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Elena A. Pearce

Florence Mazier

Signe Normand

Ralph Fyfe *School of Geography, Earth and Environmental Sciences*

Valérie Andrieu

et al. *See next page for additional authors*

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Authors

Elena A. Pearce, Florence Mazier, Signe Normand, Ralph Fyfe, Valérie Andrieu, Corrie Bakels, Zofia Balwierz, K Binka, Steve Boreham, Olga K. Borisova, Anna Brostrom, Beaulieu J-L de, Cunhai Gao, P Gonzalez-Samperiz, Wojciech Granoszewski, Anna Hrynowiecka, P Kolaczek, P Kunes, Donatella Magri, Małgorzata Malkiewicz, T Highall, Alice M. Milner, P Moller, Małgorzata Nita, Bożena Noryśkiewicz, Irena Agnieszka Pidek, Maurice Reille, Ann Marie Robertsson, J. Sakari Salonen, Patrick Schläfli, Jeroen Schokker, Paolo Scussolini, Vaida Šeirienė, Jaqueline Strahl, Brigitte Urban, Hanna Winter, and Jens Christian Svenning

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

Short title: Forest openness before *Homo sapiens*

Elena A. Pearce,[1,2]* Florence Mazier,[3] Signe Normand,[1,2,4] Ralph Fyfe,[5] Valérie Andrieu,[6] Corrie Bakels,[7] Zofia Balwierz,[8] Krzysztof Bińka,[9] Steve Boreham,[10] Olga K. Borisova,[11] Anna Brostrom,[12] Jacques-Louis de Beaulieu,[13] Cunhai Gao,[14] Penélope González-Sampériz,[15] Wojciech Granoszewski,[16] Anna Hrynowiecka,[17] Piotr Kołaczek,[18] Petr Kuneš,[19] Donatella Magri,[20] Małgorzata Malkiewicz,[21] Tim Mighall,[22] Alice M. Milner,[23] Per Möller,[12] Małgorzata Nita,[24] Bożena Noryśkiewicz,[25] Irena Agnieszka Pidek,[26] Maurice Reille,[13] Ann-Marie Robertsson,[27] J. Sakari Salonen,[28] Patrick Schläfli,[29] Jeroen Schokker,[30,31] Paolo Scussolini,[32] Vaida Šeirienė,[33] Jaqueline Strahl,[34] Brigitte Urban,[35] Hanna Winter,[36] Jens-Christian Svenning[1,2,4]

[1] Center for Ecological Dynamics in a Novel Biosphere (ECONOVO) & Center for Biodiversity Dynamics (BIOCHANGE), Department of Biology, Aarhus University, Ny Munkegade 114, DK-8000, Aarhus C, Denmark.

[2] Section for Ecoinformatics and Biodiversity, Department of Biology, Aarhus University, Ny Munkegade 114, DK-8000, Aarhus C, Denmark.

[3] Department of Environmental Geography, CNRS UMR GEODE 5602, University Toulouse Jean Jaurès, Toulouse, France.

[4] Center for Sustainable Landscapes under Global Change (SustainScapes), Department of Biology, Aarhus University, Ny Munkegade 114, DK-8000, Aarhus C, Denmark.

[5] School of Geography, Earth and Environmental Sciences, University of Plymouth, Plymouth, UK.

[6] CEREGE, CNRS, IRD, Europôle de l'Arbois, BP 80, F-13545, Aix-en-Provence, France.

[7] Faculty of Archaeology, Leiden University, Einsteinweg 2, 2333 CC, Leiden, Netherlands

[8] Department of Geology and Geomorphology, University of Łódź, Narutowicza 88, 90-139, Łódź, Poland.

[9] Faculty of Geology, University of Warsaw, Warsaw, Poland.

[10] Department of Geography, University of Cambridge, CB2 3EN, Cambridge, UK.

[11] Independent researcher, Soloviny str. 4-1-224, 117593, Moscow, Russia.

[12] Department of Geology, Lund University, Sölvegatan 12, SE-223 62, Lund, Sweden.

[13] Aix Marseille University, Avignon University, National Center for Scientific Research, National Research Institute for Sustainable Development, Mediterranean Institute for Marine and Terrestrial Biodiversity and Ecology (CNRS, IRD, IMBE), Aix-en-Provence, France.

[14] Ontario Geological Survey, 933 Ramsey Lake Road, Sudbury, Ontario, P3E 6B5, Canada.

[15] Instituto Pirenaico de Ecología, IPE–CSIC, Avda/ Montañana 1005, 50059, Zaragoza, Spain.

[16] Polish Geological Institute, National Research Institute, Carpathian Branch, Skrzatów 1, 31-560, Kraków, Poland.

[17] Polish Geological Institute – National Research Institute, Marine Geology Branch, ul. Kościerska 5, 80-328, Gdańsk, Poland.

[18] Climate Change Ecology Research Unit, Faculty of Geographical and Geological Sciences, Adam Mickiewicz University, Bogumiła Krygowskiego 10, Poznań, 61-680, Poland.

[19] Department of Botany, Charles University, Prague, Czechia.

[20] Dipartimento di Biologia Ambientale, University of Rome ‘La Sapienza’, Rome, Italy.

[21] Laboratory of Paleobotany, Department of Stratigraphical Geology, Institute of Geological Sciences, University of Wroclaw, Cybulskiego 34, 50-205, Wroclaw, Poland.

[22] Department of Geography and Environment, School of Geosciences, University of Aberdeen, UK.

[23] Department of Geography, Royal Holloway University of London, Egham, UK.

[24] Faculty of Natural Sciences, University of Silesia, Będzińska 60, 41-200, Sosnowiec, Poland.

[25] Faculty of Earth Sciences and Spatial Management, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100, Toruń, Poland.

[26] Maria Curie-Sklodowska University, Institute of Earth and Environmental Sciences, Al. Krasnicka 2 d, 20-718, Lublin, Poland.

[27] Department of Physical Geography and Quaternary Geology, Stockholm University, SE-106 91, Stockholm, Sweden.

[28] Department of Geosciences and Geography, University of Helsinki, Helsinki, Finland.

[29] Institute of Plant Sciences and Oechger Centre for Climate Change Research, University of Bern, Altenbergrain 21, 3013 Bern, Switzerland.

[30] TNO, Geological Survey of the Netherlands, Postbus 80015, 3508 TA, Utrecht, Netherlands.

[31] Faculty of Science, Department of Earth Sciences, Vrije Universiteit, Amsterdam, Netherlands.

[32] Institute for Environmental Studies, Vrije Universiteit Amsterdam, Amsterdam, Netherlands.

[33] Nature Research Centre, Institute of Geology and Geography, Akademijos 2, LT-08412, Vilnius, Lithuania.

[34] Landesamt für Bergbau, Geologie und Rohstoffe, Inselstraße 26, 03046, Cottbus, Germany.

[35] Leuphana University Lüneburg, Institute of Ecology, Lüneburg, Germany.

[36] Polish Geological Institute, 00-975, Warsaw, Poland.

*** Corresponding author:** Elena A. Pearce, elena.pearce@bio.au.dk

Abstract

The extent of vegetation openness in past European landscapes is widely debated. In particular, the temperate forest biome is traditionally defined as dense closed-canopy forests; however, some argue that large herbivores maintained greater openness or even wood-pasture conditions. Here, we address this question for the Last Interglacial period (129,000–116,000 years ago), before *Homo sapiens*-linked megafauna declines and anthropogenic landscape transformation. We applied the vegetation reconstruction method REVEALS to 96 Last Interglacial pollen records. We found that light woodland and open vegetation represented on average over 50% cover during this period. The degree of openness was highly variable and only partially linked to climatic factors, indicating the importance of natural disturbance regimes. Our results show that the temperate forest biome was historically heterogeneous rather than uniformly dense, which is consistent with the dependency of much of contemporary European biodiversity on open vegetation and light woodland.

Teaser

Landscape reconstruction using pollen data shows that European temperate forests were open and heterogeneous before modern humans.

Introduction

The extent of vegetation openness in past European landscapes is widely debated (1–4). Uncertainties are especially acute in temperate forests, where accurate estimates are needed 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 before increased human presence (1, 2). In the past two decades, proxy-based reconstructions have challenged this view of European forests (3–5). Recent pollen-based reconstructions of past land cover in the Holocene (11,700 BP–present) have shown that traditional comparisons of the percentage of arboreal to non-arboreal pollen strongly underestimate the cover of grass and heathland (6, 7). In support of this finding, fossil records from habitat-specific Mollusca (molluscs) and Coleoptera (beetles, from the British Isles) indicated that open and light woodland vegetation dominated in the early-mid Holocene (11,700–6000 BP) (8) and during the Last Interglacial period (129–116 thousand years [ka] before present [BP]) (9), respectively. Therefore, rather than comprising exclusively closed forests, Europe was potentially a heterogeneous landscape that featured a mixture of closed, open, and semi-open vegetation, such as grassland, scrub, and wood-pasture-like vegetation (4, 10). However, in the early Holocene, it is unclear how far open vegetation is an anthropogenic signal (11). The extent of vegetation openness prior to the impacts of *Homo sapiens*, in the temperate forest biome and Europe more broadly, remains poorly quantified.

Researchers have often considered the early to mid-Holocene, before the widespread 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 insufficient, primarily because of the impact of the arrival of *H. sapiens* (~54 ka BP) (11). While earlier humans, such as Neanderthals (*H. neanderthalensis*), likely had localised effects on vegetation (12), there is evidence for the widespread use of fire by *H. sapiens* to shape vegetation during the Mesolithic (13). Furthermore, *H. sapiens* are likely to have reduced the density and distribution of large herbivores far more than previous hominins did (12, 14). Large herbivores strongly influence vegetation openness (15). The global expansion of *H. sapiens* is associated with strong reductions in species richness and functional diversity of large herbivores, with particularly severe losses among larger species (14, 16). These defaunation dynamics are likely to have reduced the ability of fauna to promote openness in landscapes. Before these losses, high megafaunal diversity was typical in Europe and worldwide for more than 20 million years (17). To understand pre-*H. sapiens* vegetation dynamics and their implications for the evolutionary adaptations of species, it is important to elucidate vegetation structure before the late-Quaternary faunal downsizing (16).

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

Pollen records represent the most direct and widely available empirical data for recreating past vegetation cover (23). The dominant vegetation of temperate Europe during the Last 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 unimodal pattern of vegetation succession in central and temperate regions (24, 26). The first is the pioneer, Protocratic, *Pinus-Betula* (pine-birch) phase, in which rising temperatures and increasingly fertile soils supported light-demanding vegetation. High temperatures peaked during the temperate Mesocratic period, which is traditionally considered to be closed-forest dominated by *Quercus* (oak) and *Corylus* (hazel; early-temperate), followed by *Carpinus betulus* (hornbeam; late-temperate). Finally, towards the end of the interglacial, leached soils and falling temperatures of the Oligocratic/Telocratic phase were correlated with *Picea* (spruce) dominating along with *Pinus* and *Abies* (fir), and increasing vegetation openness (25).

