Forest or tundra? How different vegetation reconstructions of Last Glacial landscapes in Europe may shape our perception of early human dispersal processes

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Abstract

Regional variability and long-term changes of past ecosystems likely had a strong impact on hunter-gatherer population dynamics, including the expansion of anatomically modern humans and the disappearance of Neanderthals. However, our understanding of these ecosystems remains limited, even when looking at large-scale patterns, such as the extent and distribution of forested areas. Vegetation reconstructions are key to better understand ecological preferences and their influence on the spatial distribution and dispersals of early humans. Here, we compare four different vegetation reconstruction techniques, two based on pollen data and two vegetation models, between 70–20 thousand years before present in Europe. Absolute values in forest cover can differ by up to 40% between reconstruction techniques, highlighting that the choice of method can make the difference between a boreal forest and a tundra. Besides method-specific and statistical uncertainties, the reason for such a substantial offset lies in the loose definition of forest cover metrics, rendering a direct comparison between methods impossible. At the same time, we show that all reconstruction techniques accurately reconstruct ecosystem dynamics over time on continental to regional scales. We therefore highly recommend researchers to use relative forest cover measures as the more robust method to estimate past landscapes.

1. Introduction

Environmental dynamics are often said to be one of the key aspects in understanding the timing, course, and incentives of the expansion of early modern humans out of Africa and of their dispersal across the world (Maier et al., 2023; Saltré et al., 2024; Timmermann et al., 2022). Yet our comprehension of environmental dynamics during crucial periods of human dispersal remains limited. In particular, it is unclear what role forest cover played during major dispersal events and how different levels of forest cover figured in ecological preference of early hunter-gatherers (Harvati et al., 2019; Hershkovitz et al., 2018). There is growing evidence for an early dispersal of anatomically modern humans into Europe between 55 and 43 ka before present (BP), extending as far west as southern France (Slimak et al., 2022). These presumably very small and rather isolated populations (Mylopotamitaki et al., 2024; Pederzani et al., 2024; Prüfer et al., 2021; Sümer et al., 2025) were contemporaneous to late Neanderthals, who apparently also lived in rather isolated communities (Slimak et al., 2024) and highly structured populations (Rogers, 2024), but disappeared around 43 ka BP from Europe (Posth et al., 2023).

To date, there is very little evidence on how the environments that Neanderthals and Palaeolithic hunter-gatherer populations faced may have actually looked like (Fletcher et al., 2010; Tzedakis et al., 2013). Importantly, to assess the possible influence of forestation on habitat fragmentation, the geographic structure of populations, and demographic developments of both Neanderthal and anatomically modern hunter-gatherers, reliable vegetation reconstructions are prerequisite (Maier et al., 2021; Riede and Pedersen, 2018; Schmidt et al., 2021; Staubwasser et al., 2018; Timmermann, 2020; Vidal-Cordasco et al., 2023). Such quantitative reconstructions of e.g., forest cover have played a key role in combining archaeological and palaeoenvironmental data on regional scales (e.g., Alenius et al., 2021; Mehl and Hjelle, 2016) and are an important aspect of modern conservation and adaptation strategies (Alkama and Cescatti, 2016; De Lombaerde et al., 2022; Vancutsem et al., 2021). However, previous studies on continental to global scales have either focused on the LGM itself (e.g., Davis et al., 2024; Kaplan et al., 2016) or the period succeeding it (e.g., Li et al., 2025), while palaeoenvironments from the pre-LGM period remain poorly understood.

To reconstruct palaeoenvironments, researchers rely on two fundamentally different approaches: Reconstructions based on proxy data and vegetation models. Fossil pollen grains from lake sediments or peat deposits are one of the most common and widespread form of environmental proxy from terrestrial archives. Several different methods, e.g., Biomisation (Prentice et al., 1996), REVEALS (Regional Estimates of Vegetation Abundance from Large Sites; Sugita, 2007), the modern analogue technique (MAT; Zanon et al., 2018), pollen-based temperature reconstructions (Bartlein et al., 2011) transform raw pollen data into reconstructions of environmental and/or climatic conditions. However, predating the Holocene period, suitable pollen archives are scarce and heterogeneously scattered, hampering regional analyses significantly.

In contrast, vegetation models offer a continuous reconstruction of palaeoenvironments on global to regional scales (e.g., Beyer et al., 2020; Li et al., 2025) as they operate independently of proxy data and instead use climate variables, such as temperature and precipitation obtained from palaeoclimate simulations. Vegetation models can be implemented in Earth System Models (ESMs), where they are dynamically interacting with the climatic conditions. These so-called dynamic vegetation models (DVMs) are designed to reflect the broad shifts in vegetation patterns and the consequential feedback on the climate system (Dallmeyer et al., 2023). Vegetation models can also operate as static models using the output of palaeoclimate simulations. These models are then used as diagnostic tools based on a pre-defined ruleset. Vegetation models can be implemented at a high spatial resolution to assess specific research questions, such as assessing the local response of ecosystems to (sub)millennial-scale climate variability. Their output is in part validated against

modern observations or fossil pollen data (Dallmeyer et al., 2022; Li et al., 2025), but also often contradicts localised proxy-based reconstructions (Laepple et al., 2023) thus highlighting important uncertainties in vegetation reconstructions from both approaches.

To obtain as comprehensive an overview as possible of what the landscape may have looked like during the Late Glacial, we compare the different methods and also address the advantages and limitations of the available reconstruction approaches. In total, we compare four methods, the pollen-based Biomisation and REVEALS, a static vegetation model (PaleoVeg), and a DVM (JSBACH) coupled to an ESM.

2. Methods

In the following, we briefly describe all methods to reconstruct forest cover during the late Last Glacial period (70–20 ka BP). For more detailed descriptions, we refer to the references within each section. Figure 1 presents a schematic overview of the data, methods, and workflow used in this study.

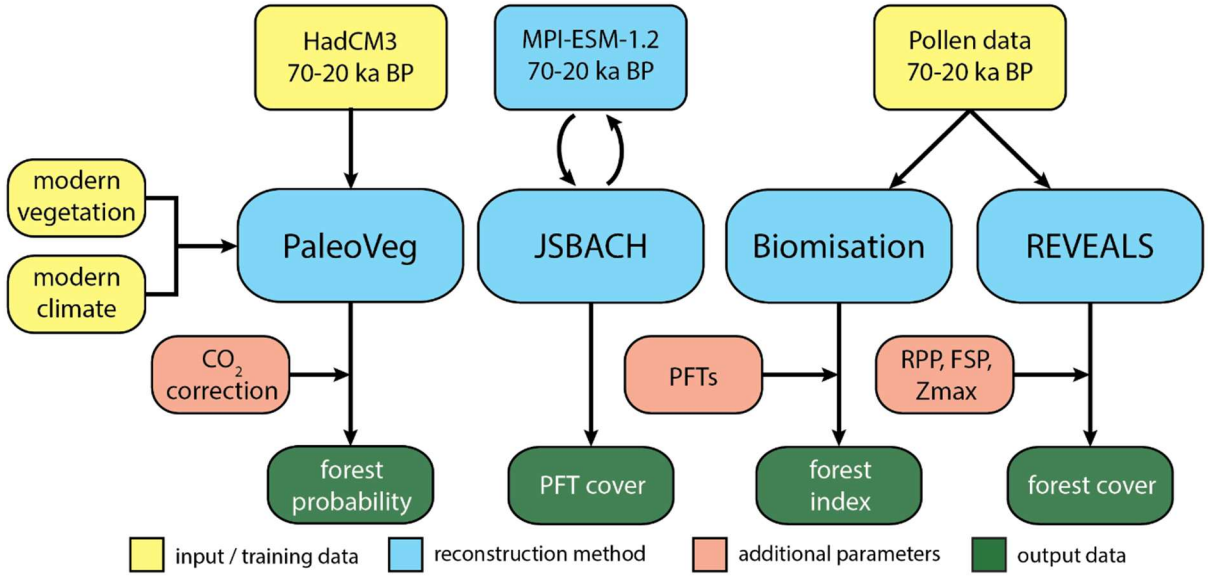

Figure 1: Schematic overview of the different data and methods used in this study to reconstruct the palaeovegetation. Input data (yellow) represent the different data sources: The output of high-resolution climate simulations HadCM3 (Beyer et al., 2020) and MPI-ESM 1.2 (Duque-Villegas et al., 2025), and the compiled fossil pollen data (Kern et al., 2025) for the period from 70–20 ka BP. Additional parameters (red) originate from other sources (e.g., global CO_2-levels, remote sensing data, reanalysis data), which are required by the respective methods (blue) to generate different types of vegetation reconstructions (green). PFT: plant functional type; RPP: relative pollen productivity; FSP: fall speed; Zmax: maximum spatial extent of the regional vegetation.

2.1. PaleoVeg

The PaleoVeg vegetation model is extensively described in Shao et al. (2018). The original model used a probabilistic statistical approach to relate vegetation types to climate variables. In this study, we utilise a more refined version with a random-forest-based implementation (https://github.com/roink/PaleoVeg; Schlüter, 2025) that is conceptually rooted in Shao et al. (2018) but not identical to that original setup. PaleoVeg predicts the probability that a certain vegetation type (including bare soil) exists in each grid cell. The probability that a grid cell is covered by forest therefore corresponds to the sum of probabilities of all forested vegetation types. Importantly, the vegetation of a grid cell does not correspond to the vegetation type probabilities (e.g., a grid cell with

50 % boreal forest and 50 % tropical forest probabilities is not covered by a mix of boreal and tropical tree taxa).

