

## Beyond the closed-forest paradigm: Cross-scale vegetation structure in temperate Europe before the late-Quaternary megafauna extinctions

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### ABSTRACT

The Last Interglacial (~129,000–116,000 years ago) provides key insights into temperate European vegetation dynamics before significant anthropogenic impacts. Using LOVE (Local Vegetation Estimates) and REVEALS (Regional Estimates of VEgetation Abundance from Large Sites) models, this study reconstructs vegetation patterns across local (~9 km<sup>2</sup>) and regional (~100 km<sup>2</sup>) scales. Local landscapes presented a heterogeneous mosaic, with averages of 17 % open vegetation, 21 % closed forests, and 63 % light woodlands, reflecting high fine-scale heterogeneity. Importantly, weak local-regional correlations highlight the importance of localised drivers. Longitude and, to a lesser extent, precipitation explained some variation in local vegetation openness, but heterogeneity remained unexplained, emphasising the role of disturbance regimes. Shannon diversity and evenness varied widely, indicating a mix of species-rich and more uniform habitats and reflecting diverse ecological dynamics. Beta diversity showed high spatial turnover, suggesting composition was shaped by localised factors rather than uniform climatic drivers. Frequently represented genera, such as *Artemisia*, *Heli-anthemum*, *Erica*, *Filipendula*, and *Plantago*, indicate diverse open and semi-open habitats, shaped by disturbances and hydrological variability. Weak climatic correlations and dominance of disturbance-adapted taxa suggest active disturbance-shaped vegetation. Large herbivorous mammals (megafauna) likely maintained vegetation openness through grazing and browsing; there is limited evidence for frequent fire activities in this period. These findings challenge the closed forest paradigm for interglacials, revealing substantial openness and heterogeneity. This scale-explicit evidence of Last Interglacial vegetation complexity offers insights into the biodiversity and

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ecological functionality of pre-anthropogenic ecosystems, with implications for modern conservation and rewilding, particularly in maintaining diversity through disturbance and megafaunal interactions.

## 1. Introduction

The Last Interglacial (Eemian; ~129,000–116,000 years ago) provides a valuable opportunity to study the structure and dynamics of vegetation in Europe's temperate forest biome before significant human-driven ecological changes. This period predates the arrival of *Homo sapiens* in Europe and the associated widespread declines of large herbivores—key factors that likely transformed natural ecosystems over time (Bergman et al., 2023; Davoli et al., 2024; Svenning et al., 2024a). These changes are compounded by the extensive habitat transformations caused by early land use practices (Fyfe et al., 2013; Horsák et al., 2019; Nielsen et al., 2012), which continue to impact even the remaining forests and semi-natural vegetation (e.g., Ellenberg, 1988; Peterken, 1996). By examining the ecosystems of the Last Interglacial, we can better understand pre-anthropogenic vegetation structures, the processes that shaped them, and the drivers of biodiversity in temperate biomes.

The temperate forest biome has traditionally been hypothesised to consist of dense, closed forests in the absence of human impacts (Bradshaw and Mitchell, 1999; Breckle, 2002; Ellenberg, 1988; Peterken, 1996). However, alternative perspectives have long highlighted the role of large herbivores as dominant drivers of vegetation structure (Owen-Smith, 1988; Zimov et al., 1995). This perspective gained prominence with Vera's (2000) influential wood-pasture hypothesis, which emphasised the role of large herbivores in shaping open landscapes, particularly in Mesolithic Europe. Shortly thereafter, a qualitative review of Middle and Late Pleistocene interglacial paleoecological evidence supported the idea of heterogeneous vegetation in northwestern Europe under climates similar to today, shaped by geodiversity and climate, and pre-dating *Homo sapiens*' arrival (Svenning, 2002). By contrast, palynological studies from the European Holocene record provided evidence countering the Vera hypothesis (Mitchell, 2005). Later reviews and synthetic analyses incorporating palaeobotanical and palaeozoological data endorsed greater heterogeneity in vegetation during the Mesolithic and the Last Interglacial (Fyfe, 2007; Whitehouse and Smith, 2010; Sandom et al., 2014), also highlighting significant differences in vegetation structure between these periods (Sandom et al., 2014). More recently, quantitative estimates of regional vegetation cover derived from pollen data have revealed higher levels of openness across Europe during the Last Interglacial and the Mesolithic. These findings have renewed debates about the key drivers of vegetation structure (Nielsen et al., 2012; Serge et al., 2023; Pearce et al., 2023). At the same time, it is increasingly clear that ecosystems in the early Holocene were widely occupied and shaped by human activities (Ellis et al., 2021), making studies on the Pleistocene interglacials important for assessing non-anthropogenic states (cf. Svenning, 2002). Pollen-based reconstructions using the REVEALS (Regional Estimates of VEgetation Abundance from Large Sites) model have shown that light woodland and open vegetation represented substantial proportions of regional-scale land cover during the Last Interglacial in Europe (Pearce et al., 2023). On average, more than 50 % of the temperate forest biome consisted of light woodland and open vegetation, with considerable geographic heterogeneity likely driven by disturbance from large megafauna (Pearce et al., 2023). Further evidence for substantial open and semi-open vegetation in the Last Interglacial has also come from other palaeoecological proxies, e.g., beetle, mollusc, and small-vertebrate assemblages (Alexandrowicz and Alexandrowicz, 2010; Sandom et al., 2014; Langford et al., 2017; Stefaniak et al., 2023) and dietary studies of large herbivores (e.g., Stefaniak et al., 2021).

Despite this growing body of evidence, quantitative studies of vegetation cover have focused on regional scales (Pearce et al., 2023,

2024). Such studies provide valuable insights into broad patterns but do not provide estimates of finer-scale heterogeneity. This is a critical gap, as local-scale vegetation structures may be shaped by specific environmental factors, such as microclimatic variations, topographic complexity, and small-scale disturbance regimes, which cannot be captured at higher spatial resolutions (Svenning, 2002; Fyfe, 2007). Understanding local-scale vegetation heterogeneity is also crucial for evaluating biodiversity capacity, as it directly determines the availability of diverse habitats for species with varying ecological requirements. Importantly, a large proportion of temperate forest-associated species in Europe prefer semi-open and open canopy conditions (Müller et al., 2013; Hilmers et al., 2018; Kwiatkowska, 1994; Lachat et al., 2016; Vild et al., 2024), thus the presence of such habitats at local and regional scales would have strong implications for pre-anthropogenic biodiversity levels. The impact of spatial scale on measures of heterogeneity has been acknowledged within landscape ecology for decades (e.g., Delcourt and Delcourt, 1988; Turner et al., 1989). Without local-scale estimates, we risk oversimplifying the dynamics of interglacial ecosystems and underestimating their complexity. To address these gaps, this study applies the Landscape Reconstruction Algorithm (LRA) to pollen data from the Last Interglacial, a method that integrates local-scale vegetation reconstructions using the LOVE (LOcal VEgetation Abundance) model with regional-scale reconstructions from the REVEALS model (Sugita, 2007a, b). This approach enables a detailed assessment of vegetation openness and heterogeneity at multiple spatial scales during the Last Interglacial.

The key questions addressed by this study are: 1) What were the levels and patterns of local-scale vegetation openness and heterogeneity in temperate Europe during the Last Interglacial, and how did these vary across different environmental settings? 2) To what extent do local vegetation patterns reflect regional-scale trends, and what factors drive the observed differences between these spatial scales? 3) How did climatic, topographic, and other geoenvironmental variables influence the structure and composition of vegetation mosaics during this period?

By addressing these questions, our study seeks to provide a more nuanced understanding of interglacial vegetation dynamics and their implications for biodiversity and ecosystem functioning. Further, based on our empirical findings, we discuss what insights the findings provide about biodiversity capacity and ecological functionality within the temperate biome in Europe prior to the immigration of modern humans (*Homo sapiens*). Although this study focuses on the Last Interglacial, the insights gained offer broader relevance for understanding temperate-biome ecosystems before significant anthropogenic impacts, a topic we further discuss along with implications for environmental management strategies in the Anthropocene.

## 2. Methods

### 2.1. Data set and study area

We used pollen data from the Last Interglacial period (Eemian, MIS 5e), as presented by Pearce et al. (2023), to reconstruct local and the associated regional vegetation composition. Our focus was on the Mesocratic I phase (Early Temperate; *Quercus-Corylus* phase), which falls within the warm-climate optimum, a forested (*sensu lato*) period lasting 11–18,000-years in Central Europe (Felde et al., 2020). Mesocratic I represents a central phase in this forested period, characterised by maximum vegetation biomass and occurring well before the onset of soil fertility decline (Felde et al., 2020). We used the Landscape Reconstruction Algorithm (LRA, Sugita 2007a, 2007b) to quantify regional and local vegetation abundance from pollen data. The LRA

consists of two models: the REVEALS model, which estimates regional vegetation, and the LOVE model, which estimates local vegetation.

