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Drivers of Vegetation Structure Differ Between Proposed Natural Reference Conditions for Temperate Europe

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ABSTRACT

Aim: Pre-degradation baseline conditions (references) provide crucial context for restoration actions. Here, we compare vegetation structure and its driving processes across the main pre-agricultural references discussed for temperate Europe: the Last Interglacial and the early-mid Holocene—before and after the arrival of *Homo sapiens*, respectively.

Location: Temperate Europe.

Time Period: The first ~4000–6000 years, excluding the initial early-successional phases, of the Last Interglacial (PAAZ III) and Holocene (8700–5700 BP).

Major Taxa Studied: Plants.

Methods: We use large datasets of pollen-based vegetation reconstructions (REVEALS) to compare open vegetation, light woodland and closed forest between the two periods. We use Random Forest modelling and downscaled climate data to assess whether climate-vegetation relations were consistent between periods, as expected if they reflected direct climatic effects on vegetation.

Results: Open vegetation was slightly higher in the early–mid Holocene than in the Last Interglacial, averaging 20% versus 16% in paired grid cells, respectively. In contrast, light woodland cover was lower in the early–mid Holocene, with mean values of 49% compared to 57% in paired cells. The combined open vegetation and light woodland cover was high in both periods, averaging 73% in the Last Interglacial and 69% in the early–mid Holocene. Closed forest cover was similar across both periods (Holocene = 24%; Last Interglacial = 23%). Notably, openness –climate relations from the early–mid Holocene cannot predict open vegetation in the Last Interglacial.

Main Conclusions: These findings suggest that vegetation in the early–mid Holocene and Last Interglacial was affected by persistent, substantial disturbances, which were not controlled by direct climate effects, and that the main drivers differed between the periods, with the rich megafauna of the Last Interglacial and Mesolithic people as the primary candidates. Our findings support that early–mid Holocene ecosystems were already strongly shaped by *Homo sapiens* and differed from earlier temperate ecosystems.

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1 | Introduction

Restoration and rewilding initiatives have gained momentum in Europe over the past decade (Jepson 2016). Today, in 2024, the Global Rewilding Alliance has more member organisations in Europe than in any other region (Global Rewilding Alliance 2024), and the EU's Nature Restoration Law has set targets to restore 20% of European land and seas by 2030 (European Parliament 2024). However, the definitions of restoration and restoration success remain ambiguous, which could result in conflicting priorities and outcomes (Prach et al. 2019). Pre-degradation reference conditions provide crucial context for restoration (Willis et al. 2005, 2010); without this, efforts may be misguided, costly and time-intensive, potentially creating unsuitable habitats for existing biodiversity (Foster et al. 2003; Willis et al. 2010). In contrast, appropriate references can help to overcome shifting baseline syndrome (Pauly 1995): the idea that each generation accepts increasingly degraded nature as references for restoration. While the use of pre-human reference conditions may seem challenging given the extensive cultural modification of landscapes in Europe, they offer valuable ecological insights for understanding the processes that shaped ecosystems before intensive human transformation. It is not suggested that these periods serve as prescriptive models for restoration, but rather as references to inform contextually relevant restoration actions.

Several pre-degradation references have been suggested for restoration in Europe (Gillson et al. 2011; Monsarrat and Svenning 2022). Most commonly, reconstructions of European vegetation focus on the early–mid Holocene, after the post-glacial period but before widespread agriculture (~9000–6000 BP) (Fyfe et al. 2013; Mitchell 2004; Nielsen et al. 2012). This time predates intensive agriculture in Europe, and data from the period is plentiful. The period is also relatively close to the present, which is generally favoured over earlier references because it provides insights into ecosystems that may still have remnants or analogues existing today. The early–mid Holocene climate across Europe was generally warmer than the pre-industrial period, though this varied by season and region (Strandberg et al. 2022). Notably, warmer winters in northern Europe and drier conditions in the Mediterranean resemble present-day trends, offering insights into ecosystem responses to warming (Strandberg et al. 2022). However, today's global climate now surpasses any previous Holocene temperatures (Gulev et al. 2021). By the start of the Holocene, *Homo sapiens* had expanded into Europe, and low-intensity subsistence practices such as early agriculture, pastoralism and vegetation burning were widespread (Bocquet-Appel et al. 2012; Ellis et al. 2021). Furthermore, the expansion of modern humans across Europe is correlated with the extinction of numerous species of megafauna during the Last Glacial Period (116,000–11,650 BP) (Davoli et al. 2024; Svenning et al. 2024). Megafauna can strongly influence vegetation structure through the consumption of large quantities of vegetation, thereby altering the biomass distribution within ecological systems (Pringle et al. 2023). Additionally, their physical activities, including trampling, debarking and rooting, can result in significant disturbances to ecosystems and contribute to the creation and maintenance of open areas (Pringle et al. 2023; Svenning et al. 2024). The Late Pleistocene extinctions are likely to have reduced the impact of fauna at the landscape scale and may have had cascading effects on vegetation communities (Pearce et al. 2023; Pearce et al. 2025). Furthermore, the effect of fire use and hunting of the remaining fauna by *H. sapiens* is likely to have further altered vegetation in the early–mid Holocene (Mason 2000; Selsing 2016). Therefore, the early–mid Holocene reference condition may not reflect European ecological systems before human-induced ecological transformation.

The Last Interglacial (Eemian; 129,000–116,000 years BP) is the most recent interglacial period before the current Holocene (Kukla et al. 2002) and has been proposed as an alternative reference condition for landscape restoration (Svenning and Faurby 2017; Svenning 2002). The period was characterised by warmer temperatures than both the early–mid Holocene and the pre-industrial modern climate, with average temperatures estimated to be 1°C–2°C higher than pre-industrial. In relation to the present warming climate, the Last Interglacial serves as an important analogue, capable of illustrating how ecosystems responded to warmer conditions, despite different climate forcing and rate of change (Otto-Bliesner et al. 2021). In addition, sufficient palynological datasets are available for meaningful comparison with the Holocene, unlike for earlier interglacial periods. The Last Interglacial pre-dates both strong defaunation (Svenning et al. 2024) and *H. sapiens* expansion into Europe (Dennell 2015). Though the period was not without human influence (Nikulina et al. 2022; Roebroeks et al. 2021), as Neanderthals (*Homo neanderthalensis*) were widespread throughout the continent (Benito et al. 2017), their population densities were likely too low to influence vegetation at a wide scale (Prüfer et al. 2014). As a result, the Last Interglacial presents a valuable opportunity to study past systems in the absence of extensive human impact at a time of climatic similarity to today.

