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RESEARCH ARTICLE

Higher abundance of disturbance-favoured trees and shrubs in European temperate woodlands prior to the late-quaternary extinction of megafauna

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Abstract

1. Large herbivorous mammals strongly influence vegetation structure by creating and maintaining open areas and causing disturbance within closed woody habitats. The herbivores alive today in Europe are only a small remnant of the large species that existed in high diversity and abundance before modern humans. The extinction of so many large herbivores during the last 50,000 years, and the loss of megaherbivores (body weight ≥1000 kg) from most of the continent before the Pleistocene–Holocene transition, is likely to have had cascading effects on vegetation structure and composition.
2. To evaluate these effects within the European temperate forest biome, we examine the abundance change of three important European woody taxa (deciduous oaks, *Quercus* spp.; hazel, *Corylus* [mainly *C. avellana*]; and yew, *Taxus baccata*) before and after the late-Quaternary downgrading of the region''s large herbivore fauna. These taxa are disturbance-favoured, depend on canopy openings for regeneration, and tend to decline in closed dense forests. *Quercus* and *Corylus* may thrive in systems affected by megafauna herbivory or fire, whilst *Taxus* is fire-sensitive but can thrive in grazed systems. Using pollen-based reconstructions (REVEALS), we investigated the proportional cover of these three focal taxa in the Last Interglacial (129,000–116,000 before present [BP]) and early–mid-Holocene (8700–5700 BP).
3. We found that woodlands in the Last Interglacial exhibited higher cover of *Corylus* and *Taxus* relative to the Holocene, with the former reaching very high percentage cover; meanwhile, *Quercus* had a consistent, moderately high percentage cover in both periods. Furthermore, we found that the cover of *Corylus* and *Taxus* appeared to be influenced more by unmeasured, non-climatic factors than *Quercus*.
4. *Synthesis*: The abundance of *Taxus* suggests a limited role of fire; whilst the observed levels of *Taxus*, *Corylus* and *Quercus* align with the potential influence of

megafauna herbivory; however, a direct quantitative link remains to be established. Our results suggest that vegetation was structurally and compositionally affected by differences in disturbance regimes between the Last Interglacial and early–mid-Holocene, with the loss of diverse disturbance regimes likely contributing to the divergence of Holocene vegetation from long-term ecological baselines.

KEYWORDS
disturbance regimes, European forests, forest structure, megafauna, reference conditions

1 | INTRODUCTION

Large herbivorous mammals (hereafter, 'megafauna') have strong interactions with vegetation. Megafauna consume vegetation in large quantities, thereby altering plant biomass, community composition and structure (Pringle et al., 2023). Megafauna also cause physical disturbance to ecosystems by trampling, debarking and rooting (Pringle et al., 2023). Due to these processes, megafauna play an important role in creating and maintaining open areas. This is the case in the temperate forest biome, where closed woody vegetation would otherwise dominate under mild climatic conditions (Svenning, 2002). Today, megafauna assemblages are a fraction of their past size (Smith et al., 2018). Larger species existed in much greater diversity and abundance before the arrival of modern humans ~50,000 years ago (Bergman et al., 2023; Smith et al., 2018). The extinction of so many megafauna species likely had cascading effects on the abundance, structure and composition of vegetation communities (Bakker et al., 2016; Svenning et al., 2024). Extant smaller species such as *Capreolus capreolus* (roe deer), *Cervus elaphus* (red deer) and *Sus scrofa* (wild boar) are unlikely to have produced functionally equivalent vegetation interactions (Pringle et al., 2023). In the European temperate forest biome, pollen-based reconstructions have revealed high percentages of open and light-woodland vegetation before modern humans (Pearce et al., 2023). Climate and other environmental processes, such as soil moisture availability (le Roux et al., 2013) and degree of continentality (Giesecke et al., 2008), may have influenced vegetation patterns at this time. However, it is likely that megafauna assemblages, and their associated disturbance regimes, had a major influence on vegetation structure, composition and species interactions (Davoli et al., 2023; Svenning et al., 2024).

Many trees and shrubs depend on disturbance for reproduction, to reduce competition from other taxa and to provide open, sunlit conditions (Vera, 2000). However, different disturbance mechanisms can have diverging effects. For example, *Pinus* (pine), *Betula* (birch) and *Salix* (willow) are positively related to fire events (Molinari et al., 2020), whereas *Quercus* (oak) and *Corylus* (hazel) are fire-tolerant but equally benefit from canopy openings driven by fire or large grazers (Molinari et al., 2020; Vera, 2000). Meanwhile, *Taxus* (yew) is sensitive to fire but can thrive in grazed systems (Busing et al., 1995; Omarova & Asadulaev, 2016). Evidence suggests that intense fire regimes may not have been widespread in Europe before the arrival of modern humans (Milner et al., 2016; Sandom, Faurby, et al., 2014). Conversely, the megafauna-rich conditions of past European landscapes may have promoted taxa such as *Quercus*, *Corylus* and *Taxus* (Pearce et al., 2023; Svenning & Magård, 1999).

Deciduous *Quercus* (deciduous oaks, with *Quercus robur* and *Q. petraea* being the most widespread and the only species in northern parts of Europe; hereafter '*Quercus*') is a light-demanding taxon that thrives in disturbed, transitional habitats (Bobiec et al., 2018). *Quercus* seed dispersal and recruitment occur mostly in dynamic, mosaic landscapes; the taxon fails to regenerate under dense canopies in modern European forests (Bobiec et al., 2018). Abundant *Corylus* (hazel; largely *Corylus avellana*: common hazel; hereafter '*Corylus*') is usually indicative of scrub woodland subject to ongoing disturbance (Vera, 2000). *Corylus* may thrive under the canopy of lightly shading trees such as *Quercus* and *Fraxinus excelsior* (common ash) (Coppins & Coppins, 2003); however, *Corylus* seedlings require high-light conditions and *Corylus* pollen production is enhanced in open and sunny sites (Bégeot, 1998; Vera, 2000). As a result, it is considered a ready coloniser of open landscapes (Kollmann & Schill, 1996; Vera, 2000) and fails to regenerate under a dense canopy (Vera, 2000). *Taxus baccata* (common yew; hereafter '*Taxus*') is usually considered a shade-tolerant taxon, but also thrives in full sun (Linares, 2013). However, in modern forests, *Taxus* depends on canopy openings for reproduction, regeneration, growth and survival and declines under a dense canopy of shading trees (Linares, 2013; Svenning & Magård, 1999). *Taxus* requires substantial light for optimal growth, experiencing significant reductions in growth rates, biomass allocation and reproductive success under shaded conditions (Iszkuło et al., 2012; Perrin & Mitchell, 2013). Limited light availability in dense canopies, dominated by faster- and taller-growing species such as *Abies alba* (silver fir) and *Fagus sylvatica* (beech), hampers *Taxus* growth, survival and regeneration (Iszkuło et al., 2012; Perrin & Mitchell, 2013). Consequently, *Taxus* populations decline in dense forests where light is scarce (Iszkuło et al., 2012; Perrin & Mitchell, 2013). Additionally, *Taxus* is highly toxic to many large herbivores, except for deer and possibly certain other ruminants (Cortinovis & Caloni, 2015; Thomas & Polwart, 2003) and therefore may outcompete species more susceptible to browsing (Dhar et al., 2007; García & Ramón Obeso, 2003). On the other hand, *Taxus* is vulnerable to fire due to its thin bark and difficulty regenerating, particularly in dry environments (Mola et al., 2014; Thomas & Polwart, 2003) and its slow growth and low seedling recruitment further delay population recovery post-fire (Thomas & Polwart, 2003). Therefore, *Taxus* would likely have been favoured in past ecosystems with high levels of herbivory provided by diverse megafauna (Davoli et al., 2023) but would have been disfavoured by frequent fires.

