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Substantial light woodland and open vegetation characterised the temperate forest biome before Homo sapiens

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1 Substantial light woodland and open vegetation characterised the temperate forest biome

MAAAS

2 before *Homo sapiens*

3 Short title: Forest openness before *Homo sapiens*

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78 Abstr	act
79	The extent of vegetation openness in past European landscapes is widely debated. In
80	particular, the temperate forest biome is traditionally defined as dense closed-canopy
81	forests; however, some argue that large herbivores maintained greater openness or even
82	wood-pasture conditions. Here, we address this question for the Last Interglacial period
83	(129,000-116,000 years ago), before Homo sapiens-linked megafauna declines and
84	anthropogenic landscape transformation. We applied the vegetation reconstruction method
85	REVEALS to 96 Last Interglacial pollen records. We found that light woodland and open
86	vegetation represented on average over 50% cover during this period. The degree of
87	openness was highly variable and only partially linked to climatic factors, indicating the
88	importance of natural disturbance regimes. Our results show that the temperate forest biome
89	was historically heterogeneous rather than uniformly dense, which is consistent with the
90	dependency of much of contemporary European biodiversity on open vegetation and light
91	woodland.
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- 93 Teaser
- 94 Landscape reconstruction using pollen data shows that European temperate forests were95 open and heterogeneous before modern humans.
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97 Introduction

98 The extent of vegetation openness in past European landscapes is widely debated (1–4).
99 Uncertainties are especially acute in temperate forests, where accurate estimates are needed

100 as baselines for ecosystem restoration. The traditional view is that closed-canopy forests, as the climax state of vegetation succession, would have dominated the temperate forest biome 101 before increased human presence (1, 2). In the past two decades, proxy-based 102 reconstructions have challenged this view of European forests (3-5). Recent pollen-based 103 reconstructions of past land cover in the Holocene (11,700 BP-present) have shown that 104 traditional comparisons of the percentage of arboreal to non-arboreal pollen strongly 105 underestimate the cover of grass and heathland (6, 7). In support of this finding, fossil 106 records from habitat-specific Mollusca (molluscs) and Coleoptera (beetles, from the British 107 Isles) indicated that open and light woodland vegetation dominated in the early-mid 108 Holocene (11,700-6000 BP) (8) and during the Last Interglacial period (129-116 thousand 109 years [ka] before present [BP]) (9), respectively. Therefore, rather than comprising 110 exclusively closed forests, Europe was potentially a heterogeneous landscape that featured 111 a mixture of closed, open, and semi-open vegetation, such as grassland, scrub, and wood-112 pasture-like vegetation (4, 10). However, in the early Holocene, it is unclear how far open 113 vegetation is an anthropogenic signal (11). The extent of vegetation openness prior to the 114 115 impacts of *Homo sapiens*, in the temperate forest biome and Europe more broadly, remains poorly quantified. 116

Researchers have often considered the early to mid-Holocene, before the widespread 118 119 adoption of agriculture, to be an appropriate reference point for pre-human vegetation structure (2, 3, 5). However, as a pre-human baseline for Europe, the early-mid Holocene is 120 insufficient, primarily because of the impact of the arrival of H. sapiens (~54 ka BP) (11). 121 While earlier humans, such as Neanderthals (H. neanderthalensis), likely had localised 122 effects on vegetation (12), there is evidence for the widespread use of fire by *H. sapiens* to 123 shape vegetation during the Mesolithic (13). Furthermore, *H. sapiens* are likely to have 124 reduced the density and distribution of large herbivores far more than previous hominins 125 did (12, 14). Large herbivores strongly influence vegetation openness (15). The global 126 expansion of *H. sapiens* is associated with strong reductions in species richness and 127 functional diversity of large herbivores, with particularly severe losses among larger species 128 (14, 16). These defaunation dynamics are likely to have reduced the ability of fauna to 129 promote openness in landscapes. Before these losses, high megafaunal diversity was typical 130 in Europe and worldwide for more than 20 million years (17). To understand pre-H. sapiens 131 vegetation dynamics and their implications for the evolutionary adaptations of species, it is 132

important to elucidate vegetation structure before the late-Quaternary faunal downsizing(16).

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The Last Interglacial in Europe (Eemian) corresponds to Marine Isotope Stage 5e (129–116 136 ka BP) (18), and predated the expansion of *H. sapiens* into Europe (19). Some early human 137 influence did exist (20), as Neanderthals were present throughout Europe (21), but they 138 likely only influenced local vegetation structure, owing to low population sizes (20). 139 Furthermore, despite different climate forcing, the Last Interglacial was characterised by 140 climates comparable to those of the present (22). As a result, it presents a valuable 141 opportunity to study vegetation openness in the absence of extensive human impact and 142 with climatic characteristics similar to today. However, there are large gaps in our 143 understanding of the vegetation cover during this period. 144

Pollen records represent the most direct and widely available empirical data for recreating 146 past vegetation cover (23). The dominant vegetation of temperate Europe during the Last 147 148 Interglacial period has been inferred by dividing pollen percentage diagrams into distinct zones based on dominant taxa (24, 25). Four common 'zones' are broadly identified as a 149 unimodal pattern of vegetation succession in central and temperate regions (24, 26). The 150 first is the pioneer, Protocratic, Pinus-Betula (pine-birch) phase, in which rising 151 152 temperatures and increasingly fertile soils supported light-demanding vegetation. High temperatures peaked during the temperate Mesocratic period, which is traditionally 153 considered to be closed-forest dominated by Quercus (oak) and Corylus (hazel; early-154 temperate), followed by *Carpinus betulus* (hornbeam; late-temperate). Finally, towards the 155 end of the interglacial, leached soils and falling temperatures of the Oligocratic/Telocratic 156 phase were correlated with *Picea* (spruce) dominating along with *Pinus* and *Abies* (fir), and 157 increasing vegetation openness (25). 158

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Vegetation openness during the Last Interglacial period has mostly been determined by comparing the raw percentages of arboreal pollen with non-arboreal pollen, which has indicated a scarcity of grassland and heathland and an overrepresentation of woody cover (2, 27). However, the use of raw pollen percentages fails to account for the nonlinearity of the pollen-vegetation relationship (27). Further, other proxies for vegetation reconstruction provide conflicting estimates. Small mammal assemblages suggest that mixed woodlands, including open grassy habitats, likely existed in West and Central Europe, with more open

- forest-steppe landscapes occurring in South and Northeast Europe (28). Beetle assemblage
 records from the British Isles similarly indicate a mixture of closed forests, wood-pasture
 and open vegetation (9). Finally, fossil finds of many large grazing animals, and
 megaherbivore diet indicators, indicate the presence of mixed woodland and open habitats
 across Europe (4).
- The pollen-vegetation relationship is influenced by spatial scale, basin size, differences in 173 sedimentary archives, and taxonomic differences in pollen productivity and dispersal 174 characteristics (27, 29). The Regional Estimates of VEgetation Abundance from Large Sites 175 (REVEALS) model corrects for biases caused by these factors and provides the regional 176 vegetation composition and land cover within a $1^{\circ} \times 1^{\circ}$ area (27). The REVEALS model 177 has been extensively validated using both modern and historical analogues (see Methods) 178 (30–32). Pollen-based REVEALS reconstructions of vegetation openness over the Holocene 179 were produced for $1^{\circ} \times 1^{\circ}$ grid cells across Europe (7). However, REVEALS has only been 180 used to reconstruct vegetation of the Last Interglacial period at single sites (33) and not at 181 the continental scale. 182
- In this study, we applied REVEALS to a large dataset of Last Interglacial pollen records 184 across Europe. We assessed vegetation openness in the European temperate forest biome, 185 186 as well as adjoining biomes, before the arrival of H. sapiens. To elucidate the processes controlling vegetation structure, we evaluated the extent to which climatic and topoedaphic 187 factors explain the variation in pre-anthropogenic vegetation openness across Europe and 188 within the temperate forest biome. Our study provides insights into the state of the temperate 189 forest biome before modern humans and contributes to the long-standing 'open' vs 'closed' 190 vegetation debate in Europe. Our results have important implications for our understanding 191 of the evolutionary ecology of Europe's native biota as well as for restoration and rewilding 192 efforts within this biome and across the continent. 193
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195 **Results**

196 Europe-wide scale

197Our results showed that, before the arrival of *H. sapiens*, highly heterogeneous vegetation198was widespread in Europe (Fig. 1). Taxa indicating open and light woodland vegetation199were strongly represented alongside the closed forests of shade-tolerant trees. In the early-200temperate period, open vegetation represented an average of 21% (95% CI [14.8, 26.2]) of

the vegetation cover, with light woodland taxa representing an additional 53% (95% CI [47.0, 58.7]). We found that 16% of the grid cells contained open vegetation over more than 50% of their area (n = 10; Fig. 1). Low levels of open-vegetation taxa, between 0% and 10%, were found in 48% of the grid cells (n = 30; Fig. 1).