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 sedimentary archives, and taxonomic differences in pollen productivity and dispersal characteristics (27, 29). The Regional Estimates of VEgetation Abundance from Large Sites (REVEALS) model corrects for biases caused by these factors and provides the regional vegetation composition and land cover within a 1° × 1° area (27). The REVEALS model has been extensively validated using both modern and historical analogues (see Methods) (30–32). Pollen-based REVEALS reconstructions of vegetation openness over the Holocene were produced for 1° × 1° grid cells across Europe (7). However, REVEALS has only been used to reconstruct vegetation of the Last Interglacial period at single sites (33) and not at the continental scale.

In this study, we applied REVEALS to a large dataset of Last Interglacial pollen records across Europe. We assessed vegetation openness in the European temperate forest biome, 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 factors explain the variation in pre-anthropogenic vegetation openness across Europe and within the temperate forest biome. Our study provides insights into the state of the temperate forest biome before modern humans and contributes to the long-standing 'open' vs 'closed' vegetation debate in Europe. Our results have important implications for our understanding of the evolutionary ecology of Europe's native biota as well as for restoration and rewilding efforts within this biome and across the continent.

Results

Europe-wide scale

Our results showed that, before the arrival of *H. sapiens*, highly heterogeneous vegetation was widespread in Europe (Fig. 1). Taxa indicating open and light woodland vegetation were strongly represented alongside the closed forests of shade-tolerant trees. In the early-temperate 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).

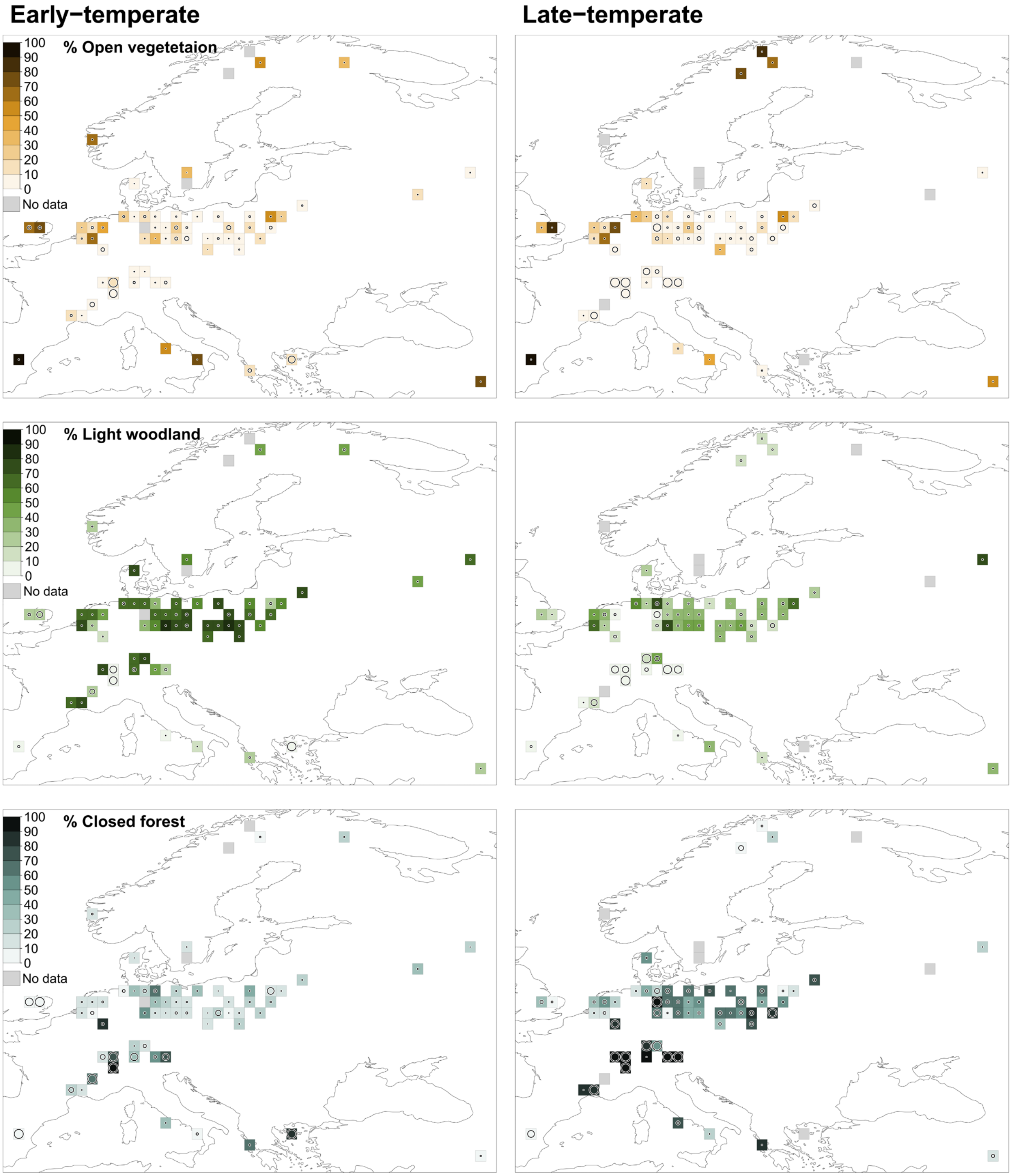

Fig. 1. REVEALS estimates. Open vegetation (**top**; herbaceous and heath taxa) light woodland (**middle**: shade-intolerant and intermediate taxa) and closed forest (**bottom**: shade-tolerant taxa) in the early-temperate (left) and late-temperate (right) periods. Each square is a regional grid cell of 1° × 1°. Darker colours show greater cover by open vegetation. 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.

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 early-temperate period, *n* = 30; Fig. 1).

During both time periods, Poaceae (grasses) and Cyperaceae (sedges) were the dominant open vegetation taxa, and *Corylus* was the dominant light-woodland taxon (Table S1). Other common taxa in the two categories were *Artemisia* (mugworts)*,* Amaranthaceae/Chenopodiaceae (gooseworts and relatives)*,* Ericaceae (various heathers and relatives), *Rumex acetosa* type (sorrel), *Calluna vulgaris* (common heather), *Betula*, *Pinus*, *Salix* (willow)*,* and *Taxus baccata* (yew; Data S1).

Temperate forest biome

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

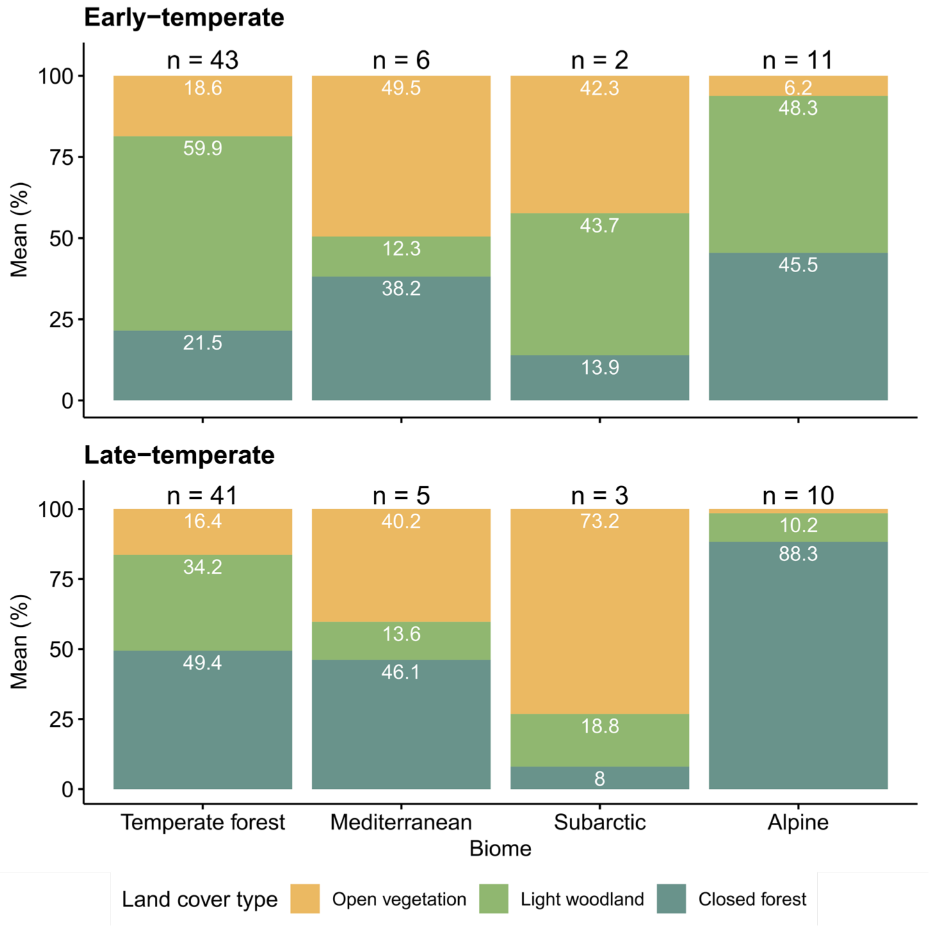

Fig. 2. Mean percentage land cover type per biome. Mean land cover (%) of open vegetation (yellow), light woodland (green) and closed forest (blue) in the temperate forest, Mediterranean, Subarctic and Alpine biomes in the early-temperate (**top**) and late-temperate (**bottom**) periods of the Last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

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*

= 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 cells, the standard error was greater than the REVEALS estimate for closed forests, raising uncertainty regarding the reliability of the results (Fig. 1; Data S2). However, the grid cells in this region were unanimous in their findings. *Picea*, *Abies alba* (silver fir), *Corylus*, and *Quercus* were dominant in the early-temperate, indicating a mixed closed and light woodland landscape. *Abies alba* was the dominant taxon in the late-temperate, indicating a closed-forest dominated landscape.

Other biomes

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

Drivers of vegetation openness

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).

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

< 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 by high openness and low precipitation in the Mediterranean. There was moderate evidence that degree of continentality decreased vegetation openness, with openness increasing towards more oceanic conditions (estimate = –0.057, *P* = 0.045; Fig. 3). There was moderate evidence that open vegetation cover was affected by terrain roughness (estimate = 0.002, *P* = 0.011; Fig. 3). Finally, a pairwise comparison of the estimated marginal means from the beta regression model revealed no difference in vegetation openness between the early-temperate and late-temperate periods (estimate = 0.028, *P* = 0.273; Fig. S2).