The REVEALS model estimates regional vegetation cover over large areas (grid cells;  $\sim 100 \text{ km}^2$ ) based on pollen data, preferably from large lakes ( $> 100 \text{ ha}$ ). However, pollen counts from multiple small lakes and/or bogs may also be used to achieve reliable results, though with larger error estimates (Sugita 2007a; Sugita et al., 2010; Mazier et al., 2012; Fyfe et al., 2013; Trondman et al., 2016). REVEALS relies on relative pollen productivity estimates and fall speed of pollen for key taxa, as well as corrections for differential pollen transport and deposition (Sugita 2007a; Hellman et al., 2008). For each grid cell, the LRA requires one large site to calculate regional vegetation abundance and at least one smaller (1–50 ha) site for local vegetation reconstruction. For grid cells with multiple potential sites but no large lakes ( $> 100 \text{ ha}$ ), we employed a "leave-one-out" approach ( $n = 6$ , Sugita et al., 2010) to reconstruct local plant abundance around each target site. Pollen data from the 'target' site of each run were used as input to the LOVE model but excluded from the REVEALS regional vegetation estimates. In total, we applied the REVEALS to sites distributed across 10 grid cells (Table S1).

The LOVE model (v.7.0) was used to estimate local vegetation abundance within smaller areas ( $9 \text{ km}^2$ ), integrating results from REVEALS to account for regional pollen contributions (Sugita 2007b). For this study, LOVE was applied to 31 sites (Table S1). Several sensitivity runs were conducted to evaluate the impact of standard error (SE) inputs and assumptions about the spatial scale of pollen source areas. Specifically, the Relevant Source Area of Pollen (RSAP), which defines the spatial scale of local vegetation reconstruction, and the Nearest Source Area of Pollen (NSAP), which applies to single-site estimates, were considered. The RSAP was determined using the "leave-one-out" approach, where the final RSAP value was set to the maximum value observed across sites in a given gridcell (Sugita et al., 2010). Following test runs, a fixed RSAP of 1690 m was adopted for the final reconstructions. This RSAP value aligns with previous estimates for similar-sized basins and landscapes (Hjelle et al., 2015). Sensitivity tests of SE values (0.1, 0.3, and 0.5) confirmed that an SE of 0.5 was appropriate for the final analysis.

## 2.2. Local open vegetation

To assess the influence of environmental conditions on vegetation openness, a beta regression model with a logit link function was fitted using the betareg package (v3.2.0; Cribari-Neto and Zeileis, 2010) in R. We used climatic, topographic and spatial variables as predictors (Supplementary Material). To address potential multicollinearity among predictors, we assessed variance inflation factors (VIF) using a stepwise selection procedure. Climate variables with  $VIF > 5$  were excluded. The final model included local longitude, elevation, and three bioclimatic variables (mean temperature of the wettest quarter, mean temperature of the driest quarter, and precipitation of the coldest quarter) as predictors. Open vegetation (%) was the response variable, and all continuous predictors were standardised to facilitate interpretation of effect sizes. Model precision was estimated with an identity link. Maximum likelihood estimation was used, and model fit was evaluated using pseudo  $R^2$  and residual diagnostics.

We assessed the relationship between local and regional open vegetation, light woodland, and closed forest cover using Pearson's correlation coefficients. We investigated whether differences in vegetation openness between local and regional scales were associated with corresponding differences in climate conditions. Predictor variables were selected using the same stepwise selection procedure as above. We calculated the difference between local and regional conditions for the resulting variables: mean temperature of wettest quarter, mean temperature of driest quarter, precipitation seasonality, precipitation of warmest quarter, and precipitation of coldest quarter. We applied a linear model with the difference in vegetation openness as the response

variable and the selected bioclimatic differences as predictors.

## 2.3. Local vegetation heterogeneity

Shannon diversity (H) and evenness (J) indices were calculated using the REVEALS/LOVE taxa for each study site to evaluate patterns of biodiversity and species abundance distributions. The mean, median, minimum, and maximum values of these indices were summarised across sites. A linear regression model was then constructed to assess the relationship between local diversity (H) and environmental predictors selected using the stepwise procedure. Final predictors were local longitude, mean temperature of the wettest quarter, mean temperature of the driest quarter, precipitation of the coldest quarter, and elevation.

We assessed whether differences in beta diversity could be attributed to local-regional differences in climate variables. We applied a Bray-Curtis dissimilarity matrix using the vegdist function in the vegan package (Oksanen et al., 2007) to quantify beta diversity for all site pairs (regional and local data). For each grid cell, mean Bray-Curtis distances were calculated by averaging the pairwise beta diversity values across all relevant site pairs. We then fitted a linear regression model with Bray-Curtis dissimilarity (per site) as the response variable and climate difference variables (difference = regional - local) as predictors. Following the stepwise selection process, the final climate variables were mean temperature of wettest quarter, mean temperature of driest quarter, precipitation seasonality, precipitation of warmest quarter, and precipitation of coldest quarter.

To better understand the composition and ecological characteristics of open vegetation, we examined the full community, including non-REVEALS taxa (genus level), of herbs, graminoids, and dwarf shrubs from the wider pollen dataset used in Pearce et al. (2023), representing 96 sites at the genus level. Dominant taxa were identified by those represented across the most sites, and their ecological preferences were inferred through expert consultation and using published literature to characterise their likely habitat associations and the environmental settings they represent (Chytrý et al., 2024). Whilst not an accurate measure of the percentage abundance of these taxa, the presence of specific taxa as indicators of open vegetation structure and functioning offered deeper insights into the ecological dynamics of these systems.

In all analyses, all continuous predictor variables were standardised to improve interpretability of effect sizes. All analyses were conducted in R version 4.4.1.

## 2.4. Climate data

We used equilibrium climate simulations for 127 ka conducted according to the PMIP4 protocol (Otto-Bliesner et al., 2017). Specifically, we used outputs from the GISS-E2-1-G Earth system model (Kelley et al., 2020), as employed in Pearce et al. (2023). This model was selected based on its superior ability to represent the distribution of *Ilex* (holly) as an indicator of oceanic climate, aligning well with evidence that oceanic conditions extended further east during the Last Interglacial (LIG) than today (Pearce et al., 2023). This alignment was confirmed by comparisons with recent Maximum Likelihood Classification analyses, which highlighted that GISS-E2-1-G captured this feature more effectively than other models (Pearce et al., 2023). Temperature and precipitation fields were downscaled to a 5-km resolution and bias-corrected, following the methodology described in Pearce et al. (2023). For regional climate, we calculated the mean value for each grid cell, while local climate was represented by the conditions at the specific location where the pollen data was collected. Bioclimatic variables were derived using the approach outlined by WorldClim (Fick and Hijmans, 2017) using the 'dismo' package in R (Hijmans et al., 2022).

### 3. Results

#### 3.1. Local vegetation openness and heterogeneity

Open vegetation locally accounted for 17 % (SD = 23) of the landscape, on average, while closed vegetation represented a similar proportion at 21 % (SD = 17). In contrast, light woodland, supporting taxa such as *Corylus* (hazel; mostly *C. avellana* [common hazel]) and deciduous *Quercus* (deciduous oak species, mostly *Q. robur* and *Q. petraea*) that rely on sunlit conditions for regeneration and persistence, dominated the landscape with a mean value of 63 % (SD = 23; Figs. 1, 2).

Shannon diversity (H) values across the study sites ranged from 0.56 to 2.09, with a mean of 1.49, indicating moderate species diversity overall. Evenness (J), which reflects the uniformity of species abundance distribution, ranged from 0.23 to 0.84, with a mean of 0.57, suggesting that species were unevenly distributed across most sites.

#### 3.2. Local vs regional scale

Compositionally, local vegetation tended to moderately reflect regional vegetation, with *Corylus*, *Pinus* and Poaceae most dominant locally, and *Corylus*, Poaceae and deciduous *Quercus* most dominant regionally (Table 1). In terms of vegetation structure, we found that the proportion of local open vegetation was only weakly correlated to regional open vegetation of the same gridcell ( $r = 0.32$ ), but that local light woodland was not correlated to regional light woodland ( $r = -0.18$ ), and local closed forest was not correlated to regional closed forest ( $r = -0.11$ ; Fig. 3, S1, S2). These results show the existence of substantial variability in vegetation structure across scales, i.e., the local prevalence of open vegetation or closed forest, for example, was often much higher or lower than the general regional level.