- 208 Fig. 1. REVEALS estimates. Open vegetation (top; herbaceous and heath taxa) light woodland (middle: shade-intolerant and intermediate taxa) and closed forest 209 (**bottom**: shade-tolerant taxa) in the early-temperate (left) and late-temperate (right) 210 periods. Each square is a regional grid cell of $1^{\circ} \times 1^{\circ}$. Darker colours show greater 211 cover by open vegetation. White/black circles inside each grid cell represent the 212 coefficient of variation (standard error / REVEALS estimate). When SE \geq 213 REVEALS estimate, the circle fills the entire grid cell, and the estimate is considered 214 unreliable. 215
- In the late-temperate period, open vegetation represented an average of 19% (95% CI [12.6, 25.4]) of the vegetation cover, with light woodland taxa representing an additional 28% (95% CI [23.3, 32.6]; Fig. 1). We found that 15% of the grid cells contained more than 50% open vegetation (n = 9; Fig. 1). The late-temperate period had more grid cells with less than 10% open vegetation taxa (58% of grid cells, n = 34, compared to 48% in the earlytemperate period, n = 30; Fig. 1).
- During both time periods, Poaceae (grasses) and Cyperaceae (sedges) were the dominant 224 open vegetation taxa, and Corvlus was the dominant light-woodland taxon (Table S1). Other 225 common taxa in the two categories were Artemisia (mugworts). 226 Amaranthaceae/Chenopodiaceae (gooseworts and relatives), Ericaceae (various heathers 227 and relatives), Rumex acetosa type (sorrel), Calluna vulgaris (common heather), Betula, 228 Pinus, Salix (willow), and Taxus baccata (yew; Data S1). 229
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231 Temperate forest biome

In the temperate forest biome (oceanic and continental sites that are not in the 'Alpine' 232 region; see Fig. S1), open and light woodland taxa combined represented 79% (95% CI 233 [74.0, 83.0]) of the vegetation, on average, in the early-temperate and 51% (95% CI [43.3, 234 57.9]) in the late-temperate period (Fig. 2). In the early-temperate, open taxa represented an 235 average of 19% (95% CI [12.8, 24.5]) of the vegetation, while light woodland taxa 236 represented an additional 60% (95% CI [54.4, 65.3]; Fig. 2). We found that 12% of the grid 237 cells contained more than 50% open vegetation (n = 5), whereas 49% of the grid cells 238 contained 0–10% open vegetation (n = 21; Fig. 1). In the late-temperate, open taxa 239 represented an average of 16% (95% CI [10.2, 22.5]) of the vegetation, and light woodland 240 taxa an additional 34% (95% CI [29.0, 39.4]; Fig. 2). We found that 10% of the grid cells 241 contained greater than 50% open vegetation (n = 4), whereas the number of grid cells with 242 less than 10% open vegetation increased slightly to 56% (n = 23; Fig. 1). During both 243

periods, the most open sites tended to occur in oceanic Europe. However, multiple exceptions existed and did not follow any spatial pattern, nor were they assigned to a particular biome (Fig. 1).

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Fig. 2. Mean percentage land cover type per biome. Mean land cover (%) of open vegetation (yellow), light woodland (green) and closed forest (blue) in the temperate forest, Mediterranean, Subarctic and Alpine biomes in the early-temperate (**top**) and late-temperate (**bottom**) periods of the Last Interglacial.

255 Alpine region

The Alpine region (Fig. S1) contained relatively little open vegetation (Figs. 1 and 2). All grid cells contained less than 20% of open vegetation taxa in the early-temperate (n = 11) and less than 10% of open vegetation taxa in the late-temperate period (n = 10; Fig. 1). The presence of light woodland taxa varied. In the early-temperate, light woodland taxa represented between 0% and 80% of the vegetation. The late-temperate contained a much lower percentage of light woodland taxa, with most grid cells containing less than 20% (n 262 = 9; Fig. 1). Most of the region was closed forest, particularly during the late-temperate period, when all grid cells contained 90-100% closed forest vegetation (Fig. 1). In most grid 263 cells, the standard error was greater than the REVEALS estimate for closed forests, raising 264 uncertainty regarding the reliability of the results (Fig. 1; Data S2). However, the grid cells 265 in this region were unanimous in their findings. Picea, Abies alba (silver fir), Corvlus, and 266 Quercus were dominant in the early-temperate, indicating a mixed closed and light 267 woodland landscape. Abies alba was the dominant taxon in the late-temperate, indicating a 268 closed-forest dominated landscape. 269

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271 Other biomes

In the subarctic and Mediterranean biomes (Fig. S1), open vegetation taxa dominated, but 272 vegetation openness was highly variable. In the Mediterranean, during the early-temperate 273 period, the six grid cells contained between 10% and 100% open vegetation, with an average 274 openness of 50% (95% CI [16.6, 73.7]; Figs. 1 and 2). In the subarctic, both grid cells 275 contained 30%–50% open vegetation (Fig. 1). The late-temperate showed a similar variation 276 in openness; in the Mediterranean, grid cells had between 0% and 100% open vegetation 277 (mean = 40%; 95% CI [8.4, 51.3]), whereas the three subarctic sites contained 60%–90%278 open vegetation (Figs. 1 and 2). A high level of light woodland taxa were present during the 279 early-temperate in the subarctic (40%-50% cover), which dropped to less than 20% in the 280 281 late-temperate (Fig. 1). In the Mediterranean, light woodland taxa represented between 0% and 30% of the vegetation in the early-temperate and between 0% and 40% in the late-282 temperate (Fig. 1). 283

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285 Drivers of vegetation openness

286 *Continental scale*

The full beta regression model included the following predictors: mean temperature of the warmest quarter (°C), precipitation of the driest month (mm), degree of continentality (the difference between the mean temperature of the warmest quarter and coldest quarter; °C), standard deviation (SD) of elevation (terrain roughness; m), occurrence in the Alpine region (1) or outside it (0), and time window (early-temperate, late-temperate). The model explained 29.9% of the variation in the data (pseudo R^2).

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The precipitation of the driest month and mean temperature of the warmest quarter had the strongest effect on vegetation openness (estimate = -0.044, P < 0.001; estimate = -0.181, P 296 < 0.001, respectively; Fig. 3). The negative effect of temperature was largely driven by high openness and low temperatures in the subarctic, and the effect of precipitation was driven 297 by high openness and low precipitation in the Mediterranean. There was moderate evidence 298 that degree of continentality decreased vegetation openness, with openness increasing 299 towards more oceanic conditions (estimate = -0.057, P = 0.045; Fig. 3). There was moderate 300 evidence that open vegetation cover was affected by terrain roughness (estimate = 0.002, P 301 = 0.011; Fig. 3). Finally, a pairwise comparison of the estimated marginal means from the 302 beta regression model revealed no difference in vegetation openness between the early-303 temperate and late-temperate periods (estimate = 0.028, P = 0.273; Fig. S2). 304

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307Fig. 3. Beta regression predictions for variables with significant effects: Mean308temperature of the warmest quarter (°C), degree of continentality (°C),309precipitation of driest month (mm), and standard deviation of elevation (m).310Two scales are shown: Europe (n = 118; all grid cells across both time windows;311solid + unfilled points, and dashed lines), and the temperate forest biome (n = 82;312oceanic and continental grid cells, excluding 'Alpine' group, across both time windows; solid points and lines).

315 **Temperate forest biome**

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The full beta regression model for the temperate forest biome explained 22.5% of the variation in the data (pseudo R^2). Increasing continentality was linked to decreasing vegetation openness to a strong degree (estimate = -0.137, P = 0.003; Fig. 4). No other explanatory variables had significant effects (Table 1; Fig. S2).

Table 1. Beta regression model output for all explanatory variables. Estimates and *P*-values are given for all explanatory variables for Europe (all grid cells) and grid cells in the temperate forest biome (oceanic and continental grid cells, excluding 'Alpine' group).

	Coefficient	Est	imate	<i>P</i> -value		
		Europe	Temperate	Europe	Temperate	
		(all grid	Forest	(all grid	Forest	
		cells)	Biome	cells)	Biome	
Ν	Mean temp. warmest quarter (°C)	-0.181	-0.189	0.001	0.164	
	Mean precip. driest month (mm)	-0.044	-0.019	4.40E-05	0.298	
	Degree of continentality (°C)	-0.057	-0.137	0.045	0.003	
	Standard deviation of elevation (m)	0.002	-0.002	0.011	0.569	
	Time window (early/late temperate)	-0.196	-0.133	0.271	0.487	
	Alpine $(0,1)$	-0.593		0.147		

339 Alpine region

Including all grid cells (n = 66) in the beta regression model revealed that the alpine sites had a moderate negative association with vegetation openness (estimate = -0.827, P = 0.029; Fig. S3). However, after removing the outlier in Southern Norway (see Methods), we found no effect (Fig. S2).

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345 **Robustness assessment**

- 346 Multiple comparisons of means using Tukey contrasts revealed that the standard errors were significantly higher for closed vegetation than for open vegetation (estimate = -18.82, P < -18.82347 1e–04) or light woodland vegetation (estimate = -15.58, P < 1e-04; Fig. S4). Furthermore, 348 the standard errors for open vegetation cover did not vary greatly across the openness levels 349 (Fig. S5). The REVEALS estimates for open vegetation were unreliable for only three grid 350 cells (Fig. 1; see the Methods section). The REVEALS estimates were unreliable in one grid 351 cell for light woodlands and 15 grid cells for closed vegetation (Fig. 1). All standard errors 352 are provided in Dataset 02. 353
- We found no effect of wetland indicators on vegetation openness. A pairwise comparison 355 of the estimated marginal means from beta regression modelling showed no difference in 356 vegetation openness between samples taken from bogs and lakes (estimate = -0.002, P =357 0.950; see also Fig. S6). We found no relationship between vegetation openness and the 358 wetland taxa Salix (estimate = 11.127, P = 0.213) and Alnus (alder; estimate = -0.627, P =359 0.919). Across Europe (all grid cells), we found moderate evidence for a relationship 360 between lake size and vegetation openness (estimate = 4.499e-05, P = 0.024). However, 361 this relationship was driven by the grid cell from Lake Van, Turkey, which is the largest 362 lake in the dataset (Table S2). When we excluded this grid cell, we found no evidence of a 363 relationship (estimate = -6.020e-05, P = 0.353). 364
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366 Discussion