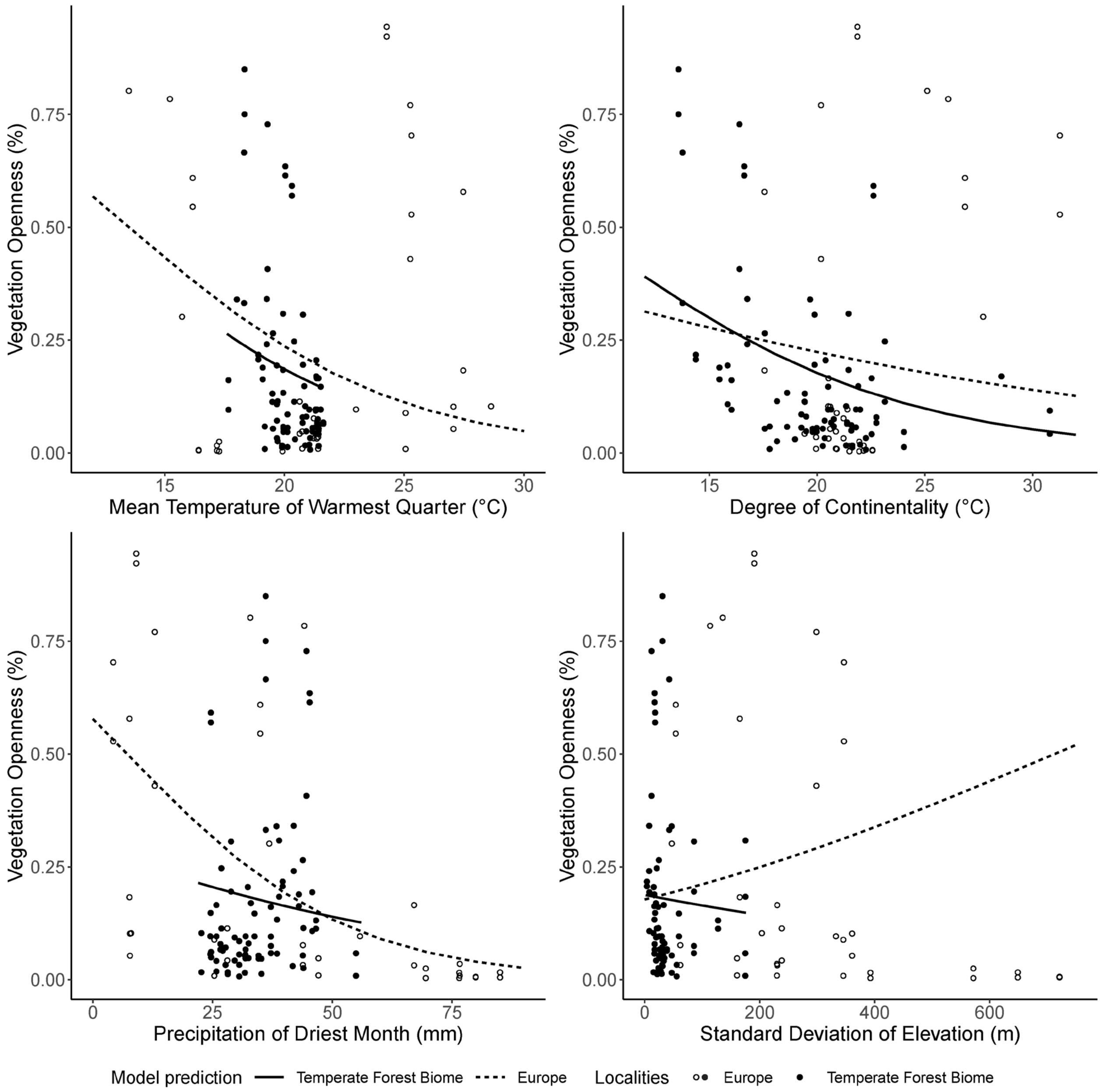

Fig. 3. Beta regression predictions for variables with significant effects: Mean temperature of the warmest quarter (°C), degree of continentality (°C), precipitation of driest month (mm), and standard deviation of elevation (m). Two scales are shown: Europe (*n* = 118; all grid cells across both time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

Temperate forest biome

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	Estimate		*P*–value	
	Europe (all grid cells)	Temperate Forest Biome	Europe (all grid cells)	Temperate Forest Biome
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	

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).

Robustness assessment

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, $P <$ 1e–04) or light woodland vegetation (estimate = –15.58, $P <$ 1e–04; Fig. S4). Furthermore, the standard errors for open vegetation cover did not vary greatly across the openness levels (Fig. S5). The REVEALS estimates for open vegetation were unreliable for only three grid cells (Fig. 1; see the Methods section). The REVEALS estimates were unreliable in one grid cell for light woodlands and 15 grid cells for closed vegetation (Fig. 1). All standard errors are provided in Dataset 02.

We found no effect of wetland indicators on vegetation openness. A pairwise comparison of the estimated marginal means from beta regression modelling showed no difference in vegetation openness between samples taken from bogs and lakes (estimate = –0.002, $P =$ 0.950; see also Fig. S6). We found no relationship between vegetation openness and the wetland taxa *Salix* (estimate = 11.127, $P = 0.213$) and *Alnus* (alder; estimate = –0.627, $P =$ 0.919). Across Europe (all grid cells), we found moderate evidence for a relationship between lake size and vegetation openness (estimate = 4.499e–05, $P = 0.024$). However, this relationship was driven by the grid cell from Lake Van, Turkey, which is the largest lake in the dataset (Table S2). When we excluded this grid cell, we found no evidence of a relationship (estimate = –6.020e–05, $P = 0.353$).

Discussion

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

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 (*Corylus avellana*), and grass-dominated open vegetation. **Top right:** Early-temperate 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);

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

The high abundance of *Corylus* and deciduous *Quercus* (hereafter *Quercus*) in the light woodland category supports the presence of semi-open landscapes, and is indicative of ongoing disturbance regimes. *Corylus* and *Quercus* were particularly visible during the 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, 37). We expected high levels of *Quercus* and *Corylus* during the early-temperate because this pattern is characteristic of many of the Last Interglacial pollen diagrams (24). However, previous studies concluded that the temperate forests were *Quercus* dominated, with *Corylus* present to a lesser degree (24). Our REVEALS model estimated greater percentages of *Corylus* than *Quercus* during the early-temperate period. Although partial *Corylus* dominance after the *Quercus* phase of the temperate period has been shown previously (38), our findings suggest a much greater role for *Corylus*. *Corylus* dominance would be consistent with scrub woodland dependent on ongoing disturbance, although *Corylus* may also thrive under the canopy of lightly shaded trees, such as *Quercus* and *Fraxinus* (ash) (37). Furthermore, *Quercus* regeneration, from seed dispersal to recruitment, occurs mostly in dynamic, heterogeneous landscapes subjected to disturbances from grazing animals and fire, for example (36). Importantly, both *Corylus* and *Quercus* fail to regenerate under a dense canopy (36, 39) and both taxa persisted for millennia through the temperate period

(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.

The variability in open vegetation across Europe raises questions about the drivers of openness, since environmental and climatic factors only partially explain the distribution of vegetation openness. In focusing our analysis on the temperate forest biome, we found that vegetation was more open in the milder oceanic grid cells (Figs. 1 and 2). From a climatic perspective, this relationship is counterintuitive because tree dominance is expected under milder temperate conditions (4). Furthermore, we found little evidence of any effects of other climatic or environmental variables in this biome (Fig. S2). It is possible that other environmental variables, such as soil type, played a role in driving open vegetation (40). However, soil type is difficult to assess for the Last Interglacial period, and comparisons to modern records are inadequate, given the transformation of relief and thus soil formation, structure, and texture following glacial cycles (41). Except for the 'Alpine' group, the 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 openness is often mediated by disturbance factors (42). Furthermore, under mild temperate conditions today, trees tend to dominate via succession in the absence of the active 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 vegetation, with potentially stronger effects under more oceanic climates.

The presence of open and light woodland taxa suggests ongoing vegetation disturbance. A plausible candidate is the rich megafaunal community of Europe during the Last Interglacial (15, 35). Large herbivores are ecological engineers capable of altering vegetation at the landscape scale (17). Their large body size requires the consumption of large quantities of plant biomass, which further affects vegetation through trampling, rooting, and debarking, as well as through seed dispersal and biogeochemical cycling (17). The effects of large herbivores on vegetation structure and wider ecosystem functioning have been well researched in recent years, especially relating to the ecosystem-wide effects of reintroductions (45). In modern European systems, large free-living herbivores can have considerable and lasting effects on vegetation composition and structure, for example, by generating or maintaining open and semi-open vegetation (46). Further, their effects might 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 home to a considerably greater number of larger-bodied herbivores (16), including elephants and other megaherbivores with strong effects on vegetation structure (15, 47). Our high openness estimates for England are consistent with previous beetle-based estimates, which also indicate high large herbivore abundances (9, 48) at a level sufficient to generate open vegetation on fertile wetland adjacent soils in Western Europe today (46). In the present study, closed forest vegetation was more abundant in the Alpine region (Figs. 1 and 2). It is possible that, due to lower accessibility (49), larger herbivores were not as prevalent in this mountainous region, and altered vegetation structure more in lowland regions (4, 9). However, terrain roughness, a measure hypothesised to reflect herbivore accessibility (49), had a moderate positive effect on vegetation openness (Fig. 3). Further research is required to understand this relationship.

Large herbivores may alter forests beyond promoting vegetation openness, such as by affecting the structure and species composition of the closed vegetation community (15). Such effects might explain the expansion of *C. betulus* in the late-temperate period. *C. betulus* is one of the few dominant European tree species able to develop a 'cage' architecture when exposed to browsing, allowing it to grow out of reach of herbivores (50). 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 regimes more readily than other dominant European tree species, but especially under high light conditions (50). This adaptation challenges the view that abiotic drivers alone influence forest structure, even when forests are denser, as in the late-temperate period (Fig. 1). Our findings support the presence of sunlit conditions that could enable *C. betulus* survival and eventual dominance (Table S1).

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 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). However, quantifying the role of fire in the rest of the temperate forest biome during the Pleistocene interglacial periods is a promising avenue for future research, particularly given megafauna-fire interactions and the widespread consequence of herbivore extinction on global fire regimes (53). Furthermore, other disturbances such agents of abnormal intensity (floods, avalanches, storms, and landslides) are likely to have played a role in opening vegetation in some settings (4). The roles of these abiotic stochastic disturbances in interglacial ecosystems and their interactions provide interesting future research opportunities.

Traditionally, closed-canopy forests are believed to have dominated the temperate forest biomes before modern humans (2, 26). Our findings show that European forests included substantial open and light woodland elements, and suggest an important role for processes that maintain open habitats. This may have important implications for European biota, and particularly for rarer species that depend on open, intermediate, and disturbed landscapes (54, 55). Consequently, common approaches to restoration, such as tree planting, risk creating unfavourable habitats for biodiversity that has evolved in heterogeneous landscapes (5, 56). Trophic rewilding and other approaches aimed at restoring natural disturbance 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 understanding the structure of a biome in conservation and restoration, we advocate for a reimagining of the temperate forest biome to reflect the substantial open vegetation and light woodland present.

Materials and methods

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

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

Pollen data collection and preparation

We collected 96 European pollen records from the European Pollen Database (www.europeanpollendatabase.net/), Pangaea (www.pangaea.de/), Neotoma (www.neotomadb.org/), and individual pollen data contributors (Fig. S1; Table S2) and applied the vegetation reconstruction method REVEALS (27). The REVEALS model reconstructs vegetation cover regionally. This is achieved by quantifying background pollen from one or more sites to produce regional vegetation for a 1° × 1° area (27). REVEALS overcomes the nonlinearity of the pollen-vegetation relationship by accounting for relative 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 (61), as well as at the European scale (62). Empirical testing against modern (59, 60, 62) and historical (31) analogues has shown that REVEALS improves the accuracy of vegetation reconstruction considerably compared to that using pollen proportions alone. Finally, REVEALS is robust to variations in site selection, sampling design, and parameter values (63), and is considered a valuable tool for reconstructing past landscapes in different settings and environments, including small sites (32), floodplains (64), and mountainous regions (31).