#### 3.3. Floristic interpretation

The local-scale, dynamic mosaic structure of the vegetation during the Last Interglacial (early temperate) is also indicated by the most frequently represented genera of shrubs and small trees (Table 2) and herbs and dwarf shrubs (Table 3). Prominent shrubs and small trees such as *Corylus avellana* (hazel), *Taxus baccata* (yew), *Juniperus* (juniper), *Ilex aquifolium* (holly), and *Viburnum* (guelder-rose, wayfaring tree), alongside other taxa like *Rhamnus* (buckthorn) and *Ligustrum vulgare* (privet) collectively are consistent with heterogeneous open-woodland vegetation characterised by substantial areas of scrub and open habitats. Dry and semi-open environments are represented by *Artemisia*, a taxon often associated with transitional zones between grasslands and open woodlands. Similarly, *Helianthemum* points to the presence of sunny, calcareous grasslands, while *Calluna vulgaris* and *Erica* are indicative of acidic heathlands. These habitats likely formed the drier, more light-demanding components of the vegetation mosaic. Wetland and riparian habitats are well-represented by taxa such as *Typha* and *Cladium*, which are associated with marshes and fens, and *Filipendula*, a characteristic species of damp meadows. *Ranunculus* suggests the presence of wet meadows, open water margins, or drier grasslands, while *Polygonum* s.l. thrives in moist, nutrient-rich soils along stream banks or disturbed wet areas. These species point to the role of hydrological variability in shaping wetland and riparian zones. Disturbed and nutrient-rich open habitats are indicated by taxa like *Plantago*, *Rumex*, and *Urtica*, which are commonly associated with grasslands, pastures, and anthropogenic-like disturbance zones in modern ecosystems. These species suggest a dynamic, heterogeneous vegetation structure influenced by natural disturbances, maintaining areas of high light availability and ecological turnover.

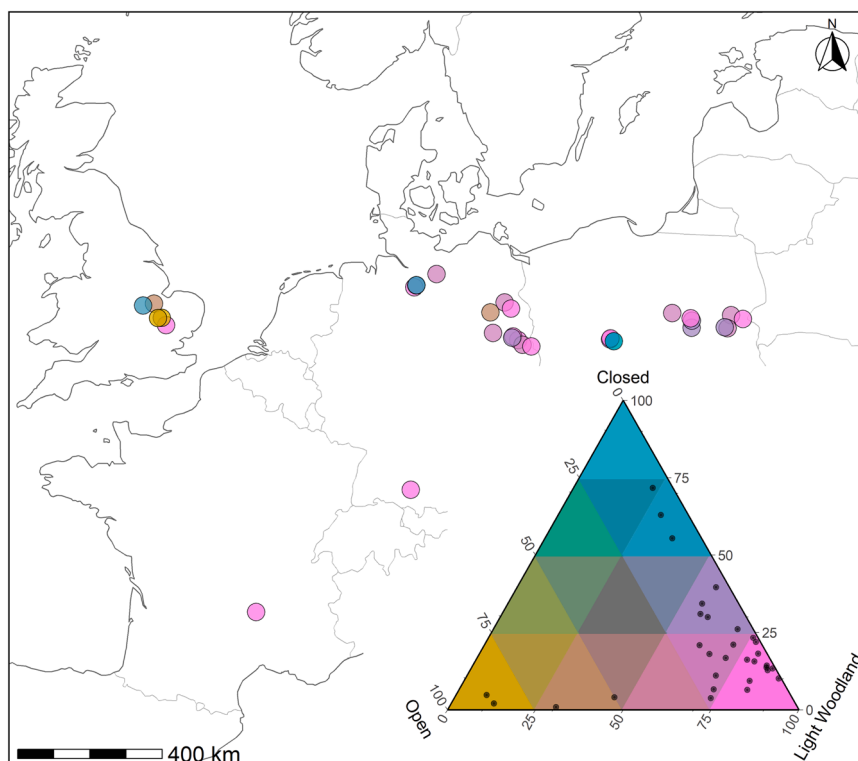
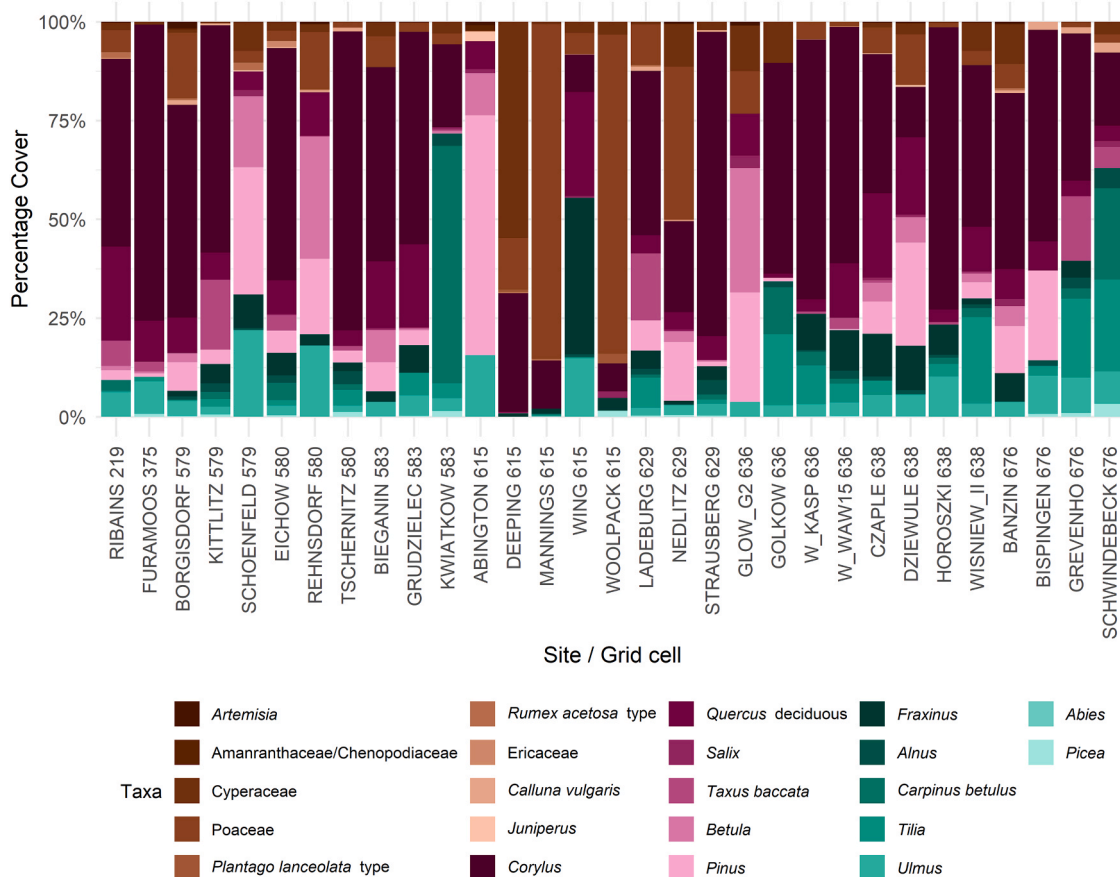


Fig. 1. Triplot of local vegetation cover estimates ( $\sim 9 \text{ km}^2$ ) during the Mesocratic phase I (early temperate) of the Last Interglacial in the 31 local sites used for this study. Site points are coloured based on dominant vegetation types.



**Fig. 2.** Local percentage cover of each taxa (browns = open vegetation, pinks = light woodland, greens = closed forest) for each site. Grid cell ID numbers are also given.

**Table 1**

Dominant taxa regionally (REVEALS) and locally (LOVE) across the subset of grid cells (REVEALS; n = 10) and sites (LOVE; n = 31) used for this study. Functional grouping is shown in parentheses: (O) Open vegetation, (LW) light woodland, and (C) closed forest.