The early–mid Holocene and the Last Interglacial are increasingly well understood in terms of vegetation cover but have not been directly compared at the continental scale. Quantified vegetation cover from transformed pollen counts has shown that, during the early–mid Holocene, maximum forest cover was ~70% ± 10% and open vegetation likely covered 20%–30% of European landscapes (Githumbi, Fyfe et al. 2022; Roberts et al. 2018). In North-Central Europe, Poaceae (grasses) were found to cover 10%–15% of the landscape at 8200 BP, with *Calluna vulgaris* (common heather) covering as much as 20% of the landscape in westernmost Denmark (Nielsen et al. 2012). Across mid-latitude Europe, broadleaf, deciduous forests were found to have increased to a maximum spatially averaged cover of ~70% between 8000 and 6000 BP, with coniferous trees abundant in upland and more eastern areas (Fyfe et al. 2015; Kuneš et al. 2015; Roberts et al. 2018). However, it is worth noting that forest cover included disturbance-dependent and shade-intolerant tree species (Fyfe et al. 2015; Kuneš et al. 2015; Roberts et al. 2018). During the temperate (mesocratic) phase of the Last Interglacial, open vegetation and light woodland represented over 50% cover in the temperate forest biome (Pearce et al. 2023; Pearce et al. 2025). Light woodland cover comprised mostly *Corylus* (hazel) and *Quercus* (oak): light-demanding species that are indicative of ongoing disturbance regimes (Pearce et al. 2023). However, the drivers of vegetation structure are difficult to assess for past landscapes.

In the early–mid Holocene, landscapes were more open in Western Europe than in East-Central Europe (Githumbi, Fyfe et al. 2022, Githumbi, Pirzamanbein, et al. 2022; Serge et al. 2023). While there is disagreement as to the cause of this pattern, climate has been shown to be a strong predictor of differences in vegetation composition before the onset of agriculture in Northern and Western Europe (Marquer et al. 2017) and is expected to have also affected vegetation structure. In Denmark and North Germany, the degree of continentality and soil type are strong predictors of open vegetation in the early–mid Holocene (Nielsen et al. 2012). Similarly, in the Last Interglacial, open vegetation was negatively correlated with the degree of continentality in the temperate forest biome (Pearce et al. 2023). However, open vegetation was likely driven by factors other than climate, and a large amount of variation in open vegetation remains unexplained (Pearce et al. 2023). Other drivers, including herbivory, fire and human modification, likely shaped past vegetation structure (Pringle et al. 2023; Selsing 2016). In particular, human vegetation and fire management practices would have promoted open vegetation during the early–mid Holocene across Europe (Bishop et al. 2015; Tallavaara et al. 2015; Ordonez and Riede 2022), with smaller, more localised effects in the Last Interglacial due to a lower population size (Prüfer et al. 2014; Benito et al. 2017; Roebroeks et al. 2021). The defaunation dynamics of the Last Glacial Period likely altered the processes driving vegetation structure in Europe (Davoli et al. 2024; Svenning et al. 2024), yet no direct comparisons of continental vegetation cover exist for the Last Interglacial and early–mid Holocene (i.e. before and after widespread defaunation). Furthermore, the limited data available for non-climatic drivers make it difficult to discern their relative influence in the two periods.

Developing a deeper understanding of the processes that shaped past and present ecosystems is crucial to anticipate the effects of restoration and to shape appropriate management actions (Perino et al. 2019), including recognising the emergence of ecological novelty in the past or likely future (Hobbs et al. 2014; Kerr et al. 2024). In this study, we compare vegetation structure between two candidate pre-degradation references in temperate Europe. We test whether vegetation structure, and the climatic mechanisms driving open vegetation, were consistent between the Last Interglacial and the early–mid Holocene, before and after the arrival of *Homo sapiens* and the late-Quaternary megafauna extinctions. Comparing the climatic mechanisms driving open vegetation serves as a pragmatic approach to infer how far the magnitude of non-climatic drivers differs between the Last Interglacial and early–mid Holocene in Europe. We hypothesise that while the mechanisms shaping vegetation structure during the Last Interglacial and early–mid Holocene may be broadly similar, the relative influence of these mechanisms likely differs. This difference arises from defaunation dynamics and the more intense anthropogenic impacts on vegetation in the early–mid Holocene, which may have led to the development of novel vegetation structures not present in the previous interglacial. By examining the differences in the structure and functioning of alternative 'natural' references (the Last Interglacial, the early–mid Holocene), we provide an important context for restoration actions and question the use of historical references that include substantial human-induced landscape modification.

2 | Methods

To compare land cover between the two time periods, we used quantified vegetation abundance derived from the application of the REVEALS model (Sugita 2007) to pollen counts from the Last Interglacial (Pearce et al. 2023) ($n = 66$ sites) and the Holocene (Serge et al. 2023) ($n = 539$ sites). The REVEALS model estimates taxon-specific vegetation cover from pollen counts at a regional scale (c. 100 km distance from the sampling location [1° x 1°]; Sugita 2007). The model has been extensively tested and validated in Europe (Hellman et al. 2008; Hjelle et al. 2015) and is robust to variations in site selection, sampling design and parameter values (Mazier 2012). The selection of pollen sites, harmonisation of pollen taxonomy and parameterisation methods for the REVEALS model are comparable and outlined in Pearce et al. (2023) and Serge et al. (2023). We aggregated the taxa into land cover types as in Pearce et al. (2023), where open vegetation included all herbaceous and heath taxa; light woodland included shade-intolerant or intermediate woody taxa that cannot regenerate under closed-canopy conditions; and closed woodland included all shade-tolerant taxa and other woody taxa that did not fit into one clear group (Table S1). We examined open vegetation, light woodland and closed forest in the temperate forest biome, as defined in Pearce et al. (2023), with the neighbouring sub-Arctic and Mediterranean biomes included in the Data S1 (Europe-wide results). We focused on the mesocratic phases of vegetation development in both the Last Interglacial (Mesocratic I; Lang 1994) and the early–mid Holocene (8700–5700 BP; H. J. B. Birks 1986) as in Pearce et al. (2024). The mesocratic phase is considered the climax phase of a typical interglacial cycle and coincides with maximum vegetation biomass and fertile soils (H. H. Birks and Birks 2004). The mesocratic phase of the Last Interglacial was characterised by an initial rise in *Quercus*, *Corylus*, *Taxus* and *Tilia* (Mesocratic I), followed by an increase in *Carpinus* and *Picea* in the latter part (Mesocratic II) (Lang 1994). The vegetation composition of Mesocratic I in the Last Interglacial most closely resembles that of the Holocene mesocratic, as there is no strong expansion of *Picea* and *Carpinus* (Pearce et al. 2024). Moreover, both phases occurred within the first 4000–6000 years of their respective interglacials, excluding the initial early-successional phases. During this time, there was some presence of *Carpinus* in both periods but not yet the strong expansions seen in later stages (Pearce et al. 2024). Given the parallels in vegetation composition and the relative timing of these phases, we centre our analysis on Mesocratic I, with an additional examination of the entire mesocratic period (including Mesocratic II: the *Carpinus*/*Picea* phase) provided in the Data S1 to assess the impact of this division on our results.

For each land cover type (open vegetation, light woodland and closed forest) in each 1° by 1° grid cell, we obtained a single percentage cover estimate and standard error (SE). These values were used to compare cover estimates between time periods for grid cells in the temperate forest biome (early–mid Holocene mesocratic: $n = 342$; Last Interglacial mesocratic: $n = 49$) and all of Europe (Holocene: $n = 539$; Last Interglacial: $n = 66$; Data S1). Uncertainty (standard error [SE]) was calculated as in Pearce et al. (2023).