Because radiocarbon dating was not possible for our study period, we selected pollen records that were dated to the Last Interglacial period based on litho- and/or bio-stratigraphical evidence (65). This is considered a robust approach for the Last Interglacial, as in Europe the Last Interglacial follows a very distinct, widely acknowledged pattern of vegetation succession by the dominant taxa, with the most closed vegetation phases occurring in the mesocratic/temperate phase (24, 26). To avoid issues of interglacial non-synchronicity across Europe, we used dominant vegetation taxa to classify the Protocratic, Mesocratic (temperate), and Telocratic periods based on defined pollen zones of the Last Interglacial (24, 25) following Lang's protocol (24). Therefore, we examined vegetation openness in the *Quercus/Corylus*- (first half of the Mesocratic: early-temperate) or *C. betulus*-dominated (second half of the Mesocratic: late-temperate) periods, rather than at specific times.

We implemented REVEALS using the protocol of Githumbi *et al.* (7), based on the LRA R package (66). The REVEALS model uses pollen count data, relative pollen productivity (RPP) estimates, and pollen fall speed to reconstruct regional vegetation cover for each taxon in each time slice (Supplementary Materials). The REVEALS model is applied to lake and bog sites separately within each 1° × 1° grid cell and combines results, from several sites when available, to produce a single mean percentage cover estimate (Data S1) and mean standard error (*SE*; Data S2) for each RPP taxon per grid cell. Site locations with respect to their grid cells are available in the supplementary material (Fig. S8). The assumptions of the REVEALS model were presented by Sugita (27). We calculated the mean percentage cover of each plant function and land-cover type by summing the mean percentage cover of each associated RPP taxon (Table 2), and averaged these values across all grid cells ($n = 66$) to provide Europe-wide estimates of vegetation openness. REVEALS calculates the uncertainty, using the delta method (67), as the *SEs* derived from the sum of the within- and between-site variations in the grid cell (Data S2) (7). We also calculated the coefficient of variation (SE/REVEALS estimate) to report *SEs*, as shown in Fig. 1. We 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 in our regression analyses as they were reflective of the surrounding grid cells.

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

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

Betula	Shade-intolerant tree	Light woodland
Pinus		
Pistacia		
Corylus	Intermediate tree	
Buxus sempervirens		
Phillyrea		
Quercus deciduous		
Taxus baccata		
Salix		
Abies	Shade-tolerant tree	Closed forest
*Alnus**		
Carpinus betulus		
Carpinus orientalis		
Castanea sativa		
Fagus		
*Fraxinus**		
Picea		
Quercus evergreen[†]		
Tilia		
Ulmus		

*Taxa considered to be 'shade-tolerant' due to their ability to thrive in shaded forest landscapes despite having high light requirements, because of their tolerance to wet soils and/or ability to recruit in small treefall gaps. [†]*Quercus* evergreen is conservatively included as shade-tolerant, based on *Quercus Ilex*. However, in the Mediterranean, other *Quercus* evergreen species may indicate more open landscapes.

Climate data and biomes

We used equilibrium simulations of the climate at 127 ka BP (the climatic optimum of the Last Interglacial; LIG) as in Scussolini et al. (68), from six Earth system models: AWI-ESM-1-1-LR (69), CNRM-CM6-1 (70), GISS-E2-1-G (71), INM-CM4-8 (72), IPSL-CM6-LR (73), and MIROC-ES2L (74). We downscaled the monthly surface air temperature and precipitation from these models to a resolution of 5 km. We then bias-corrected the values of the Last Interglacial simulation by comparing the historical simulations of the same models with the CHELSA V2 high-resolution climate dataset (75) over the period 1981–2010. From the corrected LIG values, we calculated the mean of the six models and derived the bioclimatic variables, as in WorldClim (76).

We determined the climatic biomes of the Last Interglacial period using monthly temperature and precipitation data from each of the six LIG models and the mean ensemble model to produce the first Köppen-Geiger climate classification maps, as in Beck et al. (77), for the Last Interglacial period (Fig. S7; Supplementary Material). To maintain a large sample size, we grouped the Köppen-Geiger climate classifications into four main climate 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.

Statistical analysis

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).

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.

Drivers of vegetation openness

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

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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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.

Competing Interest Statement

The authors declare they have no competing interests.

Data and Materials Availability

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

Science Advances

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Supplementary Materials for

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

Elena A. Pearce* *et al.*

*Corresponding author. Email: elena.pearce@bio.au.dk

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, up-to-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 RPP-harmonised 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 (early-temperate), 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% ± 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.

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).

			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	10.18	0.09	3.01	0	35.95	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	13.83	0.17	6.12	0.03	18.66	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	20.96	0	4.67	0	2.6	0.44	0.65
Late	Temperate Lowland Europe	SD	0.24	0.19	2.2	13.69	1.88	0.11	0.04	0.14	12.39	0.07	4.01	0.03	17.25	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	10.69	0.09	2.43	0.01	30.08	0.03	7.01	0.05	8.55	0.37	1.09
Early	Europe - all	SD	0.14	1.23	0.88	13.61	0.37	0.04	0.42	0.11	16.18	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	15.61	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	13.48	0.08	3.8	0.1	17.08	0.1	5.9	0.08	4.79	1.52	0.68

			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	19.61	0	0	0	1.03	6.66	0	4.38	3.42
Late	Temperate Lowland Europe	SD	13.85	1.66	15.99	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	18.07	1.47	6.11	4.19	0	0.66	2.28	6.84	0.67	4.78	4.21
Late	Europe - all	Mean	18.02	1.4	14.45	0.62	0	0.1	0.86	5.61	0.1	3.19	3.11
Late	Europe - all	SD	28.91	1.59	15.39	4.68	0	0.6	0.96	7.35	0.78	4.38	5.31

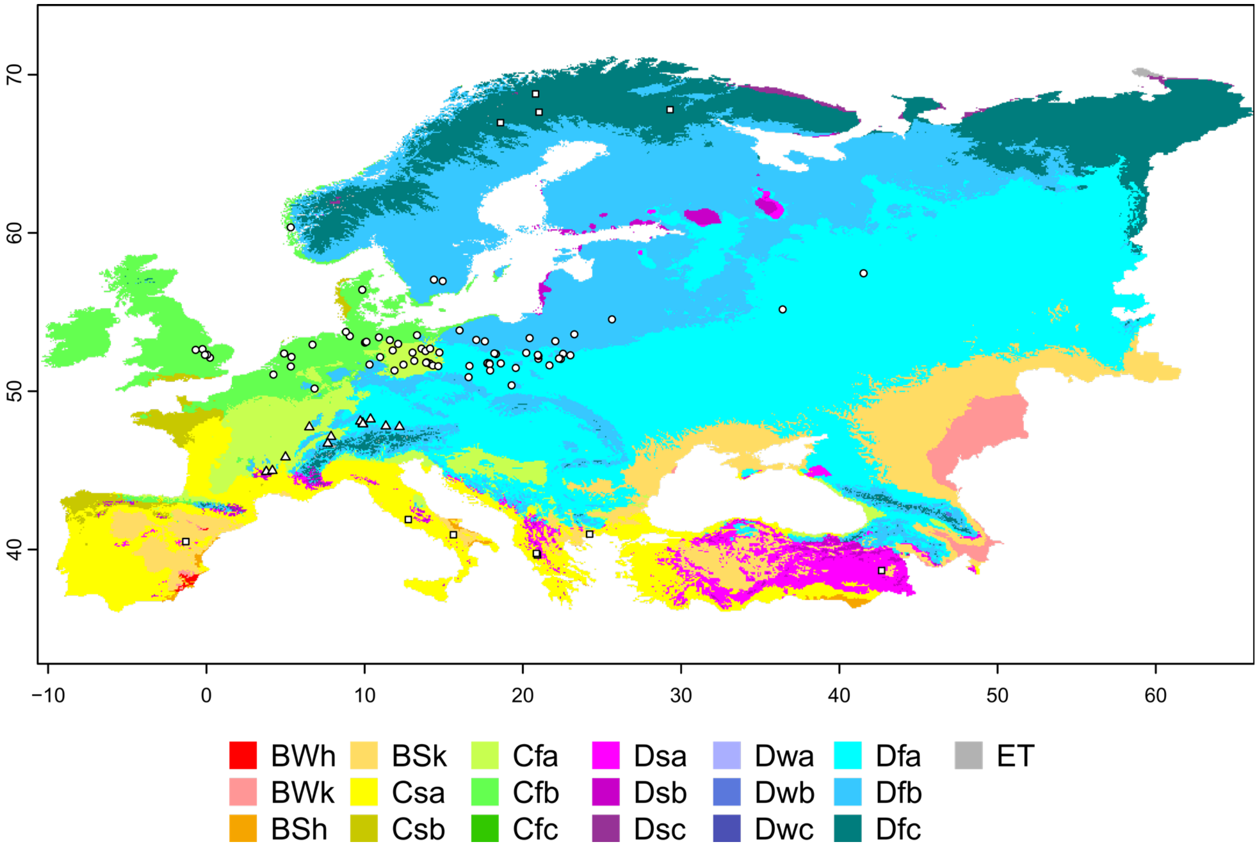


Fig. S1. Location of 96 pollen sequences (points; see Table S2) divided according to Köppen-Geiger climate classification for the Last Interglacial. We reconstructed the classifications as in Beck et al. (77), from monthly temperature and precipitation data from the GISS-E2-1-G earth system model (71). 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).