REVEALS taxa	Mean REVEALS (%)	LOVE taxa	Mean LOVE (%)
Corylus (LW)	37.5	Corylus (LW)	38.2
Pinus (LW)	12.3	Poaceae (O)	11
Poaceae (O)	10.1	Quercus deceduous (LW)	8.8
Quercus deceduous (LW)	9.2	Pinus (LW)	8.7
Ulmus (C)	6.2	Ulmus (C)	5.9
Tilia (C)	3.9	Fraxinus (C)	4.9
Cyperaceae (O)	3.9	Cyperaceae (O)	4.6
Betula (LW)	3.2	Tilia (C)	4.3
Abies (C)	3.2	Betula (LW)	4.1
Fraxinus (C)	3	Carpinus betulus (C)	3.9
Carpinus betulus (C)	3	Taxus baccata (LW)	2.4
Taxus baccata (LW)	1.3	Alnus (C)	1.1
Alnus (C)	1	Salix (LW)	0.5
Picea (C)	0.7	Picea (C)	0.4
Calluna vulgaris (O)	0.5	Calluna vulgaris (O)	0.4

### 3.4. Drivers of openness and heterogeneity

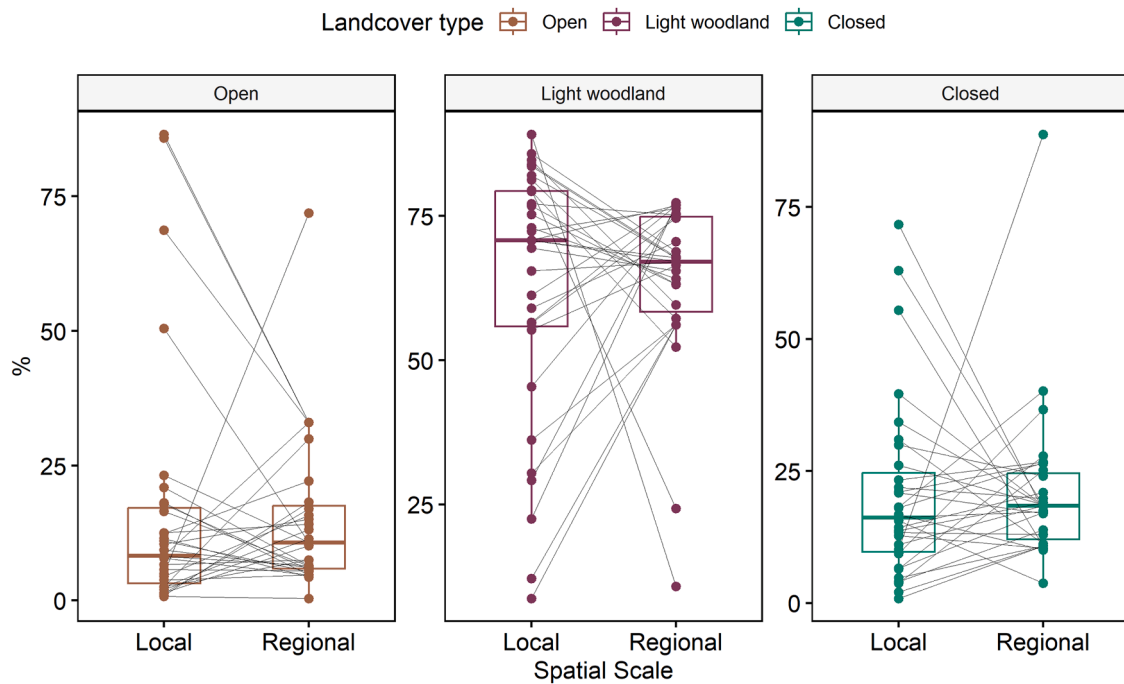
We found strong evidence that local vegetation openness was linked to longitude and moderate evidence for an effect of local precipitation. The beta regression model explained 46.1 % of the variation in local vegetation openness (pseudo R<sup>2</sup>). Negative effects were observed for

longitude (Estimate = -0.68, p = 0.012) and precipitation of the coldest quarter (Estimate = -0.56, p = 0.042), i.e., openness increased towards the west and with increasingly dry winters. Other predictors, including temperature variables and elevation, did not show significant effects (p > 0.20). The model's precision parameter was high (phi = 5.08, p < 0.001), supporting robust estimation of coefficients. Residual diagnostics showed no major violations, with quantile residuals within acceptable bounds.

We found no evidence that the difference in local and regional open vegetation was explained by the corresponding differences in climate. The linear model showed no significant relationships between open vegetation differences and any of the climate variables (all p > 0.4). The explanatory power of the model was low, with an R<sup>2</sup> value of 0.06, and the adjusted R<sup>2</sup> indicated no improvement over a null model (adjusted R<sup>2</sup> = -0.13). The overall F-statistic (F = 0.32, p = 0.897) confirmed that the model did not explain the observed variation in openness differences. The overall results indicate limited evidence that differences in bioclimatic conditions between local and regional scales drive variation in vegetation openness.

Regression analysis revealed that longitude significantly influenced Shannon diversity (Estimate = 0.102, p = 0.011), while the effects of bioclimatic variables and elevation were not statistically significant (all p > 0.2). The model explained 25.1 % of the variance in Shannon diversity (adjusted R<sup>2</sup> = 0.10), though the overall model was not statistically significant (F = 1.675, p = 0.177). These findings suggest that the east-west gradient in longitude, rather than climatic or elevational variables, was the primary driver of local diversity in the dataset.

The linear model analysing the influence of climate differences on



**Fig. 3.** Open vegetation, light woodland and closed forest percentage cover per site, locally (LOVE) and regionally (REVEALS). Sites are depicted by points, which are joined by grey lines to show direction of change between the two spatial scales. The horizontal line within each box represents the median, the box bounds represent the interquartile range (IQR; 25th to 75th percentiles), and the extended lines (whiskers) indicate data variability outside the IQR, up to 1.5 times the IQR. Outliers are depicted as individual points beyond the whiskers.

**Table 2**

Dominant local shrubs and small trees by pollen count across all sites in Pearce et al., (2023) (n = 96), excluding vines/climbers as they provide limited information on vegetation structure. The table includes all taxa, encompassing both REVEALS/LOVE and non-REVEALS/LOVE taxa. Total pollen count represents the cumulative number of pollen grains recorded for a given taxon across all sites. Minimum frequency for inclusion is 10 %.

Genus	Percentage grid cells present (%)	Total pollen count	Modern-day habitat	Representative species*
<i>Corylus</i> (Hazel)	97.8	228191	Woodlands (especially open, low, or disturbed), forest edges, hedgerows	<i>Corylus avellana</i>
<i>Taxus</i> (yew)	66.3	15561	Open or low woodlands, semi-open patches inside forests, forest edges, mosaic vegetation, slopes	<i>Taxus baccata</i> **
<i>Juniperus</i> (Juniper)	47.8	1356	Rocky slopes, grasslands, open woodlands	<i>Juniperus communis</i>
<i>Ilex</i> (Holly)	44.6	298	Woodlands, hedgerows	<i>Ilex aquifolium</i>
<i>Viburnum</i> (Wayfaring tree, Guelder-rose)	27.2	111	Forest edges, thickets, wetlands	<i>Viburnum lantana</i> , <i>V. opulus</i>
<i>Frangula</i> (Alder buckthorn)	22.8	53	Wetlands, stream banks, woodlands	<i>Frangula alnus</i>
<i>Cornus</i> (Dogwood)	17.4	32	Forest edges, hedgerows, rocky slopes	<i>Cornus mas</i> , <i>C. sanguinea</i>
<i>Ephedra</i> (Joint-pine)	16.3	55	Dry, rocky soils, saline soils, disturbed sites	<i>Ephedra distachya</i>
<i>Sambucus</i> (Elder)	16.3	56	Hedgerows, roadsides, nutrient-rich soils	<i>Sambucus nigra</i> , <i>S. racemosa</i> , <i>S. ebulus</i>
<i>Ligustrum</i> (Privet)	14.1	42	Hedgerows, forest edges, disturbed sites	<i>Ligustrum vulgare</i>
<i>Pistacia</i> (Terebinth)	10.9	138	Open woodlands, dry scrublands, rocky slopes	<i>Pistacia terebinthus</i>
<i>Rhamnus</i> (Buckthorn)	10.9	37	Forest edges, dry slopes, scrubland	<i>Rhamnus cathartica</i>

\* Widespread and common in temperate Europe today (except *Pistacia terebinthus*, a Mediterranean species that extends into Sub-Mediterranean climates).

\*\* Mostly a small tree. Can achieve old age and massive stem girths (10–15 m), but is usually still short-statured (15–20 m, but often shorter)

beta diversity (Bray-Curtis dissimilarity) revealed no significant relationships between beta diversity and any of the climate variables tested (all  $p > 0.1$ ). The overall model explained 19.45 % of the variation in beta diversity ( $R^2 = 0.195$ ), but the adjusted  $R^2$  value (0.033) suggested limited explanatory power when accounting for the number of predictors. The F-statistic for the model was not significant ( $F = 1.207$ ,  $p = 0.335$ ), indicating that the included climate variables collectively did not explain a significant proportion of the variation in local-regional beta diversity differences. These findings suggest that other factors, beyond the tested climate variables, may drive differences in beta diversity between the local and regional scales.

