

The age and post-glacial development of the modern European vegetation: a plant functional approach based on pollen data

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Abstract To assess quantitatively the age of the modern vegetated landscape of Europe and western Asia Minor, and to reconstruct Holocene dynamics in biomes and landscape openness, we convert pollen data into plant functional type (PFT) assemblages and interpolate the data in space and time with a 4D thin plate spline. We then assess overall vegetation change using the squared chord distance metric, changes in potential natural vegetation using the biomisation method, and changes in landscape openness by calculating the arboreal pollen PFT percentage. The age of the modern European vegetated landscape varies in space; while much of lowland Europe dates to ~2,000 cal years BP, some areas have remained unchanged since the beginning of the Holocene; on average, the European vegetated landscape is ~4,000 years old. Though the (PFT) assemblage became continuously more similar to present, biome assemblages changed in northern and southern Europe but stayed relatively constant in central Europe. Landscape openness as approximated by arboreal PFT % increased until the mid-Holocene and then returned to early-Holocene conditions by modern times.

The temporally continuous dominance of forest biomes suggests climate remained favourable to forest cover across Europe throughout the Holocene. Nevertheless, arboreal PFT % decreased significantly between the mid-Holocene and the present, requiring a non-climatic explanation, which can be offered by disturbance from human activity. Thus, human activity may have been a main driver of European vegetation dynamics since the mid-Holocene, suggesting it should be included in future conceptions of “natural” European vegetation dynamics.

Keywords Arboreal pollen · Biome · Holocene · Plant functional type · Squared chord distance

Introduction

The size of the human population of Europe, and the magnitude of the human impact on the landscape, increased continuously from the beginning of the Holocene (roughly 10,000 years ago) to modern times (from AD 1750 to the present day), making human activity an integral part of European post-glacial environmental history (Ellenberg 1988; Thirgood 1981; Behre 1988). Thus, the question “what is natural?”, often asked in the contexts of vegetation biogeography and conservation science, becomes problematic (Carrión and Fernández 2009; Carrión 2010; Farris et al. 2010; Loidi et al. 2010; Willis and Birks 2006). When was the European landscape last “natural”? Can a human-influenced landscape ever be “natural”? Here, we approach these questions by using pollen data to reconstruct European vegetation cover throughout the Holocene. Though previous work has been done on Northern Hemisphere Holocene vegetation history, we use novel techniques with the most current data to draw a clearer picture

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of Holocene European vegetation than has been possible to date.

Previous work using pollen data has mainly focussed on the mid-Holocene (6,000 BP), while only a few studies have looked at change throughout the Holocene. This includes interpolated maps of broad-scale European vegetation characteristics, e.g. forest cover (Cheddadi and Bar-Hen 2009) or biomes (Huntley 1990a; Guiot et al. 1996). Other studies map European vegetation reconstructions on a point basis, based on, for example, biomes (Guiot et al. 1996; Prentice et al. 1996, 2000; Gachet et al. 2003; Collins et al. 2012), more generalized vegetation assemblages (Huntley 1990c), or plant traits (Gritti et al. 2004). Still other studies focus on mapping individual plant taxa across Europe throughout the Holocene (e.g. Huntley and Birks 1983; Giesecke et al. 2007; Pearman et al. 2008). Time series with low geographic resolution have also been used to investigate the synchronicity of change between Europe and North America (Gajewski et al. 2006). Numerous studies reconstruct Holocene vegetation at the regional scale (e.g. Odgaard and Rasmussen 2000; Andric and Willis 2003; Jalut et al. 2009; Collins et al. 2012), and those at the site scale are too numerous to discuss here. European biome distributions for the mid-Holocene (Galimire et al. 2005) or the pre-industrial present (Prentice et al. 2011) have also been modelled based on climate model output, and have been used for data-model comparisons against pollen-based vegetation reconstructions (Prentice et al. 1998).