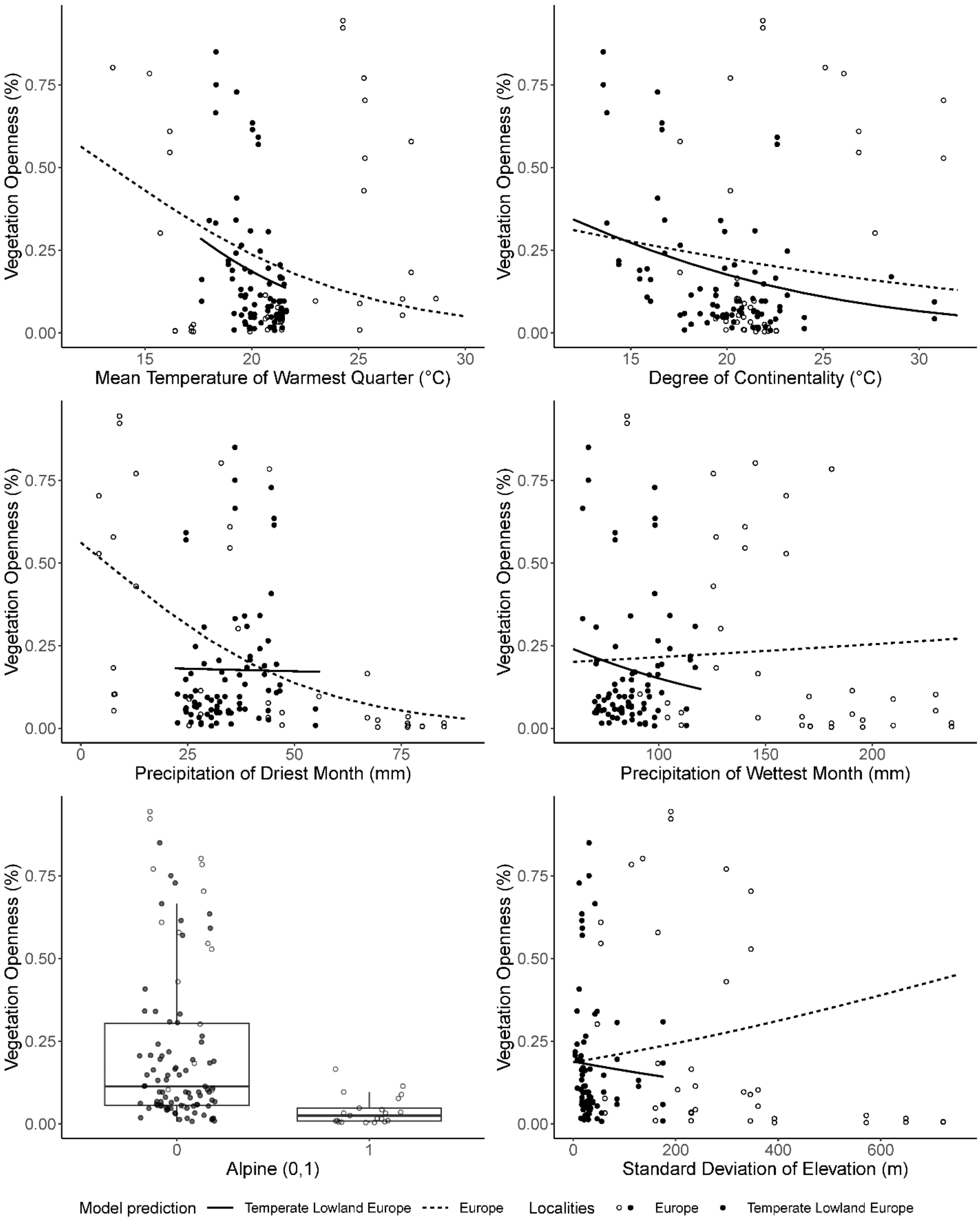


Fig. S2. Full model results of beta regression analysis, with the influencing outlier in Southern Norway (grid cell 1021) excluded.

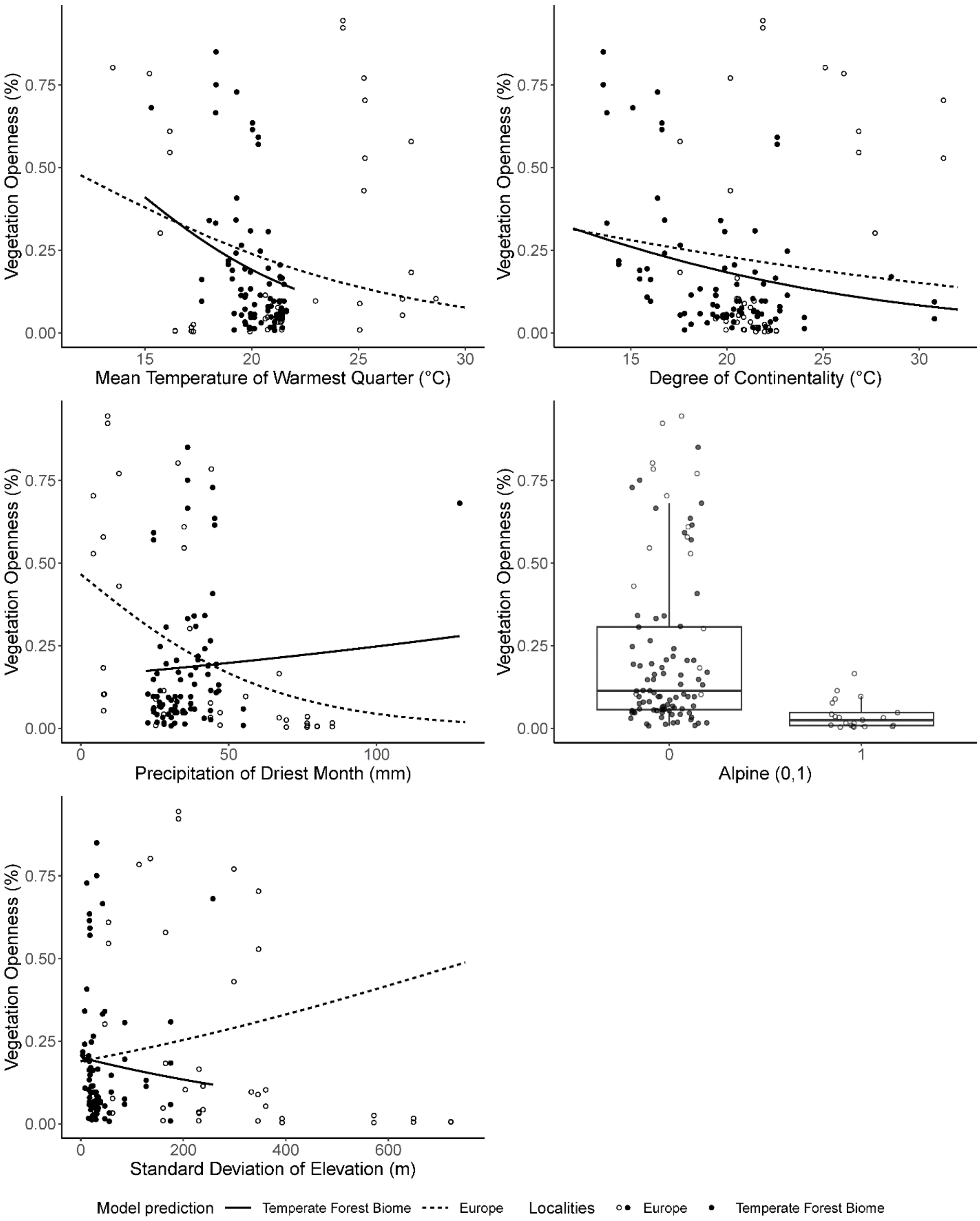


Fig. S3. Full model results of beta regression analysis, with the influencing outlier in South Norway (grid cell 1021) included.

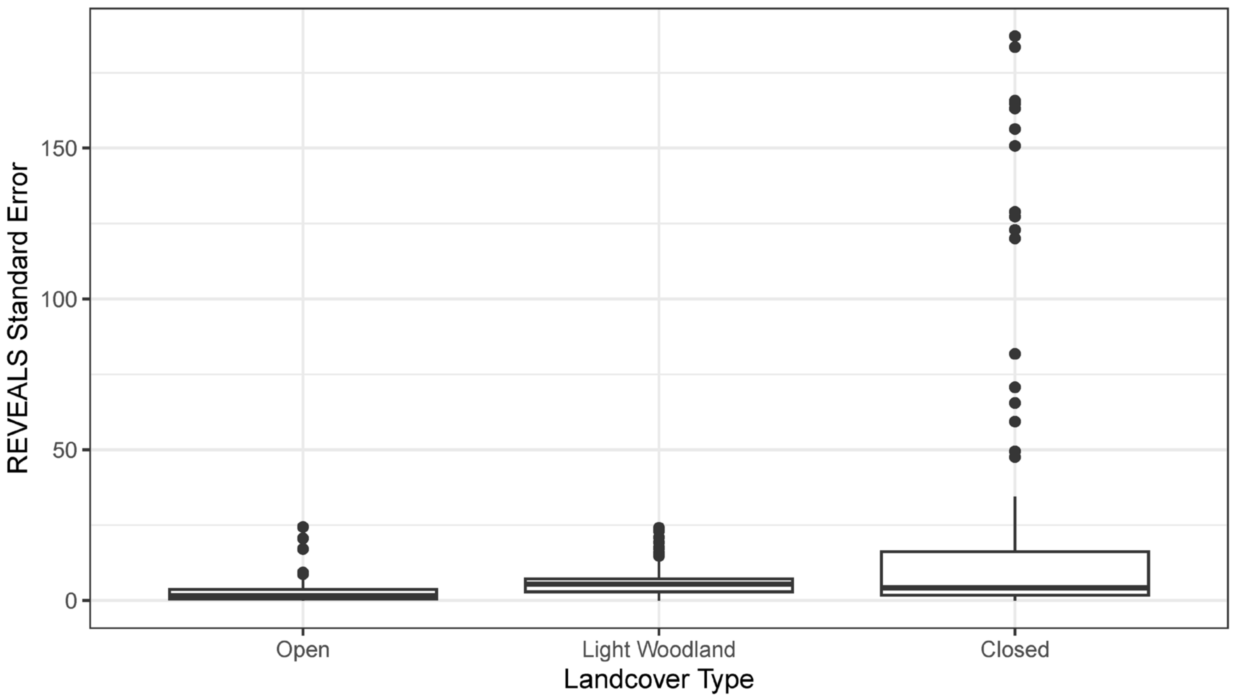


Fig. S4. Standard Errors from the REVEALS model, for all grid cells across all time windows, plotted by land cover type.