2.1 | Climate Data

We utilised equilibrium climate simulation outputs from 127 ka (Last Interglacial) and 6 ka (Holocene), following the PMIP4 protocol (Otto-Bliesner et al. 2017) as in Pearce et al. (2024). Climate data were generated using the GISS-E2-1-G earth system model (Kelley et al. 2020), downscaled to 5 km resolution, and bias-corrected as described by Pearce et al. (2023). Bioclimatic variables for each period were calculated as in the WorldClim dataset (Fick and Hijmans 2017) with the 'dismo' R package (Hijmans et al. 2022). The temperate forest biome was defined according to Köppen-Geiger climate classifications, following Beck et al. (2018; Figure S1), and included in our further analysis grid cells that were classified as belonging to this biome in either the Last Interglacial or the Holocene.

2.2 | Statistical Analyses

To compare percentage cover in paired grid cells ($n = 29$), we applied the Wilcoxon test, a non-parametric equivalent to the paired t-test. Note that, given the lack of paired data beyond Central Europe, paired tests will not capture differences in open vegetation cover in some areas, for example in the British Isles and Iberian Peninsula where open vegetation was much more prevalent. As a result, we are unable to make paired comparisons across broader gradients of openness likely present in the past, especially in regions with historically high levels of open vegetation.

To test for differences in the cover of the three vegetation types between all grid cells, we used beta regression using the 'betareg' package in R (Cribari-Neto and Zeileis 2010). Though the sample sizes between the Last Interglacial and the early-to-mid Holocene vary, this is more likely to capture Europe-wide effects. We accounted for climatic differences between the two periods by including the bioclimatic variables as potential drivers of vegetation structure. Backward stepwise selection was used to exclude explanatory variables based on high variance inflation factors (> 5) and correlation coefficients (> 0.2). The final model contained six explanatory variables: time period, mean temperature of the wettest quarter (°C), precipitation seasonality (coefficient of variation), precipitation of the warmest quarter (mm), precipitation of the coldest quarter (mm) and standard deviation of elevation (m). We also applied this model to the two time periods separately and without 'time period' as an explanatory variable to compare the climatic drivers of open vegetation between the periods. We used a pairwise comparison (z-test) of estimated marginal means from beta regression to test for a difference between the two time periods. For the paired and beta regression analyses, we used data exclusively from the temperate forest biome. We compare all grid cells (Europe-wide analyses) and all individual time windows (Table S2; Figure S2) in the Data S1.

We implemented a predictive modelling framework to test whether the relationship between climate and open vegetation was consistent between the Last Interglacial and the early–mid Holocene periods. We built a Random Forest model (Cutler et al. 2007) using the R package 'randomForestSRC' (Ishwaran and Kogalur 2023) for the Holocene using the bioclimatic variables derived from GISS-E2-1-G 6 K (see *Climate data*) as predictor variables and open vegetation (all grid cells) as the response variable. Random Forests consistently rank as one of the best methods for achieving high predictive model accuracy (Oukawa et al. 2022). This non-parametric method does not require a priori specification of model relationships (e.g. interaction terms). Instead, an algorithmic approach is used to learn the form of key relationships in the data by combining the predictions of many decision trees (Cutler et al. 2007). In this way, Random Forests: (a) can handle nonlinear relationships, (b) can use interactions in high-dimensional data to improve predictive performance, and (c) are relatively insensitive to collinearity between predictors (Dormann et al. 2013; Oppel et al. 2009). To avoid overfitting, randomness is introduced in each individual decision tree by using a random subset of data for tree building and a random subset of predictor variables at each split. We used the percent of variation explained (pseudo-R^2; 1—residual sum of squares/total sum of squares) with external cross-validation to assess model fit (Oppel et al. 2009).

In preparation for modelling, we split the Holocene grid cells into spatially separated sampling blocks: 60% for model building, 20% for testing and 20% for validating the final model (Figure S3). We ran multiple Random Forest iterations on the model building data, each time adjusting two key hyperparameters (node size, the size of terminal nodes: 1, 5, 10, 20; and mtry, the number of random variables tried at each split: 2, 4, 6, 8) to find the combination of values that maximised performance when predicting the testing data. The optimal values of these hyperparameters (node size = 10, mtry = 6) were then used to build the final model using both the training and testing data (80%). For hyperparameter selection, we used 1000 trees, and for our final model we used 2000 trees. The Holocene Random Forest [or predictive] model, relating climatic conditions to open vegetation, was applied to all grid cells to produce a map of predicted open vegetation across Europe in the early–mid Holocene. To assess the accuracy of this model, and resulting map, we compared the predictions and observed values for the spatially explicit validation data (20%) and produced a map of the model residuals. We calculated variable importance on the validation data by randomly permuting variables and comparing the resulting prediction error to the original (mean decrease in accuracy, MDA) (Cutler et al. 2007). This method takes into account the interactions between variables in the model, but can be affected by inflation of collinear variables that are related to the response (Nicodemus et al. 2010). Collinearity was present in the data and manifested as two general clusters related to temperature and precipitation (Figure S4).

Finally, we tested how well climate predicts open vegetation in the Last Interglacial. We used the Holocene Random Forest model and applied it to the Last Interglacial climate data to predict Last Interglacial open vegetation based solely on climate. We assessed the transferability of our Holocene model to the Last Interglacial by comparing the Last Interglacial open vegetation random forest predicition to the empirical open vegetation data estimates from the REVEALS model. If the application of the Holocene model achieves a similar accuracy in the Last Interglacial, it would suggest that open vegetation was determined by climate in a similar manner in both periods; conversely, a substantially lower prediction accuracy would indicate that non-climatic factors had greater influence on open vegetation in the Last Interglacial compared to the Holocene. For all analyses, we used R version 4.2.2 (2022–10-31). *P* value thresholds are given as graded measures of evidence, from 'little or no evidence' to 'very strong evidence' (Muff et al. 2022).

3 | Results

Overall, comparison of the vegetation in the two time periods showed that while open vegetation cover was slightly greater in the early–mid Holocene, there was slightly more light woodland present in the Last Interglacial. Importantly, the combined level of open vegetation and light woodland cover was very high in both periods. Cover of closed forest was less and broadly similar between the two time periods.