Though European vegetation history is clearly well studied, a large-scale synthesis in time, space, and vegetation parameters comparable to that done for North America (Overpeck et al. 1991, 1992; Williams et al. 1998, 2001, 2004) is lacking. Most of the European studies cited above either synthesize data across Europe for only one or a few time slices, or across the Holocene for a limited spatial range, or they focus on one or a few taxa, or their results are more qualitative than quantitative. Except for the work of Huntley and Birks (1983), Huntley (1990c), and Gliemerth (1997), we are unaware of any attempt to map and quantify vegetation dynamics across the whole of Europe for the entirety of the Holocene. And since those studies were published in the 1990s, great advances have been made in data availability and quality, spatial coverage, dating control, analytical techniques and computing power.

Here, we take advantage of these advances to quantitatively assess the age of the modern vegetated landscape of Europe, to measure change across time using the squared chord distance (SCD) metric (Overpeck et al. 1985), and to map the relative openness of the landscape, as well as the distribution and abundance of biomes, at 500-year intervals throughout the Holocene (11.5 ka to modern times).

Materials and Methods

Study area and data

The study area covers Europe and a small part of Asia Minor. To minimize over-interpolation, we limit our assessment to land falling consistently within 150 km of a data site at every time slice between 6 ka and the modern day. Interpolation can be expected to become less reliable with distance from individual pollen sites, and our 150 km limit represents approximately double the upper limit (25–75 km radius) at which pollen sites have been found to directly reflect their surrounding land cover (Williams and Jackson 2003). Modern coastlines and ice extent are used throughout. The data come primarily from the European Pollen Database (EPD, <http://www.europeanpollendata.net/>), with additional data as described in Collins et al. (2012). Only cores with absolute dating control were included (radiocarbon, annual laminations etc.), except where an alternative chronology was suggested by the original author, or where a clear stratigraphic correlation could be made with an independently dated adjacent core (Davis et al. 2003). The choice of age-depth model follows that of the original author where this has been published or provided with the data. For other cores, the most appropriate model was fitted (linear, polynomial etc.) based on the chronological control points and any additional published information. Average dating uncertainties range from around ± 70 years in the late Holocene to around ± 250 years in the early Holocene (Fig. S1). We used 879 selected sites (Fig. 1) containing around 60,000 samples, spanning 11,500 years, and

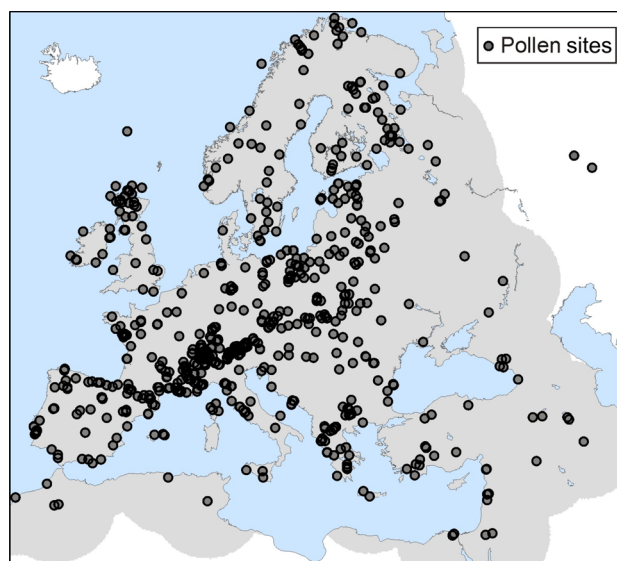


Fig. 1 The distribution of Holocene pollen sites used in the analysis

containing 2,390 terrestrial plant taxa. We performed our analyses for both the entire study area and on the northern (>55°N), middle (45–55°N), and southern (<45°N) zones separately. The data consist primarily of raw pollen counts, with minimal inclusion of digitized and percentage data.

Plant functional types

To reconstruct continental-scale vegetation patterns, we grouped pollen taxa into plant functional types (PFTs). This allowed us to handle efficiently a very large proportion of the pollen data (1,869 out of 2,390 pollen taxa present in the database) by combining ecologically similar taxa across diverse geographic regions. By combining taxa in this way, the PFT method also helps to reduce problems associated with using pollen data sourced from a wide range of individuals and projects. This is because the taxa diversity in a pollen sample is also a function of the taxonomic precision applied by the investigator, as well as the level of rarefaction that is also a function of the total pollen count (Giesecke et al. 2012), both of which will vary between sites/samples.