Our analysis of vegetation openness in Europe before *H. sapiens* revealed three principal 367 findings. First, open and light woodland vegetation were common features in the temperate 368 forest biome during the Last Interglacial. Second, vegetation cover was highly variable, with 369 the proportion of open vegetation varying widely across the entire range. Together, these 370 findings suggest that, before H. sapiens, the European temperate forest biome was a 371 heterogeneous woodland landscape with widespread but varied open and light woodland 372 vegetation (Fig. 4). Finally, variation in open vegetation cover could only be partially 373 explained by climatic and topoedaphic variables. Although the mean temperature of the 374 warmest quarter, precipitation of the driest month, and degree of continentality had some 375 effects on open vegetation cover, it is likely that other processes also played important roles 376 in shaping European landscapes before modern humans. 377



- Fig. 4. Palaeoartistic reconstructions of Last Interglacial landscapes in the European temperate forest biome, consistent with our pollen-based estimates of vegetation structure. Typical Last Interglacial fauna are shown, such as the extinct straight-tusked elephant (Palaeoloxodon antiquus), an extinct rhinoceros (Stephanorhinus kirchbergensis), and aurochs (Bos primigenius, the extinct wild form of contemporary domestic and feral cattle), alongside common extant species: fallow deer (Dama dama), a great spotted woodpecker (Dendrocopos major), a European robin (Erithacus rubecula), and greylag geese (Anser anser). Top left: Early-temperate period: Light woodland, including a mix of taller trees and the shrub hazel (Corvlus avellana), and grass-dominated open vegetation. Top right: Earlytemperate period: Open, grassy vegetation interspersed with light woodland and bordering closed forest with shade-tolerant trees. Bottom left: Late-temperate period: Light woodland, denser forest with frequent hornbeam (Carpinus), and some open vegetation (front). Bottom right: Late-temperate period: Open grass- and sedge-dominated vegetation with free-standing deciduous oaks (Quercus robur), with more closed tree stands in the background. Illustrator: Brennan Stokkermans.
- Our continental-scale analysis supports a growing body of local-level, proxy-based work. The presence of grasslands, meadows, and other open vegetation have been indicated by plant macrofossil, mollusc, and beetle records (4, 8, 9); large herbivore diet analyses (34);

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402 and the presence of forb taxa that characterise grasslands and disturbed soils, such as Artemisia, Amaranthaceae/Chenopodiaceae, and Rumex acetosa (Data S1) (20). Such 403 findings have provided useful indications of open vegetation during the Last Interglacial 404 period, but have previously conflicted with findings from pollen records. For example, in 405 the British Isles, Coleoptera assemblages indicated the presence of up to 55% wood-pasture 406 landscapes as well as open and closed habitats in the Last Interglacial period (9). In Central 407 Europe, the mammalian record indicated a mosaic environment of forested and open 408 vegetation, based on the frequent occurrence of *Equus ferus* (wild horse), *Bison* spp. (bison), 409 and Bos primigenius (aurochs) (35). Furthermore, analyses of small mammals revealed 410 diverse faunal compositions indicative of diverse habitats (28). A considerable number of 411 open landscape inhabitants (e.g. field voles Microtus agrestis and M. arvalis) as well as 412 forest-dwelling species (e.g. Apodemus sylvaticus [wood mouse] and Myodes glareolus 413 [bank vole]) were present across Europe during the Last Interglacial period (28). Our results 414 present an important step towards resolving the contradictions between the floral- and 415 faunal-based estimations of vegetation structure during the Last Interglacial period. 416

The high abundance of *Corvlus* and deciduous *Ouercus* (hereafter *Ouercus*) in the light 418 woodland category supports the presence of semi-open landscapes, and is indicative of 419 ongoing disturbance regimes. Corvlus and Quercus were particularly visible during the 420 421 early-temperate period (Fig. 1; Table S1), as these taxa are moderately light-demanding and grow opportunistically in open or light woodland areas and areas of recent disturbance (36, 422 37). We expected high levels of *Ouercus* and *Corvlus* during the early-temperate because 423 this pattern is characteristic of many of the Last Interglacial pollen diagrams (24). However, 424 previous studies concluded that the temperate forests were *Quercus* dominated, with 425 Corvlus present to a lesser degree (24). Our REVEALS model estimated greater percentages 426 of Corylus than Quercus during the early-temperate period. Although partial Corylus 427 dominance after the *Quercus* phase of the temperate period has been shown previously (38), 428 our findings suggest a much greater role for Corvlus. Corvlus dominance would be 429 consistent with scrub woodland dependent on ongoing disturbance, although *Corvlus* may 430 also thrive under the canopy of lightly shaded trees, such as *Ouercus* and *Fraxinus* (ash) 431 (37). Furthermore, *Quercus* regeneration, from seed dispersal to recruitment, occurs mostly 432 in dynamic, heterogeneous landscapes subjected to disturbances from grazing animals and 433 fire, for example (36). Importantly, both Corvlus and Ouercus fail to regenerate under a 434 dense canopy (36, 39) and both taxa persisted for millennia through the temperate period 435

(Fig. 1; Table S1). Although less common, the continued presence of *Corylus* and *Quercus*in the late-temperate period is consistent with a heterogeneous landscape with varied open
elements, suggesting the presence of ongoing disturbances.

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The variability in open vegetation across Europe raises questions about the drivers of 440 openness, since environmental and climatic factors only partially explain the distribution of 441 vegetation openness. In focusing our analysis on the temperate forest biome, we found that 442 vegetation was more open in the milder oceanic grid cells (Figs. 1 and 2). From a climatic 443 perspective, this relationship is counterintuitive because tree dominance is expected under 444 milder temperate conditions (4). Furthermore, we found little evidence of any effects of 445 other climatic or environmental variables in this biome (Fig. S2). It is possible that other 446 environmental variables, such as soil type, played a role in driving open vegetation (40). 447 However, soil type is difficult to assess for the Last Interglacial period, and comparisons to 448 modern records are inadequate, given the transformation of relief and thus soil formation, 449 structure, and texture following glacial cycles (41). Except for the 'Alpine' group, the 450 451 temperate biome grid cells revealed no clear spatial pattern of vegetation openness and no pattern likely to match any considered environmental gradient. Importantly, climate-linked 452 openness is often mediated by disturbance factors (42). Furthermore, under mild temperate 453 conditions today, trees tend to dominate via succession in the absence of the active 454 455 restoration of disturbance regimes (43), even on poor soils (44). Therefore, we propose that disturbance agents must have influenced the presence of open and light woodland 456 vegetation, with potentially stronger effects under more oceanic climates. 457

The presence of open and light woodland taxa suggests ongoing vegetation disturbance. A 459 plausible candidate is the rich megafaunal community of Europe during the Last Interglacial 460 (15, 35). Large herbivores are ecological engineers capable of altering vegetation at the 461 landscape scale (17). Their large body size requires the consumption of large quantities of 462 plant biomass, which further affects vegetation through trampling, rooting, and debarking, 463 as well as through seed dispersal and biogeochemical cycling (17). The effects of large 464 herbivores on vegetation structure and wider ecosystem functioning have been well 465 researched in recent years, especially relating to the ecosystem-wide effects of 466 reintroductions (45). In modern European systems, large free-living herbivores can have 467 considerable and lasting effects on vegetation composition and structure, for example, by 468 generating or maintaining open and semi-open vegetation (46). Further, their effects might 469

470 be stronger under mild, oceanic climates, where population sizes are less constrained by cold and drought (46). Compared to present-day Europe, the Last Interglacial period was 471 home to a considerably greater number of larger-bodied herbivores (16), including elephants 472 and other megaherbivores with strong effects on vegetation structure (15, 47). Our high 473 openness estimates for England are consistent with previous beetle-based estimates, which 474 also indicate high large herbivore abundances (9, 48) at a level sufficient to generate open 475 vegetation on fertile wetland adjacent soils in Western Europe today (46). In the present 476 study, closed forest vegetation was more abundant in the Alpine region (Figs. 1 and 2). It is 477 possible that, due to lower accessibility (49), larger herbivores were not as prevalent in this 478 mountainous region, and altered vegetation structure more in lowland regions (4, 9). 479 However, terrain roughness, a measure hypothesised to reflect herbivore accessibility (49), 480 had a moderate positive effect on vegetation openness (Fig. 3). Further research is required 481 to understand this relationship. 482

Large herbivores may alter forests beyond promoting vegetation openness, such as by 484 affecting the structure and species composition of the closed vegetation community (15). 485 Such effects might explain the expansion of C. betulus in the late-temperate period. C. 486 *betulus* is one of the few dominant European tree species able to develop a 'cage' 487 architecture when exposed to browsing, allowing it to grow out of reach of herbivores (50). 488 489 In addition, it has tough wood, a strong resprouting ability, and a folded trunk morphology that should protect against debarking. Consequently, C. betulus survives severe herbivory 490 regimes more readily than other dominant European tree species, but especially under high 491 light conditions (50). This adaptation challenges the view that abiotic drivers alone 492 influence forest structure, even when forests are denser, as in the late-temperate period (Fig. 493 1). Our findings support the presence of sunlit conditions that could enable C. betulus 494 survival and eventual dominance (Table S1). 495

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It is possible that fire regimes play a role in the unexplained patterns of vegetation openness. Feedback between fire and fire-prone grassy vegetation maintains open landscapes in some ecosystems (51). In boreal and Mediterranean ecosystems, fire disturbance is an important part of vegetation dynamics (52), and could contribute to the higher percentages of vegetation openness found in these regions. Moist temperate regions are often considered to have low fire frequencies and severity because broadleaf deciduous trees generally have high leaf moisture and little flammable material (52). Furthermore, a strong role of fire

504 would not explain openness towards oceanic conditions, which are less fire-prone. Moreover, in the British Isles, fires were infrequent during the Last Interglacial period (9). 505 However, quantifying the role of fire in the rest of the temperate forest biome during the 506 Pleistocene interglacial periods is a promising avenue for future research, particularly given 507 megafauna-fire interactions and the widespread consequence of herbivore extinction on 508 global fire regimes (53). Furthermore, other disturbances such agents of abnormal intensity 509 (floods, avalanches, storms, and landslides) are likely to have played a role in opening 510 vegetation in some settings (4). The roles of these abiotic stochastic disturbances in 511 interglacial ecosystems and their interactions provide interesting future research 512 opportunities. 513

Traditionally, closed-canopy forests are believed to have dominated the temperate forest 515 biomes before modern humans (2, 26). Our findings show that European forests included 516 substantial open and light woodland elements, and suggest an important role for processes 517 that maintain open habitats. This may have important implications for European biota, and 518 519 particularly for rarer species that depend on open, intermediate, and disturbed landscapes (54, 55). Consequently, common approaches to restoration, such as tree planting, risk 520 creating unfavourable habitats for biodiversity that has evolved in heterogeneous landscapes 521 (5, 56). Trophic rewilding and other approaches aimed at restoring natural disturbance 522 523 factors may be better suited for restoring European forest biomes because they directly promote processes that increase habitat heterogeneity (57). Because of the value in 524 understanding the structure of a biome in conservation and restoration, we advocate for a 525 reimagining of the temperate forest biome to reflect the substantial open vegetation and light 526 527 woodland present.