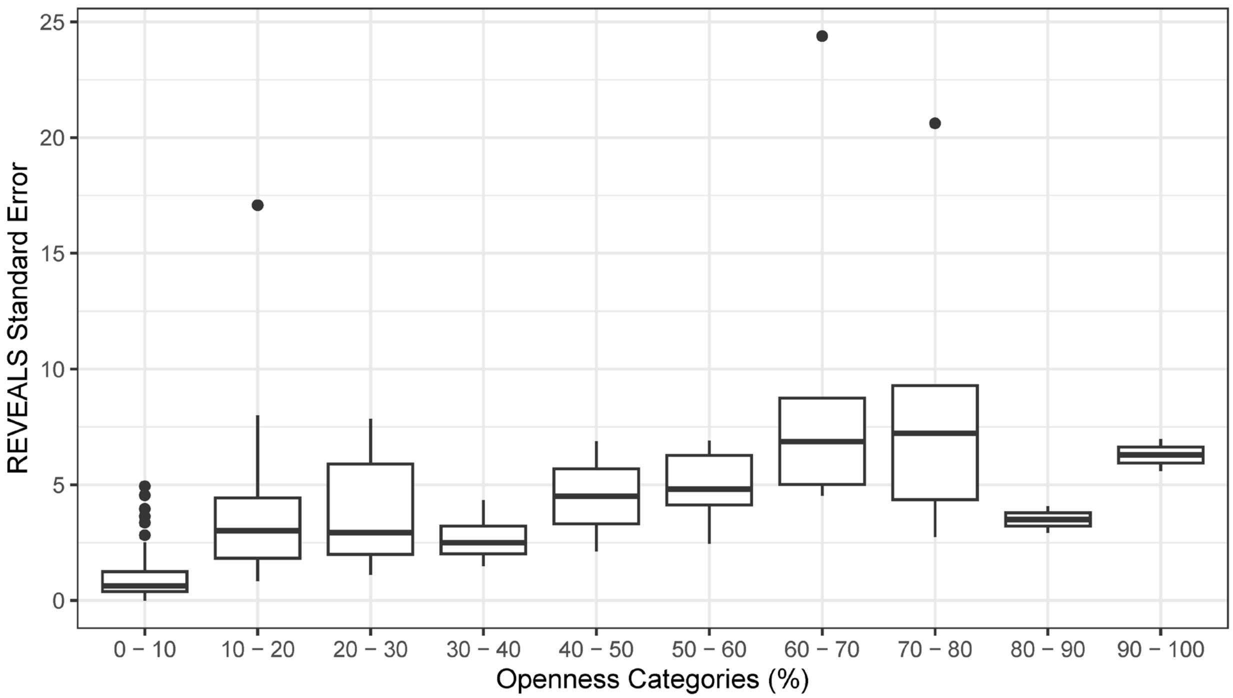
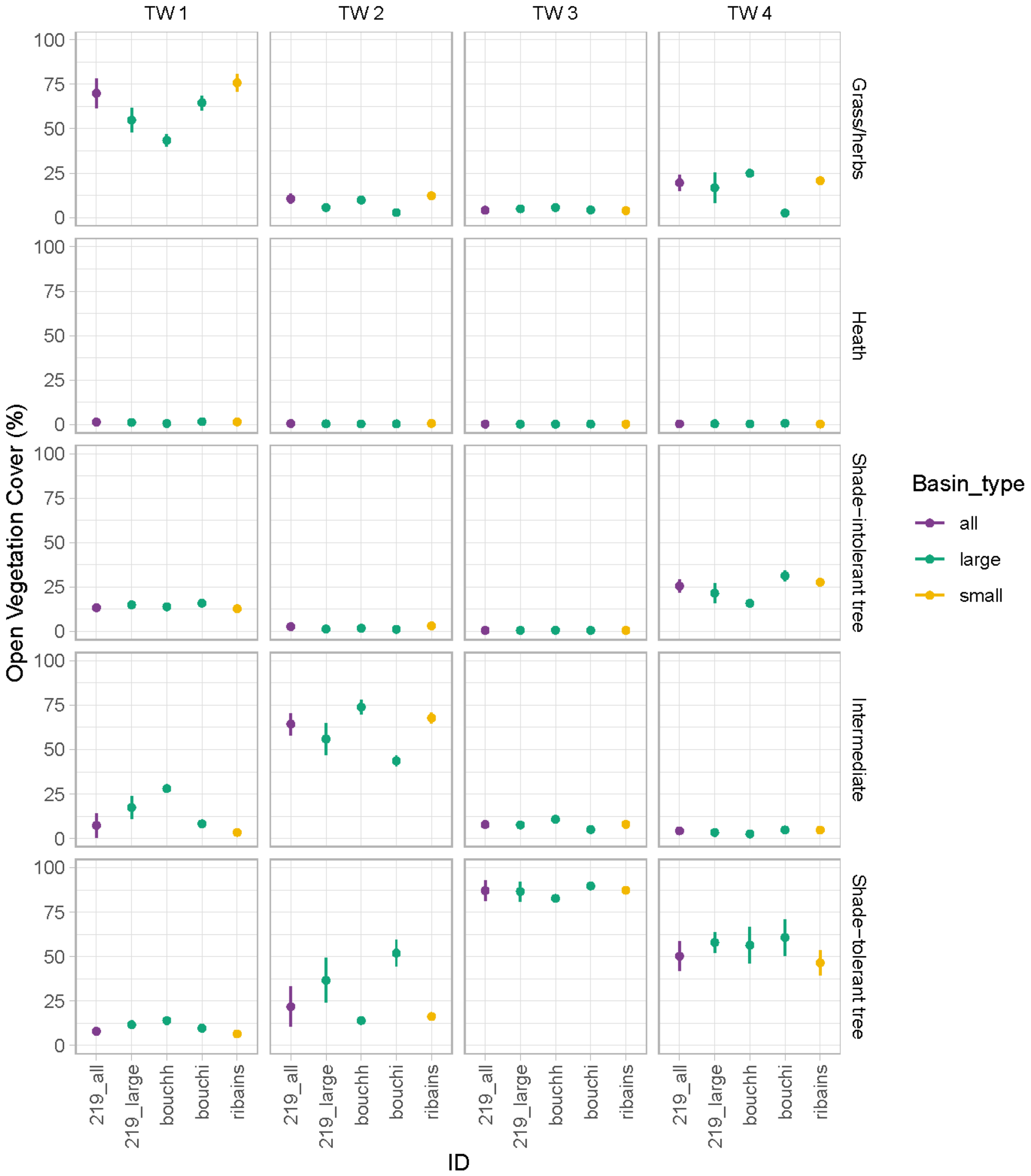
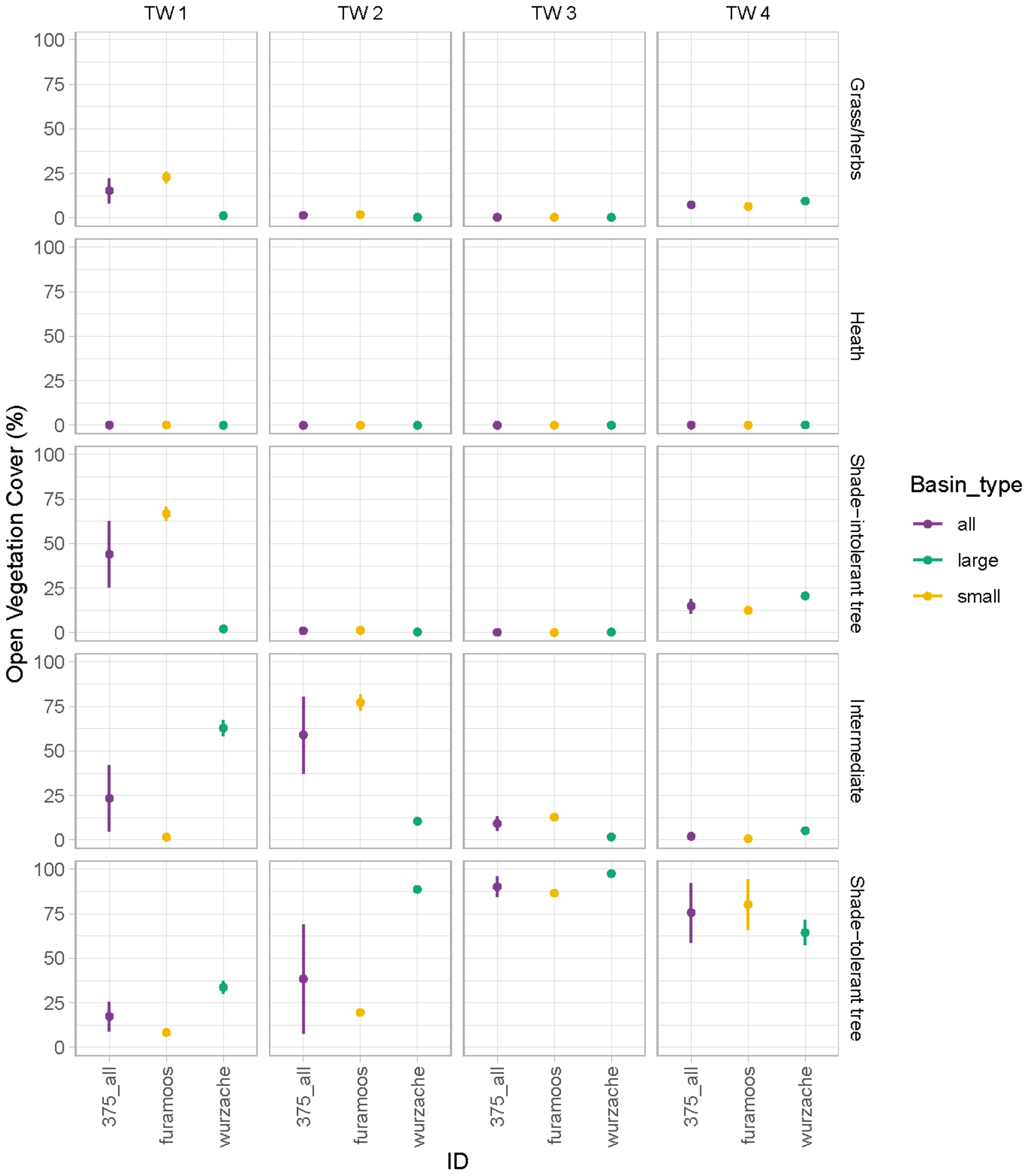
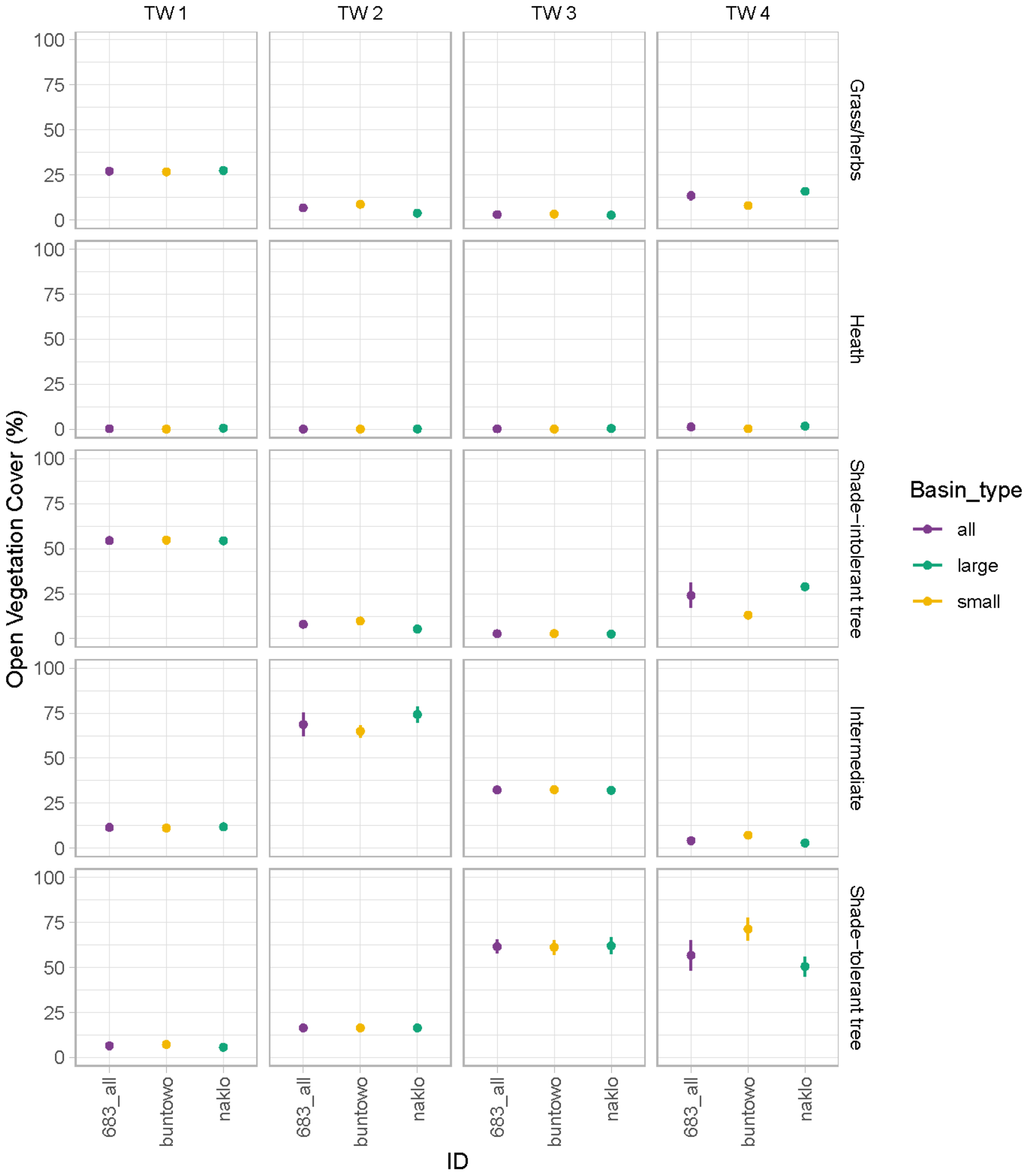


Fig. S5. Standard Errors from the REVEALS model, for all grid cells across all time windows, plotted by openness categories (%).