Multiple algorithms exist for converting pollen taxonomic data into PFTs (e.g. Prentice et al. 1996; Peyron et al. 1998; Tarasov et al. 1998; Williams et al. 1998). All follow the general procedure of (1) grouping pollen taxa into PFTs based on certain vegetation criteria (e.g. Smith et al. 1997) and (2) calculating the PFT scores as a scaled or non-scaled sum of the raw pollen counts. We chose the method of Peyron et al. (1998) (Table 1), as it is optimized for Europe and makes two key improvements over that of its European predecessor (Prentice et al. 1996).

First, the method of Peyron et al. (1998) is more sensitive to detecting changes in vegetation composition at the PFT level, as it uses more pollen taxa (77 taxa ranging in taxonomic resolution from species to family) and PFTs (22 PFTs split between 14 arboreal and 8 shrub/herbaceous types) relative to the method of Prentice et al. (1996) (41 pollen taxa, 17 PFTs). Second, Peyron et al. (1998) permit each pollen taxon to belong to only one PFT (up to 17 taxa per PFT), creating new PFTs to handle ambiguous pollen taxa; in contrast, Prentice et al. (1996) allow some taxa to belong to multiple PFTs, rendering their method less sensitive to detecting vegetation change.

The algorithm operates as follows: For each pollen sample, the abundance (percentage) of each pollen taxon is calculated relative to the sum of all of the pollen taxa included in the biomisation scheme. It should be noted that although the Peyron et al. (1998) scheme lists 77 taxa to be included (Table 1), some taxa are of high taxonomic rank (e.g. family) and therefore the actual number of pollen taxa

maybe much higher when lower ranking taxa (e.g. species) are included. In the case of our analysis, we actually included 1,869 taxa on this basis. The relative abundances are filtered to remove any values lower than 0.5 %, square-rooted to amplify the importance of the rare relative to the common taxa, and then summed into scores, using the taxon combinations relevant to each PFT. At the end of the process, every pollen sample has a score for each of the 22 PFTs.

Interpolation

Once the pollen data were transformed into PFT assemblages, we mathematically interpolated each PFT in turn onto a four-dimensional (space and time) grid. Gridding helps stabilise the effects of a changing site/sample network through time by maintaining a fixed set of positions for mapping, as well as allowing area-averages to be calculated based on the average change measured over all grid points within a fixed spatial area.

We divided the pollen samples by date into 23 500-year-long Holocene time slices, for comparison against the modern time slice, which encompassed all samples more recent than AD 1700 (0.25 ka). Within each of the 23 Holocene time slices, we interpolated the calculated scores for each of the 22 PFTs onto 1° grids using a 4D (latitude, longitude, elevation, time) thin plate spline (Fields Development Team 2006). Interpolating in time as well as space gives greater weight to data points closer to the target date and less weight to those at the edges of the time slice, minimizing temporal blurring (Davis et al. 2003). However, as the modern time slice did not have an equal balance of samples both forwards and backwards in time, we chose instead to interpolate this particular time slice using a 3D thin plate spline. For all time slices, latitude and longitude were scaled to have equal weight, and we used the scaling ratio between latitude and altitude recommended by Ozenda (1989) to capture realistically the effects of both the altitudinal and latitudinal lapse rates on vegetation. Changes in climate and hence vegetation are generally much greater over 1 km along a vertical axis than 1 km along a horizontal axis, therefore the interpolation needs to be scaled so that vertical and horizontal distances are not treated with equal weight.

To correct for over-interpolation and ground-truth the efficacy of the interpolation method, modern spatial distributions of PFTs were visually checked for plausibility against distribution maps of representative taxa in the Atlas Flora Europaea (Jalas and Suominen 1972–1999) and minimum presence/absence thresholds were applied accordingly.