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529 Materials and methods

We focused our data collection and analyses on the temperate forest biome because we were 530 explicitly interested in the vegetation openness of this bioclimatic region. We defined the 531 temperate forest biome as an oceanic or continental climate zone traditionally considered 532 dominated by temperate deciduous broadleaved or mixed deciduous broadleaf-evergreen 533 conifer forests (Fig. S7; Table S3) (58). In addition, we collected pollen data from the 534 adjoining subarctic and Mediterranean biomes to assess European vegetation cover more 535 broadly and to further our understanding of the drivers of vegetation openness (Fig. S7; 536 Table S3). We focused on the temperate period of vegetation development during the Last 537

538 Interglacial period, as it reflects the climatic optimum (24) and maximum vegetation 539 biomass development (26). Notably, open vegetation often characterises the beginning and 540 end of interglacials in pollen diagrams due to the low soil quality and temperatures 541 preceding and following glacial periods (26). Therefore, exploring openness in the central 542 temperate period is most comparable to current conditions, both in terms of climate and 543 positioning within an interglacial period.

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545 Pollen data collection and preparation

We collected 96 European pollen records from the European Pollen Database 546 (www.europeanpollendatabase.net/), Pangaea (www.pangaea.de/), 547 Neotoma (www.neotomadb.org/), and individual pollen data contributors (Fig. S1; Table S2) and 548 applied the vegetation reconstruction method REVEALS (27). The REVEALS model 549 reconstructs vegetation cover regionally. This is achieved by quantifying background pollen 550 from one or more sites to produce regional vegetation for a $1^{\circ} \times 1^{\circ}$ area (27). REVEALS 551 overcomes the nonlinearity of the pollen-vegetation relationship by accounting for relative 552 553 pollen productivity, dispersal, and deposition differences between taxa (27). The model has been extensively tested and validated at sites across Europe (59, 60) and North America 554 (61), as well as at the European scale (62). Empirical testing against modern (59, 60, 62) 555 and historical (31) analogues has shown that REVEALS improves the accuracy of 556 557 vegetation reconstruction considerably compared to that using pollen proportions alone. Finally, REVEALS is robust to variations in site selection, sampling design, and parameter 558 values (63), and is considered a valuable tool for reconstructing past landscapes in different 559 settings and environments, including small sites (32), floodplains (64), and mountainous 560 regions (31). 561

Because radiocarbon dating was not possible for our study period, we selected pollen 563 records that were dated to the Last Interglacial period based on litho- and/or bio-564 stratigraphical evidence (65). This is considered a robust approach for the Last Interglacial, 565 as in Europe the Last Interglacial follows a very distinct, widely acknowledged pattern of 566 vegetation succession by the dominant taxa, with the most closed vegetation phases 567 occurring in the mesocratic/temperate phase (24, 26). To avoid issues of interglacial non-568 synchronicity across Europe, we used dominant vegetation taxa to classify the Protocratic, 569 Mesocratic (temperate), and Telocratic periods based on defined pollen zones of the Last 570 Interglacial (24, 25) following Lang's protocol (24). Therefore, we examined vegetation 571

572openness in the *Quercus/Corylus-* (first half of the Mesocratic: early-temperate) or C.573*betulus-*dominated (second half of the Mesocratic: late-temperate) periods, rather than at574specific times.

We implemented REVEALS using the protocol of Githumbi *et al.* (7), based on the LRA R 576 package (66). The REVEALS model uses pollen count data, relative pollen productivity 577 (RPP) estimates, and pollen fall speed to reconstruct regional vegetation cover for each 578 taxon in each time slice (Supplementary Materials). The REVEALS model is applied to lake 579 and bog sites separately within each $1^{\circ} \times 1^{\circ}$ grid cell and combines results, from several 580 sites when available, to produce a single mean percentage cover estimate (Data S1) and 581 mean standard error (SE; Data S2) for each RPP taxon per grid cell. Site locations with 582 respect to their grid cells are available in the supplementary material (Fig. S8). The 583 assumptions of the REVEALS model were presented by Sugita (27). We calculated the 584 mean percentage cover of each plant function and land-cover type by summing the mean 585 percentage cover of each associated RPP taxon (Table 2), and averaged these values across 586 all grid cells (n = 66) to provide Europe-wide estimates of vegetation openness. REVEALS 587 calculates the uncertainty, using the delta method (67), as the SEs derived from the sum of 588 the within- and between-site variations in the grid cell (Data S2) (7). We also calculated the 589 coefficient of variation (SE/REVEALS estimate) to report SEs, as shown in Fig. 1. We 590 591 considered SEs to be unreliable when they were greater than the REVEALS estimate. We identified three unreliable grid cells for open vegetation (Data S2; Fig. 1), but retained these 592 593 in our regression analyses as they were reflective of the surrounding grid cells.

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Table 2. Taxa harmonised according to relative pollen productivity (RPP taxa, n	ı =
30) and grouped into land cover and plant functional types.	

RPP taxa	Plant functional	Land cover type		
	type			
Amaranthaceae/Chenopodiaceae	Herbaceous	Open vegetation		
Artemisia				
Cyperaceae				
Filipendula				
Plantago lanceolata type				
Poaceae				
Rumex acetosa type				
Calluna vulgaris	Heath			
Ericaceae				
Juniperus				

	Betula	Shade-intolerant	Light woodland
	Pinus	tree	
	Pistacia	T . 11	
	Corylus	Intermediate tree	
	Buxus sempervirens		
	Philiprea Quarcus deciduous		
	Tarus baccata		
	Salir		
	Abies	Shade-tolerant	Closed forest
	Alnus*	tree	
	Carpinus betulus		
	Carpinus orientalis		
	Castanea sativa		
	Fagus		
	Fraxinus*		
	Picea		
	Quercus evergreen [†]		
	l illa Litera a		
507	Ulmus *Taxa considered to be 'shade telere	nt' due to their shil	ity to thrive in sheded forest
597	landscapes despite having high	light requirements be	ecause of their tolerance to wet
599	soils and/or ability to recrui	t in small treefall	gans [†] Ouercus evergreen is
600	conservatively included as sha	de-tolerant. based on	<i>Ouercus Ilex.</i> However, in the
601	Mediterranean, other Quercu	s evergreen species	s may indicate more open
602	landscapes.	C 1	, 1
603			
604	Climate data and biomes		
605	We used equilibrium simulations of the	e climate at 127 ka B	P (the climatic optimum of the
606	Last Interglacial; LIG) as in Scussolir	ni et al. (68), from siz	x Earth system models: AWI-
607	ESM-1-1-LR (69), CNRM-CM6-1 (70)), GISS-E2-1-G (71),	INM-CM4-8 (72), IPSL-CM6-
608	LR (73), and MIROC-ES2L (74). We a	downscaled the month	nly surface air temperature and
609	precipitation from these models to a re	solution of 5 km. We	then bias-corrected the values
610	of the Last Interglacial simulation by	comparing the histo	orical simulations of the same
611	models with the CHELSA V2 high-re	solution climate datas	set (75) over the period 1981-
612	2010. From the corrected LIG values, v	ve calculated the mean	n of the six models and derived
613	the bioclimatic variables, as in WorldC	clim (76).	
614			
615	We determined the climatic biomes	s of the Last Interg	glacial period using monthly
616	temperature and precipitation data from	n each of the six LIG 1	models and the mean ensemble
617	model to produce the first Köppen-Gei	ger climate classificati	ion maps, as in Beck et al. (77)
618	for the Last Interglacial period (Fig	S7. Supplementary N	Material) To maintain a large
610	sample size we around the Können (Seiger climate classifi	ications into four main climate
013	sample size, we grouped the Koppen-C	Serger enniale etassiii	

- types for the analysis: oceanic, continental, subarctic, and Mediterranean (Fig. S7; Table
 S3). We also included an Alpine category to separate this mountainous region from the
 predominantly lowland regions. The Alpine grid cells had continental or oceanic climates
 and experienced higher precipitation (>100 mm in the wettest month) and/or a higher
 standard deviation of elevation (>500 m).
- Whilst we examined '*Quercus/Corylus*-dominated' and '*C. betulus*-dominated' vegetation in place of a given time window, the climate data reflected a specific time (127 ka). We acknowledge this limitation but argue that the interglacial climatic peak should correspond well to the temperate phase of vegetation (24), as well as to a more stable climate (78). Furthermore, macroclimatic variables exhibited broad trends. Although we cannot infer more localised events (78) from the available vegetation and climate data, elucidation of broader climatic trends is consistent with the aims of this study.
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634 Statistical analysis

635 Robustness assessment

We tested for a relationship between land-cover type and *SE* using a one-way ANOVA and Tukey's HSD. We tested the reliability of the REVEALS model for data from the Last Interglacial period to establish its suitability for scarce data. Specifically, we examined grid cells with small basins that violated the assumptions of the REVEALS model (27). We compared the reconstructions using small lakes and bogs to those using large lakes to separate the effects of wetland vegetation at the margins of small lakes and bogs from those of regional grasslands (Supplementary Material).