#### 4. Discussion

Our study highlights substantial vegetation heterogeneity in temperate Europe during the Last Interglacial, indicating a high capacity for biodiversity. Local landscapes consisted of mosaics of open vegetation (17 %), closed forest (21 %), and light woodlands (63 %), providing diverse habitats for species with varying ecological needs. Weak to no correlations between local and regional vegetation patterns suggest that local vegetation was shaped by factors beyond regional trends. Widespread herbs and dwarf shrubs indicate diverse habitat types, including dry grasslands and disturbed ground, heathlands, shrublands, and open

**Table 3**

Dominant local herbs, graminoids, and dwarf shrubs by pollen count across all sites in Pearce et al., (2023) (n = 96). The table includes all taxa, encompassing both REVEALS/LOVE and non-REVEALS/LOVE taxa. Total pollen count represents the cumulative number of pollen grains recorded for a given taxon across all sites. Minimum frequency for inclusion is 15 %.

Genus	Percentage grid cells present (%)	Total pollen count	Modern-day habitat	Representative species*
<i>Artemisia</i> (Mugwort, Wormwood)	89.1	2470	Disturbed soils, grasslands, open woodlands, sandy soils	<i>Artemisia absinthium</i> , <i>A. campestris</i> , <i>A. vulgaris</i>
<i>Rumex</i> (Docks, Sorrels)	76.1	1022	Meadows, pastures, wetlands, nutrient-poor and nutrient-rich soils, roadsides, streams	<i>Rumex acetosa</i> , <i>R. acetosella</i> , <i>R. conglomeratus</i> , <i>R. crispus</i> , <i>R. hydrolapathum</i> , <i>R. obtusifolius</i>
<i>Typha</i> (Cattails)	60.9	1127	Wetlands, ponds, lakes	<i>Typha angustifolia</i> , <i>T. latifolia</i>
<i>Plantago</i> (Plantains)	57.6	525	Pathways, meadows, grasslands, saline soils, disturbed soils	<i>Plantago lanceolata</i> , <i>P. major</i> , <i>P. maritima</i> , <i>P. media</i>
<i>Calluna</i> (Heather)	50	867	Heathlands, moorlands	<i>Calluna vulgaris</i>
<i>Pteridium</i> (Bracken)	48.9	919	Acidic soils in woodlands, heaths, grasslands	<i>Pteridium aquilinum</i>
<i>Filipendula</i> (Meadowsweet)	47.8	192	Damp meadows, stream banks, dry calcareous grasslands	<i>Filipendula ulmaria</i> , <i>F. vulgaris</i>
<i>Urtica</i> (Nettles)	44.6	198	Nutrient-rich, disturbed soils, cultivated areas, woodlands, hedgerows	<i>Urtica dioica</i> , <i>U. urens</i>
<i>Erica</i> (Heathers)	42.4	1140	Acidic heathlands, moors, bogs, wet or sandy soils	<i>Erica cinerea</i> , <i>E. tetralix</i>
<i>Thalictrum</i> (Meadow rues)	40.2	213	Damp meadows, riverbanks, rocky habitats, moist woodlands	<i>Thalictrum aquilegifolium</i> , <i>T. flavum</i> , <i>T. minus</i>
<i>Ranunculus</i> (Buttercups)	32.6	407	Wet meadows, marshes, grasslands, aquatic habitats, woodlands	<i>Ranunculus acris</i> , <i>R. bulbosus</i> , <i>R. flammula</i> , <i>R. repens</i> , <i>R. sceleratus</i> , <i>R. polyanthemos</i> , <i>R. auricomus</i> , <i>R. lanuginosus</i>
<i>Humulus</i> (Hops)	30.4	707	Hedgerows, moist wood margins, fertile riverbanks	<i>Humulus lupulus</i>
<i>Polypodium</i> (Polypods)	25	98	Shaded rocks, old walls, humid woodlands	<i>Polypodium interjectum</i> , <i>P. vulgare</i>
<i>Polygonum</i> s.l. (Knotweeds)	17.4	265	Fields, wetlands, disturbed areas, riverbanks, moist meadows	<i>Persicaria amphibia</i> , <i>P. bistorta</i> , <i>P. hydropiper</i> , <i>P. maculosa</i> , <i>Polygonum aviculare</i>
<i>Helianthemum</i> (Rock roses)	16.3	23	Sunny calcareous grasslands, rocky limestone habitats, dry areas	<i>Helianthemum canum</i> , <i>H. nummularium</i>
<i>Cladium</i> (Great fen-sedge)	16.3	184	Nutrient-poor, base-rich wetlands, fens, bogs	<i>Cladium mariscus</i>
<i>Osmunda</i> (Royal fern)	15.2	168	Wetlands, stream banks, open damp woodlands	<i>Osmunda regalis</i>
<i>Thelypteris</i> ** (Marsh fern)	15.2	1683	Marshes, fens, wetlands	<i>Thelypteris palustris</i>

\* Widespread and common in temperate Europe today

\*\* May include *Gymnocarpium* spp. (oak ferns) in older pollen diagrams. *Gymnocarpium* is linked to rocky outcrops and humid woodlands.

wetlands, underscoring the ecological complexity of these systems (Fig. 4). Longitude and, to an extent, winter precipitation emerged as drivers of local vegetation openness, albeit with weak effects that were contrary to physiological expectations. The high vegetation heterogeneity across scales provides key insights into the structure and dynamics of pre-anthropogenic temperate ecosystems.

#### 4.1. High levels of local and cross-scale vegetation heterogeneity

Our study reveals substantial vegetation openness and high vegetation heterogeneity during the Last Interglacial in temperate Europe, evident at the local and regional scale. Local landscapes consisted of mosaics of open vegetation (19 %), closed forests (20 %), and light woodlands (61 %). Local landscapes exhibited high vegetation heterogeneity, with Shannon diversity values ranging from 0.56 to 2.09 (mean = 1.46) and evenness values (J) ranging from 0.23 to 0.84 (mean = 0.56), indicating that no single vegetation type dominated most sites and highlighting their structural diversity. Floristic interpretation of the more widespread herb and dwarf shrub taxa supports the occurrence of a diversity of vegetation types such as dry grasslands, open wetlands, and heathlands, albeit their detailed nature remains to be understood.

Importantly, we demonstrate that this structural heterogeneity was enhanced by deviations between local vegetation composition and regional averages. For example, while light woodland dominated regionally, local landscapes often exhibited higher proportions of either open vegetation or closed forests, contributing to the heterogeneity of the vegetation structure. This local-regional divergence also emphasises the importance of considering scale when reconstructing past vegetation patterns. The potential for scale dependence in land cover heterogeneity has long been recognised within landscape ecology (Milne, 1991; Turner

et al., 1989). The evidence for multi-scale heterogeneity sets our study apart from prior research, which showed high heterogeneity during the Last Interglacial (Pearce et al., 2023, 2024) but focused exclusively on regional-scale vegetation. By integrating local and regional estimates, we provide direct evidence that local vegetation patterns were not simply scaled-down reflections of regional trends but rather represented unique compositions that amplified the heterogeneity of the landscape.

Sandom et al. (2014) also provided support for the local occurrence of heterogeneous vegetation with substantial open and semi-open vegetation during the Last Interglacial using beetle assemblages as proxies, highlighting the role of herbivores in shaping vegetation dynamics (also see Langford et al., 2017). However, their study was geographically limited to Great Britain and did not incorporate direct plant-based quantifications. By contrast, our study builds on this foundation by drawing on records that span a much broader area of the European temperate biome, allowing us to directly quantify vegetation openness and heterogeneity across both local and regional scales, offering a more expansive view of Last Interglacial vegetation dynamics. Together, these findings not only complement earlier localised studies but also provide the basis for a deeper exploration of vegetation patterns at finer scales.