The model statistically reconstructs the palaeovegetation by applying a present-day vegetation-climate relationship to climatic states of the past. It was trained using remote sensing data with a spatial resolution of 8 km from the Advanced Very High Resolution Radiometer (AVHRR, Loveland et al., 2000) and the WorldClim 2.1 data based on 1970-2000 climate (Fick and Hijmans, 2017). The approach has been validated by reconstructing the modern vegetation using the WorldClim data and comparing it to the original AVHRR vegetation dataset (Shao et al., 2018). The model then applies the same relationship to past climate states in order to statistically reconstruct the palaeovegetation following a modified classification by the International Geosphere-Biosphere Programme (Loveland et al., 2000) adapted to the pre-Holocene period (e.g., removal of "urban land" and "cropland"). The final classification consists of 10 vegetation types and bare ground. As input data, we use the downscaled and bias-corrected palaeoclimate data based on the HadCM3 global climate model (GCM; Beyer et al., 2020). The HadCM3 dataset comprises 17 bioclimatic variables (BCVs) for 120–0 ka BP in 1,000-year (22–0 ka BP) and 2,000-year (120–22 ka BP) time steps at a spatial resolution of 0.5° and is accessible through the *pastclim* R package (Leonardi et al., 2023).

Atmospheric CO_2 considerably influenced photosynthesis efficiency in past ecosystems (Prentice and Harrison, 2009). The PaleoVeg thus also factors in a CO_2 correction factor (f_{CO2}) that was initially inferred from palaeovegetation reconstructions for the LGM (Woillez et al., 2011). Assuming a linear relationship between CO_2 levels and photosynthesis rates (where $f_{CO2} = 1$ for the present), we extrapolated f_{CO2} for the entire study interval (see Supporting Information) using atmospheric CO_2 data from Antarctic ice cores (Indermühle et al., 2000; Veres et al., 2013).

2.2. MPI-ESM-1.2 and its land component JSBACH

We use the vegetation output of a transient simulation (Duque-Villegas et al. 2025) performed in the comprehensive Earth System Model MPI-ESM-1.2 (Max-Planck-Institute Earth System model version 1.2, Mauritsen et al., 2019). This simulation covers the entire Last Glacial, but we concentrate on the period from 70 to 20 ka BP. The MPI-ESM 1.2 includes the land surface and dynamic vegetation model JSBACH3.2 (Reick et al., 2013) that represents vegetation in the form of eight plant functional types (PFTs) as a fraction of land-cover in any given grid cell. These include extratropical and tropical trees that can either be deciduous or evergreen, raingreen and cold-resistant shrubs, and C3 and C4 grasses. JSBACH uses a "mosaic" approach, where each land surface grid cell is tiled so that all PFTs could in principle coexist within a grid cell. The PFTs are limited by temperature thresholds reflecting their bioclimatic tolerance (e.g., cold resistance, chilling, and heat requirements). Shifts in PFT cover are driven by the relative differences in net primary productivity (NPP) between the PFTs, which depend on factors such as moisture availability or atmospheric CO_2-levels, and reflect inter-PFT competition (Brovkin et al., 2009). The JSBACH version used in this simulation does not include permafrost, dynamic soil development, or seed dispersal. Thus, timescales of vegetation migration are relatively short compared to reality (Dallmeyer et al., 2022). The spatial resolution of the simulation is T31, i.e. 400 km x 400 km grid-cell size on a Gaussian grid.

2.3. Pollen data

We compiled 61 palynological records from palaeoclimate archives located in Europe and the surrounding areas (Fig. 2) that contain pollen data from the late Last Glacial period, specifically the interval from 70–20 ka BP (Kern et al., 2025). Pollen samples were selected within ± 500 years of the defined time step (e.g., 30,000 ± 500 years BP). If multiple data points fall into this window, pollen counts were aggregated into a single sample. Prior to data analyses, all taxa were harmonised to the

genus (woody and major herbaceous taxa) or the family level (other herbaceous taxa) (Kern et al., 2025). This fossil pollen dataset forms the basis for the Biomisation and REVEALS reconstructions (Fig. 1). It is important to note that both pollen-based methods can only represent the vegetated area (since pollen data are unable to represent bare soil).

The Biomisation process describes the grouping of plant taxa into plant functional types (PFTs) based on their climatic preferences and similar traits (e.g., life form, leaf morphology, and phenology). Sets of PFTs are then arranged in combinations to form a relatively small number of biomes, i.e., a biological community that formed as a result of environmental and climatic factors. The Biomisation algorithm (Prentice et al., 1996) utilises PFTs of the total pollen sum to calculate the most probable biome. This relatively simple reconstruction algorithm has been shown to perform moderately well and addresses differences in pollen productivities between tree/shrub and forb taxa (Binney et al., 2017). In this study, we use 30 PFTs to reconstruct 12 biomes after Bigelow et al. (2003) and Binney et al. (2017). The Biomisation algorithm yields so-called biome affinity scores, dimensionless scores that measure the similarity of the record to a predefined set of biomes (Prentice et al., 1996). The biome with the highest affinity score is then assigned to a site. We here introduce a quantitative measure (forest index) to estimate the probability that a site is covered by a forested biome. This is calculated as the maximum affinity score within all forested biomes (e.g., cool mixed forest) minus the maximum affinity score within all non-forested biomes (e.g., cushion-forb tundra), which is then rescaled to 0-100.

The REVEALS algorithm reconstructs land-cover estimates (Sugita, 2007) and has been described and discussed extensively in previous studies (Githumbi et al., 2022; Kern et al., 2025; Pearce et al., 2023; Serge et al., 2023). REVEALS yields land-cover percentages for every taxon (Sugita, 2007); tree cover can then be calculated as the sum of land-cover by all tree taxa. The unique feature of REVEALS is the addition of taxa-specific parameters, such as the relative pollen productivity (RPP) estimates and the fall speed of pollen (FSP), to the raw pollen counts. Multiple compilations of RPP and FSP values on regional to continental scales exist (e.g., Githumbi et al., 2022; Schild et al., 2025; Serge et al., 2023; Wieczorek and Herzschuh, 2020) and have been validated and optimised through comparison with satellite-based land-cover reconstructions (Hansen et al., 2013; Schild et al., 2025). Lastly, REVEALS accounts for wind speed, and the maximum extent of regional vegetation (Zmax), which were set to 3 m/s and 100 km, respectively (Trondman et al., 2015). REVEALS provides land-cover percentages for each taxon, which can be assigned to e.g., biomes based on the individual research questions (e.g., Githumbi et al., 2022; Kern et al., 2025).