Quantifying vegetation communities before and after the late-Quaternary megafauna extinctions is challenging. The extinctions occurred with the arrival of *Homo sapiens* ~50,000 BP, during the last glacial period (Bergman et al., 2023; Svenning et al., 2024), when forests and their tree species had strongly reduced distributions and abundances due to the cold, dry climate (Svenning et al., 2008; Willis & van Andel, 2004). Modern conservation practices are increasingly focused on restoring ecological function (Perino et al., 2019) and the role of long-term data (e.g. on functional baselines) has been recognised for almost 20 years (Willis et al., 2005, 2010). Pre-degradation baselines can provide unique ecological insights into systems before human-induced degradation, supplying modern restoration efforts with important context. However, we note that reconciling these insights with modern restoration efforts requires acknowledging contemporary ecological complexities, such as changing climate regimes and other anthropogenic influences, such as wildfire initiation, which may necessitate additional considerations beyond pre-degradation baselines alone. To establish a pre-degradation baseline for current and future systems, warm interglacial conditions are most relevant. The Last Interglacial in Europe (Eemian; ~129,000–116,000 BP) is the most recent interglacial period prior to the Holocene. It occurred before the late-Quaternary megafauna extinctions and had a faunal structure broadly comparable to the preceding 10 million years or more (Blanco et al., 2021; Croitor & Brugal, 2010). This period is geologically recent enough to limit evolutionary changes, as most extent species were already present (Van Kolfschoten, 2000). Finally, the Last Interglacial is climatically comparable to the warming Holocene, particularly in its central mesocratic phases, and has been described as a testbed for assessing environmental responses and climate feedbacks under conditions warmer than the pre-industrial benchmark (Kalis et al., 2003; Kühl et al., 2007; Salonen et al., 2018). Therefore, the Last Interglacial presents a long-term representative baseline for vegetation structure and dynamics under warm conditions prior to the late-Quaternary faunal downgrading (Smith et al., 2018).

Pollen-based vegetation reconstruction using the REVEALS model (Sugita, 2007) has shown that *Quercus* and *Corylus* were present in high abundance during the Last Interglacial in Europe (Pearce et al., 2023). Studies using raw pollen data from the Last Interglacial have shown a *Corylus* peak of up to 50% (Rychel et al., 2014; Suchora et al., 2022). Past abundances of *Quercus* and *Corylus* are better known for the Holocene, where REVEALS modelling shows 1%–15% *Quercus* cover and 10%–15% mean *Corylus* cover at 8200–5700 BP (Githumbi et al., 2022; Serge et al., 2023). *Taxus* was present during the Last Interglacial to a varying degree (3%–15% in Central Europe; Malkiewicz, 2018; Schläfli et al., 2021). In the Holocene, *Taxus* pollen is infrequent and cover is considered low (2%–6%; Deforce & Bastiaens, 2007; Pérez Díaz et al., 2013). However, in both the Holocene and the Last Interglacial, *Taxus* cover has only been examined using raw pollen percentages, which are less robust than REVEALS modelling for reconstructing past cover (Anderson et al., 2006; Sugita, 2007).

In this study, we compare the abundances of *Quercus*, *Corylus* and *Taxus* to assess how their populations changed before and after the late-Quaternary megafauna extinctions in the temperate forest biome. We quantify percentage cover for each taxon in the Last Interglacial and early–mid-Holocene using the latest REVEALS reconstructions (Pearce et al., 2023; Serge et al., 2023). Whilst direct testing of megafauna impact on vegetation was unfeasible in this study, we assess the extent to which observed abundance differences relate to climatic variations and estimate the residual variance. We were specifically interested in answering the following research questions: (1) How does the percentage cover of *Quercus*, *Corylus* and *Taxus* differ between the Last Interglacial and the early–mid-Holocene (before the onset of agriculture)? (2) How far can these differences be explained by climatic differences between the two periods? Overall, we expected that *Quercus*, *Corylus* and *Taxus* would be less abundant in the early–mid-Holocene than in the Last Interglacial as they depend on disturbed, transitional habitats for regeneration (Bobiec et al., 2018; Coppins & Coppins, 2003; Svenning & Magård, 1999), although human-enhanced fire regimes (Milner et al., 2016) may have compensated for the megafauna decline in the case of *Quercus* and *Corylus*. Furthermore, if changes in the abundance of these taxa were caused by human-linked changes in megafauna herbivory (Svenning et al., 2024), we expect that climate variables will have poor predictive ability. Together, our research questions will shed light on the pre-degradation abundances of important European tree species and their potential drivers, with implications for restoration initiatives and forest management (Lindbladh et al., 2007; Palli et al., 2023).

2 | METHODS

We used the latest pollen-based reconstructions of deciduous *Quercus*, *Corylus* and *Taxus* from the Last Interglacial (Pearce et al., 2023) and the early–mid-Holocene (Serge et al., 2023). The early–mid-Holocene dataset was missing *Taxus* reconstructions, which we produced using the same protocols as Serge et al. (2023). The two datasets and our early–mid-Holocene *Taxus* reconstructions were produced using the REVEALS model (Sugita, 2007) and following the same protocols developed by the LandClim and PAGES Land-cover6K projects (Gaillard et al., 2010; Githumbi et al., 2022). The REVEALS model transforms pollen count data to produce quantitative reconstructions of regional vegetation (Sugita, 2007). It overcomes the nonlinearity of the pollen–vegetation relationship by accounting for relative pollen productivity (RPP), dispersal and deposition differences between taxa. It is important to note that accurate RPP estimates for *Taxus* do not yet exist. In the absence of this, the estimate for *Juniperus* is used as a comparable substitution (Kuneš et al., 2011; Pearce et al., 2023). Whilst there therefore may be more uncertainty regarding the absolute percentages of *Taxus*, this study is concerned with the relative abundance of *Taxus* in the Holocene and the Last Interglacial. For this comparison, it is most important that our method of measuring *Taxus* cover is consistent across time periods.

The REVEALS model was developed to transform pollen data from large lakes but can also produce regional vegetation cover estimates from multiple small-sized lakes and bogs (Trondman et al., 2016) and floodplains (Hoevers et al., 2022). The REVEALS model has been extensively tested and validated in Europe (Abraham et al., 2014; Hellman et al., 2008; Hjelle et al., 2018) and is robust to variations in site selection, sampling design and parameter values (Mazier, 2012). Pollen selection, harmonisation and REVEALS model parameterisation are comparable and available from Pearce et al. (2023) and Serge et al. (2023).