Our findings based on LOVE modelling are consistent with a range of local studies that also highlight the dynamic and heterogeneous nature of Last Interglacial vegetation. In Denmark, pollen and macrofossils from a Last Interglacial deposit in a small and shallow lake basin reveal a mix of herbaceous species associated with shaded, semi-shaded, and open wet and dry habitats, e.g., *Lycopus europaeus* (gypsywort), *Ranunculus sceleratus* (celery-leaved buttercup), *Ajuga reptans* (bugle), *Sanicula europaea* (sanicle), and *Osmunda regalis* (royal fern; Andersen, 1975). The woody assemblage includes light-woodland species such as *Corylus*



(caption on next page)



**Fig. 4.** Reconstruction of Last Interglacial vegetation and likely drivers in the European temperate forest biome, integrating this study's pollen-based vegetation estimates with additional palaeoecological evidence from other studies (cited in the text). Top: Depiction of a vegetation structure consistent with the LOVE and REVEALS estimates, featuring key species inferred from pollen data, including privet (*Ligustrum vulgare*), pedunculate oak (*Quercus robur*), yew (*Taxus baccata*), elder (*Sambucus nigra*), Scots pine (*Pinus sylvestris*), hazel (*Corylus avellana*), and meadowsweet (*Filipendula ulmaria*). Middle: Illustration of megafaunal influences on vegetation structure, highlighting the likely role of large herbivores such as the straight-tusked elephant (*Palaeoloxodon antiquus*) in shaping the landscape, akin to the ecological effects of extant elephants. Also depicted are starling (*Sturnus vulgaris*), hare (*Lepus europaeus*), great spotted woodpecker (*Dendrocopos major*), and abundant hazel (*Corylus avellana*). Bottom: Riverside environment illustrating how water bodies likely attracted large herbivores in line with the piosphere effect (Carvalho & Campbell, 2023), fostering more open conditions (Svenning, 2002). Shown species include narrow-nosed rhino (*Stephanorhinus hemitoechus*), fallow deer (*Dama dama*), horse (*Equus ferus*), aurochs (*Bos primigenius*), boar (*Sus scrofa*), bison (*Bison priscus*), and straight-tusked elephant (*Palaeoloxodon antiquus*). Birds present include lapwing (*Vanellus vanellus*) and raven (*Corvus corax*). All illustrated species are documented in Last Interglacial records from the region. Illustrator: Hodari Nundu.

*avellana* (hazel) in high abundance, *Quercus* (oak), and *Taxus baccata* (yew) (cf. Pearce et al., 2024), and tall, shade-tolerant trees like *Tilia* spp. (lime) and *Carpinus betulus* (hornbeam), alongside shrubby *Ilex aquifolium* (holly) (Andersen, 1975), which thrives across light to shaded environments. Last Interglacial sites from north-eastern Germany display the consistent occurrence of open dry and wet habitat forbs along with abundant trees and shrubs, including many light-woodland species (Börner et al., 2015; Hrynowiecka et al., 2021). The forbs include taxa such as *Artemisia* (mugwort), *Rumex acetosella* (sheep's sorrel), *Anthemis* (mayweed), *Plantago media* (hoary plantain) from pollen, and *Eupatorium cannabinum* (hemp-agrimony) and *Ranunculus sceleratus* from macrofossils. *Calluna vulgaris* (common heather) exhibits consistent pollen presence. Light-woodland shrubs and trees include taxa such as *Corylus*, *Quercus*, *Taxus baccata*, *Pinus sylvestris* (Scots pine), *Sambucus nigra* (elder), *Viburnum* (guelder-rose), *Buxus sempervirens* (box), and *Frangula alnus* (alder buckthorn).

Similar findings are reported from south-western Poland (Malkiewicz, 2002), in central Poland (Bober et al., 2023), and in eastern Poland (Granoszewski, 2003; Bińska and Nitychoruk, 2003; Pidek and Terpiłowski, 1993), including the consistent presence of the light-demanding shrubs *Ligustrum vulgare* (privet) and *Buxus sempervirens* (box) (Bober et al., 2023). Behre et al. (2005) also describe tree-rich ecosystems in northwest Germany but with plant and beetle macrofossils indicating the presence of open wet and dry habitats. Keen et al. (1999) reconstruct a largely treeless floodplain in Lincolnshire, England, with adjacent forests dominated by disturbance-dependent *Quercus* (Dietz et al., 2022), suggesting a mosaic of open vegetation and light woodland (in line with Langford et al., 2017). Pop and Bakels (2015) provide evidence of semi-open conditions at Neumark-Nord 2, Germany, supported by pollen and macrofossils reflecting a mix of grasslands, shrubs, and forest patches. Jolly-Saad and Dabkowski (2021) report from the Resson tufa plant macrofossil record in France a landscape of mixed deciduous woodland, featuring *Taxus baccata* (English yew), and *Corylus avellana* (common hazel). Light-demanding shrubs such as *Ligustrum vulgare* and *Buxus sempervirens* are also present here along with charophytes and mosses of open wetland habitats. Light-demanding shrubs and small trees are likewise well-represented in German tufas from the Last Interglacial, including *Cotoneaster* (cotoneaster), *Crataegus monogyna* (common hawthorn), *Malus sylvestris* (crab apple), *Prunus spinosa* (blackthorn), *Rhamnus* (buckthorn), and *Syringa* (lilac), in combination with more shade-tolerant shrubs as well as both light-demanding and shade-tolerant taller trees (Jolly-Saad and Dabkowski, 2021). Schokker et al. (2004) highlight dynamic vegetation at a Dutch site, shaped by fluvial processes and interspersed with open patches, while Stefaniak et al. (2021) link megaherbivore diets to mosaics of grasslands and woodlands in Poland, consistent with the role of herbivores in maintaining openness.

These studies, utilising diverse datasets such as plant macrofossils, pollen, molluscs, beetles, and herbivore fossils, consistently reveal heterogeneous vegetation where abundant trees coexisted with open and transitional habitats, in line with findings for the Pleistocene oceanic interglacials more broadly (Svenning, 2002). Together, this growing body of evidence supports our findings, underscoring the importance of local environmental variability, disturbance dynamics, and biotic

interactions in shaping the Last Interglacial temperate biome. These insights provide a broader geographical and ecological context for understanding the diverse vegetation structures of the Last Interglacial.

These findings challenge the long-standing closed forest paradigm, which posits that moist temperate climates naturally favour dense, closed forests (Breckle, 2002). This paradigm has been a dominant framework for understanding interglacial vegetation, assuming that climatic stability in such regions results in vegetation systems trending toward closed dominance. However, our results reveal that substantial openness and heterogeneity existed even under warm, moist interglacial conditions. The observed patterns suggest that closed forests were not the inevitable natural state of temperate biomes. Instead, vegetation openness and heterogeneity likely resulted from natural disturbances and environmental variability, including local-scale processes such as microclimatic differences, topographic complexity, and inherent stochasticity in vegetation dynamics.

These insights align with the concept of alternative biome states proposed by Pausas and Bond (2020), which emphasise that open and closed biomes can coexist even in climates capable of supporting closed forests. This perspective highlights the crucial role of disturbances, such as herbivory and fire, in maintaining open ecosystems as long-term components of the landscape, rather than merely transitional or degraded states. Our findings further support critiques of the closed forest paradigm, arguing for a more nuanced view of temperate forest biomes as dynamic, structurally complex, semi-open woodland mosaics shaped by interactions between environmental drivers and disturbance regimes, rather than static, predominantly tall-canopied, shaded systems.

#### 4.2. Drivers of vegetation patterns

Whilst the broad-scale distribution of biomes is conventionally seen as controlled by large-scale climatic patterns (e.g., Breckle, 2002), this view is now increasingly questioned, with a stronger general role for disturbance factors being argued (e.g., Pausas and Bond, 2020). At the local scale, reconstructed by our LOVE analysis (~9 km<sup>2</sup> scale), vegetation exhibited high heterogeneity within the context of a broadly forest-conducive interglacial climate (Felde et al., 2020), likely reflecting a complex interplay of factors. Importantly, we find limited evidence for strong climate-linked controls at this localised level, echoing our earlier regional-scale results (Pearce et al., 2023). Along with weak correlations between local and regional vegetation patterns, these findings suggest that other influences may have played an important role at both scales, but likely even more so at local scales. Moreover, the observed correlations run counter to expectations based on climate-driven productivity; for example, openness increases in regions with higher winter precipitation, a trend inconsistent with the typically denser vegetation associated with more productive climates.