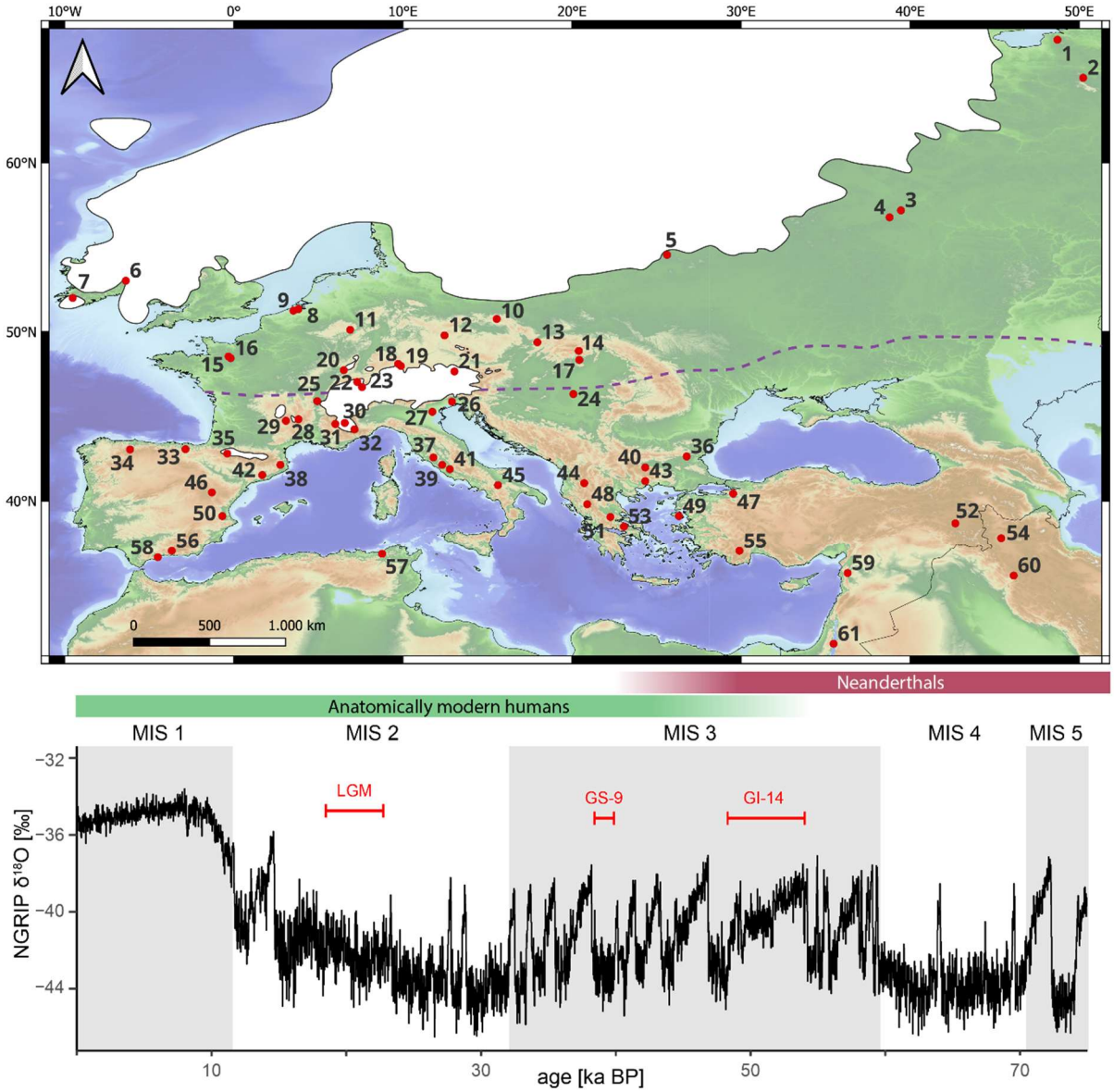

Figure 2: Pollen archives included in this study (after Kern et al., 2025) next to NGRIP $\delta^{18}O$ for the last 75 ka (Rasmussen et al., 2014). The extent of ice-sheets (Ehlers et al., 2011) and permafrost (Stevens et al., 2025) is shown for the Last Glacial Maximum. The three red intervals (LGM, GS-8, and GI-14) are referred to in the results and discussion section. Coloured bars indicate the estimated presence of different human species in Europe (after Slimak et al., 2022). Marine Isotope Stages (MIS) after Lisiecki and Raymo (2005).

2.4. Definition of forest cover

Forest cover is often interpreted as the density and extent of tree cover and has been extensively used in palaeoecological studies (Pearce et al., 2023; Zanon et al., 2018) and climate-vegetation feedback studies on albedo or evapotranspiration, where forest cover is often more relevant than the vegetation composition (Bright et al., 2015; Reichstein and Carvalhais, 2019). However, the term "forest cover", albeit widely used, is only loosely defined. Forest cover can mean that the dominant biome is a type of forest, that the probability of a forested biome domination is higher than a threshold (e.g., 50 %), or that the sum of forest biome probabilities is higher than a threshold. Furthermore, it is often incorrectly associated with the term "tree cover", although a forest is very rarely composed only of trees (in terms of land cover, i.e., a fully closed canopy).

Palaeovegetation reconstructions can be used to reconstruct forest cover, but they typically vary in their respective outputs, including categorical (e.g., presence/absence, biomes), semiquantitative

(e.g., biome affinity scores, a dimensionless score to determine the most plausible biome), and quantitative data (e.g., biome percentages, taxon percentages, tree cover fractions). Additionally, methods can treat unvegetated areas (e.g., bare soil) differently in their calculations (e.g., Dallmeyer et al., 2025; Li et al., 2025; Strandberg et al., 2022; Sun et al., 2022). As a consequence, the respective absolute values of forest index (Biomisation), forest cover (REVEALS), tree cover fraction (JSBACH), and forest probability (PaleoVeg) must be interpreted differently.

A direct comparison of such techniques has been successfully implemented in various studies, covering a wide range of temporal and spatial scales (Dallmeyer et al., 2023; Hallett et al., 2025; Pearce et al., 2025; Schild et al., 2025; Zanon et al., 2018). However, this requires the introduction of a universal biome definition scheme across methods (Dallmeyer et al., 2019). This becomes increasingly difficult when more than two methods are compared and often entails a loss of information from oversimplification. In this study, we therefore decided to evaluate and compare the different representations of forest cover for each respective vegetation reconstruction technique, without trying to shoehorn them into an overarching scheme. As a consequence, absolute values of forest cover should be interpreted with caution. Instead, we focus on temporal trends, amplitudes of change, and regional patterns in the vegetation. To facilitate the direct comparison between methods, we standardise all datasets by subtracting the respective mean and dividing by the standard deviation. The resulting values (also known as Z-scores) have a mean of 0, with positive values indicating above average forest cover and vice versa.

2.5. Chronological uncertainty

Chronological uncertainties are typically reported in studies as errors in direct dating techniques (e.g., radiocarbon dating or luminescence dating) or as model uncertainties. However, most of the time, chronological uncertainties are difficult to quantify as they result from a complex interplay of multiple factors that contribute differently at any given time in a time series. These factors include, but are not limited to, dating uncertainty, interpolation between absolute dates, uncertainties resulting from correlation techniques, sampling uncertainties, temporal binning of data, and phase shifts.

To investigate the level of chronological uncertainty and to avoid misinterpretation of datasets, we employed two methods to quantify whether chronological uncertainties substantially contribute to potential agreements or mismatches between reconstruction techniques: Time-lagging and dynamic time warping (DTW). Time-lagging describes the temporal shift of one dataset by one or more time steps in either direction. Subsequent analyses such as the Root Mean Square Deviation can then identify whether the time-lagged data are a better fit than the original, which might indicate a systematic temporal offset.

DTW works similar to time-lagging, but on a point-by-point basis. It computes the local stretch or compression applied to two timeseries in order to minimise the observed distance between both (Giorgino, 2009). The DTW distance then yields information on the similarity between two time series after alignment and thus corrects for potential chronological uncertainties. Furthermore, we compare the Root Mean Square Deviation before and after DTW was applied for each method pair. DTW was performed on standardised Z-scores in R using the package *dtw* and employing the Rabiner-Juang step pattern type “VI-c” (Giorgino, 2009).

3. Results

3.1. Temporal evolution of mean forest cover

We employed forest-cover reconstructions for all methods from 70 ka BP to 20 ka BP in time steps of 2000 years (i.e., 26 time steps). For this calculation, we consider only grid cells (PaleoVeg and JSBACH) where pollen data are available for the same time step. Overall, JSBACH consistently reconstructed the highest (mean 55 %) and REVEALS the lowest (mean 17 %) levels of forest cover across all time steps. Biomisation (mean 40 %) and PaleoVeg (mean 38 %) range in-between (Fig. 3). Importantly, we observe a clear offset between methods across all time steps. Compared to PaleoVeg and the Biomisation values, the forest reconstructions of JSBACH and REVEALS consistently range higher and lower, respectively. Based on the definition of forest cover and the differences in the calculation of forest cover from the individual method outputs (as discussed in section 2.4), this behaviour was expected and hinders a direct comparison between methods, because the absolute values are not comparable.

To circumvent this general offset in forest cover reconstruction, each method was normalized by calculating their respective Z-scores. The resulting data from of all methods highlight several important features (Fig. 4): The overall patterns of reconstructed forest cover are in agreement across all methods and broadly represent the climatic conditions during the Last Glacial period. Lower forest values from 70–60 ka BP broadly correspond to MIS 4, although the different methods show some disagreement on the exact timing of the MIS 5a–MIS 4 transition. An abrupt increase in forest values across all methods signals the transition into MIS 3, with the highest values between 60–50 ka BP and a gradual decrease to lower values until ca. 30 ka BP. Within this gradual decrease, several smaller increases in values can be observed that may correspond to interstadials, but these are not consistent across methods. The absence of individual interstadials is likely due to the binning of data into relatively broad bins of 2 kyr, which is longer than most interstadials during MIS 3. The transition into early MIS 2 and the LGM is hardly discernible from the data.

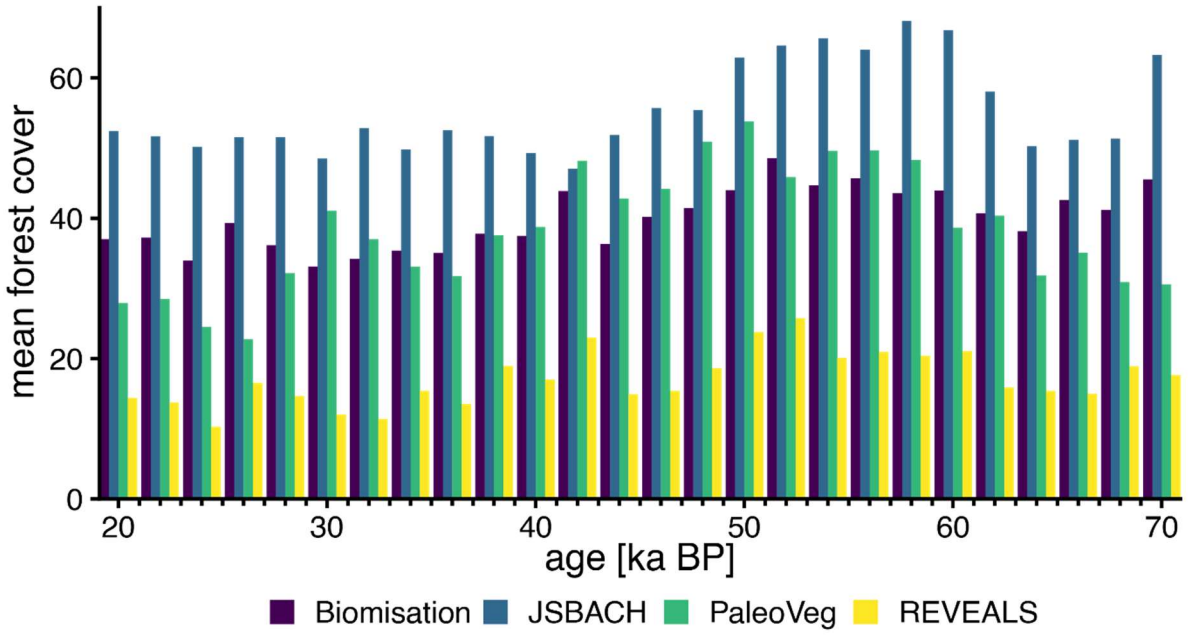

Figure 3: Comparison of the mean forest cover generated by each method in Europe during the 70–20 ka BP interval. The respective means for PaleoVeg and JSBACH were only calculated across grid cells where pollen data was available at a given time step. Absolute values can differ by up to 40 % (JSBACH and REVEALS) resulting from the different definitions of forest