Table 1 Assignments used to reconstruct plant functional types (PFTs) and biomes (reproduced from Peyron et al. 1998)

Pollen taxa to PFT assignment		
PFT	Code	Taxa included in PFT
Boreal summergreen	bs	<i>Larix</i>
Boreal summergreen arctic-alpine	bs/aa	<i>Betula</i>
Boreal evergreen conifer	bec	<i>Picea</i> , <i>Pinus</i> subgen. <i>Haploxylon</i>
Boreal evergreen/cool-temperate conifer	bec/ctc	<i>Abies</i>
Intermediate temperate conifer	ctc1	<i>Cedrus</i> , <i>Taxus</i>
Eurythermic conifer	ec	<i>Juniperus</i> , <i>Pinus</i> subgen. <i>Diploxylon</i>
Temperate/boreal summergreen/arctic-alpine	ts/bs/aa	<i>Alnus</i> , <i>Salix</i>
Temperate/boreal summergreen	ts/bs	<i>Populus</i>
Temperate summergreen	ts	<i>Acer</i> , <i>Fraxinus excelsior</i> , <i>Quercus</i> (deciduous)
Cool-temperate summergreen	ts1	<i>Carpinus</i> , <i>Ulmus</i> , <i>Corylus</i> , <i>Fagus</i> , <i>Frangula</i> , <i>Tilia</i> , <i>Ulmus</i>
Warm-temperate summergreen	ts2	<i>Castanea</i> , <i>Platanus</i> , <i>Ostrya</i> , <i>Fraxinus ornus</i> , <i>Vitis</i> , <i>Juglans</i>
Warm-temperate broad-leaved evergreen	wte	<i>Quercus</i> (evergreen)
Cool-temperate broad-leaved evergreen	wte1	<i>Buxus</i> , <i>Hedera</i> , <i>Ilex</i>
Warm-temperate sclerophyll trees/shrub	wte2	<i>Acacia</i> , <i>Cistus</i> , <i>Rhus</i> , <i>Myrtus</i> , <i>Olea</i> , <i>Phillyrea</i> , <i>Pistacia</i> , <i>Ceratonia</i>
Cold grass shrub	cgs	<i>Hippophaë</i> , <i>Polygonum</i>
Warm grass shrub	wgs	Fabaceae, <i>Zizyphus</i> , Scrophulariaceae, <i>Ephedra fragilis</i> , Brassicaceae, Crassulaceae
Steppe forb/shrub	sf	Apiaceae, Asteraceae, <i>Armeria</i> , Boraginaceae, Campanulaceae, Caryophyllaceae, Centaurea, Dipsacaceae, <i>Helianthemum</i> , <i>Plantago</i> , Plumbaginaceae, <i>Ranunculus</i> , Rosaceae, Rubiaceae, <i>Rumex</i> , <i>Sanguisorba</i> , <i>Thalictrum</i>
Steppe/desert forb/shrub	sf/df	<i>Artemisia</i> , Chenopodiaceae
Desert forb/shrub	df	<i>Ephedra</i> , Zygophyllaceae
Arctic-alpine dwarf shrub	aa	<i>Alnus fruticosa</i> , <i>Betula nana</i> , <i>Saxifraga</i> , <i>Empetrum</i> , <i>Dryas</i> , <i>Rhododendron</i> , <i>Vaccinium</i>
Grass	g	Poaceae
Heath	h	Ericaceae, <i>Calluna</i>
PFT to biome assignment		
Biome	Code	PFTs included in Biome
Cold Deciduous Forest	CLDE	bs, bs-aa, h, ts-bs, ts-bs-aa
Cold Mixed Forest	CLMX	bec-ctc, bs, bs-aa, ctc1, ec, h, ts-bs, ts-bs-aa, ts1
Cool Conifer Forest	COCO	bec, bec-ctc, bs, bs-aa, ec, h, ts-bs, ts-bs-aa, ts1
Cool Mixed Forest	COMX	bec, bec-ctc, bs, bs-aa, ec, h, ts, ts-bs, ts-bs-aa, ts1, ts2
Cool Steppe	COST	cgs, g, sf, sf-df
Desert	DESE	df, sf-df
Taiga	TAIG	bec, bec-ctc, bs, bs-aa, ec, h, ts-bs, ts-bs-aa
Temperate Deciduous Forest	TEDE	ctc, bs, bs-aa, ctc1, ec, h, ts-bs, ts-bs-aa, ts1, ts2, wte1
Tundra	TUND	aa, bs-aa, g, h, ts-bs-aa
Warm Mixed Forest	WAMX	ec, h, ts, ts-bs, ts-bs-aa, ts1, ts2, wte, wte1
Warm Steppe	WAST	g, sf, sf-df, wgs
Xerophytic Woods/Scrub	XERO	ec, g, wte, wte2