Fire constitutes a disturbance factor with capacity to shape vegetation across scales (e.g., Pausas and Bond, 2020). Fire, whether natural or anthropogenic, appears to have had a minimal impact on vegetation patterns, given the prevalence of the fire-sensitive *Taxus baccata* (Pearce et al., 2024). Additionally, beetle assemblages from Last Interglacial deposits in Great Britain, as analysed by Sandom et al. (2014), lack

fire-associated taxa, further pointing to a limited role for fire as a driving force in Last Interglacial landscapes. Further, although Neanderthals may have influenced vegetation patterns through fire management (Roebroeks et al., 2021), their impacts were likely limited by their small population sizes during the Last Interglacial (Mellars and French, 2011; Li et al., 2024). In contrast, human activities appear to have strongly shaped landscape-scale fire regimes across the Central European lowlands in the later part of the Mesolithic (Dietze et al., 2018), in line with general evidence for elevated fire regimes driven by *Homo sapiens* (e.g., Caldararo, 2002; also see Sandom et al., 2014). These findings highlight the need to explore alternative drivers to explain the observed patterns of vegetation heterogeneity and openness in the Last Interglacial.

The role of large herbivores in shaping vegetation heterogeneity and openness during the Last Interglacial is strongly supported by multiple lines of evidence. Pearce et al. (2023), (2024) provide evidence of semi-open regional landscapes in the Last Interglacial, highlighting the likely influence of herbivory in maintaining mosaics of grasslands, woodlands, and open areas. Davoli et al. (2024) go further by estimating herbivore diversity, density, and vegetation consumption rates, finding these to have been much higher in the Last Interglacial compared to conditions in modern natural areas (in line with contemporary empirical estimates; Fløjgaard et al., 2022). Their findings suggest that the Last Interglacial herbivore guild, which included large species such as *Palaeoloxodon antiquus* (straight-tusked elephant), *Stephanorhinus* spp. (rhinoceroses), and large bovids (*Bison* spp., *Bos primigenius*, *Bubalus murrensis*), had the capacity to exert strong pressure on vegetation. Sandom et al. (2014) provide further evidence of high abundances of large herbivores and associated vegetation heterogeneity during the Last Interglacial in Great Britain by examining beetle assemblages. A process-based model of vegetation dynamics in temperate Europe also supports that large herbivores can generate substantial openness by their consumption of vegetation (Schulze et al., 2018). Further, empirical studies from natural areas with wild-living large bovids and horses in contemporary Europe show their capacity to generate and maintain open and semi-open vegetation under productive temperate climates, as discussed further below (e.g., Ejrnæs et al., 2024). This body of work aligns with evidence from other regions, indicating likely strong effects of large herbivores on vegetation prior to the late-Quaternary megafauna extinctions (e.g., Bakker et al., 2016; Svenning et al., 2024a).

The high inter-site variability and limited regional-local scale coupling in vegetation structure could potentially reflect the interplay between geodiversity and herbivore-driven processes. Geodiversity, encompassing variations in topography, soil types, and hydrology, creates diverse environmental conditions that mediate how herbivores interact with vegetation, in addition to their direct impacts on vegetation. Such environmental heterogeneity likely shaped the spatial distribution of herbivore impacts, with spatially varying disturbances promoting vegetation mosaics, as has been suggested for the forest steppe in eastern Europe (Erdős et al., 2022). The concept of piospheres, empirically demonstrated by Carvalho and Campbell (2023), highlights the effects of elephant-mediated herbivory on tree cover in modern-day African savannas. Their study used remote sensing to quantify vegetation gradients radiating from water sources, showing that areas closer to water points experienced the highest levels of tree cover reduction due to concentrated elephant activity. This selective browsing and trampling created zones of intensified openness, with tree cover gradually increasing further from water points. These findings provide a contemporary analogue for how megafauna-driven spatial gradients could have operated during the Last Interglacial, where large herbivores, including the massive *Palaeoloxodon antiquus*, should have had the capacity to generate vegetation heterogeneity (cf. Gordon et al., 2023).

#### 4.3. Implications for past ecosystems

The heterogeneous vegetation mosaics revealed in this study provide crucial insights into the ecological dynamics of temperate Europe during

the Last Interglacial. These mosaics, comprising open vegetation, light woodland, and closed forests, created a structurally-diverse landscape that supported high biodiversity capacity. By providing a variety of habitats, these mosaics enabled the coexistence of species with differing ecological requirements, from grassland specialists in open areas to species associated with dense forests. Dynamic vegetation patterns likely played a critical role in supporting megafauna populations. Megafauna likely benefited from a combination of grazing and browsing resources, as well as the seasonal availability of diverse habitats and food sources that facilitated resource partitioning (Rivals and Ziegler, 2018; Stefaniak et al., 2021). The role of megafauna likely extended beyond their dependence on these landscapes, as their grazing, browsing, and trampling activities had the capacity to shape the mosaic structure by maintaining open areas and preventing tree encroachment, as outlined above.

While the focus of this study is on the humid-temperate biome during the Last Interglacial, the observed mosaics align with broader patterns of temperate-biome structure that persisted before the late-Quaternary megafauna extinctions. Similar dynamics involving megafauna and vegetation heterogeneity likely characterised European ecosystems more broadly and during earlier periods, such as the Middle and Early Pleistocene, Pliocene, and Miocene (e.g., Costeur et al., 2013; Svenning, 2002). For example, during the Last Interglacial, Carrión et al. (2024a) highlight highly heterogeneous landscapes in the Balkans, where deciduous and Mediterranean forest patches were interspersed with open vegetation, pointing to erosion and herbivory as key drivers. Similarly, the work by Carrión et al. (2024b) on southeastern Spain, during the warm-temperate and seasonally variable climate of the Early Pleistocene (~1.6–1.2 million years ago), demonstrates a mosaic of open and wooded habitats, with suggested links to hydrological variability and megafaunal activity. These wider and deeper temporal links point to the persistence of heterogeneous landscapes in Europe over millions of years, at least partially shaped by megafauna (Szabó et al., 2022; Costeur et al., 2013; Saarinen and Lister, 2016). In summary, the Last Interglacial vegetation mosaics likely exemplify the ecosystem structure across temperate Europe during warm periods generally, in the absence of strong human impacts. These findings provide valuable context for understanding the structure of pre-extinction temperate biomes and the critical role of megafauna in shaping their complexity and stability.

The mosaic structure of Last Interglacial vegetation and earlier warm periods have implications for pre-*sapiens* hominids, whose survival strategies would have been closely linked to the availability of diverse resources in close proximity. Open areas and light woodlands offered hunting grounds and access to plant resources. Such landscape diversity likely allowed Neanderthals to adopt flexible subsistence strategies, enhancing their ability to inhabit interglacial environments (Roebroeks et al., 2021; Uzunidis et al., 2024). This perspective contrasts with the traditional view of uniformly dense forests during interglacials and the associated debate on the challenges for Neanderthals and earlier hominids in terms of limited availability of accessible resources (Roebroeks et al., 1992).

#### 4.4. Relevance to modern and future ecosystems

The ongoing trend in Europe toward succession-driven vegetation closure poses significant challenges for biodiversity and ecosystem functionality. Land-use extensification in the absence of substantial megafauna is leading to widespread vegetation densification across Europe, as reported by large-scale studies (Buitenwerf et al., 2018; Fayet et al., 2022). Similar patterns of successional homogenisation are widely reported in local studies, e.g., in Central European forests (Prach and Kopecký, 2018; Cholewińska et al., 2020) and abandoned wet meadows (Czortek et al., 2021), resulting in losses of habitat diversity and species adapted to open or semi-open landscapes. Studies of Białowieża Forest further illustrate this dynamic, with late-successional shifts toward dense, old-growth forest conditions in the absence of major disturbances

(Brzeziecki et al., 2020). These processes reduce the availability of light-demanding or disturbance-adapted species, homogenising landscapes and diminishing structural and functional diversity essential for broader biodiversity (Hilmers et al., 2018; Vild et al., 2024).

Trophic rewilding offers a promising solution to counteract this trend by restoring trophic complexity through the restoration of functionally diverse megafaunas (Svenning et al., 2024b). Notably, wild and semi-wild large herbivores in European natural areas maintain open and semi-open habitats, reduce the dominance of competitive tall-statured species, and promote species richness (e.g., Henning et al., 2017; Konvička et al., 2021). For example, evidence from Oostvaardersplassen demonstrates the capacity of feral horses (*Equus ferus caballus*), feral cattle (*Bos primigenius taurus*), and red deer (*Cervus elaphus*) to maintain open vegetation and promote plant species richness, while supporting species otherwise in decline, even under a mild, productive climate on fertile soil (Ejrnæs et al., 2024). Another example from Białowieża Forest demonstrates how European bison (*Bison bonasus*) can limit woody encroachment in open habitats within woodland ecosystems, highlighting their role in maintaining habitat heterogeneity even in tree-rich settings (Kowalczyk et al., 2021). These cases align with broader findings on the ecological benefits of trophic rewilding, which highlight the restoration of key ecosystem functions like nutrient cycling, seed dispersal, and natural disturbance regimes (Svenning et al., 2024b).

