-cover could compare the results using several vegetation models (*i.e.* Dallmeyer et al., 2023), undertake a detailed intercomparison with established and emerging pollen-indicator type approaches (e.g. Deza-Aruajo et al., 2022), draw on more extensive compilations of pollen records, as well as investigate potential impact of bare ground in pollen-based reconstructions (e.g. through the application of the Modern Analogue Technique demonstrated by Sun et al., 2022). In addition, incorporating ALCC estimates in the workflow and introducing plant consumption by megafauna would allow further analysis of underlying processes behind detected land-cover changes.

680

681 4.6. More than agriculture – pre-agricultural practices and land-cover naturalness

Despite the limitations of our study, the significant relationship between the HPI and HYDE 3.2 population 682 density (Fig.7) supported the suggestion that relatively high HPI values in the Mid-Holocene were mainly 683 attributed to human vegetation cover modifications by the means of early agricultural and non-agricultural 684 practices during the periods preceding TW14 (5700-6200 BP). It should be noted that HYDE 3.2 population 685 estimates are highly debated in the land use community due to their uncertainties related to strong 686 dependency on a few historical population sources, such as McEvedy and Jones (1978), Maddison (2001) and 687 Livi-Bacci (2007) (uncertainty ranges reported by Goldewijk et al., 2017b). However, our conclusion on partially 688 non-agricultural nature of high HPI values at Mid-Holocene is also supported by the widespread evidence of 689 hunter-gatherer land use, which indicates that land-cover were largely transformed by humans prior to 690 agricultural onset (Bos and Urz, 2003; Finsinger et al., 2006; Nikulina et al., 2022; Roebroeks et al., 2021; 691 Scherjon et al., 2015). Moreover, findings of Ellis et al. (2021), based on the analysis of spatially explicit global 692 reconstruction of historical human populations and land use, show that nearly three guarters of Earth's land 693 was already inhabited by hunter-gatherer and/or early agricultural societies at the beginning of the current 694 interglacial interval, transforming wildlands into cultured anthromes. Their conclusions are in line with our 695 findings that indicate around 70% difference between reconstructed and potential natural state of land-cover at 696 5700-6200 BP (Fig. 5, TW14). Contrastingly, KK10 land use indicates 17% of land-cover change over the 697 same study area at 5700-6200 BP (Fig. 6, right panel, TW14), which is rather an indicator for adoption of 698 agriculture, than land-cover "naturalness". Notably, high HPI values at TW14 are concentrated in the 699 Mediterranean region (see Fig. 2). In support of our findings, a synthesis of existing sedimentary charcoal 700 records (Marlon et al., 2013) reports significant fire activity during the early Holocene in the Mediterranean 701 region. While the study of Marlon et al. (2013) acknowledges that it is difficult to analyse complex fire-702 vegetation-climate dynamics over the Mediterranean region, they suggest strong dependence of the European 703 704 early Holocene fire history on climate rather than human activity. However, HPI increase across the continent throughout our study period aligns with fire intensity patterns in northeastern and central Europe reported by 705 Marlon et al. (2013), which during this time they hypothesise to be driven primarily by human activity. Hence, 706 707 alongside the use of the climate-driven baseline in our study, high charcoal index, KK10 index and long history of archaeological evidence of human presence across the Mediterranean region support our findings that 708 suggest high human pressure on vegetation "naturalness" of the region and call for a more extensive analysis 709

of HPI against charcoal records. Thus, our findings do not support the hypothesis of a relatively natural land-710 cover in the Mid-Holocene in Europe, and suggest high levels of anthropogenic modifications to vegetation 711 composition due to cumulative effect of changes introduced by early agricultural and non-agricultural activities. 712 The HPI values indicate that at TW1 (present -100 BP) nearly 87% of the studied land-cover differed from the 713 potential natural state, which accounts for changes due to agricultural activity as well as impact of non-714 agricultural activities, accumulated throughout the long history of human-environment interaction. These values 715 are comparable with previously published estimates, indicating that from 75 to 95% of the global area is 716 somewhat transformed by human societies (Ellis et al., 2010, 2021; Williams et al., 2015). It is, however, 717 challenging to estimate the full extent of anthropogenic impact on land-cover from the existing literature, as 718 lands that are described as "natural" often exhibit long histories of use, including protected areas, managed 719 forest and cultural landscapes (Ellis et al., 2021). Using a quantitative approach, our results validated high 720 levels of cumulative anthropogenic change of vegetation cover at 6000 BP (nearly 72%) and in the modern 721 period (nearly 87%) and emphasized that while agriculture was an important driver of land-cover change in the 722 Holocene, other human practices also significantly contributed to divergence of land-cover from its natural 723 state. Similar conclusions were reported by Strona et al. (2016), who compared forest structure data with PNV 724 simulations, and indicated that at present day European forests are far from a natural condition, showing only 725 moderate signals of the ecological spatial structure typical of undisturbed vegetation (mostly at higher 726 latitudes). It should be noted that while HPI values reflect time-cumulative anthropogenic impact on 727 landscapes, they do not represent exclusively unstable or disturbed ecosystems. If, after an anthropogenic 728 disturbance, an area recovered into a stable and mature ecosystem which is different to the existing pre-729 disturbance ecosystem, it is still considered to have been altered by human activity through our analysis. 730 Hence, our findings are not directly comparable with a concept of disturbed ecosystems used in ecology. since 731 this study quantifies magnitude by which humans shifted vegetation off its natural climate-driven course 732 regardless of the end-state of the resulting ecosystem. Our findings, however, contribute to the debate on the 733 start of Anthropocene (Lewis and Maslin, 2015; Ruddiman et al., 2016; Ruddiman, 2013, 2018; Smith and 734 Zeder, 2013; Waters et al., 2016; Zalasiewicz et al., 2021), highlighting the importance of acknowledging the 735 long history of anthropogenic land-cover modifications. 736