cover (see section 2.4), but the overarching temporal pattern is shared across all datasets and broadly follows the climate signal observed in the Northern Hemisphere (Fig. 2, Rasmussen et al., 2014).

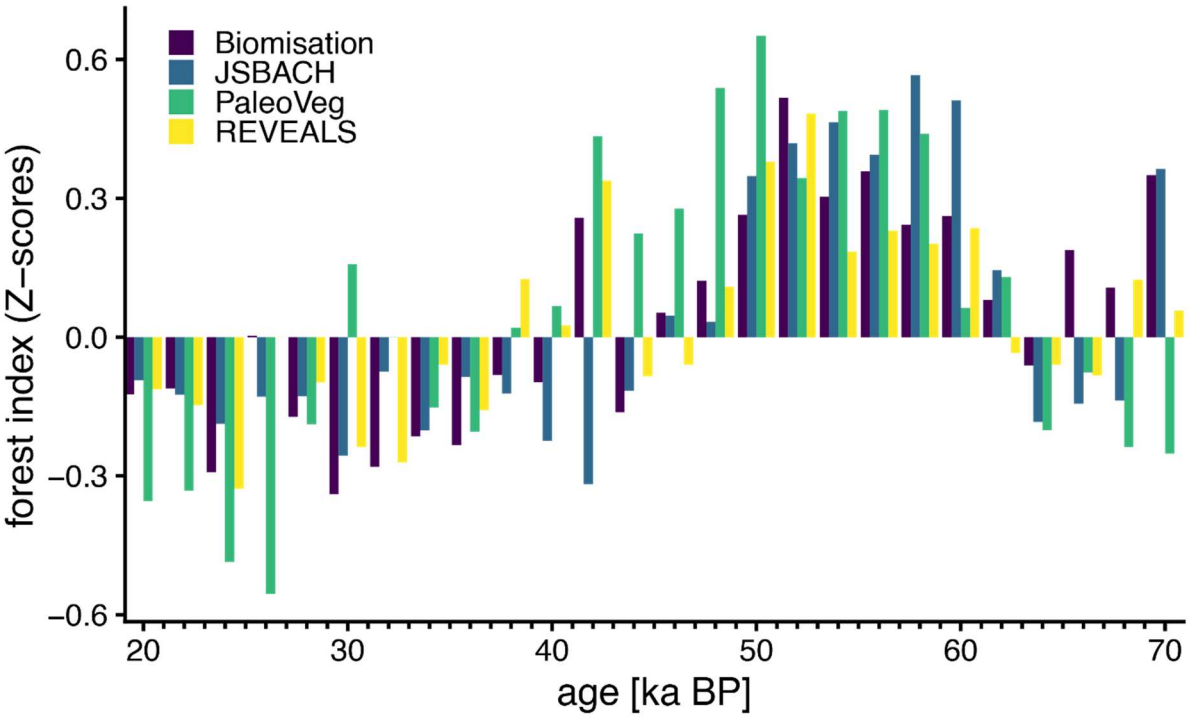

Figure 4: Temporal evolution of forest reconstructions from 70–20 ka BP in Europe after Z-score normalisation. Standardisation removes the general offset between datasets (Fig. 3) and highlights that all methods share a similar temporal trend.

3.2. Time-lagging and dynamic time warping

To evaluate a potential chronological offset between datasets, we calculated the correlation coefficients (R) between method pairs after shifting one dataset by one time step in either direction (i.e., ±2000 years). In the majority of cases, correlation decreased substantially after time-lagging. Two exceptions include the Biomisation-JSBACH and PaleoVeg-JSBACH pairs, where the R values improved marginally from 0.589 to 0.595 and 0.808 to 0.818, respectively. However, lagging the JSBACH dataset by one time step also reduces the correlation between the REVEALS-JSBACH pair substantially (from 0.704 to 0.606). Hence, we chose not to systematically lag any dataset for future analyses.

Instead, we investigated how well-aligned individual datapoints are across all datasets. For this, we performed pairwise DTW on the mean forest cover percentages across the entire domain for every time step (Giorgino, 2009). DTW calculates the cost of the optimal warping path (DTW distance; low distances indicate a higher similarity). Here, we chose the step pattern “Rabiner-Juang type VI-c”, which resulted in a minor time-series alignment at the cost of warping the time series to an extent. The observed DTW distances (Tab. 2) after alignment range from 0.60 to 0.86 indicating a weak to moderate similarity. Overall, the improvements in the correlation coefficient before and after alignment were minor; the only exception being the JSBACH-Biomisation pair, where the correlation coefficient after alignment improved by 0.22.

In summary, both time-lagging and DTW revealed no systematic offset between datasets. Minor improvements can be achieved by DTW for specific data-pairs, but this would also negatively affect the correlation between other pairs. Hence, we refrain from aligning datasets only to improve the correlation of specific method-pairs.

Table 1: Correlation coefficient (R) of the warped mean forest cover time series after dynamic time warping (R before time-warping in parentheses). The REVEALS-Biomisation pair is omitted from the analysis, because both methods originate from the same pollen dataset.

	REVEALS	JSBACH	Biomisation	PaleoVeg
PaleoVeg	0.74 (0.65)	0.86 (0.81)	0.60 (0.54)	-
JSBACH	0.76 (0.70)	-	0.81 (0.59)	0.86 (0.81)

3.3. Spatio-temporal distribution of forest cover

In the following, we briefly present changes in forest-cover reconstructions for each method at three selected time intervals: Greenland Interstadial 14 (GI-14; ca. 52 ka BP), Greenland Stadial 8 (GS-8, ca. 36 ka BP) and the Last Glacial Maximum (LGM, ca. 22 ka BP). These snapshots represent interstadial, stadial, and full glacial conditions during MIS 2–3, respectively. Importantly, the timing of stadials and interstadials is well-aligned between the NGRIP $\delta^{18}O$ climate reference dataset (Rasmussen et al., 2014), the MPI-ESM simulation (including JSBACH) (Duque-Villegas et al., 2025), and the HadCM3 output (used for PaleoVeg; Beyer et al., 2020). Forest-cover reconstructions are presented as standardised Z-scores, i.e., as deviations from the mean forest cover of the respective method, to compensate for the systematic offset between methods (Figs. 3 and 4).

3.3.1. Forest cover during GI-14 (interstadial conditions)

The forest cover in Europe during GI-14 (52 ka BP; Fig. 5) represent the maximum forest cover in the investigated time frame (70–20 ka BP). High levels of forest cover are observed north of the Alps and in the Central Mediterranean region, while Northern Africa and the Middle East remained mostly treeless and the Western and Eastern Mediterranean (the Iberian Peninsula and Anatolia) are characterised by lower forest cover compared to the rest of Europe. All methods agree that the northernmost ice-free regions of Central Europe were likely forested, but the individual amount (with respect to their means) can vary substantially. In contrast, the Alpine region shows lower forest cover in all methods except JSBACH.