We focused on the distributions of *Quercus*, *Corylus* and *Taxus* in the temperate forest biome (Sensu Pearce et al., 2023). We also included pollen-based reconstructions from the adjoining sub-Arctic and Mediterranean biomes, to test for a Europe-wide effect, but only report these in the Supporting Information. *Quercus*, *Corylus* and *Taxus* are dependent on disturbance regimes that open the forest canopy for regeneration, often declining in dense, closed forests (Bobiec et al., 2018; Coppins & Coppins, 2003; Linares, 2013). Furthermore, the three taxa spread early at the beginning of interglacial periods and so are not strongly dispersal limited (Svenning et al., 2008). We focused on the mesocratic phases of vegetation development in both the Last Interglacial (Lang, 1994) and the Holocene (Birks, 1986). The mesocratic is the temperate, middle phase of an interglacial and thus is least affected by preceding and proceeding glacial conditions. In a typical interglacial cycle (i.e. one absent of pressure from modern humans), the mesocratic reflects the climatic optimum (Caspers et al., 2002) and maximum vegetation biomass development (Birks & Birks, 2004).

For the Last Interglacial, the mesocratic was identified by increases in *Quercus*, *Corylus*, *Taxus* and *Tilia* (first half of the mesocratic: Mesocratic I), followed by *Carpinus* and *Picea* (second half of the mesocratic: Mesocratic II) (Lang, 1994). Visual interpretation found that the vegetation community composition of Last Interglacial Mesocratic I was most comparable to the Holocene mesocratic, as there is no strong expansion of *Picea* and *Carpinus*. Furthermore, the Last Interglacial was a shorter interglacial period than the Holocene, with higher vegetation turnover (Felde et al., 2020). We therefore focus our analyses on Mesocratic I in the Last Interglacial. To test whether our choice to split the mesocratic affected our results, we analyse the full mesocratic period (including Mesocratic II: *Carpinus*/*Picea* phase) in the Supporting Information.

To assess the impact of megafauna extinction and other early, pre-agricultural human impacts on each taxon, we looked at *Quercus*, *Corylus* and *Taxus* abundance before the onset of substantial agriculture in the Holocene. We used REVEALS reconstructions of percentage *Cerealia* (members of the Poaceae family that are well-known indicators of agricultural activities) cover (Serge et al., 2023) as a proxy for the anthropogenic conversion of past landscapes to cropland. *Cerealia* cover began increasing exponentially at 5700 BP. As a result, we defined the mesocratic in the Holocene as encompassing 8700–5700 BP, before the rise in *Cerealia* but after the protocratic phase and the associated disturbances of the preceding glacial period (Birks, 1986). For the main analysis, we used the reconstructions of our three focal taxa for the selected mesocratic phases in each time period (Last Interglacial: Mesocratic I; Holocene: 8700–5700 BP; Table S1). We also included reconstructions that divided the mesocratic phases into individual time windows (Holocene: $n=6$; Last Interglacial, $n=2$) to provide more detail (Table S1).

We ensured our definition was restricted to periods where our three focal taxa were widespread in the temperate forest biome so that abundance variation would represent local ecological factors rather than large-scale biogeography. We captured early increases in *Quercus* and *Taxus*; however, we note that the early Holocene rise in *Corylus* precedes the mesocratic phase. *Corylus* expanded rapidly in the Holocene protocratic, particularly in Northwest Europe (Birks, 1986; Birks et al., 2016). As a result, our definition of the mesocratic in the Holocene misses the initial rise in *Corylus* cover. To test whether this exclusion impacted our results, we include a separate comparison of *Corylus* cover between the Holocene protocratic and Last Interglacial mesocratic in the Supporting Information.

Pollen-based reconstruction using REVEALS provides regional vegetation cover for 1-degree by 1-degree grid cells. A mean percentage cover estimate and mean standard error (SE) are given for each taxon per grid cell (Pearce et al., 2023; Serge et al., 2023). We averaged these values across grid cells to provide mean cover estimates for the temperate forest biome (Holocene: $n=342$; Last Interglacial: $n=49$) and Europe (Holocene: $n=539$; Last Interglacial: $n=66$; Supporting Information). The REVEALS model calculates uncertainty as the SEs derived from the sum of the within- and between-site variation in the REVEALS results in the grid cell (Githumbi et al., 2022). We used a coefficient of variation (SE/REVEALS estimate) to report SEs. When SE was greater than the REVEALS estimate, we considered the estimate unreliable.

2.1 | Climate data and zones

We used results from equilibrium simulations of climate, at 127 ka (Last Interglacial) and 6 ka (Holocene), executed according to the PMIP4 protocol (Otto-Bliesner et al., 2017). We used the results of the GISS-E2-1-G (Kelley et al., 2020) earth system model, as in Pearce et al. (2023). Temperature and precipitation fields were downscaled to a resolution of 5 km and bias-corrected, as in Pearce et al. (2023). We derived bioclimatic variables, as in WorldClim (Fick & Hijmans, 2017), for each time period using the 'dismo' package in R (Hijmans et al., 2022). Using this data, the temperate forest biome was defined using Köppen–Geiger climate classifications, produced as in Beck et al. (2018) (Figure S1). Köppen–Geiger climate classifications were grouped into oceanic, continental, sub-Arctic, arid and Mediterranean categories following Pearce et al. (2023, Table S2). We defined the temperate forest biome as lowland grid cells that had an oceanic or continental climate in the Last Interglacial and/or

Holocene (Table S2). Lowland grid cells were defined as those where the standard deviation of elevation was <500 m.

2.2 | Statistical analyses

Where we had data for a given grid cell in both the Holocene mesocratic and the Last Interglacial mesocratic, we applied the paired Wilcoxon test for non-parametric data to compare percentage cover ($n = 29$ paired grid cells). Using paired grid cells is more robust for measuring vegetation changes between the two time periods. However, the sample size is much smaller than using all grid cells and paired grid cells were mostly limited to Central Europe.

We used beta regression to assess the spatial, temporal and environmental drivers of each taxon across all grid cells in the temperate forest biome, as beta regression is appropriate for modelling continuous proportion data (Douma & Weedon, 2019). This is less robust than the paired analysis, as the sample sizes vary, but is more likely to capture Europe-wide effects. We selected explanatory variables based on known drivers of the distributions of each taxon from the literature (Berti & Svenning, 2020; Normand et al., 2011; Svenning, 2002). We included the above-mentioned bioclimatic variables and latitude (to assess disequilibrium dynamics following glaciation; Normand et al., 2011). We also included the standard deviation (SD) of elevation (Fischer et al., 2008) to assess the role of terrain roughness/herbivore accessibility on each taxon (c.f. Berti & Svenning, 2020). We tested for an effect of time period on each taxon by including time period (Last Interglacial; Holocene) as an explanatory factor. We used a pairwise comparison (z-test) of estimated marginal means from beta regression to test for a difference between the two time periods. We used backwards stepwise selection to exclude explanatory variables based on high variance inflation factors (>5) and correlation coefficients (>0.2).