737 Conclusions

In this study we examined the relationship between simulated potential vegetation (PNV) and pollen-based 738 regional estimates of vegetation abundance (REVEALS) to guantify human pressure on land-cover over the 739 second half of the Holocene (6200 BP – AD 2015). With this method we observed a northward increase of 740 anthropogenic pressure in time, expressed in a form of a human pressure index (HPI) in the largest part of 741 continental Europe (41 to 54°N) throughout the second half of the Holocene. The time and location of this 742 increase coincide in trajectory and evolution with well-known anthropogenic land-cover change (ALCC) 743 scenarios, KK10 and HYDE 3.2, as well as with findings of the ArchaeoGLOBE initiative. Similar to KK10 and 744 Archaeoglobe, in the Mid-Holocene HPI values suggest anthropogenic land-cover modifications across 745 Mediterranean Europe, and partial modifications in central and northern Europe. From there, HPI extends 746 towards the north, with increasing intensity around 1200-1700 BP, following patterns similar to the ALCC 747 scenarios. Our study found that almost 60% of grid cells exhibited a significant increase in HPI values during 748 the modern time (TW1), compared to 5700-6200 BP (TW14). These findings align with estimates of ALCC: 749 nearly 56% of the study area's land-cover was transformed by human activities during the modern era (TW1) 750 based on KK10 estimates, while HYDE 3.2 estimates suggest that agriculture impacted nearly 45% of the land-751 cover, with grazing accounting for 18% and cropland accounting for 27%. However, our inferred human impact 752 on vegetation (as indicated by HPI values) was greater than suggested by the KK10 deforestation index, and 753 HYDE 3.2 cropland and grazing estimates. We observed high initial values of HPI at 5700-6200 BP, indicating 754 up to 70% of the vegetation composition was affected by humans, as well as the absence of correlation 755 756 between presence of agricultural taxa in REVEALS. These findings suggest that our approach demonstrates human impact on land-cover in a broader aspect than agriculture. Significant correlation of HPI with HYDE 3.2 757 population density (r = 0.75, p-value < 0.005) indicates that the HPI is strongly associated with human activity. 758 759 Our findings suggest that up to 70% of vegetation composition in Europe may have been affected by both early agricultural and pre-agricultural human practices prior to the Mid-Holocene. In the context of the debate about 760 the chronology of the Anthropocene, this study suggests that anthropogenic land-cover change transcends the 761 762 boundaries of agriculture. It highlights the significance of cumulative effect of pre-agricultural practices on the state of land-cover in the Mid-Holocene, and calls for a more comprehensive exploration of the complex 763 interactions between humans and the environment during that era. 764

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TW	Age range cal BP	TW length(years)
1	AD 2015-1850	165
2	100-350 BP	250
3	350-700 BP	350
4	700-1200 BP	500
5	1200-1700 BP	500
6	1700-2200 BP	500
7	2200-2700 BP	500
8	2700-3200 BP	500
9	3200-3700 BP	500
10	3700-4200 BP	500
11	4200-4700 BP	500
12	4700-5200 BP	500
13	5200-5700 BP	500
14	5700-6200 BP	500

Supplementary table 1. Definition of time windows used in this study.



Supplementary figure 1. Difference in WMR between the TW1 (present -100 BP) and each consequent TW. P:
positive slope (more recent time window has lower WMR/ higher human pressure index); N: negative slope

- 317 (more recent time window has higher WMR/lower human pressure index); S: significant; NS: non-significant.



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Supplementary figure 2. Difference in WMR between the two neighbouring TWs. P: positive slope (more recent
time window has lower WMR/ higher human pressure index); N: negative slope (more recent time window has
higher WMR/lower human pressure index); S: significant; NS: non-significant.



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Supplementary Figure 3. Comparison of human pressure index (HPI) versus HYDE 3.2 simulated cropland estimates (left panel) and HYDE 3.2 simulated grazing (right panel), expressed as fraction of croplands and grazing over latitudinal zones in Europe for TW14 (5700-6200 BP).



- 330 Supplementary Figure 4. Comparison of human pressure index (HPI) versus KK10 simulated land use,
- expressed as fraction of croplands and grazing over latitudinal zones in Europe for TW14 (5700-6200 BP).



- Supplementary Figure 5. Human pressure index (HPI) values of grid cells with (blue) and without (orange) the presence of agricultural taxa in REVEALS estimates, represented by Cerealia t. and *Secale cereale* pollen at TW14 (5700-6200 BP).
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340 Supplementary Figure 6. Agricultural onset in REVEALS vegetation reconstructions, marked by first 341 appearance of Cerealia t. and *Secale cereale* pollen in the dataset.



Supplementary Figure 7. Fraction of bare ground simulated by CARAIB at TW14 (5700-6200 BP). Due to the similarities observed among all studied TWs, the plotting of other TWs was omitted. The presented pattern of bare ground distribution can be considered representative for all TWs included in the current study.



Supplementary Figure 8. Fraction of each of the analysed plant functional types at the starting point of our analysis (TW14; 5700-6200 BP), modelled by CARAIB vegetation model. The data for all TWs is provided as a supplementary dataset to this article.