Analyses

We used the interpolated, gridded PFT scores described above to perform three different types of analyses of

Holocene European vegetation age and change. All analyses were performed for the entirety of the study area, as well as for the north, middle, and southern zones separately, and all calculations were done individually for each pixel of the grid.

Squared chord distance (SCD)

To determine the age of the modern vegetation and to assess change during the Holocene, we compared the PFT assemblage of each time slice to that of modern conditions using the SCD dissimilarity coefficient (Overpeck et al. 1985; Huntley 1990b). The SCD provides a quantitative assessment of the similarity or difference between vegetated landscapes. Simpson (2012) has proposed alternative dissimilarity metrics, but SCD remains the most commonly applied method for evaluating pollen data. The SCD is calculated using the following formula:

$$d_{ij} = \sum_k \left(p_{ik}^{1/2} - p_{jk}^{1/2} \right)^2$$

where d_{ij} is the SCD between a pixel in a given time slice i and the same pixel at the modern day j , and p_{ik} is the proportion ($0.0 \leq p_{i(j)k} \leq 1.0$) of PFT k in that pixel for time slice i (j) (Overpeck et al. 1985). It should be noted that the SCD calculation involves square rooting the PFT scores, which are themselves composed of square rooted values. This double square root transformation will reduce the differences within the dataset in absolute terms, but since this is applied equally to the entire dataset, the differences will nevertheless remain in relative terms.

The calculated SCD can theoretically range from 0 to 2, where 0 indicates a perfect match and 2 indicates maximum possible difference; observed values usually range between 0 and 1 (Overpeck et al. 1991; Huntley 1990b). Though dissimilarity is a continuous concept, a threshold value distinguishing analogous from non-analogous pixel pairs can be empirically derived from the data. We identified a threshold of 0.2 by comparing the SCD scores of pixel pairs having the same biome (cf. subsection B below) against those of pixel pairs having different biomes (Fig. 2). 67 % of pixel pairs with $SCD < 0.2$ (> 0.2) had the same (different) biome while 33 % had different (same) biomes. Thus, crossing this threshold is functionally equivalent to passing from one biome to another (e.g. Williams et al. 2001) 67 % of the time, or with a probability of roughly one standard deviation.

There is no single established threshold SCD value that determines when one vegetation type changes to another. Overpeck et al. (1985) and Huntley (1990b) derive SCD analogue thresholds of 0.15 and 0.3 for modern pollen taxa for their pollen datasets from North America and Europe, respectively. Our approach differs from these studies in two ways.

First, their calculations were done using point site data, while ours were performed for each pixel of our interpolated surfaces. Second, they performed their calculations using a smaller selection of pollen taxa (~30 woody/10 herbaceous families/genera in Overpeck et al. 1985; ~38