Open vegetation cover was higher in the Holocene ($\text{mean} = 31.7\% \pm 22.1\%$) than in the Last Interglacial ($\text{mean} = 17.9\% \pm 18.8\%$; all grid cells in the temperate forest biome). Pairwise comparison (z-test) of estimated marginal means from beta regression found strong evidence for this difference ($\text{estimate} = -0.139$, $p < 0.0001$; Figure 1). In contrast, light woodland cover was greater in the Last Interglacial ($\text{mean} = 58.7\% \pm 20.0\%$) compared to the Holocene ($\text{mean} = 44.2\% \pm 18.5\%$), with very strong evidence for this change ($\text{estimate} = 0.187$, $p < 0.0001$; Figure 1). Closed forest cover remained similar across both periods, with little difference observed ($\text{Holocene} = 24.1\% \pm 18.2\%$;

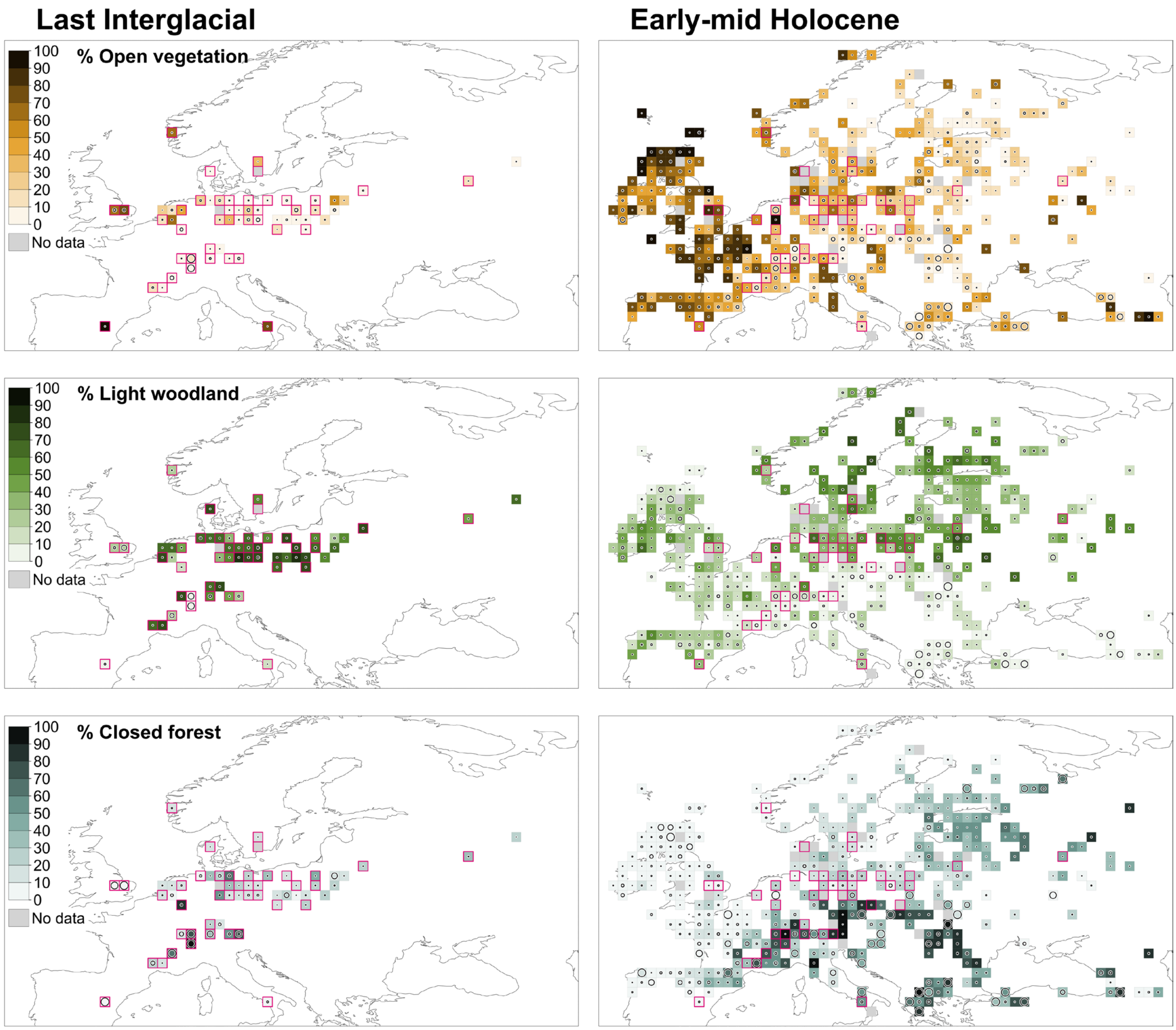

FIGURE 1 | REVEALS estimates of open (yellow), light woodland (green), and closed (blue) vegetation percentage cover in the Last Interglacial (left) and early-mid Holocene (right) in the temperate forest biome. Each square is a regional grid cell of 1° × 1°. Darker colours show greater respective cover. Paired grid cells have a pink outline. White/black circles inside each grid cell represent the coefficient of variation (standard error/REVEALS estimate). When SE ≥ REVEALS estimate, the circle fills the entire grid cell, and the estimate is considered unreliable.

Last Interglacial = 23.5% ± 17.7%; estimate = −0.002, $p = 0.978$; Figure 1).

For paired grid cells, Wilcoxon testing found moderate evidence that open vegetation was lower in the Last Interglacial (mean = 16.3% ± 17.5%) compared to the Holocene (mean = 19.7% ± 12.6%; $p = 0.048$; Figure 2; Figure S4). Conversely, there was moderate evidence for higher light woodland cover in the Last Interglacial (56.6% ± 21.4% mean cover) compared to the Holocene (49.0% ± 12.8% mean cover; $p = 0.051$; Figure 2; Figure S4). We found only weak evidence for a difference in closed forest cover (Last Interglacial = 27.1% ± 21.1% mean cover; Holocene = 31.3% ± 16.2% mean cover; $p = 0.080$; Figure 2; Figure S4).

The abundance of closed forest taxa remained largely similar between the two time periods, though *Carpinus betulus* (hornbeam) was more common in the Last Interglacial (3.3% ± 7.1%) mean cover compared to 0.2% ± 0.8% mean cover in the early–mid Holocene (Table S3). Open taxa *Calluna vulgaris* (common heather), Cyperaceae (sedges) and Poaceae (grasses) all had greater mean cover in the Holocene than the Last Interglacial (Table S3). The largest changes in individual taxon cover were in the light woodland group, where *Corylus avellana* (hazel) had almost 20% greater mean cover in the Last Interglacial (Last Interglacial: 36.8% ± 17.6%; Holocene: 16.9 ± 13.0). Deciduous *Quercus* (oak) cover had lower cover in the Holocene (Last Interglacial: 9.6% ± 6.4%; Holocene: 5.6 ± 5.9), whereas *Betula* (birch) and *Pinus* (pine) both had greater cover (6.4% and 3.3% increase, respectively; Table S3). All other taxa remained largely similar (Table S3).

In the Last Interglacial, beta regression found little to no evidence that climatic variables affected open vegetation in the temperate forest biome. The only climatic variable with any effect was mean temperature of the wettest quarter, though this was weak (estimate = −0.056, $p = 0.08$). However, there was strong evidence that the standard deviation of elevation affected open vegetation (estimate = −0.003, $p = 0.01$). Overall, the Last Interglacial model explained ~24% variation in open vegetation (pseudo R^2). In the Holocene period, there was very strong evidence for precipitation of the warmest quarter (estimate = −0.002, $p > 0.0001$) and strong evidence for precipitation of the coldest quarter (estimate = 0.001, $p = 0.01$), mean temperature of the wettest quarter (estimate = −0.044, $p = 0.01$), and standard deviation of elevation (estimate = −0.001, $p = 0.01$) affecting open vegetation. There was weak evidence that precipitation seasonality (coefficient of variation) affected open vegetation (estimate = 0.014, $p = 0.06$). Overall, the Holocene model explained ~19% variation in open vegetation (pseudo R^2).