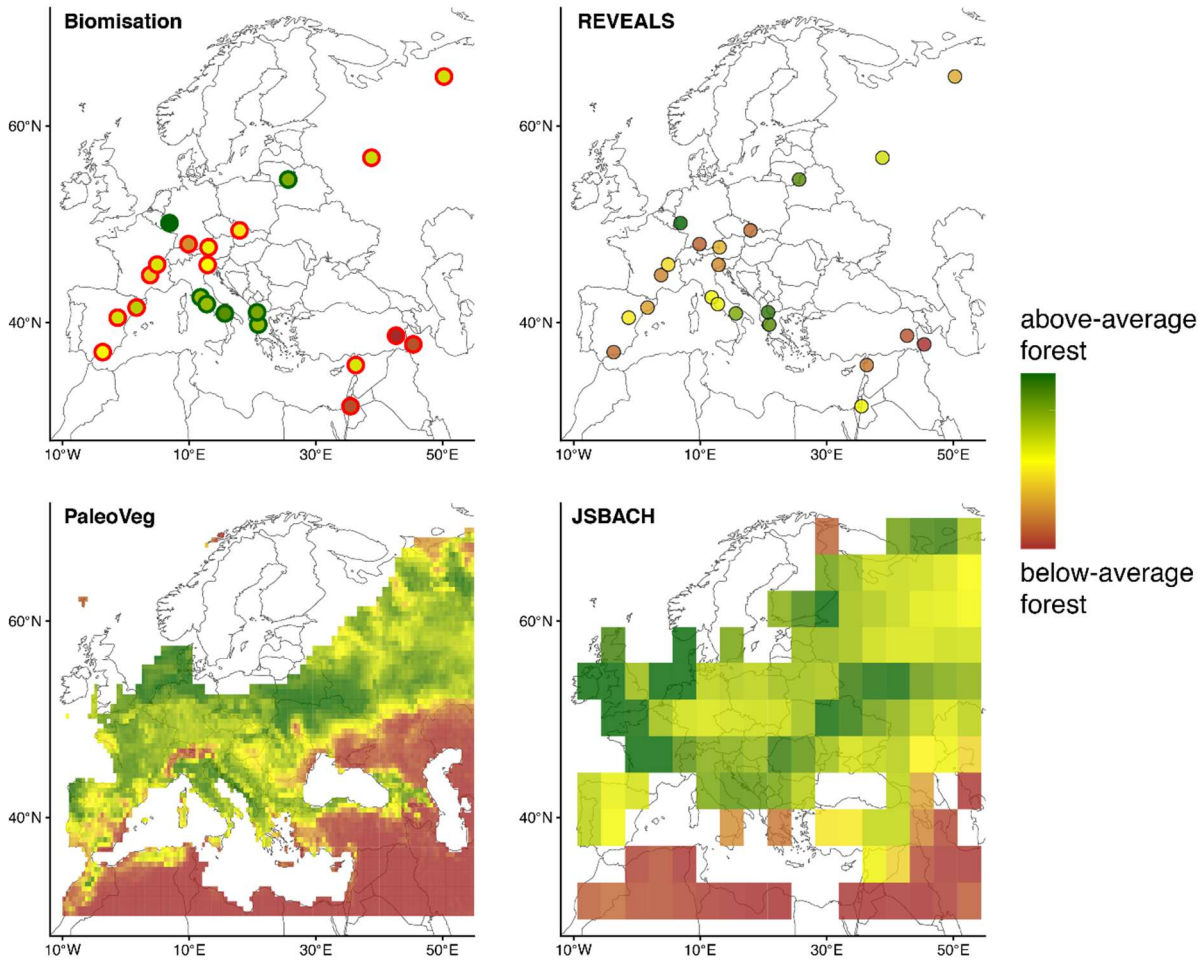

Figure 5: Forest cover Z-scores (with respect to the 70–20 ka BP interval) for all different methods in Europe during Greenland Interstadial 14 (GI-14; 52 ka BP). Green values depict a above-average forest cover, while red values show below-average forest cover. For Biomisation, the borders of each site indicate whether the Biomisation predicted a forest biome (green) or a non-forest biome (red).

3.3.2. Forest cover during GS-8 (stadial conditions)

Compared to GI-14, the mean forest cover during GS-8 (36 ka BP; Fig. 6) are considerably lower and closer to the respective means for the entire study interval (i.e., yellow in Fig. 6). The overall pattern of forests across Europe remains similar to that of GI-14, but with a stronger North-South divide. Regions of high forest cover stretch across Central and Eastern Europe in an E-W belt, while forest cover levels, especially in the pollen-based methods, have decreased substantially south of the Alps. Particular the Italian Peninsula and the Balkans show lower forest cover compared to GI-14. The remainder of the Mediterranean and the Middle East remain unchanged. The site in Tunisia highlights that while the majority of Northern Africa is virtually treeless, small islands of forests can persist if the local conditions are favourable.

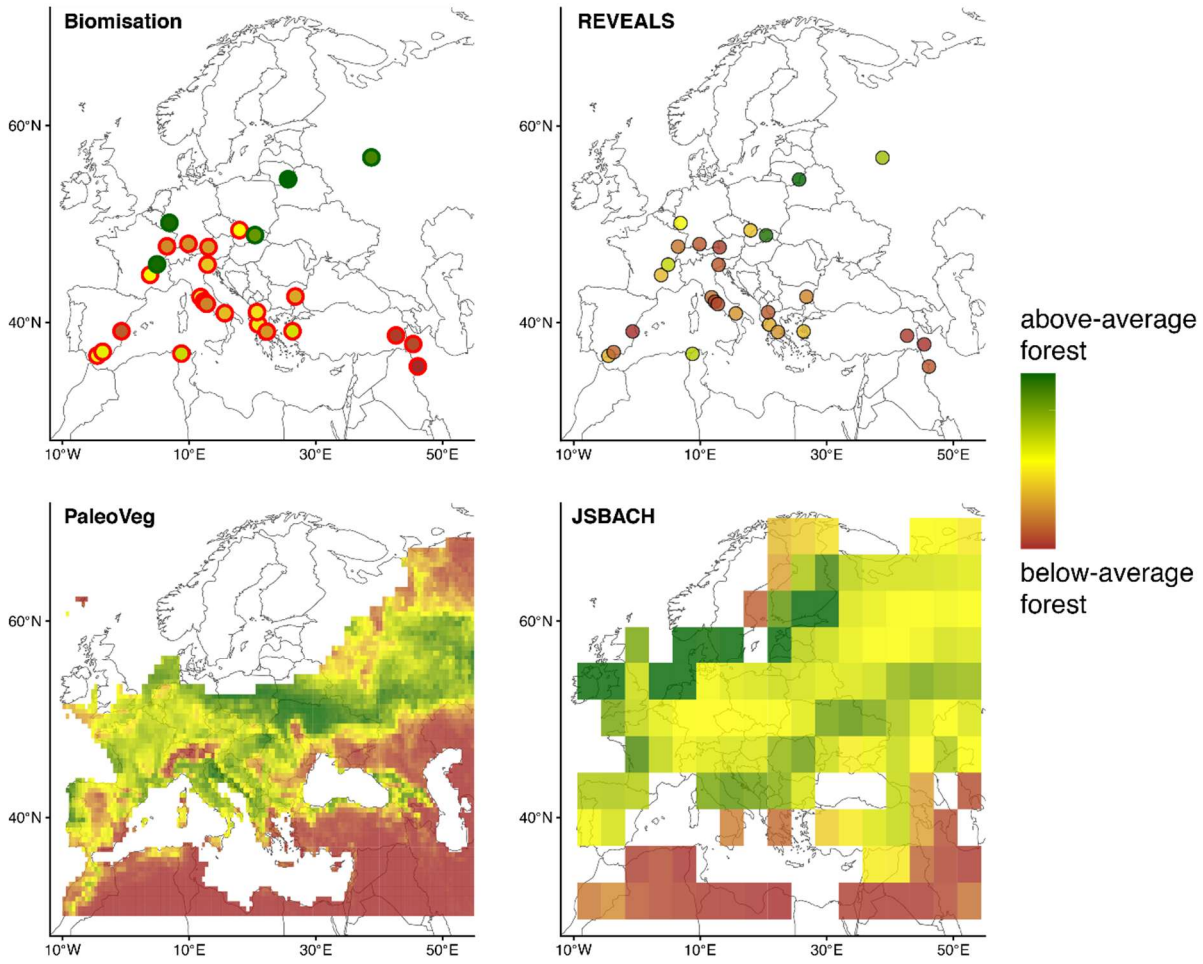

Figure 6: Forest cover Z-scores (with respect to the 70–20 ka BP interval) for all different methods in Europe during Greenland Stadial 8 (GS-8; 36 ka BP). Green values depict a above-average forest cover, while red values show below-average forest cover. For Biomisation, the borders of each site indicate whether the Biomisation predicted a forest biome (green) or a non-forest biome (red).

3.3.3. Forest cover during the LGM (full glacial conditions)

During the full glacial conditions of the LGM (22 ka BP; Fig. 7) levels of forest cover are close to their minima. Nonetheless, isolated regions with above-average forest cover remain throughout Europe, but primarily in coastal regions of Southern Europe (Iberian Peninsula and Adriatic coast) and Eastern Europe (Pannonian Basin and the East European Plain). In contrast, the levels of forest cover have decreased substantially from GS-8 and GI-14 in North-Eastern Russia, Central and Western Europe. No methods predict a significant presence of forests in Northern Africa and the Middle East.