643

We used beta regression (Supplementary Material) to test for a relationship between vegetation openness and bog presence as well as key wetland taxa, i.e. willow (*Salix*) and alder (*Alnus*). We also tested the relationship between lake size and vegetation openness. Because the REVEALS model relies on pollen deposited in large lakes, we wanted to ensure that any openness found was not an expansion of open woodlands near lake margins. We summed the radii of each lake per grid cell to form our explanatory variable and performed a beta regression analysis with vegetation openness as the response variable.

651

652 Drivers of vegetation openness

653	We used beta regression to test the relationship between vegetation openness and potential
654	drivers thereof (explanatory variables) (4). These included precipitation and temperature
655	extremes, degree of continentality (the difference between mean temperature of the warmest
656	and coldest quarters) (33), latitude (to assess disequilibrium dynamics following glaciation)
657	(79), and timing within an interglacial period. We included the standard deviation of
658	elevation to assess the role of terrain roughness on vegetation openness, for example, in
659	relation to megaherbivore accessibility, where more energetically expensive sites (49)
660	would be less grazed and therefore contain less open vegetation taxa (15). We also included
661	a binary variable indicating whether a grid cell was 'Alpine' or not, to capture any effect of
662	lowland vs. mountain areas (Fig. S1). We used backward stepwise selection to exclude
663	explanatory variables based on high-variance inflation factors (>5) and correlation
664	coefficients (>0.2). Our final model contained six explanatory variables: mean temperature
665	of the warmest quarter (°C), precipitation of the driest month (mm), degree of continentality
666	(°C), SD of elevation (m), alpine (0, 1), and time window (early-temperate; late-temperate).
667	

For all analyses, we used R version 4.2.2 (2022-10-31). *P*-value thresholds are given as
graded measures of evidence, from 'little or no evidence' to 'very strong evidence' (80).

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972 Author Contributions

- JCS, FM, RF, SN, and EAP designed the research; VA, CB, ZB, KB, SB, OKB, AB, JLB,
 CG, PGS, WG, AH, PK, PK, DM, MM, TM, AMM, PM, MN, BN, IAP, MR, AMR, JSS,
 PS, JS, PS, VS, JS, BU, and HW contributed to the data and expertise; EAP, FM, and RF
 analysed the data; and EAP, JCS, FM, SN, and RF wrote the paper.
- 977

978 Competing Interest Statement

- 979 The authors declare they have no competing interests.
- 980

981 Data and Materials Availability

All data needed to evaluate the conclusions in the paper are present in the paper and/or theSupplementary Materials.



Supplementary Materials for

Substantial light woodland and open vegetation characterised the temperate forest biome before *Homo sapiens*

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This PDF file includes:

Supplementary Text Figs. S1 to S8 Tables S1 to S3

Other Supplementary Materials for this manuscript include the following:

Data S1 to S2

Supplementary Text

REVEALS model

Pollen selection and harmonisation

For pollen selection and for running the REVEALS model, we used protocols developed by the LandClim and PAGES Land-cover6K projects (6, 7, 81) adapted to the Last Interglacial period. Relative pollen productivity (RPP) estimates exist for many European plant taxa, and there are several syntheses of RPP estimates and pollen fall speeds. Here, we used the most complete, upto-date synthesis (7), which has been well-validated against modern data in Europe (62). We did not include Secale and Cerealia-type taxa as separate from Poaceae, given that the Last Interglacial occurred before the onset of agriculture. Where these taxa were present, we grouped them as wild plants under Poaceae. Additionally, in the absence of an RPP estimate for *Taxus* baccata (yew), an important taxon for the Last Interglacial, we used the estimate for Juniperus (juniper), as in Kuneš et al. (40). We excluded several entomophilous (insect-pollinated) taxa and rare taxa, as recent work has shown that the addition of a large number of such taxa does not improve REVEALS reconstructions (62, 63). We harmonised the taxonomy and nomenclature of pollen morphological types from the 96 pollen records, and then assigned them to 1 of 30 RPPharmonised taxa (from now on referred to as RPP taxa; Table 2), following the protocol outlined in Githumbi et al. (7). The 30 RPP taxa were grouped to five plant functional types and three land cover types (Table 2), and aggregated into the Protocratic, early-Mesocratic (earlytemperate), late-Mesocratic (late-temperate), and Telocratic zones. To check how representative the RPP taxa were of the whole pollen sample, we calculated the proportion of pollen grains within each sample that were included in the RPP taxa. The REVEALS taxa (n = 31) represented $95.5\% \pm 5.1$ of the total terrestrial pollen sum.

Model Parameters

The REVEALS model relies on pollen sequences collected from large lakes. It has also been shown to work well with multiple smaller lakes or bogs, though the standard error is larger (63, 81). While it is therefore appropriate to use pollen records from small sites to increase the number of pollen records included in a REVEALS reconstruction, estimates using pollen assemblages from large bogs should be interpreted with caution (63; see Fig. S8). The REVEALS model requires estimates of basin size for sites used; however, the exact basin size can be difficult to define for interglacial deposits. Where possible, we obtained site type and radius information from original publications or directly from individual pollen data contributors. Otherwise, we measured the modern basin and/or elevation data following Mazier *et al.* (63). Finally, where this information was absent or uncertain, we assigned the basin size of remaining sites as small (5 m radius; n = 12).

We applied a Gaussian plume model for pollen dispersal and deposition models for bogs (29, 82) and lakes (27). We used a constant wind speed of 3 m s-1 (7, 81) and the maximum extent of the regional vegetation (Zmax) was set to 50 km, roughly corresponding to a 1°×1° grid cell (63).

Köppen-Geiger climate classification maps

When a palaeoclimate (i.e. the LIG) is simulated with different models, then differences in the setup of the models can produce different results because their sensitivities to a change in forcings is different, even though their present-day climates are similar (83). To know which model produced the best representation of the palaeoclimate, we used the distribution of *Ilex* (holly) as an indicator of oceanic climate (84), and compared this to the oceanic-continental boundary present in the classification maps. The eastern-most distribution of *Ilex* agreed with recent Maximum Likelihood Classification analysis (85) that an oceanic climate extended much further East in the Last Interglacial than today. We found that this pattern was best reflected in GISS-E2-1-G (71), and therefore used this model to produce our final climate classification map (Fig. S7) for regression analyses. For comparison, the mean ensemble model results are also presented in Fig. S7.

Robustness assessment: model comparisons

We produced REVEALS estimates for grid cells that included both reliable (model assumptions met: large lakes) and unreliable (model assumptions unmet: small lakes/bogs) sites (Fig. S8). For these grid cells, we ran REVEALS for 1) all reliable sites, 2) all unreliable sites, and 3) all reliable + unreliable sites (Fig. S6). We also wanted to test the suitability of using marine and riverine sites for REVEALS. These form only a small proportion (marine = 0.05; riverine = 0.03; Fig. S2) of our dataset, but also violate the assumptions of the REVEALS model. However, we did not have reliable sites within the same grid cells to use for comparison. We acknowledge this limitation in our dataset, and show the relevant, less reliable grid cells in Fig. S8.

Robustness assessment: local vegetation effects

In some grid cells, both Cyperaceae and Poaceae could represent wetland taxa, such as *Phragmites*, particularly in the early-temperate period and some Mediterranean grid cells (86). Floodplains are likely to characterise riverine sites (87), which explains the high proportions of herbaceous taxa found in all British Isles grid cells (Fig. 1). However, it is important to note that temperate floodplains in Europe today tend to become densely wooded in the absence of land use or restoration actions, whereas grasslands often dominated floodplains in the Last Interglacial period (6, 88). While the wetland vegetation surrounding the lakes and bogs likely had a small local effect in this study (7), validations of the REVEALS model against modern analogues in Europe (59, 60) and North America (61) (see Methods) showed that the model accounted well for the local effects of vegetation. Large bogs may present more uncertainty (32), but most of the pollen sequences used in this study were from lakes (Fig. S8). Furthermore, we found no effect for the presence of bogs or the wetland taxa Alnus and Salix on vegetation openness. We also found no correlation between lake size and vegetation openness, suggesting that the presence of open vegetation was not due to local expansion at lake margins. These results agree with the interpretations in the literature for the temperate forest biome during the Last Interglacial period. In Neumark Nord, Germany (Table S2), researchers found that high proportions of Poaceae and Cyperaceae did not represent increases in wetland-indicating taxa, but rather tracked increases in other non-arboreal pollen (20). Furthermore, the presence of dry grasslands, meadows, and other non-wetland open vegetation have been indicated by plant macrofossil, mollusc, and beetle

records (4, 8, 9); large herbivore diet analyses (34); and the presence of forb taxa that characterise grasslands and disturbed soils, such as *Artemisia*, Amaranthaceae/Chenopodiaceae, and *Rumex acetosa* (Data S1) (20). It is therefore likely that, for most of our grid cells in the temperate forest biome, the representation of open vegetation is reflective of regional cover in the Last Interglacial period and likely indicates grasslands.

Beta regression

We used beta regression using the "betareg" R package (89) to examine possible spatial, temporal and environmental drivers of vegetation openness. Beta regression is appropriate for modelling continuous proportion data (90) and produces two sub-models: a location model and a precision model (89). The location model predicts the mean and is estimated by a logit link. The precision model, with a log link, produces a *phi* coefficient, where the higher *phi* corresponds to higher precision or lower variance.