The Random Forest model relating climate to open vegetation for the Holocene had a performance of 49% variation explained (pseudo R^2) on the spatially segregated validation data (Figure S3). Applying this model to all European grid cells produced estimates of open vegetation based solely on climate (Figure 3a). The model predicted high open vegetation generally, with the highest values in oceanic regions, particularly in Northwest Europe, and lower open vegetation in more continental regions (Figure 3a). The residuals showed that the model over-predicted open vegetation in grid cells with low levels of open vegetation and under-predicted open vegetation in grid cells with high levels of open vegetation (Figure 3b,c). In the Random Forest model, the top four predictors of open vegetation in the early–mid Holocene were mean temperature of the coldest quarter, mean temperature of the warmest quarter, mean temperature of the driest quarter, and precipitation seasonality, respectively (Figure S5). Mean temperature of the

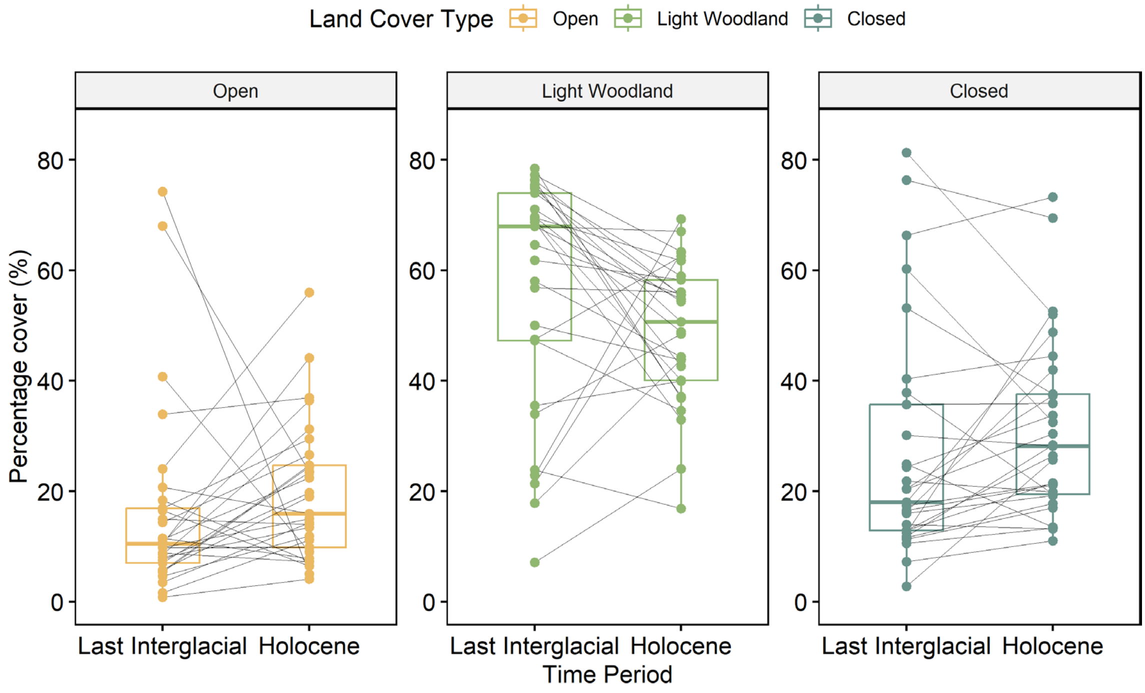

FIGURE 2 | Boxplots of open vegetation (yellow), light woodland (green) and closed forest (blue) cover for paired grid cells in the Last Interglacial and the early-mid Holocene. Grid cells are depicted by points, which are joined by grey lines to show direction of change between the two time periods.