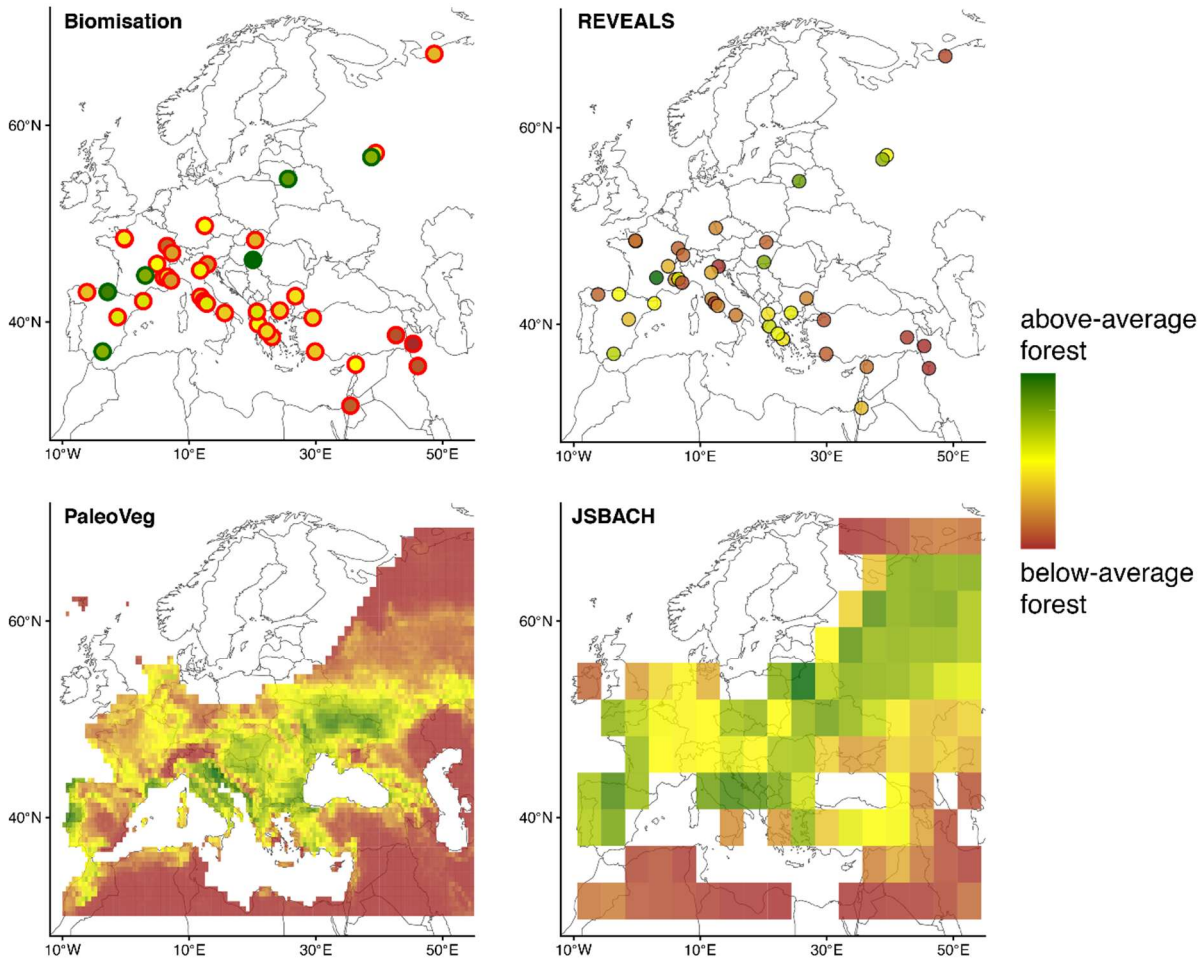

Figure 7: Forest cover Z-scores (with respect to the 70–20 ka BP interval) for all different methods in Europe during the Last Glacial Maximum (LGM; 22 ka BP). Green values depict a above-average forest cover, while red values show below-average forest cover. For Biomisation, the borders of each site indicate whether the Biomisation predicted a forest biome (green) or a non-forest biome (red).

4. Discussion

Environmental change in Europe during the Last Glacial was naturally tied to the long- and short-term climatic evolution. Over longer timescales of several millennia, terrestrial ecosystems in Europe are broadly in tune with the climatic patterns observed in Greenland ice cores (Rasmussen et al., 2014). The fully glacial climates of MIS 4 and MIS 2 led to cold and dry conditions across Europe, which substantially limited the proliferation and spread of tree taxa (e.g., Fletcher et al., 2010; Kaplan et al., 2016). During MIS 3, more mild and humid climatic conditions favoured an increase in forest cover and the expansion of tree species into the higher latitudes. This was particularly pronounced during interstadials – transient bursts of warming and increased moisture availability – which led to a rapid afforestation across wide areas of Europe (Allen et al., 2000; Britzius et al., 2024; Kern et al., 2022). Although the return to stadial conditions entailed forest contractions, the overall levels of forest cover during MIS 3 remained well above those during the full glacial conditions of MIS 4 and MIS 2.

This overarching pattern of climate-ecosystem coupling is well-represented in all methods investigated in this study (Figs. 3 and 4). On continental scales, the resulting reconstructions show a moderate to high correlation with each other. However, on local scales, the reconstruction of forest at a specific site and the associated grid-cell may vary substantially. To an extent, this is to be expected and stems from of a combination of factors such as statistical variance, chronological

uncertainty, and model and proxy data (in-)accuracy. In the following, we explore in more detail the regional patterns of forest cover in Europe during the Last Glacial, how the different methods perform, as well as their strengths and weaknesses.

4.1. Regional forest cover

The reconstructions of regional forest cover exhibit a wide range of potential palaeoenvironments in Europe during the Last Glacial (Fig. 5–7). Regions at lower latitudes, such as Northern Africa and the Middle East, experience little variability in forest cover throughout the entire time interval. To some extent, the reconstructions in these regions even suggest a slight afforestation during cold intervals such as the LGM compared to the preceding MIS 3. This is likely related to the southward shift of moisture belts, increasing overall precipitation and decreasing precipitation seasonality in proxy-based and model-based climate reconstructions (Arpe et al., 2011; Davis et al., 2024; Ludwig et al., 2016). Despite the cooler LGM temperatures and lower CO_2 levels stunting tree growth (Woillez et al., 2011), higher moisture availability outweighs these factors at lower latitudes to an extent.

In the Mediterranean, the vegetation response pattern to climatic variability is highly differentiated. While much of the Mediterranean region exhibits a moderate decrease in forest cover from interstadial to stadial as well as stadial to full glacial climates (Figs. 5–7), smaller sub-regions diverge from the overall pattern. For example, the north-western Iberian Peninsula, the Balkans, and Central Italy exhibit a certain resilience to climatic perturbations. Model data show that these areas retained a high forest cover during e.g., the LGM, indicating that these areas may have acted as glacial refugia during the Last Glacial. Unfortunately, these model predictions cannot be validated due to the limited number of pollen-based reconstructions (Fig. 2; c.f. Fletcher et al., 2010) and plant macrofossil data (e.g., Tzedakis et al., 2013) in these critical areas.

Changes in forest cover in response to climatic perturbations are relatively homogeneous in Western and Central Europe. Interstadial conditions favoured the widespread expansion of trees and resulted in vast regions of high forest cover (Fig. 5). During stadial conditions, intermediate levels of forest cover reflect transitional ecological conditions (Fig. 6). Full glacial conditions are dominated by open landscapes, albeit the datasets hint at the persistence of isolated tree populations in localized areas (Fig. 7). The existence of such refugia is subject of a long-standing discussion in the palaeoecology community (Bennett et al., 1991; Petit et al., 2003; Tzedakis et al., 2013). Such refugia are often linked to favourable microclimates that may occupy areas too small to be resolved by climate and vegetation models (Dobrowski, 2011; Rull, 2010; Timbrell et al., 2024; Vercauteren et al., 2013).

The ecological changes associated with interstadial, stadial, and full glacial climate conditions are most drastic and diverse in Eastern Europe (Fig. 5–7). Both vegetation models predict several states of forest cover coexist during all stages of the Last Glacial. However, these observations are difficult to validate using pollen data due to the lack of suitable archives in Eastern Europe. North of 50°N and in the Carpathian Mountains, model-based and pollen-based reconstructions show a high agreement. During intermediate to warm conditions (i.e., GI-14) forests dominate the landscape. Climatic cooling during MIS 3 and 2 induces a gradual decline in the Eastern European forests in a clearly discernible latitudinal gradient, resulting in a widespread distribution of tundra in the northern parts and forest-tundra or forest-steppe ecotones further south (i.e., closer to 50°N). Further south, in the Pontic–Caspian region (i.e., the area stretching from north of the Black Sea eastward to the Caspian Sea), such forest-tundra or forest-steppe ecotones characterise the interstadial vegetation. By the time of the LGM, these forest populations have been largely replaced by open landscapes akin to the modern Eurasian steppe.

4.2. Proxy-model mismatch

On a continental scale, the different forest-cover reconstructions show a remarkable similarity in the temporal dynamics of forest cover during the Last Glacial. Overall, all methods capture the long-term sequence of forest expansions and retractions associated with climatic variability during MIS 4–2. While there is some variability that can be attributed to Greenland Stadials and Interstadials, the limited temporal resolution impedes a more extensive analysis of the impact of the abrupt climatic transitions on the forest populations in Europe.