In total, we ran four beta regression models. To look at the effect of time period whilst accounting for climate and other environmental factors, the first model (hereafter, 'the full model') contained six explanatory variables after variable selection: time period (Last Interglacial; Holocene), mean temperature of the wettest quarter (°C), precipitation seasonality (coefficient of variation;°C), precipitation of warmest quarter (mm), precipitation of coldest quarter (mm) and SD of elevation (m). To look at the relative importance of climate compared with time period, we removed time period from the full model to see if the model accuracy changed. A large drop in model accuracy after removing the time period variable from the full model would suggest that unmeasured, non-climatic variables account for a large part of explained variation (i.e., are important). For the third and fourth models, we ran the full model separately for the Last Interglacial and the Holocene to investigate any differences in climatic or environmental drivers between the two periods. We did not include interaction terms in any model, as we did not expect the physiological relationship between climate and vegetation to change between the Last Interglacial and the Holocene.

For the paired and beta regression analyses, we only used data from the temperate forest biome. Results for all grid cells (Europe-wide analyses) and for individual time windows (Table S3) are presented in the Supporting Information.

2.3 | Sensitivity analyses

To assess the robustness of our findings, we performed several sensitivity analyses. Due to *Abies* being susceptible to bias in vegetation cover estimates—especially in larger sedimentation basins—because of its high pollen fall speed and the limitations of GPM-based pollen productivity estimates (Abraham et al., 2014), we tested whether adjusting the RPP for *Abies* would influence our results for *Quercus*, *Corylus* and *Taxus*. Additionally, we tested the effects of excluding small sites and potentially local taxa (Cyperaceae) from the REVEALS reconstructions, as these factors may not align with the model's assumptions and could influence regional estimates. Lastly, we compared megafauna disturbance between the Last Interglacial and Holocene periods by comparing weighted mean grazing pressure values for herbaceous taxa in each period (Midolo et al., 2023). Detailed results for these analyses are presented in the Supporting Information.

3 | RESULTS

3.1 | *Corylus* (hazel)

We found considerably higher *Corylus* cover during the Last Interglacial mesocratic compared with the Holocene mesocratic in the European temperate forest biome. Paired analysis of grid cells using Wilcoxon testing showed strong evidence for a difference in *Corylus* cover between the two time periods ($p = 0.002$; Figures 1 and 2; $n = 29$ paired grid cells). In paired grid cells, cover was lower in the Holocene by an absolute mean of 14.0% ± 21.8. This represents a relative decrease of 38.9% from the mean value of 36.0% in the Last Interglacial. *Corylus* cover was lower in all paired continental grid cells and 72% of paired oceanic grid cells (Figure S2).

Across all grid cells, the Last Interglacial mesocratic had 36.8% ± 17.6 SD mean cover by *Corylus*, whereas the Holocene mesocratic had 16.9% ± 13.0 mean cover (Figure 3). A pairwise comparison (z-test) of estimated marginal means from beta regression found very strong evidence for lower *Corylus* cover in the Holocene mesocratic than the Last Interglacial mesocratic (estimate = −0.19, $z = -6.40$, $p < 0.0001$; all Holocene and Last Interglacial grid cells in the temperate forest biome). There was strong evidence that *Corylus* had lower cover in all time windows in the Holocene mesocratic than in Mesocratic I, but no evidence for a difference between the Holocene time windows and Mesocratic II (Table S3; Figure S3).

Corylus abundance was only partially explained by climatic variation between the two time periods. The full beta regression model

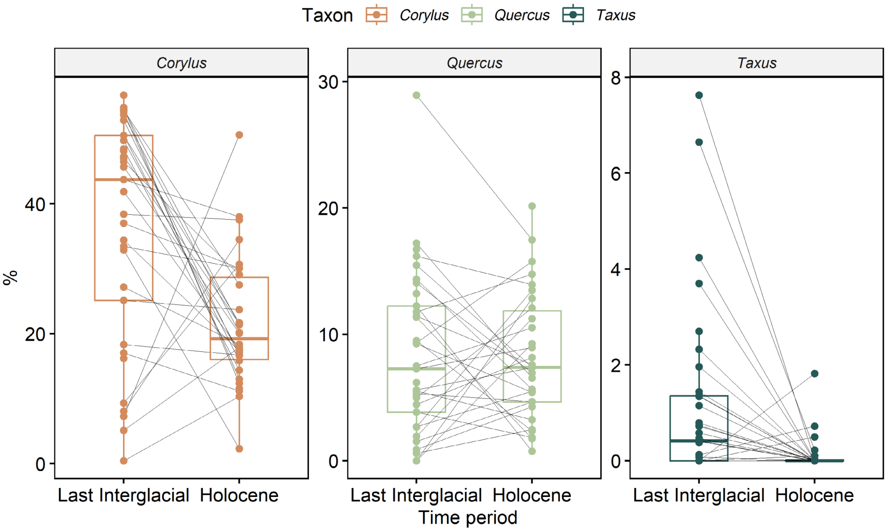

FIGURE 1 *Corylus*, *Quercus* and *Taxus* percentage cover in paired grid cells for the Last Interglacial and the early–mid-Holocene. Grid cells are depicted by points, which are joined by grey lines to show direction of change between the two time periods.