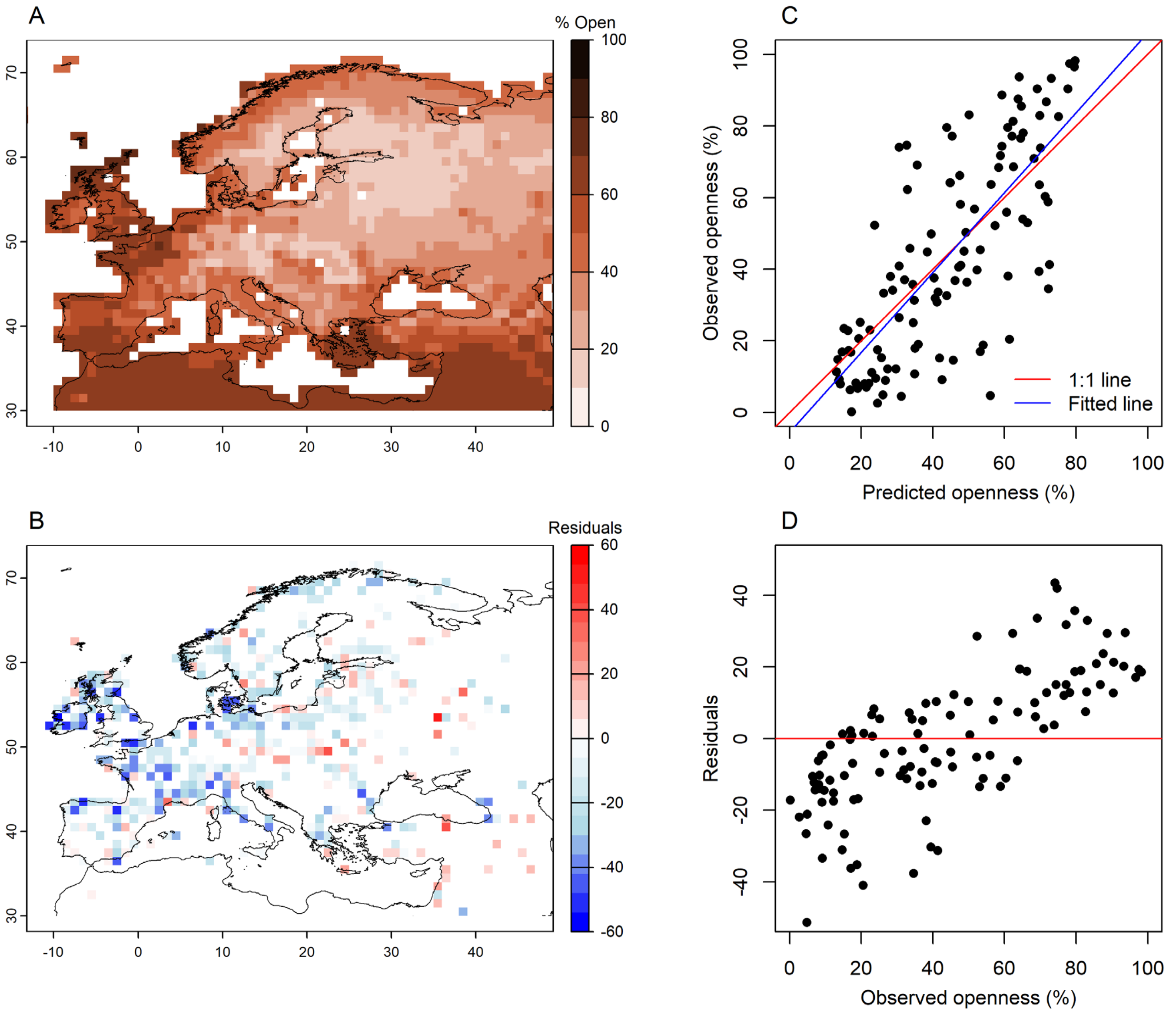

FIGURE 3 | Random Forest predictions for open vegetation (%) in the early-mid Holocene, based on 12 bioclimatic variables. (A) Predicted values of percentage open vegetation from Random Forest model. (B) Map of residuals presented as the difference between the Holocene REVEALS estimates and the Holocene climate-predicted estimates using Random Forest. (C) Holocene REVEALS estimates plotted against Holocene climate-predicted estimates using Random Forest. (D) Residual plot of residuals (*y* axis) against REVEALS estimates (*x* axis) and 1:1 line (red).

coldest and warmest quarters had particularly strong effects on open vegetation (Figures S5 and S6): we found a unimodal relationship between temperature and open vegetation, where open vegetation was negatively affected under more extreme mean temperatures (approximately $<0°C$ and $>15°C$) and positively affected under milder mean temperatures (approximately $>0°C$ and $<15°C$; Figure S6a,b).

Using the Holocene model to predict Last Interglacial vegetation from its climate data (GISS-E2-1-G 127K) resulted in poor predictive power and failed to predict open vegetation for the Last Interglacial (negative pseudo R^2; Figure 4). The model mostly predicted higher open vegetation than observed in REVEALS reconstructions of the Last Interglacial (Figure 4). Climatic variables in the Last Interglacial and Holocene followed broadly similar distributions (Figure S7), so differences in climatic range could not explain the disparity between these relationships. This equivalence was true for the main predictors of open vegetation in the Holocene, though precipitation of the coldest quarter was slightly higher and more variable in the Holocene (Figure S7). Overall, precipitation variables had generally slightly higher and temperature variables slightly lower values in the Holocene compared to the Last Interglacial (Figure S8).

4 | Discussion

Our comparison of vegetation structure and its drivers between two proposed restoration references revealed three principal findings. First, open vegetation was slightly higher in the early–mid Holocene compared to the Last Interglacial. Second, light woodland cover was slightly lower in the early–mid Holocene. Importantly, the combined level of open vegetation and light woodland cover was high in both periods. Third,

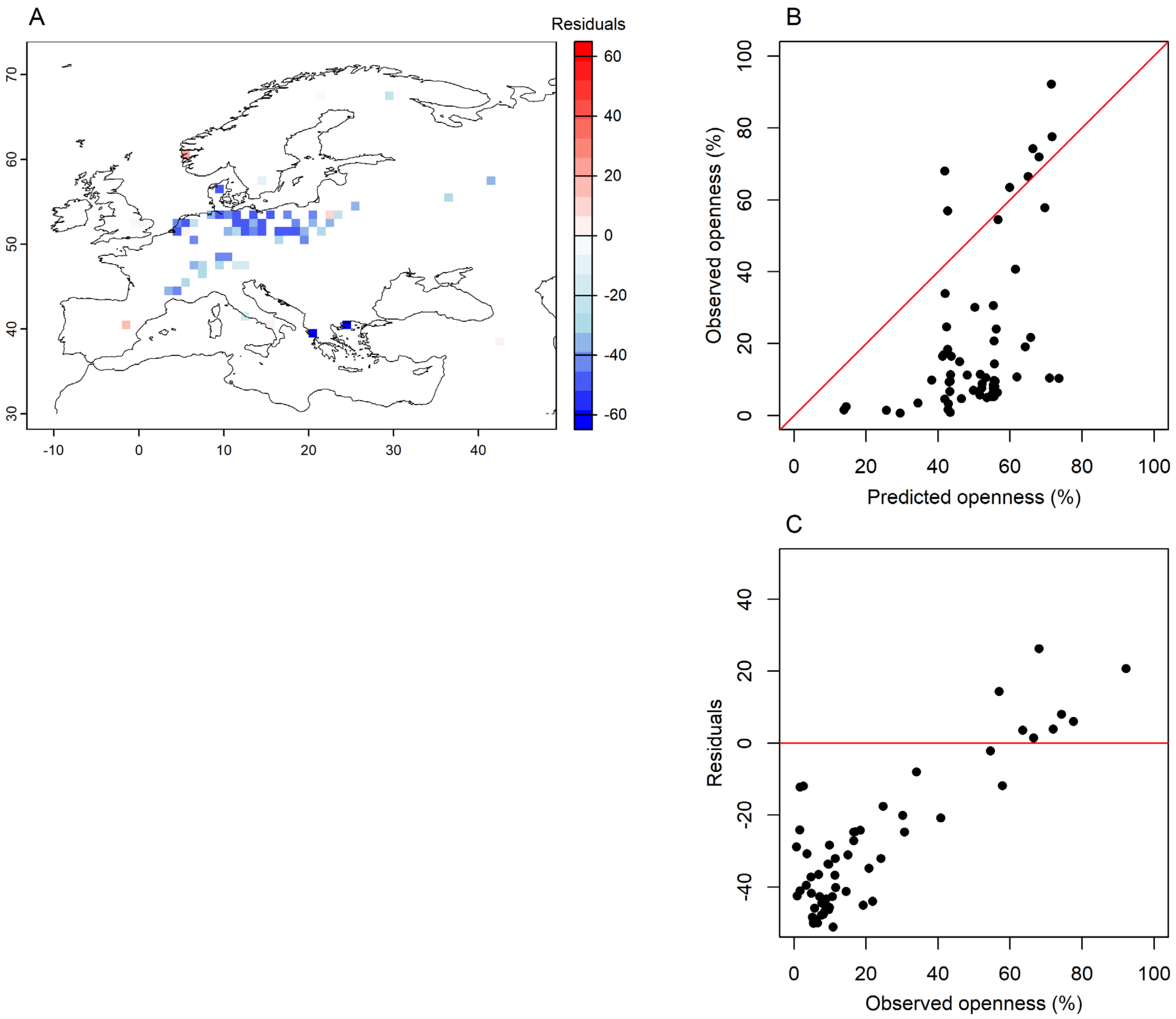

FIGURE 4 | Random Forest predictions for open vegetation (%) in the Last Interglacial. (A) Map of residuals presented as the difference between the Last Interglacial REVEALS estimates and the Last Interglacial climate-predicted estimates using Random Forest. (B) The Last Interglacial REVEALS estimates plotted against the Last Interglacial climate-predicted estimates using Random Forest. 1:1 line is shown in red. (C) Residual plot of residuals (*y* axis) against REVEALS estimates (*x* axis) and 1:1 line (red).

climatic predictors did not explain open vegetation cover in the Last Interglacial, and the predictors of open vegetation cover in the Holocene could not predict open vegetation in the Last Interglacial. These findings indicate that during the Holocene and Last Interglacial periods, landscapes exhibited differences not only in vegetation structure but also in the intensity of the mechanisms influencing it. Furthermore, the primary structural patterns and variances cannot be solely attributed to direct climate effects.