On regional scales, proxy-model agreement is highest in Eastern Europe, the Iberian Peninsula, and the Middle East. In turn, the agreement between methods is weak in Western and Central Europe as well as the central Mediterranean region, where models suggest moderate to high forest cover, while pollen data indicate widespread tundra and/or steppe landscapes. Previous studies, both on pollen data (Bigelow et al., 2003; Binney et al., 2017; Tarasov et al., 2000) and model reconstructions (Harrison and Prentice, 2003; Strandberg et al., 2011), have observed similar forest-cover distributions during glacial climates (primarily during the LGM). In particular, these patterns of model-proxy agreement and mismatch have been known to the community (Davis et al., 2024; Kaplan et al., 2016) and are not limited to glacial climates only (Dallmeyer et al., 2023; Marquer et al., 2017; Strandberg et al., 2022).

Despite capturing the general trend of forest cover dynamics during the Last Glacial, there exists a fundamental offset in the mean forest-cover reconstructions (Fig. 3). This can inspire very different interpretations of the Last Glacial landscapes, from barren tundra or steppe environments to open (boreal) forests, with wide-ranging consequences for data interpretation, e.g., the inference of ecological preferences of Palaeolithic hunter-gatherer groups. The apparent overrepresentation of trees north of the Alps by vegetation models has been previously reported (Davis et al., 2024; Kaplan et al., 2016) and is not in agreement with the general consensus that Europe was predominantly treeless during the LGM (Bigelow et al., 2003; Binney et al., 2017; Tarasov et al., 2000). It also contradicts our understanding of glacial landscapes in Europe during the Late Pleistocene with regards to large herbivore presence (Ukkonen et al., 2011), aDNA evidence (Willerslev et al., 2014), permafrost presence (Stevens et al., 2025), and speleothem data (Fleitmann et al., 2009; Genty et al., 2010; Staubwasser et al., 2018), which all indicate harsh climatic conditions and a mosaic of tundra, steppe, and open forest environments (Britzius et al., 2024; Holm and Svenning, 2014; Pederzani et al., 2023). At the same time, the comparison of methods in this study suggests that REVEALS reconstructions may underestimate forest cover, predicting mostly tundra and steppe landscapes during all periods of the Last Glacial. This is most apparent in the low magnitude of forest expansions during periods of climate amelioration, when (open) forests (re-)emerged in Central Europe as documented by raw pollen data (Britzius et al., 2024; Fletcher et al., 2010; Kern et al., 2022; Woillard, 1978).

As stated in the methods section, the most likely explanation for this mismatch lies in the different outputs that all methods generate as well as their interpretation in the context of forest cover. While a unified scheme that allows for a 1-to-1 comparison is unlikely to accommodate for all the intricacies of the different reconstruction methods, it remains essential to be able to compare and validate datasets. For this reason, we investigate the particular limitations of the different methods, briefly discuss how to interpret their respective output in a wider context, and explore potential solutions for future vegetation reconstructions efforts.

4.3. Model limitations

Vegetation models have substantially improved over the last decade and have been successfully applied to answer various research questions on various temporal and spatial scales. Nonetheless,

high model-complexity comes at the cost of spatial and/or temporal resolution (Laepple et al., 2023) and whether a high-complexity or a high-resolution model (or something in-between) is more suitable depends on the research question.

Global vegetation models, such as JSBACH (within the MPI-ESM), rely on climatic and climate-related parameters to reconstruct the vegetation on global scales. As such, PFT definitions are relatively broad to reflect all general vegetation types and thus limited in their ability to represent vegetation patterns on regional to local scales. A major advantage of the PFT approach is that it can predict the percentage of land cover, e.g., the percentage of land covered by different types of trees, shrubs, grasses, and bare soil within a grid cell. As such, it represents the actual landscape one would observe, which makes it straightforward to interpret the data. These models often also include the parameterisation of complex processes that affect plant growth, decline, or disturbance, e.g., soil moisture and soil dynamics (le Roux et al., 2013). Many of these parameters and thresholds are necessarily tuned to and validated by modern vegetation data (Dallmeyer et al., 2023) or to a mean climate state that is established for a given time period, such as the LGM (Laepple et al., 2023). Vegetation models often do not include (mostly) treeless environments such as permafrost soils, peatlands, or wetlands and therefore may not recognize these areas as open vegetation and incorrectly predict a much higher forest cover (Dallmeyer et al., 2023). Considering that permafrost landscapes (Stevens et al., 2025) and wetlands (Čížková et al., 2013) were widespread across Last Glacial Europe, this contributes to the overall overestimation of the forest cover in affected regions. The extent of global ice sheets is often prescribed from reconstructions that can vary a lot and effect the climate variability in particular during time periods with strong fluctuations e.g., during MIS 3 (Menviel et al., 2020). This simplification of ice sheets might further contribute to the lack of regional variability observed in models (Laepple et al., 2023).

In light of modern climate change and anthropogenic land-use, the present-day climate-vegetation relationship is increasingly at a disequilibrium (Sandel et al., 2025; Svenning and Sandel, 2013) and thus does not accurately represent the bioclimatic relationships accordingly. Climate or vegetation states in the past may have differed to the point that there exists no (near-)analogue in today's world (Correa-Metrio et al., 2012; Magyari et al., 2014; Williams and Jackson, 2007). Using present-day data for training, calibration, and validation of vegetation models also implies that the calibrated parameters are constant over time (Dallmeyer et al., 2023). However, it has been shown that plant physiological traits are dynamic in response to various factors (e.g., water availability, CO_2, and the ecological context) and vary across species, lineages, and timescales (Becklin et al., 2014; Beerling and Woodward, 1993; Franks et al., 2013). Vegetation models also assume that the palaeovegetation is at an equilibrium with the palaeoclimate, which introduces additional uncertainties when interpreting such data. Lastly, PaleoVeg generates probabilities for the occurrence of all vegetation types within a grid cell. While these probabilities can yield information on forest cover (by summing up the probabilities of all forested vegetation types) the actual vegetation composition remains unknown.

4.4. Pollen data limitations

Pollen data as a proxy for palaeoenvironmental conditions have a long-standing tradition and are one of the major indicators used to reconstruct terrestrial ecosystems. As with all proxy data, pollen archives often provide data at different temporal resolutions, include hiatuses, and/or cover only limited time periods within a study interval. Suitable pollen archives are sparse, and their geographic distribution is highly heterogeneous (Fig. 2), especially on global scales. However, researchers have used the properties of windborne pollen dispersal (>100 km; Robledo-Arnuncio, 2011) and deposition to their advantage as pollen archives capture the vegetation signal from a wider region, which often compensates for the lack of spatial coverage. Nonetheless, all future reconstructions

would benefit from the emergence of new well-dated pollen datasets with a high temporal resolution.

Early on, researcher have identified non-linear relationships between fossil pollen data and the palaeovegetation (Parsons and Prentice, 1981; Prentice, 1985). First and foremost, wind-pollinated plants produce many more pollen grains than insect-pollinated plants and thus are drastically overrepresented in pollen data. But even within the group of wind-pollinated plants, production estimates can vary by a factor of >1000. Variability within a genus or family is reported as high as a factor of ~100 (Githumbi et al., 2022; Schild et al., 2025). These effects may be further exacerbated by different preservation capabilities post-deposition (Havinga, 1967; Li et al., 2005). The range of wind-dispersed pollen grains is also species-specific (pollen morphology and density) and varies with the local topography and wind patterns (Markgraf, 1980; Niklas, 1985). Modern vegetation reconstruction techniques aim to address these non-linear relationships by including a range of assumptions (Chevalier et al., 2020; Davis et al., 2024; Fyfe et al., 2010; Prentice et al., 1996; Sugita, 2007; Theuerkauf and Couwenberg, 2018).

Overall, studies have hinted that vegetation shifts often appear too strong in pollen-based methods. The overrepresentation of tree cover during the Holocene is typically attributed to the much higher (several orders of magnitude) pollen productivity of trees per area. Modern vegetation reconstruction techniques account for this (Binney et al., 2017; Serge et al., 2023), but the very same approach can lead to an underrepresentation of tree cover during glacial periods (Kern et al., 2025). The fact that pollen-productivity estimates are based on modern interglacial conditions and therefore less accurate for different climate states such as during the Last Glacial might be a major component of this uncertainty (Dallmeyer et al., 2025).

A major restriction of pollen-based reconstructions (including REVEALS and Biomisation) is that they implicitly assume complete (100%) vegetation cover, because they can only represent the vegetation that is present and not the lack thereof. However, during the Last Glacial period, large areas of Europe were either approaching or had already surpassed the environmental limits of vegetation growth, especially in the higher latitudes, at high altitudes, and in close vicinity to ice sheets (Allen et al., 2010; Bigelow et al., 2003; Davis et al., 2024). Consequently, the assumption that these areas were nearly completely covered by vegetation does not hold and pollen-based data should be interpreted carefully as they might only represent a small fraction of the actual landscape.

Lastly, the characterisation and differentiation of (sub-)biomes (e.g., shrub tundra and cushion-forb tundra) is often based on the exact species (e.g., *Betula* or *Salix*) and/or growth form (e.g., *Corylus avellana* or *Alnus* spp.) of certain indicator taxa. Often it is near-impossible to distinguish fossil pollen data on a species level, which may lead to erroneous assumptions about the palaeoenvironment when interpretating and incorporating such data. Despite the taphonomic and depositional biases, pollen data provide a snapshot of the palaeovegetation at a given point in time that encapsulated all factors that have affected the vegetation, which almost always extent beyond climatic factors alone.