For the beta regression analyses, we removed an influencing outlier in Southern Norway. The reconstructed climatic data reported monthly precipitation for this grid cell at much greater values than expected – nearly twice the value than any other grid cell. We ran the model both with and without this grid cell and found that the results varied considerably. In the main text, we report results of the model that excluded the outlier, given our rationale that the precipitation values here are unreliable. Results including the outlier can be found in supplementary material (Fig. S3) for comparison.

	Open Vegetation									Light Woodland											
Temperate Phase	Area	Measure	Amanranthaceae/ Chenopodiaceae	Artemisia	Calluna vulgaris	Cyperaceae	Ericaceae	Filipendula	Juniperus	Plantago lanceolata type	Poaceae	Rumex acetosa_t	Betula	Buxus sempervirens	Corylus avellana	Phillyrea	Pinus	Pistacia	Quercus deciduous	Salix	Taxus
Early	Temperate Lowland Europe	Mean	0.07	0.22	0.62	6.41	0.1	0.02	0.08	0.02	10.1 8	0.09	3.01	0	35.9 5	0	8.11	0	8.9	0.43	0.79
Early	Temperate Lowland Europe	SD	0.1	0.28	1.01	9.19	0.33	0.05	0.41	0.1	13.8 3	0.17	6.12	0.03	18.6 6	0	6.57	0	5.93	0.57	1.26
Late	Temperate Lowland Europe	Mean	0.07	0.07	1.07	6.98	0.38	0.04	0.02	0.03	6.23	0.03	1.84	0.01	20.9 6	0	4.67	0	2.6	0.44	0.65
Late	Temperate Lowland Europe	SD	0.24	0.19	2.2	13.6 9	1.88	0.11	0.04	0.14	12.3 9	0.07	4.01	0.03	17.2 5	0	6.65	0	2.62	1.6	0.75
Early	Europe - all	Mean	0.08	0.36	0.42	7.3	0.13	0.02	0.14	0.03	10.6 9	0.09	2.43	0.01	30.0 8	0.03	7.01	0.05	8.55	0.37	1.09
Early	Europe - all	SD	0.14	1.23	0.88	13.6 1	0.37	0.04	0.42	0.11	16.1 8	0.18	5.48	0.04	21.5	0.17	7.89	0.23	6.73	0.54	1.86
Late	Europe - all	Mean	0.13	0.23	0.73	7.98	0.4	0.03	0.08	0.04	7.32	0.04	1.7	0.04	15.6 1	0.02	3.76	0.01	2.85	0.48	0.5
Late	Europe - all	SD	0.54	0.73	1.88	16.3	1.67	0.09	0.26	0.18	13.4 8	0.08	3.8	0.1	17.0 8	0.1	5.9	0.08	4.79	1.52	0.68

Table S1. Mean REVEALS estimate and standard deviation (SD) per taxa per time window (early-temperate; late-temperate). Mean and SD measures are given for temperate lowland Europe (temperate forest biome, n = 45) and Europe – all (all grid cells, n = 66).

_		Closed Forest												
Temperate Phase	Area	Measure	Abies alba	Alnus glutinosa	Carpinus betulus	Carpinus orientalis	Castanea	Fagus sylvatica	Fraxinus	Picea	Quercus evergreen	Tilia	Ulmus	
Early	Temperate Lowland Europe	Mean	0.52	1.42	3.45	0	0	0	2.22	2.98	0	4.7	5.27	
Early	Temperate Lowland Europe	SD	1.61	1.64	7.19	0	0	0.01	1.77	5.64	0	5.3	4.21	
Late	Temperate Lowland Europe	Mean	7.98	1.93	19.6 1	0	0	0	1.03	6.66	0	4.38	3.42	
Late	Temperate Lowland Europe	SD	13.8 5	1.66	15.9 9	0	0	0.01	0.94	8.09	0	4.62	3.4	
Early	Europe - all	Mean	6.34	1.05	2.55	0.65	0	0.14	2.32	3.56	0.09	3.39	4.93	
Early	Europe - all	SD	18.0 7	1.47	6.11	4.19	0	0.66	2.28	6.84	0.67	4.78	4.21	
Late	Europe - all	Mean	18.0 2	1.4	14.4 5	0.62	0	0.1	0.86	5.61	0.1	3.19	3.11	
Late	Europe - all	SD	28.9 1	1.59	15.3 9	4.68	0	0.6	0.96	7.35	0.78	4.38	5.31	



Fig. S1. Location of 96 pollen sequences (points; see Table S2) divided according to Köppen-Geiger climate classification for the Last Interglacial. We reconstructed the classifications as in Beck et al. (77), from monthly temperature and precipitation data from the GISS-E2-1-G earth system model (71). For further methods and choice of model, see "climate data and zones" in main methods. Circular points are within the temperate forest biome, triangular points show "Alpine" sites, and square points the remaining sites (Mediterranean and sub-Arctic).



Fig. S2. Full model results of beta regression analysis, with the influencing outlier in Southern Norway (grid cell 1021) excluded.



Fig. S3. Full model results of beta regression analysis, with the influencing outlier in South Norway (grid cell 1021) included.



Fig. S4. Standard Errors from the REVEALS model, for all grid cells across all time windows, plotted by land cover type.



Fig. S5. Standard Errors from the REVEALS model, for all grid cells across all time windows, plotted by openness categories (%).









Fig. S6. Grid cell-based REVEALS estimates of vegetation openness (left Y-axis) for each PFT (right Y-axis) in grid cells 219, 375, 676, and 683 (Fig. S1, Table S2). Four time windows (top X-axis – TW1, TW2, TW3 and TW4: Protocratic, early-temperate (early Mesocratic), late-temperate (late Mesocratic) and Oligo/Telocratic, respectively) are shown. Pollen assemblages from 1-3 small lakes/bogs (yellow circles; <400 m radius) and 1-3 large lakes (green circles; 400 - 1300 m radius) were used for the REVEALS reconstructions for each time window. The REVEALS estimates obtained with pollen data from the single lakes/bogs, and the REVEALS

estimates obtained with pollen data from all lakes/bogs (purple circles), are shown with standard errors. We also grouped lakes/bogs according to size (676_small and 219_large) for further comparison to single large or small sites, respectively. Where standard error is very small, the error bars are smaller than the symbol size and therefore not visible.

Pollen Data Contributor	Pollen Sequence	Sequence Country	Database	Lon (°)	Lat	Radius (m)	Model	Publication(s)	DOI
Steve Boreham	Abington Hall G	United Kingdom	Authors	0.23	52.1	550	Lake	Boreham & Leszczynska, 2019, Quaternary	https://doi.org/10.3 390/quat2030024
Jeroen Schokker	Amersfoort I (B32B0119)	Netherland s	Geological Survey of the Netherlands	5.38	52.2	1500	Lake	Zagwijn, 1961, Mededelingen van de Geologische Stichting; Cleveringa et al., 2000, Netherlands Journal of Geosciences	NA
Werner Ricken	Aschenhütte	Germany	Pangaea	10.3	51.7	43	Lake	Ricken & Grüger, 1988, EGQSJ, PANGAEA	https://doi.pangae a.de/10.1594/PAN GAEA.729508
Jeroen Schokker	Amsterdam- Terminal (B25E0913)	Netherland s	Geological Survey of the Netherlands	4.91	52.4	10000	Lake	Van Leeuwen et al., 2000, Netherlands Journal of Geosciences	https://doi.org/10.1 017/S0016774600 023647
Jeroen Schokker	Amersfoort New (B32B2092)	Netherland s	Geological Survey of the Netherlands	5.38	52.2	1500	Lake	Kasse et al., 2022, Netherlands Journal of Geosciences	https://doi.org/10.1 017/NJG.2022.4
Anna Hrynowieck a	Banzin	Germany	Authors	10.9	53.4	5	Lake	Börner et al, 2015, Quaternary International	https://doi.org/10.1 016/j.quaint.2014. 10.022
Anna Hrynowieck a	Beckenthin	Germany	Authors	11.6	53.2	30	Bog	Hrynowiecka et al , 2021, Quaternary International	https://doi.org/10.1 016/j.quaint.2021. 01.025
Małgorzata Malkiewicz	Bieganin	Poland	Authors	17.8	51.8	110	Lake	Malkiewicz, 2003, Geological Quarterly	NA
Helmut Müller	Bispingen	Germany	Neotoma	10	53.1	564	Lake	Müller, 1974, Geologisches Jahrbuch	doi:10.21233/gx58 -4a75
Jaqueline Strahl	Borgisdorf	Germany	Geological Survey of Brandenburg	13.1	51.9	5	Lake	Hermsdorf & Strahl, 2008, Geowiss	NA
Jeroen Schokker	Boxtel- Breede Heide 2 (B51B0307)	Netherland s	Authors	5.34	51.6	100	Bog	Schokker, Cleveringa & Murray, 2004, Journal of Quaternary Science	https://doi.org/10.1 002/jqs.808
Malgorzata Malkiewicz	Buntowo	Poland	EECRG(digitis ed)	17.1	53.2	356	Lake	Malkiewicz, 2018, Quaternary International	https://doi.org/10.1 016/j.quaint.2016. 07.006
Olga K. Borisova	Butovka	Russia	EPD	36.4	55.2	219	Bog	Borisova, 2005, Polish Geological Institute Special Papers	NA
Krzysztof Bińka	Czaple	Poland	Authors	22.5	52.4	75	Lake	Bińka & Nitychoruk, 2011, Rev. Palaeobot. Palynol	https://doi.org/10.1 016/j.revpalbo.201 0.11.003
Tim Mighall	Deeping St James	United Kingdom	Authors	-0.25	52.7	22.2	Lake	Keen et al., 1999, JQS	https://doi.org/10.1 002/(SICI)1099- 1417(199908)14:5 %3C411::AID- JQS447%3E3.0.C O:2-M
Wilhelmus De Gans	Drentsche Vallev	Netherland s	Digitised	52.9	6.71	24	Lake	De Gans, 1981, IAEA	NA
Krzysztof Bińka	Dziewule	Poland	Authors	22.4	52	60	Lake	Bińka & Nitychoruk, 2003, Geological Quarterly	NA
Jaqueline Strahl	Eichow	Germany	Geological Survey of Brandenburg	14.1	51.7	166.41	Lake	Hermsdorf & Strahl, 2008, Geowiss	NA
Hans- Jürgen Beug	Eurach	Germany	Pangaea	11.3	47.8	4184.1	Lake	Beug, 1979, Geologica Bavarica	https://doi.org/10.1 594/PANGAEA.58 939
Jan Mangerud	Fjøsanger	Norway	EECRG(digitis ed)	5.33	60.4	1204.8	Lake	Mangerud, Sejrup, Sønstegaard & Haldorsen, 1981, BOREAS	https://doi.org/10.1 111/j.1502- 3885.1981.tb0047 9.x
Ulrich C. Müller	Füramoos	Germany	EPD	9.88	48	138.2	Lake	Müller, Pross & Bibus,	doi:10.1016/S0033 -5894(03)00005-X