In the Holocene, Random Forest modelling found that the climate variables in our model were moderately successful in predicting open vegetation. We found a unimodal relationship between temperature extremes and open vegetation, where open vegetation was negatively affected under more extreme mean temperatures and positively affected under milder mean temperatures (Figure S6a,b). This observation aligns with our broader finding of higher open vegetation in oceanic Europe compared to continental Europe (Figure 3). Oceanic climates are characterised by milder temperatures due to moderation by large bodies of water (i.e. the North Sea and Atlantic Ocean). However, from a plant ecological perspective, the relationship we found between temperature and open vegetation is counterintuitive. Typically, in colder climates, less tree cover (and therefore more open vegetation) is expected due to the shorter growing seasons, lower temperatures and often poorer soil quality (Schlesinger and Bernhardt 2020). Hotter and drier climates are also generally expected to result in reduced tree cover (and more open vegetation) due to lower water availability (Larcher 2003). While we did find a small positive effect of mean temperature of the driest month on open vegetation (Figure S6c), the effect was smaller (Figure S6) and less important (Figure S5) than mean temperature of the warmest quarter and mean temperature of the coldest quarter. While climatic predictors did not explain open vegetation cover in the Last Interglacial, the standard deviation of elevation was a significant predictor and had a negative correlation with open vegetation. This may indicate lower herbivore impacts in steeper terrain, where access and therefore grazing pressure could be reduced, contributing to more closed vegetation in these areas (Berti and Svenning 2020).

Higher open vegetation in oceanic areas has been described previously for Europe in the Holocene (Githumbi, Fyfe et al. 2022, Githumbi, Pirzamanbein, et al. 2022). The continentality gradient originating from the North Sea (Giesecke et al. 2008) has been shown to influence vegetation patterns observed in Northwest and Central Europe in the early and mid-Holocene (Kalis et al. 2003; Nielsen et al. 2012). It has been suggested that, in coastal regions, the oceanic climate promoted the formation of extensive raised bogs (Nielsen et al. 2012). It is also possible that higher wind speeds in oceanic regions could influence open vegetation, as strong winds have been linked to tree mortality (Wolf et al. 2004) and wind speeds decrease progressively from the North Sea towards the east and south (Yan et al. 2002). It is also possible that the relationship between continentality and open vegetation that we observe in the Holocene was driven by an unmeasured factor that is correlated to climate, rather than by climate itself. Notably, human population density was likely higher in Western (oceanic) Europe and lower further East (continental Europe) at 13 kya (Tallavaara et al. 2015; Ordonez and Riede 2022) and *Homo sapiens* are known to have shaped European landscapes before the spread of agriculture via low-intensity subsistence practices, vegetation burning and indirectly by hunting megafauna (Ellis et al. 2021).

Our climate-based model was unable to predict open vegetation in the Last Interglacial. The temperatures were slightly warmer, and precipitation was slightly lower in the Last Interglacial compared to the early–mid Holocene. This could have several important implications for predicting open vegetation. Under classic temperature –vegetation theory, vegetation zones may have been shifted poleward or to higher elevations compared to those during the Holocene (Overpeck et al. 2006). Furthermore, warmer temperatures in the Last Interglacial could have accelerated the growth and reproduction rates of certain plant species, leading to denser vegetation in some regions. On the other hand, considerably higher temperatures and lower precipitation may limit vegetation and lead to increased open vegetation in very warm areas (Larcher 2003). Nonetheless, while there were differences in the spatial pattern of climate variables between the Holocene and the Last Interglacial, we found that their overall range and distribution were similar (Figure S7). Shifts in the climatic range are therefore unlikely to explain the disparity in climate –vegetation relationships between the two time periods.

Given that the constituent plant taxa are largely identical between the Holocene and Last Interglacial periods (Lang 1994; Beaulieu and Reille 1984), we would expect consistent climate –vegetation relationships between the two time periods if climate was the principal driver of vegetation structure via physiological responses. As we found that climate –vegetation relationships varied between the Holocene and the Last Interglacial, we suggest that open vegetation in the Last Interglacial was not determined by climate in a similar manner to the Holocene. It is likely instead that climate –vegetation relationships were mediated by non-climatic factors that differed between the two periods (Selsing 2016; Smith et al. 2018).

Our finding of substantial and slightly higher open vegetation in the Holocene compared to the Last Interglacial was unexpected. Vegetation is either resource- or consumer-mediated (Bond 2005), and we hypothesised that the defaunation dynamics of the Last Glacial Period (Svenning et al. 2024) would have cascading effects on open vegetation in the early–mid Holocene. Megafauna alter vegetation biomass distribution and contribute to the creation and maintenance of open areas (Malhi et al. 2016). We expected that reduced megafauna populations would result in less open vegetation in the Holocene due to reduced vegetation consumption (Davoli et al. 2024; Svenning et al. 2024). As this was not the case, additional consumer or resource mechanisms likely drove open vegetation in the early–mid Holocene. However, light woodland cover was less prevalent in the Holocene than during the Last Interglacial. Though this difference was small, this could indicate a reduction of the intermediate and transitional habitats that reflect natural disturbance regimes (Bobiec et al. 2018). This raises questions as to the drivers of vegetation structure in the two periods and how they differed.

It is likely that *H. sapiens* affected vegetation structure in the early–mid Holocene, even before the advent of agriculture. Anthropogenic land use estimates for the Holocene have shown that, as early as 12,000 BP, only 3.9% of global temperate woodlands were uninhabited wildlands (Ellis et al. 2021). Hunter-gatherers and early pastoralists shared regional landscapes in the Mesolithic (Battentier et al. 2018) and altered them with low-intensity subsistence practices (Ellis et al. 2021; Nikulina et al. 2022). Practices such as hunting, vegetation burning, nomadic settlements and tree felling had ecologically transformative effects on vegetation structure (Ellis et al. 2021; Nikulina et al. 2022; Smith et al., Smith 2011). The resulting land clearance (Innes et al. 2013) may have driven open vegetation to a level exceeding that of the Last Interglacial.