TW 1
TW 2
TW 3
TW 4
Grass/herbs
Heath
Shade−intolerant tree
Intermediate
Shade−tolerant tree
Open Vegetation Cover (%)
100
75
50
25
0
219_all
219_large
bouchh
bouchi
ribains
ID
Basin_type
all
large
small


TW 1
TW 2
TW 3
TW 4
Grass/herbs
Heath
Shade−intolerant tree
Intermediate
Shade−tolerant tree
Open Vegetation Cover (%)
0
25
50
75
100
ID
375_all
furamoos
wurzache
Basin_type
all
large
small


TW 1
TW 2
TW 3
TW 4
Grass/herbs
Heath
Shade−intolerant tree
Intermediate
Shade−tolerant tree
Open Vegetation Cover (%)
0
25
50
75
100
ID
683_all
buntowo
naklo
Basin_type
all
large
small

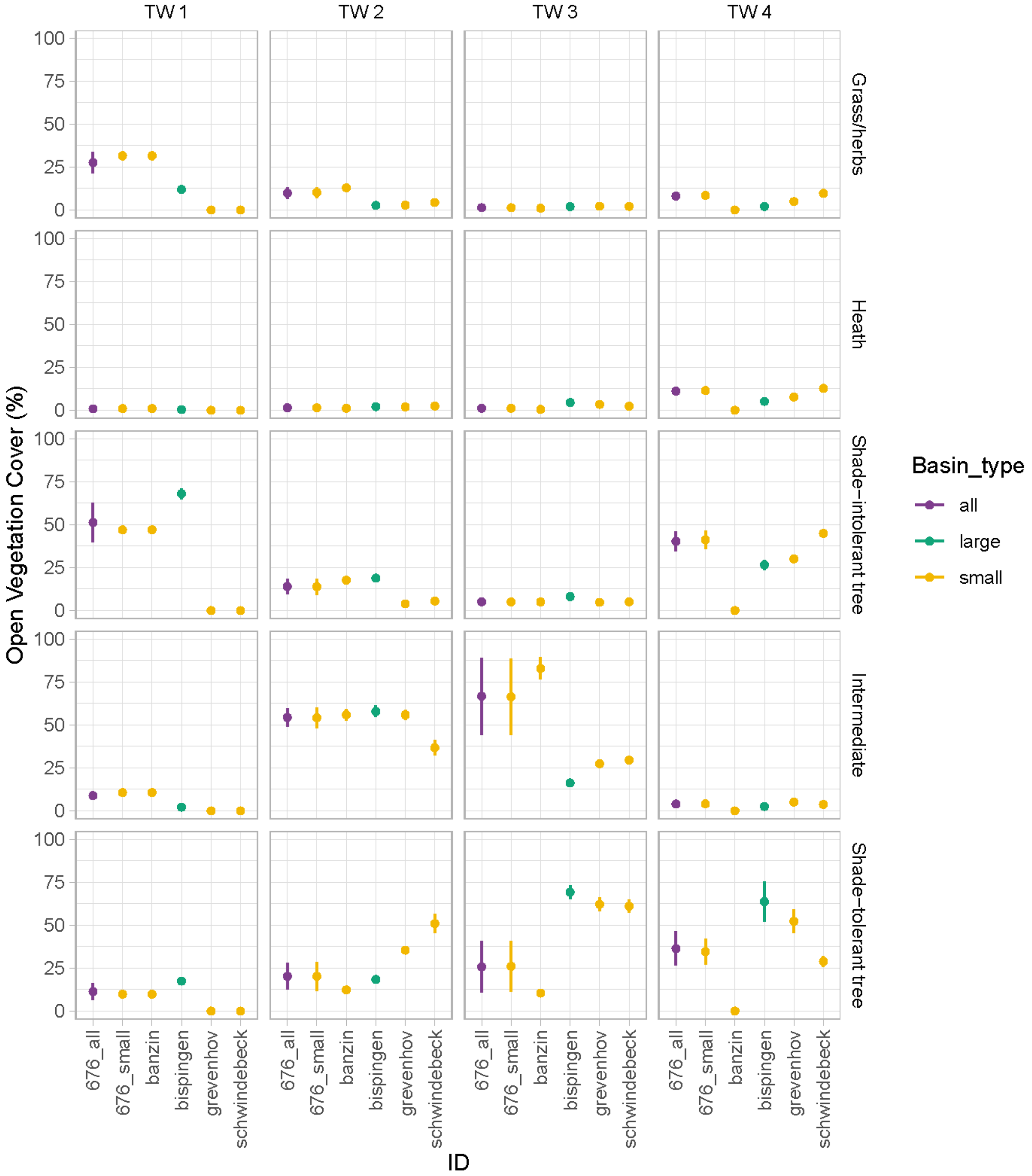


Fig. S6. Grid cell-based REVEALS estimates of vegetation openness (left Y-axis) for each PFT (right Y-axis) in grid cells 219, 375, 676, and 683 (Fig. S1, Table S2). Four time windows (top X-axis – TW1, TW2, TW3 and TW4: Protocratic, early-temperate (early Mesocratic), late-temperate (late Mesocratic) 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.

Table S2. Metadata for all pollen sequences.

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/10.3390/quat2030024
Jeroen Schokker	Amersfoort I (B32B0119)	Netherlands	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.pangaea.de/10.1594/PANGAEA.729508
Jeroen Schokker	Amsterdam-Terminal (B25E0913)	Netherlands	Geological Survey of the Netherlands	4.91	52.4	10000	Lake	Van Leeuwen et al., 2000, Netherlands Journal of Geosciences	https://doi.org/10.1017/S0016774600023647
Jeroen Schokker	Amersfoort New (B32B2092)	Netherlands	Geological Survey of the Netherlands	5.38	52.2	1500	Lake	Kasse et al., 2022, Netherlands Journal of Geosciences	https://doi.org/10.1017/NJG.2022.4
Anna Hrynowiecka	Banzin	Germany	Authors	10.9	53.4	5	Lake	Börner et al, 2015, Quaternary International	https://doi.org/10.1016/j.quaint.2014.10.022
Anna Hrynowiecka	Beckenthin	Germany	Authors	11.6	53.2	30	Bog	Hrynowiecka et al , 2021, Quaternary International	https://doi.org/10.1016/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)	Netherlands	Authors	5.34	51.6	100	Bog	Schokker, Cleveringa & Murray, 2004, Journal of Quaternary Science	https://doi.org/10.1002/jqs.808
Malgorzata Malkiewicz	Buntowo	Poland	EECRG(digitised)	17.1	53.2	356	Lake	Malkiewicz, 2018, Quaternary International	https://doi.org/10.1016/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/10.1016/j.revpalbo.2010.11.003
Tim Mighall	Deeping St James	United Kingdom	Authors	-0.25	52.7	22.2	Lake	Keen et al., 1999, JQS	https://doi.org/10.1002/(SICI)1099-1417(199908)14:5%3C411::AID-JQS447%3E3.0.CO;2-M
Wilhelmus De Gans	Drentsche Valley	Netherlands	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/10.1594/PANGAEA.58939
Jan Mangerud	Fjøsanger	Norway	EECRG(digitised)	5.33	60.4	1204.8	Lake	Mangerud, Sejrup, Sønstegaard & Haldorsen, 1981, BOREAS	https://doi.org/10.1111/j.1502-3885.1981.tb00479.x
Ulrich C. Müller	Füramoos	Germany	EPD	9.88	48	138.2	Lake	Müller, Pross & Bibus,	doi:10.1016/S0033-5894(03)00005-X

								2003, *Quaternary Research*	
Jaqueline Strahl	Gloewen	Germany	Geological Survey of Brandenburg	12.1	53	5	Lake	Hermsdorf & Strahl, 2008, Geowiss	NA
Jerzy Niklewski	Główczyn G2	Poland	Pangaea	20.2	52.4	143.84	Lake	Niklewski, 1968, Monographiae Botanicae	https://doi.pangaea.de/10.1594/PANGAEA.739263
Zofia Janczyk-Kopikowa	Golkow	Poland	Pangaea	21	52.1	195.44	Lake	Janczyk-Kopikowa, 1966, *Kwartalnik Geologiczny*	https://doi.org/10.1594/PANGAEA.760378
Samuel Wegmüller	Gondiswil-Seilern	Switzerland	EECRG(digitised)	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.pangaea.de/10.1594/PANGAEA.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 Granoszewski	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	Ioannina 249	Greece	EPD	20.9	39.7	269.4	Lake	Tzedakis, Frogley & Heaton, 2003, Global and Planetary Change	https://doi.org/10.1016/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/10.1016/S0921-8181(02)00182-0
Bożena Noryśkiewicz	Jałówka	Poland	Authors	23.2	53.6	100	Lake	Rychel et al, 2014, Quaternary International	https://doi.org/10.1016/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/10.1111/j.1502-3885.1988.tb00564.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.pangaea.de/10.1594/PANGAEA.739381
Burkhard Frenzel	Krumbach I	Germany	Pangaea	10.4	48.2	218.51	Lake	Frenzel, 1991, Stuttgart	https://doi.pangaea.de/10.1594/PANGAEA.736436
Bożena Noryśkiewicz	Kwiatków Las	Poland	Authors	17.9	51.7	15	Lake	Noryśkiewicz, 1995, Mat. Arch. Zak. Geomorf. Univ. Łódz	NA
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/10.1006/qres.2002.2340