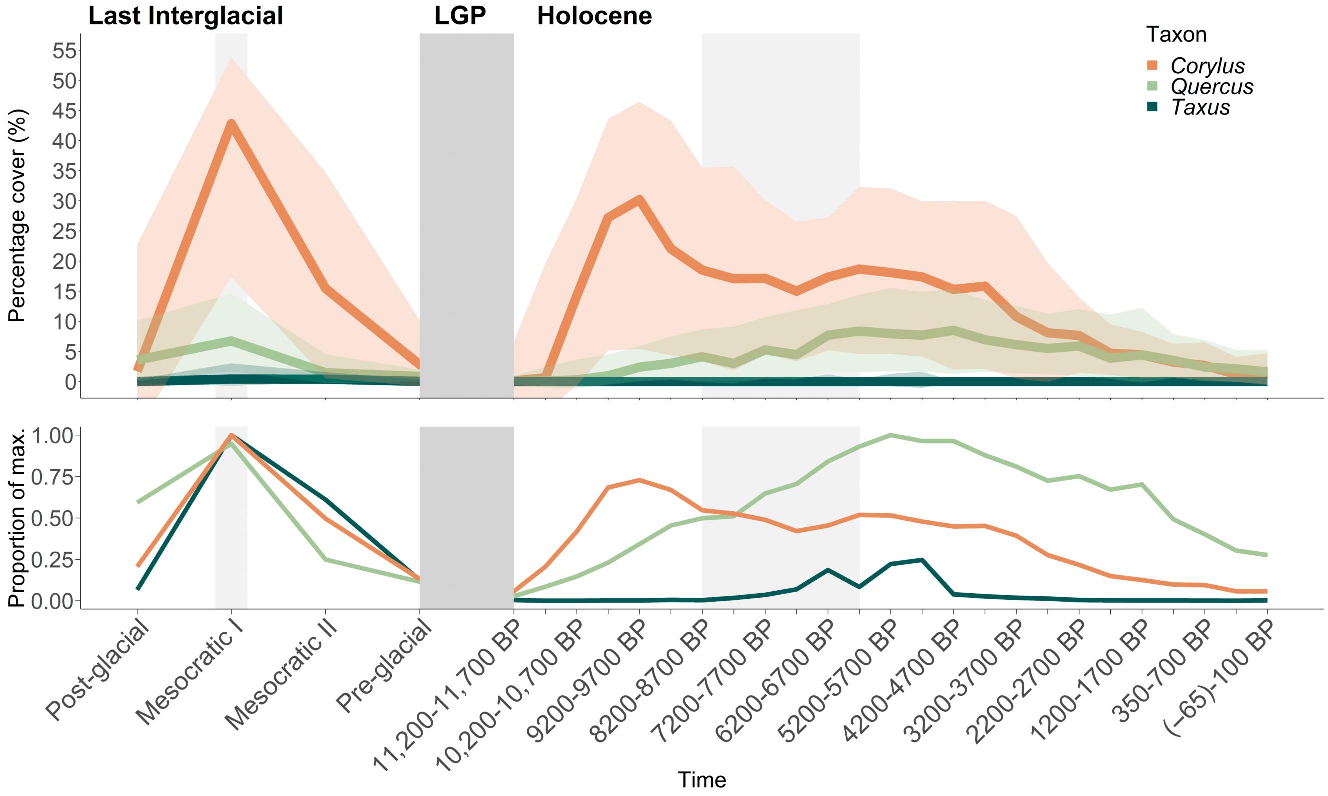

FIGURE 2 Change in mean *Corylus*, *Quercus* and *Taxus* cover in paired grid cells ($n=29$) in the Last Interglacial and Holocene (all time windows). Time windows in the Last Interglacial are given as phases relating to vegetation cover, whereas Holocene time windows have been dated (see Section 2). The darker grey box depicts the Last Glacial Period (LGP), for which we did not collect data. Lighter grey boxes depict the mesocratic phase of each time period, which we used for all analyses. Top panel: Mean and standard deviation (SD; shaded area) of *Corylus*, *Quercus* and *Taxus* percentage cover (%). Bottom panel: Cover of each taxon as a proportion of the maximum cover reached per taxon.

explained 22.5% of the variation in the data (pseudo R^2) and 13.1% when time period was removed (Table S4). The Last Interglacial model explained 12.7% of the variation in the data and the Holocene model explained 19.4% of the variation in the data (Table S4). In the Last Interglacial model, we found no evidence of any environmental or climatic driver of *Corylus* cover (Figure S4). In the Holocene model, we found very strong evidence that *Corylus* cover was linked to precipitation seasonality (estimate $=-0.054$, $p<0.0001$) and moderate evidence that cover was linked to precipitation of the coldest quarter (estimate $=0.002$, $p=0.020$; Figure S4).

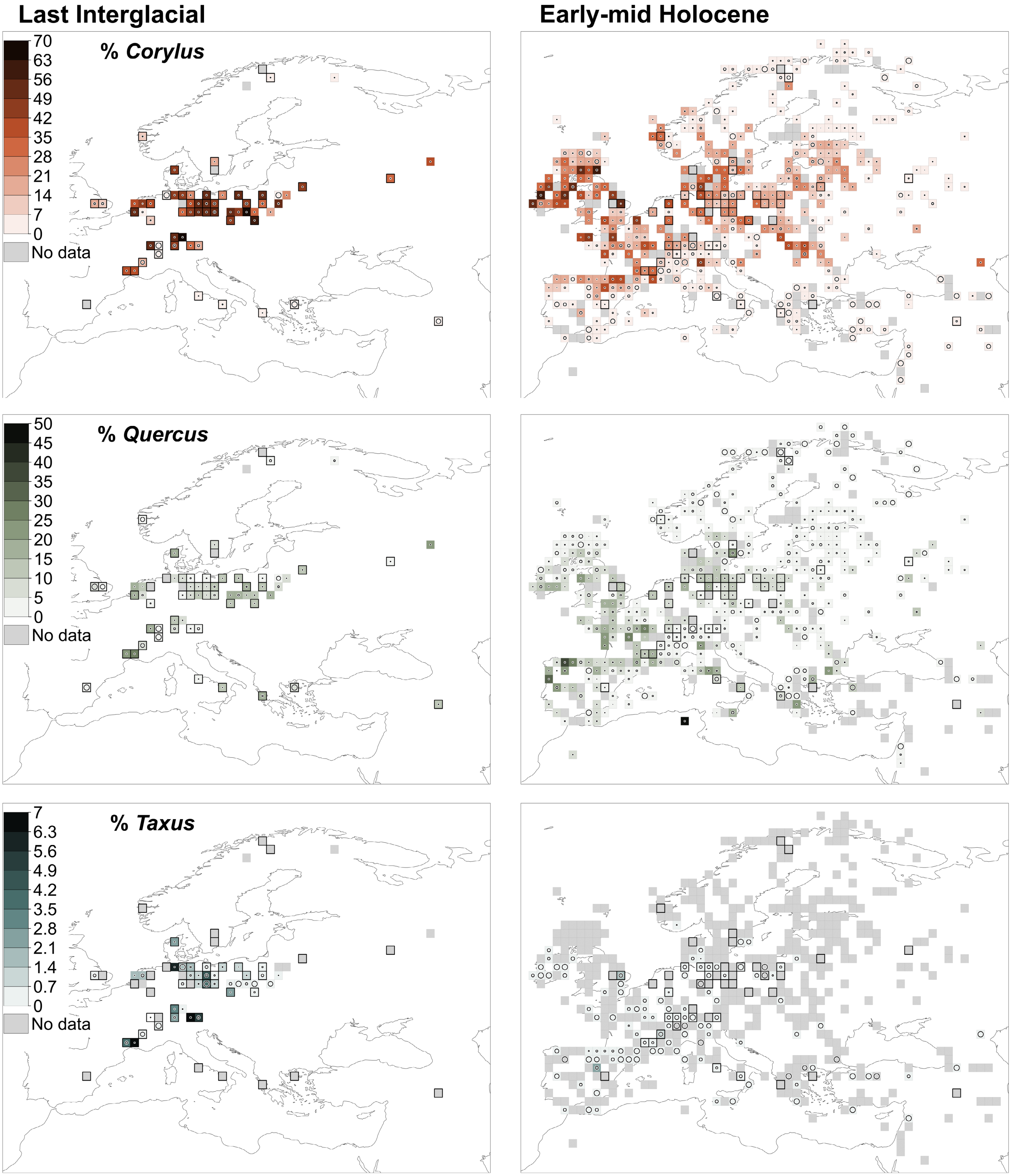

FIGURE 3 REVEALS estimates of *Corylus* (top panel), *Quercus* (middle panel) and *Taxus* (bottom panel) percentage cover in the Last Interglacial mesocratic (left) and early–mid-Holocene mesocratic (right). Each square is a regional grid cell of 1° × 1°. Darker colours show greater cover by the given taxon. Paired grid cells are shown by a black 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. Note the difference in scales of percentage cover between taxa.