Fire dynamics may explain the higher open vegetation in the early–mid Holocene compared to the Last Interglacial. Fire was more prevalent across Europe during the Holocene period. In the British Isles, 9% of early Holocene beetle species were fire-adapted, compared to none in the Last Interglacial (Sandom et al. 2014). Fire-sensitive *Taxus* was almost 90% more abundant, on average, in the Last Interglacial compared to the early–mid Holocene in European temperate forests (Pearce et al. 2024). In the Mediterranean, Holocene charcoal influx was greater and more variable than during the Last Interglacial (Lawson et al. 2013). Similarly, in Northwest Europe, the late Mesolithic saw repeated fires in woodlands, promoting a mosaic of vegetation (Innes et al. 2013). Increased fire frequency is globally linked to *Homo sapiens* through direct burning and megafauna loss (Karp et al. 2021), likely contributing to more frequent fires in temperate Europe during the early–mid Holocene (Pokorný et al. 2022). While natural fire regimes in European deciduous forests are subject to debate, human influence is considered a primary factor in the higher fire activity seen during this period (Feurdean et al. 2019). In Southwest Germany, frequent low-intensity fires and vegetation disturbances coincided with phases of Mesolithic occupation (Heidgen et al. 2022). This intentional fire use likely expanded open areas for resources such as hazel, aiding subsistence strategies during this period (Heidgen et al. 2022). Similarly, in the Southeastern Iberian Peninsula, fire peaks did not coincide with dry periods but were linked to Mesolithic practices, revealing a strong anthropogenic influence on fire regimes (Sánchez-García et al. 2024). Our findings are consistent with higher fire presence in the early–mid Holocene compared to the Last Interglacial. Frequent, low-intensity fires are associated with the presence of *C. vulgaris* (common heather), *Pinus* (pine) and *Betula* (birch) (Molinari et al. 2020; Feurdean et al. 2019; Whitehouse 2000). *C. vulgaris* rapidly produces seeds post-fire, and its meristems are located below-ground, where they are protected by the soil and facilitate regrowth after fire (Molinari et al. 2020). Despite having fast-flammable needles, *Pinus* grow quickly and self-prune lower branches to increase the fuel gap and become non-flammable (Pausas et al. 2017). *Betula* quickly colonise post-disturbance soils and resprout vegetatively (Carter et al. 2018). Our findings of higher percentages of *C. vulgaris*, *Pinus* and *Betula* in the early–mid Holocene support this increased fire presence.

Effects on individual taxa may provide insight into the different processes driving open vegetation in the Last Interglacial and Holocene. Whilst fire may have driven the distributions of certain species in the Holocene, *Corylus*, *Quercus* and *C. betulus* were more abundant in the Last Interglacial. Whilst these species are fire-tolerant, they are not as fire-adapted as *C. vulgaris*, *Pinus* and *Betula* (Molinari et al. 2020). It is possible that the lower fire frequencies but higher herbivory pressure of the Last Interglacial (Sandom et al. 2014) favoured *Corylus*, *Quercus* and *C. betulus*. *Quercus* seed dispersal and recruitment occur mostly in dynamic, variegated landscapes and the species fails to regenerate under a closed canopy (Bobiec et al. 2018). Similarly, *Corylus* is usually indicative of open and scrub woodland subject to ongoing disturbance, and successfully resprouts very quickly (Leonardsson and Götmark 2015). In modern ecosystems, *Corylus* and *Quercus* are often found in traditionally grazed areas (Bobiec et al. 2011). *C. betulus*, due to its ability to develop a 'cage' architecture, survives severe herbivory regimes more readily than other dominant European tree species (Churski et al. 2022). These mechanisms would have favoured *Corylus*, *Quercus* and *C. betulus* in the Last Interglacial, whereas, despite being rather fire-tolerant, they may have been outcompeted by more fire-favoured species in the Holocene.

Of the open taxa, proportions of Cyperaceae, Poaceae and *C. vulgaris* changed most between the two time periods; all three were more abundant in the Holocene compared to the Last Interglacial. Cyperaceae exhibited the largest difference, which may present a wetland signal in the Holocene that is consistent with the cooler, wetter climate patterns (Barrett 2013). However, *C. vulgaris* and other heath taxa are not specifically associated with wetlands but also had a higher abundance in the Holocene. It is likely instead that the open landscapes and light-canopy conditions in the early–mid Holocene benefitted Cyperaceae. Furthermore, fire effects on moist grasslands and mires, where *C. vulgaris*, *Pinus* and *Betula* can all grow, may have further increased Cyperaceae populations (Whitehouse 2000).

Our findings are partly consistent with other studies of Holocene open vegetation. Pollen-based reconstructions showed that, during the early–mid Holocene, open vegetation likely covered ~30% of European landscapes (Githumbi, Fyfe et al. 2022, Githumbi, Pirzamanbein, et al. 2022), which is consistent with our findings here. However, previous studies have concluded that, across Europe, coniferous and deciduous forests reached a spatially averaged extent of ~70% (Fyfe et al. 2015; Githumbi, Fyfe et al. 2022; Githumbi, Pirzamanbein, et al. 2022; Kuneš et al. 2015). We found that, in the early–mid Holocene, dense, closed-canopy forests only reached a spatially averaged extent of ~25% cover, and that light woodland was the dominant vegetation cover. We attribute this difference to previous studies grouping taxa into broad 'arboreal' and 'non-arboreal' categories to indicate closed and open landscapes (Roberts et al. 2018). In this study, we defined vegetation cover by the ecological requirements and niches of the taxa investigated and included a light woodland category for trees that are unable to regenerate under closed-canopy conditions (Bobiec et al. 2018; Coppins and Coppins 2003). In doing so, we show that open and light-woodland taxa dominated both the Last Interglacial and Holocene periods, rather than the closed-canopy forests often envisioned.

5 | Conclusions

In this study, we compared vegetation structure and its drivers between two pre-degradation reference conditions in temperate Europe. Our analysis reveals that not only did these references differ in vegetation structure, but also in the underlying mechanisms shaping it. Holocene conditions, even those preceding agriculture, diverge from earlier temperate woodland landscapes that existed before the arrival of *H. sapiens* in Europe and were likely altered by human activities such as defaunation and fire use. This supports findings that temperate woodlands were not uninhabited wildlands at the start of the Holocene (Ellis et al. 2021). Consequently, Holocene reference conditions may not adequately predict future ecosystem responses to land abandonment and trophic rewilding, nor represent the optimal conditions under which Europe's biodiversity evolved. We recommend restoration strategies focus on reinstating lost ecosystem processes and draw on reference conditions that better reflect the evolutionary, long-term state of European landscapes.

Author Contributions

J.-C.S., E.A.P., C.W.D., F.M., R.F. and S.N. designed the research; F.M., M.-A.S. and P.S. contributed data; E.A.P. and C.W.D. analysed the data; E.A.P. wrote the paper, with input from all co-authors.

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Ethics Statement

The authors have nothing to report.

Consent

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data used in this study are available from data.InDoRES: https://doi.org/10.48579/PRO/J5GZUO (Holocene; Serge et al. 2023) and OSF: https://doi.org/10.17605/OSF.IO/NEJBZ (Last Interglacial; Pearce et al. 2024). The R code is available from OSF: https://doi.org/10.17605/OSF.IO/G93SJ.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.