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/10.1016/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/10.1016/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.pangaea.de/10.1594/PANGAEA.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/10.1111/j.1502-3885.1984.tb00066.x
Jan Lundqvist	Leveäniemi	Sweden	EECRG(digitised)	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.pangaea.de/10.1594/PANGAEA.711922
Steve Boreham, Cunhai Gao	Mannings Farm Beds	United Kingdom	Authors	0.05	52.3	20	Lake	Gao & Boreham, 2010, Boreas	https://doi.org/10.1111/j.1502-3885.2010.00191.x
Vaida Šeirienė	Medininkai117	Lithuania	Authors	25.6	54.5	30	Lake	Šeirienė, Kühl & Kisielienė, 2017, Quaternary Research	https://doi.org/10.1016/j.yqres.2014.04.004
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/10.1594/PANGAEA.707088
Bożena Noryśkiewicz	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.pangaea.de/10.1594/PANGAEA.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/10.1016/j.revpalbo.2012.06.003
Krzysztof Bińka	Nidzica	Poland	Authors	20.4	53.4	750	Lake	Bińka, Nitychoruk & Dzierżek, 2011, Boreas	https://doi.org/10.1111/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/10.1002/jqs.2665
Karl-Ernst Behre	Oerel 61	Germany	EPD	9.06	53.5	250	Lake	Behre & van der Plicht, 1992, Vegetation History and Archaeobotany	https://doi.org/10.1007/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.pangaea.de/10.1594/PANGAEA.739625
Olga K. Borisova	PLES	Russia	EPD	41.5	57.5	500	Lake	Borisova, 2007, Quaternary Science Reviews	https://doi.org/10.1016/j.quascirev.2007.07.001
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/10.1007/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.pangaea.de/10.1594/PANGAEA.726866
Jaqueline Strahl	Schönfeld	Germany	Geological Survey of Brandenburg	13.9	51.8	115	Lake	Erd, 1991, Sonderheft	NA
Brigitte Urban	Schöningen	Germany	Authors/Neotoma	11	52.2	500	Lake	Urban et al, 1991, E&G Quaternary Sci	https://doi.org/10.3285/eg.41.1.07
Karl-Ernst Behre	Schwindebeck	Germany	Pangaea	10.1	53.1	39.894	Lake	Behre, 1962, Flora	https://doi.pangaea.de/10.1594/PANGAEA.894473
Ann-Marie Robertsson	Seitevare	Sweden	Authors	18.6	67	12500	Lake	Robertsson & Rodhe, 1988, BOREAS	https://doi.org/10.1111/j.1502-3885.1988.tb00564.x
Filip Van Beirendonck	Sint-Amands	Belgium	Authors	4.23	51	750	Bog	Verbruggen, 1999, Geologica Belgica	https://doi.org/10.20341/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 Salonen	Sokli	Finland	Authors	29.3	67.8	2500	Lake	Salonen et al., 2018, Nature communications	https://doi.org/10.1038/s41467-018-05314-1
Patrick Schläfli	Spiezberg	Switzerland	Authors	7.67	46.7	8500	Lake	Schläfli, 2021, Quaternary Science Reviews	https://doi.org/10.1016/j.quascirev.2021.106975
Valérie Andrieu-Ponel	St. Front	France	Authors	4.17	45	309.02	Lake	Martin et al, 2019, Organic Geochemistry	https://doi.org/10.1016/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/10.1002/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/10.1016/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/10.1016/j.quascirev.2016.10.016
Frank Sirocko	Trockenmaar_HL2	Germany	Pangaea	6.84	50.2	282.09	Lake	Sirocko et al., 2005, Nature	https://doi.pangaea.de/10.1594/PANGAEA.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/10.1016/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/10.1016/1040-6182(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/10.1016/j.quaint.2010.06.026
Penélope González-Sampériz	Villarquemado	Spain	Authors	-1.3	40.5	1828.2	Lake	González-Sampériz et al., 2020, Quaternary Science Reviews	https://doi.org/10.1016/j.quascirev.2020.106425
Krzysztof M Krupinski	Warszawa Kasprzak St	Poland	Pangaea	21	52.2	375	Lake	Krupinski & Morawski, 1993, Acta Palaeobotanica	https://doi.pangaea.de/10.1594/PANGAEA.739950
Krzysztof M Krupinski	Warszawa Wawrzyszew 15	Poland	Pangaea	20.9	52.3	398.94	Lake	Krupinski & Morawski, 1993, Acta Palaeobotanica	https://doi.pangaea.de/10.1594/PANGAEA.739948
Allan Hall	Wing	UK	EECRG(digitised)	-0.68	52.6	50	Lake	Hall, 1978, New Phytologist	https://doi.org/10.1111/j.1469-8137.1978.tb01655.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/10.1016/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.pangaea.de/10.1594/PANGAEA.713702

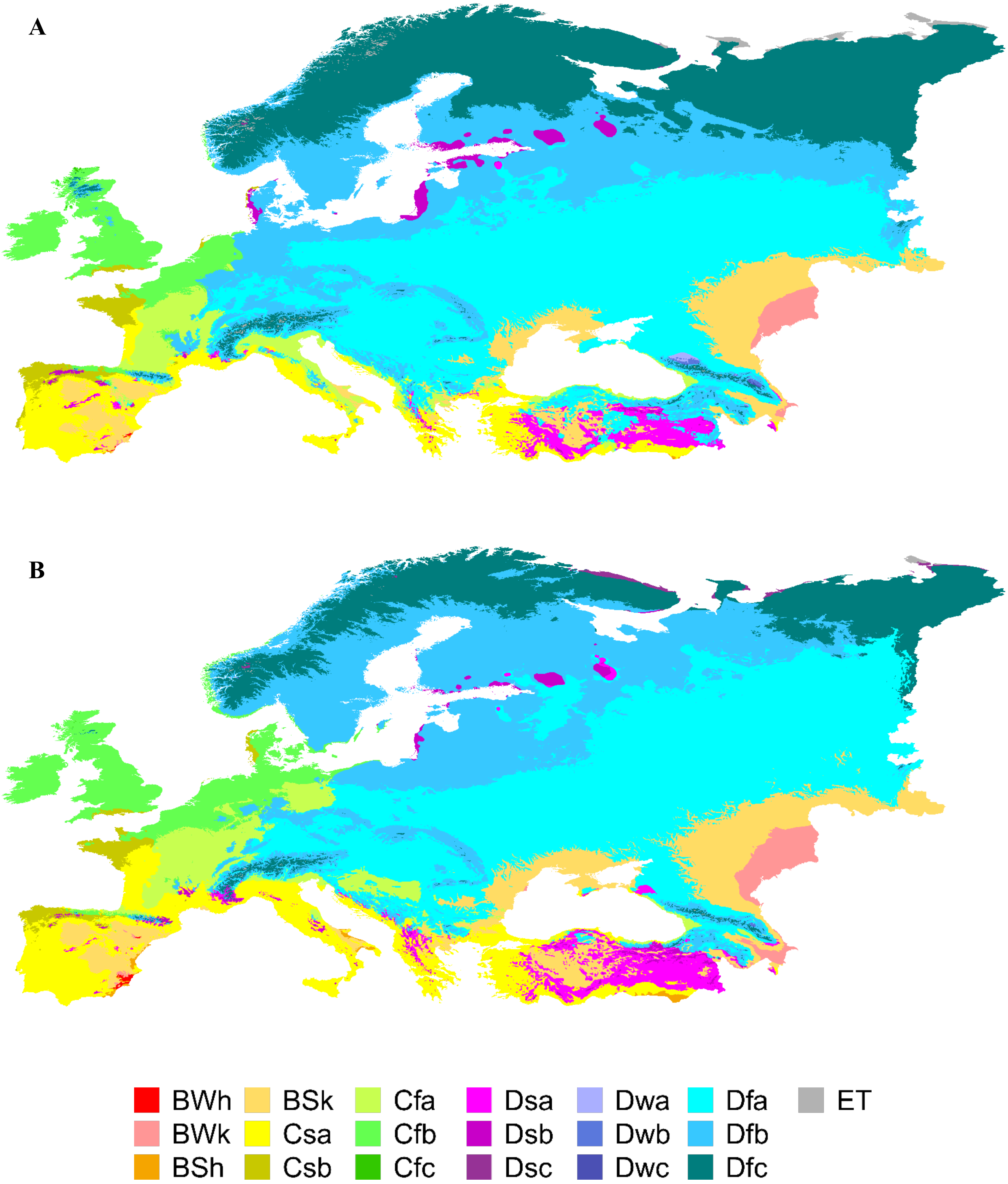


Fig. S7. Köppen-Geiger climate classification maps produced with mean ensemble model (A) and GISS-E2-1-G model (B; 71). The colour scheme was adopted from Beck *et al* (77).

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

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

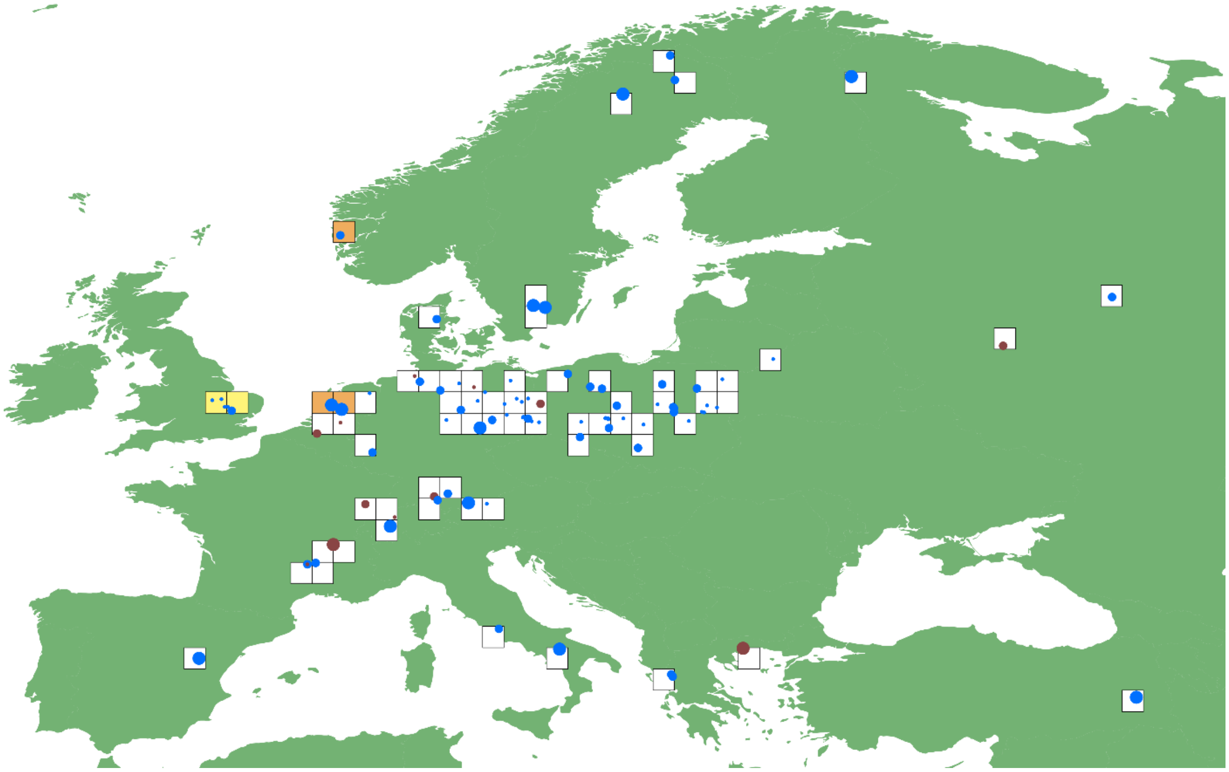


Fig. S8. Map of individual pollen sequences taken from lakes (blue points) and bogs (brown points). Small sites (<150 m radius), medium sites (150 – 1500 m radius) and large sites (>1500 m radius) correspond to small, medium and large points. Riverine (yellow) and marine (orange) grid cells are considered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