3.2 | *Quercus* (oak)

Overall, there was no difference in *Quercus* abundance between the Last Interglacial and the Holocene. Paired analysis of grid cells showed no evidence of a difference in *Quercus* cover between the two time periods ($p=0.798$; Figures 1 and 2; $n=29$ paired grid cells). *Quercus* cover was lower in the Holocene in 80% of paired continental grid cells and 28% of paired oceanic grid cells (Figure S2).

Across all grid cells, the Last Interglacial mesocratic had 9.6% ± 6.4 mean cover by *Quercus* ($n=47$), whereas the Holocene mesocratic had 5.6% ± 5.9 mean cover ($n=292$; Figure 3). A pairwise comparison (z-test) of estimated marginal means from beta regression found no evidence for a difference in *Quercus* cover between the Holocene and Last Interglacial (Estimate = 0.006, $z=-3.71$, $p=0.368$). When we compared the Holocene and Last Interglacial mesocratic time windows individually, we found evidence for higher percentage cover in the Holocene mesocratic time windows than in the Last Interglacial Mesocratic II, but no difference to Mesocratic I (Table S3; Figure S3).

The full beta regression model explained 24.3% of the variation in the data (pseudo R^2) and 24.1% when time period was removed, suggesting that climate was the most dominant driver that we measured (Table S4). The Last Interglacial model explained 27.1% of the variation in the data and the Holocene model explained 25.3% of the variation in the data (Table S4). In the Last Interglacial model, there was strong evidence that *Quercus* cover was linked to precipitation seasonality (coefficient of variation; estimate = 0.038, $p=0.001$) and weak to moderate evidence that *Quercus* cover was linked to precipitation of the warmest quarter (estimate = −0.004, $p=0.053$; Figure S5). In the Holocene mesocratic model, we found very strong evidence that *Quercus* cover was linked to precipitation seasonality (estimate = −0.043, $p<0.0001$), mean temperature of the wettest quarter (estimate = 0.077, $p<0.0001$), precipitation of the warmest quarter (estimate = −0.004, $p<0.0001$) and precipitation of the coldest quarter (estimate = 0.003, $p<0.0001$; Figure S5).

3.3 | *Taxus* (yew)

We found much higher *Taxus* cover during the Last Interglacial mesocratic compared with the Holocene mesocratic. Paired analysis of grid cells using Wilcoxon testing showed strong evidence for a difference in *Taxus* cover between the two time periods ($p=0.002$; Figures 1 and 2; $n=29$ paired grid cells). In paired grid cells, cover was lower in the Holocene by an absolute mean of 1.1% ± 2.0. This represents a relative decrease of 88.4% from the mean value of 1.3% in the Last Interglacial. *Taxus* cover was lower in all paired continental grid cells, as well as in 67% of paired oceanic grid cells (Figure S2).

Across all grid cells, the Last Interglacial mesocratic had 1.1% ± 1.8 mean cover whereas the Holocene mesocratic had 0.02% ± 0.1 mean cover (Figure 3). A pairwise comparison (z-test) of estimated marginal means from beta regression found very strong evidence for a lower *Taxus* cover in the Holocene mesocratic compared with the Last Interglacial mesocratic (estimate = −0.004, $z=-7.22$, $p<0.0001$). At every time window in the Holocene mesocratic, there was very strong evidence that *Taxus* had lower cover than in both time windows in the Last Interglacial mesocratic (Table S3; Figure S3).

Taxus abundance was only partially explained by climatic variation between the two time periods. The full model explained 39.4% of the variation in the data (pseudo R^2) and 17.8% when time period was removed (Table S4). The Last Interglacial model explained 12.4% of the variation in the data and the Holocene model explained 8.6% of the variation in the data (Table S1). In the Last Interglacial model, beta regression found strong evidence that *Taxus* cover was linked to precipitation of the warmest quarter (estimate = −0.007, $p=0.001$) and precipitation of the coldest quarter (estimate = 0.004, $p=0.004$) and weak to moderate evidence *Taxus* cover was linked to the mean temperature of the wettest quarter (estimate = 0.044, $p=0.055$; Figure S6). In the Holocene model, we found strong evidence that *Taxus* cover was liked to precipitation seasonality (estimate = −0.008, $p=0.006$; Figure S6).

4 | DISCUSSION

Our analysis of the pre-degradation abundances of *Quercus*, *Corylus* and *Taxus* before and after the late-Quaternary megafauna extinctions revealed two principal findings. First, woodlands in the Last Interglacial of temperate Europe exhibited higher cover of *Corylus* and *Taxus* relative to the early–mid-Holocene, with the former reaching a very high percentage cover; meanwhile, *Quercus* had a consistent, moderately high percentage cover in both periods. Second, we found that the cover of *Corylus* and *Taxus* appeared to be influenced by unmeasured, non-climatic factors that differed between the two time periods, as the abundance of these two taxa was explained better by models that accounted for time period. Together, these findings suggest that, as a result of different drivers, forest structure differed between the two periods and from the classical, closed-canopy expectations (Figure 4).

Our findings are inconsistent with classic vegetation succession theory (Hilmers et al., 2018; Lienard et al., 2015). Within an interglacial period, vegetation succession is considered light-driven, as the dominant vegetation shifts from light-demanding to shade-tolerant taxa and forests form closed canopies with greater competition for light (Ellenberg, 1988). Therefore, *Quercus* and *Corylus*, as light-demanding taxa that rely on open and semi-open vegetation, should decline as they are out-competed by shade-tolerant species (Ellenberg, 1988). Indeed, earlier work concluded that declines in *Quercus* and *Corylus* pollen percentages indicate that much of the landscape was closed forest in the Last Interglacial (Svenning, 2002). Whilst phases of high *Quercus* and *Corylus* are a recognised feature of the early Last Interglacial (Suchora et al., 2022) and could be attributed to early vegetation succession, our REVEALS-based findings indicate that a high abundance of both taxa was a more persistent feature of Europe's temperate forest biome. We found that *Quercus* and particularly *Corylus* were abundant throughout