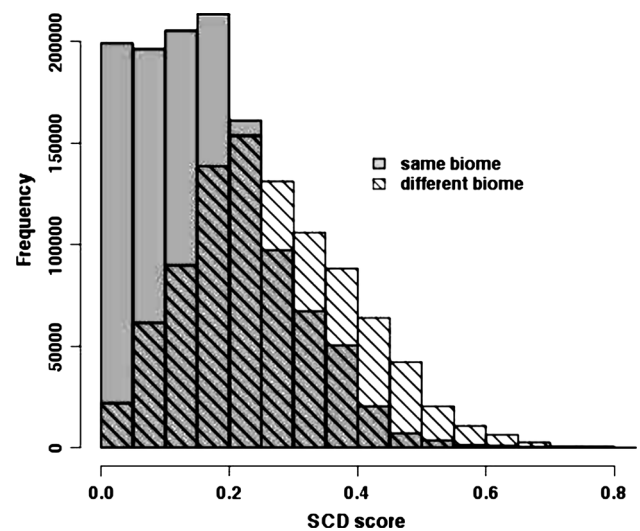


Fig. 2 Frequency distribution of squared chord distance (SCD) scores used to derive difference threshold of 0.2 (as used in Figs. 3, 4, 5). SCD scores of all pixel pairs having the same vegetation type (biome) are compared to all pixel pairs having a different vegetation type. Probability of two pixels having an SCD score greater (less) than 0.2 and having different (same) biomes is $\sim 1 \sigma$ (~ 67 %). Frequency refers to number of pixel pairs compared

woody/6 herbaceous families/genera/species in Huntley 1990b), while we instead transformed a larger selection of pollen taxa (~39 woody/39 herbaceous families/genera/species) into 22 PFTs. Despite these methodological differences, our threshold value of 0.2 is nevertheless roughly in agreement with these authors' findings.

Biomes

To map vegetation units at each time slice, we converted pollen PFT scores into biomes for each grid-point. The biomisation method (Prentice et al. 1996; Peyron et al. 1998) was designed to reconstruct vegetation in equilibrium with climate and is relatively unbiased by human activity. We calculated biomes by assigning each of 12 pollen biomes a score, calculated as the sum of the scores of the PFTs comprising that biome (where each biome is defined as a certain unique combination of PFTs). The biome with the highest score “wins”, or is called the “dominant” biome for a given PFT score assemblage. When two biomes had the same score, the biome ranking higher in the dominance hierarchy was chosen as the “winner” (c.f. Table 4 in Peyron et al. 1998; Prentice et al. 1996).

APFT%

To estimate relative landscape openness at each time slice, we computed the proportion of arboreal to non-arboreal

pollen based on the PFT scores. This was done by dividing the sum of the 14 arboreal PFT scores into the sum of all 22 PFT scores inclusive of the 8 non-arboreal PFTs (Table 1). The result was then multiplied by 100 and is expressed hereinafter as the APFT%, or the percentage contribution of arboreal PFTs to the total PFT sum. A higher APFT% corresponds to a relatively more closed landscape, e.g. a higher percentage of arboreal/woody over herbaceous vegetation. APFT% in this study has not been evaluated against actual land cover data (as required by the REVEALS method; e.g. Gaillard et al. 2010); therefore, we stress that APFT% is a *relative* rather than absolute metric of landscape openness.

Results

SCD temporal dynamics

The European vegetated landscape begins in the Holocene substantially different from modern conditions and converges towards them at a fairly steady rate throughout the study period (i.e. SCD scores start out high and decrease to zero). The northern, middle and southern zones behave fairly similarly to one another, but subtle differences occur. Variations in the convergence rate at the European and zonal scales suggest dividing the Holocene into five phases (Fig. 3).

Starting from the past and working towards the present, the five phases can be characterized as follows: (5)