Rewilding large herbivores can reverse the impacts of vegetation homogenisation, as these animals actively create dynamic, varied vegetation states, fostering greater biodiversity and functional complexity (Svenning et al., 2024b; Trepel et al., 2024). The broader potential of trophic rewilding extends beyond countering homogenisation, offering a pathway to restore the ecological roles of megafauna lost due to human-caused extinctions and extirpations. In modern natural areas in Europe, large-herbivore densities are mostly very low (Fløjgaard et al., 2022). Where densities are higher, it primarily reflects abundant deer. However, faunas dominated by deer, in the absence of larger herbivores and carnivores, form degraded assemblages with reduced functionality, as such mesoherbivores simplify plant communities through their selective browsing (Atkinson et al., 2024). By reintroducing natural processes into human-dominated landscapes, trophic rewilding addresses ecological challenges under novel biosphere conditions, providing a forward-looking approach to biodiversity conservation and ecosystem resilience. Addressing successional homogenisation through trophic rewilding helps modern and future ecosystems maintain the structural and functional diversity necessary to sustain life despite warming climates, rising atmospheric CO<sub>2</sub> levels, and increasing alien plant invasions (Svenning et al., 2024b). Implementing trophic rewilding pragmatically requires considering societal context and trade-offs with ecological functionality (Pedersen et al., 2020). Effective rewilding must adopt nuanced strategies tailored to local socio-ecological contexts to restore trophic complexity and ecosystem functionality.

#### 4.5. Limitations and future research directions

The current study focused on the Mesocratic I (Early Temperate) phase of the Last Interglacial. Expanding this work to the Mesocratic II (Late Temperate) phase - characterised by a greater representation of *Carpinus betulus* and *Picea* in the region - as well as to earlier temperate periods, would provide a more comprehensive understanding of humid temperate vegetation structure prior to the late-Quaternary megafauna extinctions, a unique global event in the Cenozoic (Svenning et al., 2024a).

The LOVE model provides proportional estimates of vegetation at a ~9 km<sup>2</sup> spatial resolution. This is a major advance on interpretations of original pollen proportions, as it effectively removes the confounding influence of background pollen. However, it does not provide detailed insights into the finer-scale structure of vegetation within these broader areas. Where dense networks of pollen sites, with robust chronological

control, exist, it may be possible to use LOVE reconstructions to infer finer-scale patterning (e.g. using the BACKLAND approach of Plancher et al., 2022), but this is unlikely to be realised for prior interglacials, with sparse records and poor chronological control. This is important, as vegetation may have been structured in more complex, non-analogue mixes of trees, shrubs and herbs even within a 9 km<sup>2</sup> area. Further, more complex vegetation structures may not be well represented in modern pollen-vegetation calibration datasets. Importantly, insect-pollinated plants, such as the species-rich Rosaceae, are under-represented in pollen records due to low pollen production and limited dispersal and are unable to be incorporated into the LRA, as this method uses wind-pollinated taxa primarily, further complicating the reconstruction of vegetation mosaics. Finally, while the REVEALS model has been extensively tested and validated in Europe (Hellman et al., 2008; Mazier, 2012), the LOVE model has undergone comparatively less evaluation. Increased validation studies would enhance its robustness.

Studying carbon stable isotopes ( $\delta^{13}\text{C}$ ) in plant macrofossils provides a promising complementary approach, as  $\delta^{13}\text{C}$  values in C<sub>3</sub> plants can reflect light availability, distinguishing between open and shaded environments (Styring et al., 2024). This method offers localised insights that complement pollen-based reconstructions and can enhance the resolution of fine-scale vegetation heterogeneity. Mechanistic approaches, such as Dynamic Vegetation Modelling tailored to include megafaunal disturbances, would also provide valuable insights into the drivers of vegetation dynamics at these scales. Furthermore, developing localised calibration datasets for shrub-tree mixes and pairing LOVE outputs with faunal and geodiversity data would offer a more nuanced understanding of fine-scale vegetation structure dynamics. A key opportunity would be targeted sampling of vegetation mosaics and gradients in the rising number of trophic rewilding sites in Europe (e.g. Konvička et al., 2021). Such approaches have potential to improve the reconstruction of complex vegetation structures and deepen our understanding of past ecosystems.

## 5. Conclusion

The Last Interglacial (Eemian; ~129,000–116,000 years ago) presents an informative period for understanding the dynamics of pre-anthropogenic temperate ecosystems. This study provides robust evidence of substantial vegetation openness and heterogeneity at both local and regional scales in temperate Europe. Local landscapes consisted of mosaics of open vegetation, light woodland, and stands of shade trees, supporting diverse habitats and demonstrating a high biodiversity capacity. Weak correlations between local and regional vegetation patterns highlight the significance of local-scale drivers, such as geodiversity and herbivory, in shaping vegetation dynamics.

The prevalence of disturbance-adapted taxa and existing evidence of megafauna abundance, diversity and impacts (Bergman et al., 2023; Davoli et al., 2024; Sandom et al., 2014) underline the likely critical role of megafauna as ecosystem engineers in Last Interglacial ecosystems, maintaining openness and heterogeneity through grazing, browsing, and trampling, in line with their role in modern ecosystems (Bakker et al., 2016; Svenning et al., 2024a; Trepel et al., 2024). These findings challenge the closed-forest climate paradigm, emphasising the importance of natural disturbances and environmental variability in shaping temperate biomes under warm, moist interglacial conditions. Further, they support the idea that open and closed biomes can coexist in climates suitable for forests and challenge the notion that open ecosystems are merely transient or degraded states (Pausas and Bond, 2020).

Beyond the Last Interglacial, these insights align with broader patterns of European vegetation structure preceding the late-Quaternary megafauna extinctions (e.g., Carrión et al., 2024a; Carrión et al., 2024b), illustrating the long-term ecological importance of vegetation mosaics shaped by herbivory and geodiversity. Understanding these dynamics provides valuable context for interpreting the biodiversity and functionality of pre-anthropogenic ecosystems and offers critical

perspectives for addressing contemporary challenges of landscape homogenisation and biodiversity loss.

Future research integrating fine-scale analyses, such as stable isotope studies of plant macrofossils and process-based vegetation modelling incorporating megafaunal impacts, will further enhance our understanding of the intricate interplay between biotic and abiotic drivers in shaping past ecosystems. These approaches can provide a more nuanced view of biome structure and vegetation dynamics, informing conservation and rewilding strategies to restore ecological complexity and resilience in modern and future landscapes.

#### Author contributions

JCS, EAP, FM, CWD and OB designed the research, EAP, FM, CWD and OB analysed the data; JCS and EAP wrote the paper, with input from all co-authors.

#### CRedit authorship contribution statement

**Hrynowiecka Anna:** Data curation, Writing – review & editing. **Malkiewicz Małgorzata:** Data curation, Writing – review & editing. **Davison Charles W:** Conceptualization, Formal analysis, Investigation, Methodology, Writing – review & editing, Visualization. **Mighall Tim:** Data curation, Writing – review & editing. **Noryskiewicz Bożena:** Data curation, Writing – review & editing. **Czyżewski Szymon:** Writing – review & editing. **Pidek Irena Agnieszka:** Data curation, Writing – review & editing. **Baines Oliver:** Formal analysis, Investigation, Methodology, Writing – review & editing. **Strahl Jaqueline:** Data curation, Writing – review & editing. **Fyfe Ralph:** Conceptualization, Methodology, Writing – review & editing. **Winter Hanna:** Data curation, Writing – review & editing. **Bińka Krzysztof:** Data curation, Writing – review & editing. **Svenning Jens-Christian:** Conceptualization, Funding acquisition, Investigation, Methodology, Supervision, Writing – original draft, Writing – review & editing. **Boreham Steve:** Data curation, Writing – review & editing. **de Beaulieu Jacques-Louis:** Data curation, Writing – review & editing. **Gao Cunhai:** Data curation, Writing – review & editing. **Granoszewski Wojciech:** Data curation, Writing – review & editing. **Pearce Elena A:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Validation, Visualization, Writing – original draft, Writing – review & editing. **Mazier Florence:** Conceptualization, Formal analysis, Investigation, Methodology, Writing – review & editing, Supervision, Validation.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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#### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.hisbio.2025.100022](https://doi.org/10.1016/j.hisbio.2025.100022).

#### Data availability

The data used in this study are available from OSF: <https://osf.io/mnw5g/> (DOI: [10.17605/OSF.IO/MNW5G](https://doi.org/10.17605/OSF.IO/MNW5G)).

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