Table S2. Metadata for all pollen sequences.

								2003, Quaternary	
Jaqueline	Gloewen	Germany	Geological	12.1	53	5	Lake	Hermsdorf & Strahl.	NA
Strahl	0.000.000	Connainy	Survey of Brandenburg			0	20110	2008, Geowiss	
Jerzy Niklewski	Glówczyn G2	Poland	Pangaea	20.2	52.4	143.84	Lake	Niklewski, 1968, Monographiae Botanicae	https://doi.pangae a.de/10.1594/PAN GAEA 739263
Zofia Janczyk- Kopikowa	Golkow	Poland	Pangaea	21	52.1	195.44	Lake	Janczyk-Kopikowa, 1966, <i>Kwartalnik</i> Geologiczny	https://doi.org/10.1 594/PANGAEA.76 0378
Samuel Wegmüller	Gondiswil- Seilern	Switzerlan d	EECRG(digitis ed)	7.88	47.1	79.788	Bog	Wegmüller, 1986, Quaternaire	NA
Karl-Ernst Behre	Grevenhof	Germany	Pangaea	10.1	53.1	127.41	Lake	Behre, 1962, Flora	https://doi.pangae a.de/10.1594/PAN GAEA.894223
Lothar Eissmann	Grobern94	Germany	EPD	12.5	51.7	1082.3	Lake	Eissman & Litt, 1992, INQUA Subcommision on European Quaternary Statigraphy	NA
Małgorzata Malkiewicz	Grudzielec	Poland	Authors	17.8	51.8	5	Lake	Malkiewicz, 2002, Acta Societatis Botanicorum Poloniae	doi:10.5586/asbp. 2002.037
Małgorzata Malkiewicz	Gutów	Poland	Authors	17.9	51.8	15	Lake	Malkiewicz, 2010, Geological Quarterly	
Jaqueline Strahl	Hinterste Mühle	Germany	Geological Survey of Brandenburg	13.3	53.5	10	Lake	Strahl, 2000, Geowiss	NA
Svend Th. Andersen	Hollerup	Denmark	Neotoma	9.85	56.4	150	Lake	Andersen, 1965, Meddelelser fra Dansk Geologisk Forening	doi:10.21233/z3x6 -1z53
Wojciech Granoszew ski	Horoszki Duże	Poland	Polish Pleistocene Pollen database	23	52.3	5	Lake	Granoszewski, 2003, Szafer Inst. of Botany	
Mamakowa Kaziemira	Imbramowice	Poland	EPD	16.6	50.9	282.09	Lake	Mamakowa, 1989, Acta Palaeobotanica	NA
Polychronis C. Tzedakis	loannina 249	Greece	EPD	20.9	39.7	269.4	Lake	Tzedakis, Frogley & Heaton, 2003, Global and Planetary Change	https://doi.org/10.1 016/S0921- 8181(02)00182-0
Polychronis C. Tzedakis	Ioannina 284	Greece	Authors	20.9	39.8	269.4	Lake	Tzedakis, Frogley & Heaton, 2003, Global and Planetary Change	https://doi.org/10.1 016/S0921- 8181(02)00182-0
Bożena Noryśkiewic z	Jałówka	Poland	Authors	23.2	53.6	100	Lake	Rychel et al, 2014, Quaternary International	https://doi.org/10.1 016/j.quaint.2013. 09.018.
Ulrich C. Müller	Jammertal	Germany	Neotoma	9.73	48.1	356.82	Bog	Müller, 2000, Vegetation History and Archaeobotany	doi:10.21233/5pjf- 4p55
Ann-Marie Robertsson	Ketkijärvet	Sweden	Authors	20.8	68.8	995	Lake	Robertsson & Rodhe, 1988, BOREAS	https://doi.org/10.1 111/j.1502- 3885.1988.tb0056 4.x
Jaqueline Strahl	Kittlitz	Germany	Geological Survey of Brandenburg	13.9	51.8	25	Lake	Erd, 1973, Z. geol. Wiss	NA
Zofia Janczyk- Kopikowa	Kletnia Stara	Poland	Pangaea	21.7	51.6	126.16	Lake	Janczyk-Kopikowa, 1989, Kwartalnik Geologiczny	https://doi.pangae a.de/10.1594/PAN GAEA.739381
Burkhard Frenzel	Krumbach I	Germany	Pangaea	10.4	48.2	218.51	Lake	Frenzel, 1991, Stuttgart	https://doi.pangae a.de/10.1594/PAN GAEA.736436
Bożena Noryśkiewic z	Kwiatków Las	Poland	Authors	17.9	51.7	15	Lake	Noryśkiewicz, 1995, Mat. Arch. Zak. Geomorf. Univ. Łódz	NĀ
Jacques- Louis de Beaulieu, Maurice Reille	La Grande Pile	France	EPD	6.5	47.7	282.09	Bog	Kukla et al., 2002, Quaternary Research	https://doi.org/10.1 006/qres.2002.234 0

Jacques- Louis de Beaulieu, Maurice Reille	Lac du Bouchet H	France	EPD	3.78	44.9	635.81	Lake	Reille et al, 1998, Quaternary Science Reviews	https://doi.org/10.1 016/S0277- 3791(97)00093-0.
Jacques- Louis de Beaulieu, Maurice Reille	Lac du Bouchet I	France	EPD	3.78	44.9	635.81	Lake	Reille et al, 1998, Quaternary Science Reviews	https://doi.org/10.1 016/S0277- 3791(97)00093-0.
Jaqueline Strahl	Ladeburg	Germany	Geological Survey of Brandenburg	13.6	52.7	5	Lake	Hermsdorf & Strahl, 2008, Geowiss	NA
Nadine Pickarski	Lake Van	Turkey	Pangaea	42.7	38.7	33729	Lake	Pickarski, 2015, Palaeogeogr. Palaeoclimatol. Palaeoecol.	https://doi.pangae a.de/10.1594/PAN GAEA.853729
Zofia Balwierz	Łanięta	Poland	Authors	19.3	50.4	800	Lake	Balwierz & Roman, 2002, Geological Quarterly	NA
Małgorzata Malkiewicz	Lechitów	Poland	Authors	16.6	51.6	5	Lake	Malkiewicz, 2002, Acta Societatis Botanicorum Poloniae	doi:10.5586/asbp. 2002.037
Jacques- Louis de Beaulieu, Maurice Reille	Les Echets	France	Authors	5	45.8	2034.2	Bog	de Beaulieu & Reille, 1984, BOREAS	https://doi.org/10.1 111/j.1502- 3885.1984.tb0006 6.x
Jan Lundqvist	Leveäniemi	Sweden	EECRG(digitis ed)	21	67.6	406.84	Lake	Lundqvist, 1971, Davidson	NA
Krzysztof M Krupinski	Lomzyca Lomza2	Poland	Pangaea	22.1	53.2	472.03	Lake	Krupinski, 1992, Stud. Geol. Pol.	https://doi.pangae a.de/10.1594/PAN GAEA.711922
Steve Boreham, Cunhai Gao	Mannings Farm Beds	United Kingdom	Authors	0.05	52.3	20	Lake	Gao & Boreham, 2010, Boreas	https://doi.org/10.1 111/j.1502- 3885.2010.00191. x
Vaida Šeirienė	Medininkai11 7	Lithuania	Authors	25.6	54.5	30	Lake	Šeirienė, Kühl & Kisielienė, 2017, Quaternary Research	https://doi.org/10.1 016/j.yqres.2014.0 4.004
Małgorzata Nita	Mikorzyn I Mlodszy	Poland	Authors	18.3	52.4	225	Lake	Stankowski & Nita, 2004, Geological Quarterly	NA
Judy Allen	Monticchio	Italy	Pangaea	15.6	40.9	3612.6	Lake	Allen et al., 1999, Nature	https://doi.org/10.1 594/PANGAEA.70 7088
Bożena Noryśkiewic z	Nakło	Poland	Pangaea	17.6	53.2	437.02	Lake	Noryśkiewicz, 1975, Reihe; Noryśkiewicz, 1978, Acta Palaeobotanica; Noryśkiewicz, 1979, Quaternary studies in Poland	https://doi.pangae a.de/10.1594/PAN GAEA.739576
Jaqueline Strahl	Nedlitz	Germany	Geological Survey of Brandenburg	13	52.4	5	Lake	Hermsdorf & Strahl, 2008, Geowiss	NA
Corrie Bakels	Neumark Nord	Germany	Authors	11.9	51.3	1723	Lake	Bakels, 2012, Review of Palaeobotany and Palynology	https://doi.org/10.1 016/j.revpalbo.201 2.06.003
Krzysztof Bińka	Nidzica	Poland	Authors	20.4	53.4	750	Lake	Bińka, Nitychoruk & Dzierżek, 2011, Boreas	https://doi.org/10.1 111/j.1502- 3885.2010.00179. x
Anna Brostrom, Per Möller	Nybygget	Sweden	Authors	14.9	57	2154.1	Lake	Lemdahl et al., 2013, JQS	https://doi.org/10.1 002/jqs.2665
Karl-Ernst Behre	Oerel 61	Germany	EPD	9.06	53.5	250	Lake	Behre & van der Plicht, 1992, Vegetation History and Archaeobotanv	https://doi.org/10.1 007/BF00206091
Karl-Ernst Behre	Osterwanna	Germany	EPD	8.82	53.7	23.937	Bog	Behre, Göttlich & Werner, 1974, Bundesanstalt für Bodenforschung	NA