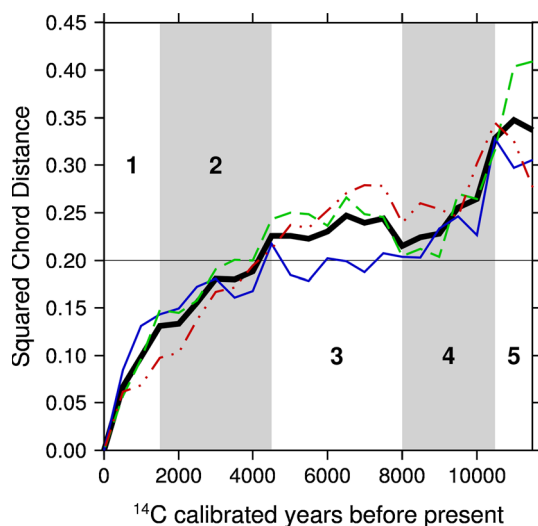


Fig. 3 Area-weighted average difference (SCD) between the vegetation (PFT assemblage) for Europe at 500-year intervals throughout the Holocene, relative to modern times (*black curve*). *Red, green, and blue curves* show the results of the same analysis done respectively for the north, middle and southern zones (Fig. 4). The *horizontal line* at 0.2 indicates the difference threshold (see Fig. 2)

diversity of rates/directions in the trends; (4) generally consistent, and relatively rapid, decrease in SCD scores; (3) reversal (i.e. increase) in SCD scores, followed by period of plateau or gradual decrease; (2) slightly higher rate of decrease; (1) rapid decrease to modern conditions (i.e. SCD score = 0). While the southern zone does experience a plateau/slow rate of decrease during the third phase, this is not preceded by the reversal that the northern and middle zones experienced. Also, the northern zone appears to maintain a steady rate of decrease during the second and first phases, rather than accelerating during the first phase as the middle and southern zones do.

Age of the modern landscape

The age of the modern vegetated landscape of Europe, as determined by the first date in the past at which the 0.2 SCD threshold is crossed, varies strongly by location. On average, the modern European vegetated landscape came into being in phase 2, around 4 ka; this is the date at which the area-weighted average curve for the whole of Europe crosses the SCD analogue threshold of 0.2 (Fig. 3). When the northern, middle, and southern zones are analysed separately, different dates emerge. The vegetation of the southern zone is on average older; its area-weighted average curve first crosses the SCD threshold between 5.5 and 6 ka (phase 3) and then oscillates around the threshold until it definitively drops below 0.2 between 4 and 4.5 ka (phase 2). The vegetation of the middle zone is on average younger, crossing the SCD threshold between 3.5 and 3 ka (phase 2). The vegetation of the northern zone matches the continental average, crossing the SCD threshold at 4 ka (phase 2).

The geographic distribution of “older” versus “younger” areas is highly variable (Figs. 4, 5). Parts of southwestern Spain, the Alps, Greece, eastern Europe, and northern Fennoscandia already had vegetation similar to modern conditions in the early Holocene, while the vegetation cover of much of central/western Europe dates to 2,000 years ago or less. The majority of the European vegetated landscape appears to be 4,000 years old or younger. By 1 ka, nearly all of Europe had crossed the SCD threshold (Fig. 5), meaning the modern European vegetated landscape is at least 1,000 years old, in terms of PFT distribution and abundance.

Biomes and APFT%

The SCD analyses presented thus far allow an estimation of the age of the modern European vegetation and an overview of its Holocene temporal and spatial dynamics, in terms of the difference between the modern vegetated landscape and the landscape of the Holocene past.