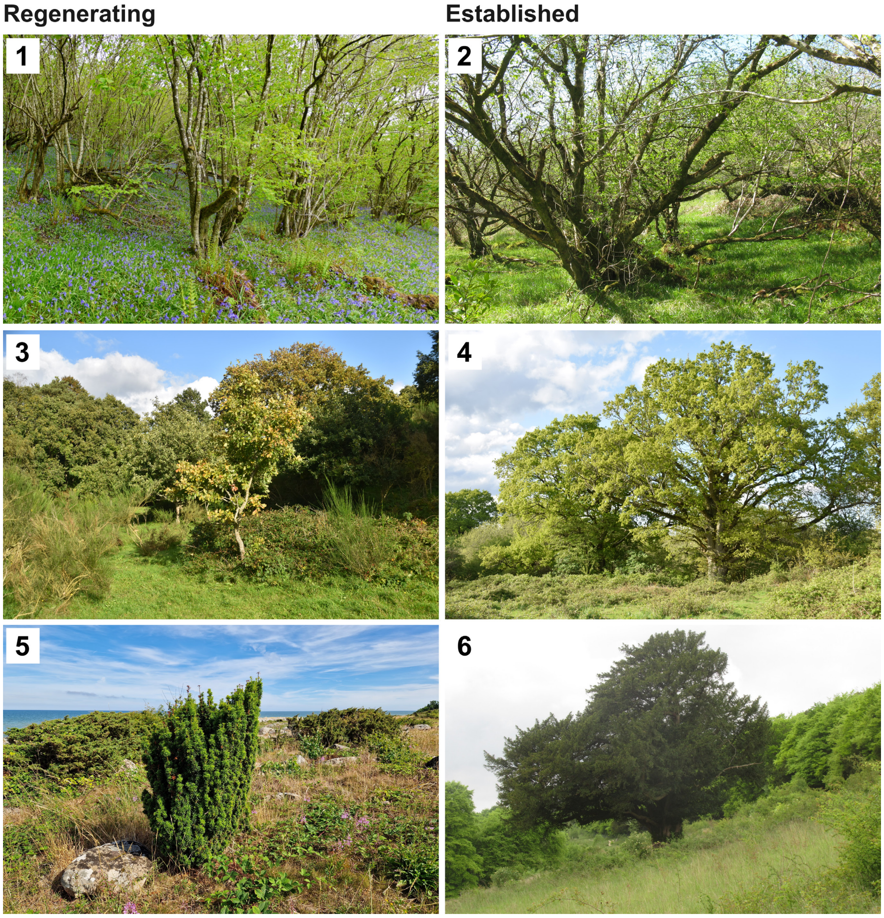

FIGURE 4 Examples of open and semi-open vegetation in Europe with regenerating (left) and established (right) *Corylus avellana* (top), *Quercus robur* (middle) and *Taxus baccata* (bottom). Photo credits: 1: Andrew Curtis, Wikimedia Commons, licensed under CC BY-SA 2.0; 2: Hazel Coppice at Torr Mhuilinn by M J Richardson, Wikimedia Commons, licensed under CC BY-SA 2.0; 3-5: Jens-Christian Svenning; Michael Geiser, iNaturalist (observation no. 115965559), licensed under CC BY-NC 4.0.

both the Last Interglacial mesocratic phases as well as in the pre-agricultural Holocene. Whilst *Corylus* did decline in the second half of the Last Interglacial mesocratic, its cover remained much higher than would be considered possible under a closed canopy (Coppins & Coppins, 2003). Instead, it is possible that the *Corylus* persisted as the dominant taxa for thousands of years, forming a stable and long-term community (Coppins & Coppins, 2003).

Habitat disturbance resulting in open vegetation may enable *Corylus* to outcompete taller-growing, shade-producing trees (Hicks, 2022). *Corylus* pollen production is enhanced in more open settings (Bégeot, 1998) and female flowers are three times more productive in direct sunlight than in shady conditions (Azarenko et al., 1997). Furthermore, *Corylus* has a relatively deep rooting system and a strong capacity for regeneration, providing it with an advantage in post-fire vegetation recovery dynamics (Tallantire, 2002). Similarly, *Quercus* thrives in disturbed open and semi-open habitats, but not under closed canopies (Bobiec et al., 2018). Even with moderate shade, *Quercus* growth is slower and saplings are less likely to survive (Jones, 1959). In contrast, *Quercus* has a strong capacity for resprouting after damage from herbivory (Bobiec et al., 2018) or fire (Jones, 1959), particularly in open sites that enable higher rates of photosynthesis (Bobiec et al., 2018).

Whilst *Taxus* can tolerate some shade, it often declines in closed forest environments due to its poor competitive ability and the shading from taller- and faster-growing species, which limits its growth and regeneration (Iszkuło et al., 2012; Perrin & Mitchell, 2013). Passive conservation approaches, such as passive rewilding or creating untouched forests are often not suitable for maintaining *Taxus* populations and active management strategies, including thinning competing species, are reported to be necessary to support its survival (Dobrowolska et al., 2017; Iszkuło et al., 2012). *Taxus* can withstand repeated pruning, continues growth under severe browsing pressure and is highly poisonous to many extant mammal species, even in small amounts (Cortinovis & Caloni, 2015). Deer are considered an exception and do browse *Taxus* in modern systems where their populations are not regulated by carnivores; at high population levels, deer can strongly depress *Taxus baccata* (Mysterud & Østbye, 2004), as well as other *Taxus* species (Windels & Flaspohler, 2011). However, such mesoherbivores are subject to strong predation effects and are expected to have had reduced abundance, in contrast to bigger herbivores, in the complex pre-extinction megafauna assemblages (Svenning et al., 2024). Importantly, non-ruminants are particularly sensitive to *Taxus* toxicity and produce little browsing damage as a result (Thomas & Polwart, 2003). *Taxus* is therefore likely to have good defences against the diverse fauna of large and megaherbivores that were widespread in Europe in the Last Interglacial (Davoli et al., 2023). This effect may be strengthened by the ability of *Taxus* seedlings to thrive in grazed systems via herbivore-mediated nurse shrubs (García & Ramón Obeso, 2003). Conversely, *Taxus* is sensitive to fire due to its thin bark and difficulty regenerating in dry environments (Calvia et al., 2023; Mola et al., 2014; Thomas & Polwart, 2003), which is likely to have affected its abundance in the Holocene.

Corylus and *Taxus* were both less abundant in the Holocene mesocratic than in the Last Interglacial. Divergent natural disturbance regimes between the two periods may help to explain these findings. Whilst direct testing of the impact of megafauna or other non-climatic disturbance agents was not feasible and this study does not provide direct evidence of their role, we estimated residual variance by considering climatic and environmental effects. Even after accounting for these variables, the residual variation in the data suggests that unexplained factors played a substantial role in driving vegetation openness. Climatic differences between the Last Interglacial and the Holocene did not account for a substantial proportion of the variation in *Corylus* and *Taxus* abundance. The high importance of the 'time period' factor in our analysis indicates that other factors influencing abundance varied between these periods and were not captured by the explanatory variables. In contrast, *Quercus* abundance, which remained consistent across both periods, was mostly explained by climatic variables in our models. If climatic differences between the periods had strongly affected vegetation, we would expect *Quercus* cover to have changed more than *Corylus* and *Taxus* cover given that it was more explained by climate variables; however, *Quercus* cover changed the least. Overall, the inconsistent climate relations between taxa across different time periods suggest that other disturbance regimes likely played a role in driving open vegetation. We suggest a high level of herbivory by a diverse, abundant megafauna in the Last Interglacial and anthropogenic ecosystem management in the early–mid-Holocene are the most plausible candidates.