Hanna Winter	Ostrow	Poland	Pangaea	19.6	51.5	35.682	Lake	Klatkowa & Winter, 1990, Acta Geographica Lodziensia	https://doi.pangae a.de/10.1594/PAN GAEA.739625
Olga K. Borisova	PLES	Russia	EPD	41.5	57.5	500	Lake	Borisova, 2007, Quaternary Science Reviews	https://doi.org/10.1 016/j.quascirev.20 07.07.001
Hanna Winter	Radówek	Poland	Authors	14.7	52.4	218.51	Bog	Urbański & Winter, 2005, Przegląd Geologiczny	NA
Jaqueline Strahl	Rehnsdorf	Germany	Geological Survey of Brandenburg	14.3	51.6	60	Lake	Kühner & Strahl, 2008, Zeitschrift der Deutschen Gesellschaft für Geowissenschaften	doi:10.1127/1860- 1804/2008/0159- 0191
Jacques- Louis de Beaulieu	Ribains maar	France	EPD	3.78	44.9	141.61	Bog	de Beaulieu & Reille, 1992, Vegetation History and Archaeobotany	https://doi.org/10.1 007/BF00189500
Hanna Winter	Rzecino	Poland	Authors	16	53.8	400	Lake	Winter, Dobracka & Ciszek, 2008, Biuletyn Państwowego Instytutu Geologicznego	NA
Eberhard Grüger	Samerberg I	Germany	Pangaea	12.2	47.8	100	Lake	Grüger, 1979, Geologica Bavarica	https://doi.pangae a.de/10.1594/PAN GAEA.726866
Jaqueline Strahl	Schönfeld	Germany	Geological Survey of Brandenburg	13.9	51.8	115	Lake	Erd, 1991, Sonderheft	NA
Brigitte Urban	Schöningen	Germany	Authors/Neoto ma	11	52.2	500	Lake	Urban et al, 1991, E&G Quaternary Sci	https://doi.org/10.3 285/eg.41.1.07
Karl-Ernst Behre	Schwindebec k	Germany	Pangaea	10.1	53.1	39.894	Lake	Behre, 1962, Flora	https://doi.pangae a.de/10.1594/PAN GAEA.894473
Ann-Marie Robertsson	Seitevare	Sweden	Authors	18.6	67	12500	Lake	Robertsson & Rodhe, 1988, BOREAS	https://doi.org/10.1 111/j.1502- 3885.1988.tb0056 4.x
Filip Van Beirendonc k	Sint-Amands	Belgium	Authors	4.23	51	750	Bog	Verbruggen, 1999, Geologica Belgica	https://doi.org/10.2 0341/gb.2014.013
Małgorzata Nita	Slawoszewek 1999	Poland	Polish Pleistocene Pollen database	18.2	52.4	62.5	Lake	Stankowski, Bluszcz & Nita, 1999, Wydawnictwo Instytutu Fizyki Politechniki Śląskiej	NA
J. Sakari Salo nen	Sokli	Finland	Authors	29.3	67.8	2500	Lake	Salonen et al., 2018, Nature communications	https://doi.org/10.1 038/s41467-018- 05314-1
Patrick Schläfli	Spiezberg	Switzerlan d	Authors	7.67	46.7	8500	Lake	Schläfli, 2021, Quaternary Science Reviews	https://doi.org/10.1 016/j.quascirev.20 21.106975
Valérie Andrieu- Ponel	St. Front	France	Authors	4.17	45	309.02	Lake	Martin et al, 2019, Organic Geochemistry	https://doi.org/10.1 016/j.orggeochem. 2019.06.005
Anna Brostrom, Per Möller	Stora Gäddevik	Sweden	Authors	14.4	57	2417.2	Lake	Lemdahl et al, 2013, Journal of Quaternary Science	https://doi.org/10.1 002/jqs.2664
Jaqueline Strahl	Strausberg	Germany	Geological Survey of Brandenburg	13.8	52.5	5	Lake	Hermsdorf & Strahl, 2008, Geowiss	NA
Małgorzata Malkiewicz	Szklarka	Poland	Authors	17.9	51.3	250	Lake	Malkiewicz, 2018, Quaternary International	https://doi.org/10.1 016/j.quaint.2016. 09.026
Alice M. Milner	Tenaghi Philippon 2005	Greece	Authors	24.2	41	9339	Bog	Milner et al, 2016, Quaternary Science Reviews	https://doi.org/10.1 016/j.quascirev.20 16.10.016
Frank Sirocko	Trockenmaar _HL2	Germany	Pangaea	6.84	50.2	282.09	Lake	Sirocko et al., 2005, Nature	https://doi.pangae a.de/10.1594/PAN GAEA.472208
Jaqueline Strahl	Tschernitz	Germany	Geological Survey of Brandenburg	14.6	51.6	5	Lake	Hermsdorf & Strahl, 2008, Geowiss	NA
Jaqueline Strahl	Uchte flats	Germany	Geological Survey of Brandenburg	11.8	52.6	85	Lake	NA	NA

Piotr Kołaczek	Ustków	Poland	Authors	18.6	51.8	50	Lake	Kołaczek et al, 2012, Quaternary International	https://doi.org/10.1 016/j.quaint.2012. 05.004
Donatella Magri	Valle Di Castiglione	Italy	Authors	12.8	41.9	500	Lake	Follieri, Magri, & Sadori, 1989, Quaternary International	https://doi.org/10.1 016/1040- 6182(89)90076-1
Jaqueline Strahl	Vevais	Germany	Geological Survey of Brandenburg	14.1	52.7	30	Lake	Lüthgens et al., 2011, Quaternary International	https://doi.org/10.1 016/j.quaint.2010. 06.026
Penélope González- Sampériz	Villarquemad o	Spain	Authors	-1.3	40.5	1828.2	Lake	González-Sampériz et al., 2020, Quaternary Science Reviews	https://doi.org/10.1 016/j.quascirev.20 20.106425
Krzysztof M Krupinski	Warszawa Kasprzak St	Poland	Pangaea	21	52.2	375	Lake	Krupinski & Morawski, 1993, Acta Palaeobotanica	https://doi.pangae a.de/10.1594/PAN GAEA.739950
Krzysztof M Krupinski	Warszawa Wawrzyszew 15	Poland	Pangaea	20.9	52.3	398.94	Lake	Krupinski & Morawski, 1993, Acta Palaeobotanica	https://doi.pangae a.de/10.1594/PAN GAEA.739948
Allan Hall	Wing	UK	EECRG(digitis ed)	-0.68	52.6	50	Lake	Hall, 1978, New Phytologist	https://doi.org/10.1 111/j.1469- 8137.1978.tb0165 5.x
Irena Agnieszka Pidek	Wiśniew II	Poland	Authors	22.3	52.1	5	Lake	Pidek & Terpiłowski, 1993, Ann. UMCS	NA
Steve Boreham	Woolpack Farm site	United Kingdom	Authors	-0.1	52.3	15	Lake	Gao et al., 2000, Quaternary Science Reviews	https://doi.org/10.1 016/S0277- 3791(99)00028-1
Eberhard Grüger	Wurzach	Germany	Pangaea	9.89	47.9	500	Lake	Grüger& Schreiner, 1993, Neues Jahrb. fur Geol. Palaontol Abh.	https://doi.pangae a.de/10.1594/PAN GAEA.713702



Fig. S7. Köppen-Geiger climate classification maps produced with mean ensemble model (A) and GISS-E2-1-G model (B; 71). The colour scheme was adopted from Beck *et al* (77).

Dfc	Cold, no dry season, cold summer	Subarctic		
Dfb	Cold, no dry season, warm summer	Continental		
Dfa	Cold, no dry season, hot summer	Continental		
Cfb	Temperate, no dry season, warm summer	Ossenia		
Cfa	Temperate, no dry season, hot summer	Oceanic		
Csa	Temperate, dry season, hot summer	Maditamanaan		
BSk	Arid, steppe, cold	Wednerranean		
Dsa	Cold, dry season, hot summer			

Table S3: Main climate zones covered by the 96 pollen sequences, grouped according to their description in the paper.



Fig. S8. Map of individual pollen sequences taken from lakes (blue points) and bogs (brown points). Small sites (<150 m radius), medium sites (150 - 1500 m radius) and large sites (>1500 m radius) correspond to small, medium and large points. Riverine (yellow) and marine (orange) grid cells are considered less reliable.

Data S1. (separate file)

REVEALS mean percentage cover estimates for each RPP taxon per grid cell.

Data S2. (separate file)

REVEALS mean standard error estimates for each RPP taxon per grid cell.