4.5. Non-climatic factors that impacted vegetation patterns

Ecosystems are highly complex and the sheer number of external factors that influence its dynamics cannot be reliably accounted for in vegetation reconstructions. The challenge hereby is two-fold: (a) incorporating these factors into vegetations models, and (b) disentangling the proxy data signal, in which these external factors are implicitly embedded.

In recent times, the primary external factor that influenced vegetation patterns, density, structure, and biodiversity has been human land use, which has exponentially increased since the onset of farming practices in the Early Holocene (Ellis et al., 2013). Before that, the human impact on Last

Glacial environments was comparably low and limited to two processes: a direct impact by the usage of fire and an indirect impact through hunting of medium to large herbivores. The magnitude of impact from both processes is naturally tied to the overall human population, which seems to have gradually – although not linearly – increased in Europe during the Late Pleistocene (Schmidt et al., 2021; Tallavaara et al., 2015).

Wildfires have the potential to transform landscapes on large scales. But due to the cold climatic conditions and reduced vegetation cover, natural wildfire activity during the Last Glacial in Europe was comparably lower than today (Daniau et al., 2010; Haas et al., 2023). Before the advent of agriculture during the early Holocene and the targeted use of fire to clear patches of land, human-caused fires have likely been accidental. Anthropogenically caused fires likely have had a substantial impact on the post-LGM vegetation (Kaplan et al., 2016) and concrete evidence for large scale impacts on ecosystems exists from the Late Glacial and early Holocene period onwards (Connor et al., 2019; Dietze et al., 2018; Feurdean et al., 2020; Robin and Nelle, 2014). Prior to the LGM, evidence for the use of fire is abundant, but the ecological impact was very local (Nikulina et al., 2024, 2025; Roebroeks et al., 2021).

Hunting of large herbivores, thereby reducing their distribution and density, by Neanderthals and anatomically modern humans has influenced ecosystems on regional scales (Nikulina et al., 2024, 2025; Sandom et al., 2014). Recent studies have demonstrated that the abundance and diversity of large herbivore strongly decreased after the arrival of modern humans in Europe ca. 50 ka BP (Bergman et al., 2023; Smith et al., 2018). Prior to that, European ecosystems were characterised by much higher proportions of open a light-woodland (Pearce et al., 2023) and habitat mosaics (Johnson, 2009), which are directly linked to the influence of large herbivores on vegetation structure and composition (Davoli et al., 2024; Svenning et al., 2024). Herbivorous megafauna engineer ecosystems globally by increasing heterogeneity in plant cover and biomes as well as decreasing plant biomass and -cover through consumption, trampling and wallowing (Johnson, 2009; Trepel et al., 2024). Moreover, fire activity has increased in grassy ecosystems in response to herbivore extinction – these grassy ecosystems have covered a larger area during the Last Glacial than today (Karp et al., 2021) – and plant taxa that coevolved with large herbivores have disappeared (Davoli et al., 2024; Johnson, 2009). The global decline of large herbivores in the context of the arrival of modern humans also has broader implications for anthropogenic climate change and biodiversity (Pringle et al., 2023; Svenning et al., 2024).

4.6. Implications for understanding human dispersal processes

In terms of human-environmental interaction, environmental preferences, and derived models of human dispersal (e.g., Shao et al., 2024), it makes a great difference whether a non-, medium- or high-forested landscape is assumed. When compared to the overall mean, the dispersal of modern humans between 60 and 43 ka is connected to a period of relatively high forest cover (Fig. 4). Absolute estimates, however, vary between 15 % and 70 % (Fig. 3) and are thus too broad for meaningful statements on ecological preferences. Nonetheless, it is conspicuous that one of the most pronounced demographic turnovers in Europe – namely the disappearance of the last Neanderthals alongside the pre-Aurignacian anatomically modern humans and the dispersal of the Aurignacian population at around 43 ka (Posth et al., 2023), coincides with a transition from a relatively high to a relatively low forest cover in the vegetation estimates with particularly inconsistent signals from the different models (Fig. 4). Despite the inconsistencies between different models for the individual time bins, the general trend indicates that a profound change in the European vegetation from rather forested to rather open landscapes with all its ecological consequences contributed to this demographic shift. The continued decrease in relative forest cover

indicates an increase in steppe or tundra environments, which may also support the idea of a decrease in net primary production (Maier et al., 2022).

During the LGM, the results indicate a roughly binary division of the European landscape (Fig. 7). From the Cote d'Azur over the Italian Peninsula and the Balkans up to the Eastern European steppe, intermediate to above-average forest cover is indicated, while the Iberian Peninsula (except the Atlantic coast), Western, and Central Europe north of the Alps and Carpathians are characterised by below-average values. Interestingly, this ecological boundary coincides with the boundary between the Epigravettian in the former area, and the Solutrean in the latter. The finding that LGM settlement areas of the Epigravettian seem to be located in intermediate to above-average forested areas while, at the same time, being (Maier et al., 2016) situated well within the zone of continuous permafrost (Stevens et al., 2025), challenges our perception of the nature of these refugial areas and concomitant human adaptation (Maier et al., 2016). Given the right conditions in favourable microclimate, boreal trees can grow in continuous permafrost, let alone the option of small isolated pockets of discontinuous permafrost that could have also occurred. Maier et al., (2016), PaleoVeg, and JSBACH agree that the western coast of the Iberian Peninsula maintained relatively mild climates and lightly forested areas – the only area in Western Europe that also maintained stable population numbers and densities throughout the climatic developments towards the LGM (Maier et al., 2016; Maier and Zimmermann, 2017).

5. Conclusions

Palaeovegetation reconstructions are an important aspect of understanding past ecosystems and how they have shaped demographic developments of hunter-gatherers across Europe during the Last Glacial period. In this study, we show that exploiting more than one dataset is required to fully utilise the potential of palaeovegetation reconstructions.

Overall, we highlight that all methods used in this study are capable of accurately reconstructing the changing vegetation throughout the late Last Glacial (70–20 ka BP) on continental scales. Irrespective of the method used, the general vegetation patterns follow the climatic variability observed in this period and thus indicate higher forest cover during early MIS 3 that gradually decreases to a minimum during the LGM. On local scales, the reconstructions may vary due to inherent uncertainties within all of the methods. Importantly, we show that absolute values of forest cover can vary by up to 40 % depending on the method and can therefore not be interpreted at face value. This is likely related to the lack of a clear definition of forest cover as well as the widely different outputs generated by each method.

The implications of these findings for the use of vegetation reconstructions with regards to demographic developments of humans in Europe during the Last Glacial are highly significant: Depending on the chosen method, a population of hunter-gatherers would have lived in a boreal forest environment or an arctic tundra with minimal vegetation. Instead, we highly recommend using relative measures and avoiding absolute values when discussing forest cover. Relative decreases in forest cover can independently of the method and unequivocally be interpreted as an opening of the landscape and vice versa. In cases where the absolute forest cover is strictly necessary, employing multiple methods and combining results can lead to a much more robust signal. However, in this case it is imperative to keep the individual method-specific limitations in mind when interpreting the results.

Pollen-based methods present snapshots of past vegetation states reflecting the local to regional interplay between different factors, such as climate, soil conditions, and flora-fauna interaction. While they typically represent a wider area, they remain limited in their geographic coverage due to the scarcity of available datasets. Therefore, pollen-based data are ideally suited to accompany e.g.,

archaeological data at specific points in time. Concerning the vegetation models in this study, JSBACH offers a considerably higher complexity compared to PaleoVeg, but lacks representation of permafrost soils, peatlands, and wetlands, which were abundant during the Last Glacial. PaleoVeg can be applied at the spatial resolution of the input predictor layers, which enables easier access to high resolution vegetation data and thus offers valuable insights when input data and model parameters are well constrained. These palaeovegetation models provide continuous data in space and time, making them powerful tools to identify broad-scale patterns such as ecosystem dynamics, migration pathways, and habitat connectivity. Such continuous data are also extremely valuable to inform suitability landscapes used to model human dispersal processes, such as the human existence potential (HEP) included in the Our Way Model Framework (e.g., Klein et al., 2021; Shao et al., 2024).

Future research will continue to improve the output of individual methods, by e.g., increasing the number of pollen records available, improving the accuracy of external parameters (such as the RPP), increasing the spatial resolution of vegetation models (e.g., by generating higher-resolution palaeoclimate data), and using more accurate calibrations of various processes within vegetation models. Nonetheless, combining methods will always provide a more comprehensive view of the palaeovegetation than a single method ever will. A promising avenue of research lies in the integration of pollen-based data into a vegetation model using data assimilation. That way, real world data from pollen archives would inform and improve vegetation models directly, rather than just being compared to at a later stage.

To facilitate the process of data exploration and interpretation, we introduce PALVEG 2.0 (https://oakern.shinyapps.io/palveg_v2/), a visualisation framework to quickly glance over the data generated in this study. The aim of PALVEG 2.0 is to help researchers identify areas/intervals of interest, explore the data in detail, and to reduce the time and effort required to get a first glance on how the palaeovegetation might have looked like based on the four different methods used in this study.

Data availability

All datasets generated in this study are available in the Zenodo database (https://doi.org/10.5281/zenodo.19630750; Kern et al., 2026).

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