Megafauna abundance, species richness and functional diversity declined severely in the LGP, particularly amongst larger species (Davoli et al., 2023; Sandom, Ejrnæs, et al., 2014; Schowanek et al., 2021; Smith et al., 2018). Given the role of larger megafauna in creating and maintaining open and semi-open vegetation, defaunation is likely to have had cascading effects on forest community composition (Bakker et al., 2016). Our results for *Corylus* and *Taxus* are consistent with this hypothesis. Interestingly, however, *Quercus* is usually considered to benefit most from open, disturbed landscapes (Bobiec et al., 2018), yet, we found no evidence of a difference in *Quercus* cover; abundances were similar in the Last Interglacial and the Holocene mesocratic periods. This indicates that temperate forests in the Holocene mesocratic also had substantial openness (Serge et al., 2023), as in the Last Interglacial, but this was likely driven by factors other than megafauna due to their lower numbers in the Holocene (Bergman et al., 2023; Smith et al., 2018). We suggest that there may be an interplay between the effects of megafauna decline and additional factors that influence open and semi-open vegetation, which resulted in *Corylus* and *Taxus* being less abundant in the Holocene mesocratic.

Fire regimes were more frequent and intense in the Holocene than in the Last Interglacial (Lawson et al., 2010), which may have maintained open and semi-open vegetation. Increased fire activity was likely due to direct fire management by *Homo sapiens* (Ellis et al., 2021), though it is also possible that the late-Quaternary megafauna extinctions contributed, as megafauna reduce flammable biomass (Karp et al., 2021). Increased fire activity, but less herbivory, in the Holocene compared with the Last Interglacial may have affected *Corylus* abundance by promoting more fire-tolerant taxa like *Pinus* (pine) and *Betula* (birch) (Molinari et al., 2020). *Pinus* and *Betula* may not have had a competitive advantage in the Last Interglacial as, though they are light-demanding, they are less tolerant of herbivory (Amsten et al., 2021).

In the early-mid-Holocene, high *Corylus* levels could have been promoted by *H. sapiens*, as hazelnuts were an important part of the Mesolithic diet (Bishop et al., 2023; Jacomet & Vandorpe, 2022; Jahns & Wolters, 2021). Deliberate coppicing of *Corylus* could promote flowering and therefore increase pollen production (Waller et al., 2012); however, the surviving browsing megafauna could have had the same effect (Vera, 2000). Moreover, whilst the human consumption of hazelnuts in the Mesolithic is well-documented, there is limited evidence of deliberate coppicing (Bishop et al., 2015). Finally, we found that *Corylus* presence was higher in the Last Interglacial than in the early Holocene. Although studies of archaeological sites have found charred hazelnut shells, indicating their consumption by *Homo neanderthalensis* (Neanderthals) (Salazar-García et al., 2013; Richter, 2016), the smaller population size of Neanderthals compared with later *H. sapiens* (Prüfer et al., 2014) is unlikely to have impacted *Corylus* abundance so substantially. This suggests that factors other than human activity played a role in promoting *Corylus* abundance, with megafauna likely having the strongest effects in the Last Interglacial and potentially also playing a role in the early-mid-Holocene (Vera, 2000).

Our findings show that disturbance-favoured *Corylus* and *Taxus* existed in greater abundance in the Last Interglacial, before the late-Quaternary megafauna extinctions. Interestingly, climate was not a primary driver of these abundance variations, emphasising the influence of unaccounted disturbance regimes in shaping past vegetation dynamics and opening an important avenue for future research. We conclude that the results presented here support active disturbance regimes in the Last Interglacial and are consistent with these being caused by megafauna herbivory rather than fire, given the higher abundance of *Taxus*. Megafauna existed in great abundance in Europe and world-wide for more than 30 million years (Smith et al., 2018). Our results indicate that the abundances of *Corylus* and *Taxus* in the early–mid-Holocene diverged from long-term baselines, which may have important implications for forest management and restoration initiatives (Bobiec et al., 2018; Mysterud & Østbye, 2004; Svenning & Magård, 1999). Modern management practices, characterised by either low densities of larger herbivores or high densities of mesoherbivores, do not reflect the greater diversity of herbivory modes and likely increased heterogeneity in herbivory that shaped past ecosystems (Atkinson et al., 2024). Consequently, trophic rewilding with a more diversified megafauna likely better aligns with long-term ecological conditions, promoting more resilient and functionally diverse woodland ecosystems.

AUTHOR CONTRIBUTIONS

Jens-Christian Svenning, Elena A. Pearce, Florence Mazier, Ralph Fyfe and Signe Normand designed the research, Florence Mazier, Maria-Antonia Serge and Paolo Scussolini contributed data; Elena A. Pearce and Charles W. Davison analysed the data; Elena A. Pearce wrote the paper, with input from all co-authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare they have no conflicting interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data used in this study are available from data.InDoRES: https://data.indores.fr/dataset.xhtml?persistentId=doi:10.48579/PRO/J5GZUO (Holocene; Serge, 2023) and OSF: https://osf.io/nejbz/ (Last Interglacial; DOI: 10.17605/OSF.IO/NEJBZ; Pearce et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. REVEALS time windows (TW) and years before present (BP; Holocene only) grouped to the interglacial phases used in this study (Last Interglacial mesocratic and Holocene mesocratic).

Table S2. Main climate zones covered by the Last Interglacial and Holocene pollen cores, grouped according to their description in the paper.

Table S3. Pairwise comparisons (*z*-test) of the estimated marginal means from beta regression modelling for each taxon across every time window.

Table S4. Model output (estimates and *p* values) for the four beta regression models per taxa.

Figure S1. Köppen-Geiger climate classification for the Last Interglacial (127 k) and Holocene (6 k). We reconstructed the classifications as in Beck et al. (2018), from monthly temperature and precipitation data from the GISS-E2-1-G earth system model (Kelley et al., 2020). For further methods and choice of model, see "climate data and zones" in main methods.

Figure S2. Maps showing the difference in percentage cover of *Quercus*, *Corylus* and *Taxus* for paired grid cells, from the Last Interglacial to the Holocene. More red colours show a decrease in cover, whereas more blue colours show an increase.

Figure S3. Boxplots of taxa percentage cover in the temperate forest biome (paired grid cells), at every time window, for the Last Interglacial (Protocratic to Telocratic) and the Holocene (11,700 – (-65) BP).

Figure S4. Beta regression predictions of *Corylus* cover for variables where we found evidence of an effect in the Last Interglacial or Holocene: Mean Temperature of the Wettest Quarter (°C), Precipitation Seasonality (mm) and Precipitation of the Warmest Quarter (mm) and Precipitation of the Coldest Quarter (mm).

Figure S5. Beta regression predictions of *Quercus* cover for variables where we found evidence of an effect in the Last Interglacial or Holocene: Mean Temperature of the Wettest Quarter (°C), Precipitation Seasonality (mm) and Precipitation of the Warmest Quarter (mm) and Precipitation of the Coldest Quarter (mm).

Figure S6. Beta regression predictions of *Taxus* cover for variables where we found evidence of an effect in the Last Interglacial or Holocene: Mean Temperature of the Wettest Quarter (°C), Precipitation Seasonality (mm) and Precipitation of the Warmest Quarter (mm) and Precipitation of the Coldest Quarter (mm).

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