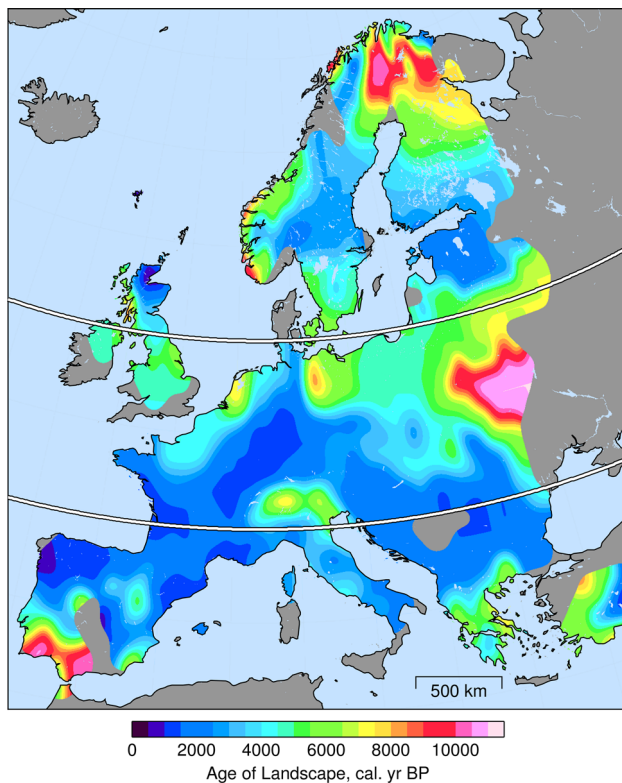


Fig. 4 Approximate age of the European vegetated landscape. “Age” calculated as the date at which SCD relative to modern times (1750 AD to present) first exceeds the difference threshold of 0.2 (Fig. 2). SCD calculations were based on interpolated plant functional type (PFT) assemblages, derived from fossil pollen data. Land area in grey falls outside the 150 km radius of a sample site. Divisions at 45°N and 55°N delineate northern, middle, and southern zones as described in the text. All maps in this paper use a Lambert azimuthal equal-area projection centered on 7°E, 52°N with the same scale

However, the SCD difference metric says nothing about the ecological nature of the changes. Here, we go beyond the question of “how much change?” to explore the types of vegetation change occurring between the beginning of the Holocene and modern times. Conversion of pollen PFT scores into pollen biomes (potential natural vegetation) gives an overview of ecological vegetation units formed primarily in response to climatic conditions (Prentice et al. 1996). Comparing the ratio of arboreal to non-arboreal pollen PFTs allows an approximation of relative landscape openness, which, for the latter half of the Holocene at least, can be seen as a rough proxy for human impact on the landscape.

Biomes

At the European scale, non-forest biomes decrease in relative abundance during the early Holocene (phases 5 and 4) and different cold forest biomes alternate in dominance

throughout the Holocene. Relative abundance of *temperate deciduous forest* increases during phase 5 to become the dominant biome by phase 4, a status it retains up to the present (Fig. 6a).

The northern and southern zones (Fig. 6b, d) drive the European-scale biome dynamics of the cold forest and non-forest biomes, respectively, while the middle zone (Fig. 6c) drives the dominance of the *temperate deciduous forest* biome. In both the northern and southern zones, *temperate deciduous forest* abundance peaks in phase 3, then declines in phases 2 and 1.

In the northern zone, *taiga* is relatively more abundant at the early and late Holocene, *cold mixed forest* is abundant only in the early Holocene, *cool mixed forest* is abundant only in the late Holocene, and *tundra* is present during phase 5 but disappears in phase 4.

In the middle zone, the *temperate deciduous* and *cool mixed forests* dominate in roughly consistent proportions throughout the Holocene, after the *cold mixed forest* and *taiga* disappear in phases 5–4 (Fig. 6c).

In the southern zone, the non-forest *steppe* biomes decrease in relative abundance during phases 5 and 4, reach a low stand in phase 3, and then increase again slightly in phases 2 and 1. The *xerophytic* non-forest biome maintains a relatively constant abundance throughout the Holocene. *Warm mixed forest* first appears in phase 4, increases in abundance during phase 3 as the *temperate deciduous forest* declines in abundance, and maintains a constant level of abundance during phases 2 and 1.

Spatially, these trends manifest as a large northward advance and then southward retreat of *temperate deciduous forest* relative to the other cold forest biomes in northern Europe, general spatial stability of forest biome distribution in the middle of Europe, and a subtle advance and retreat of the southern limit of *temperate deciduous forest* relative to the non-forest biomes in southern Europe (Fig. 7).

APFT%

European APFT% increased from less than 60 to 80 % between phases 5 and 3, reached a plateau in phase 3, dropped gradually to 70 % in phase 2, then dropped steeply back to 60 % in phase 1 (Fig. 8). The APFT% of the northern and middle zones follow this same general pattern, with slight differences in timing and magnitude, while the APFT% of the southern zone rises steadily between phases 5 and 3 and then drops steadily between phases 3 and 1.

Throughout the Holocene, APFT% is consistently lowest in the southern zone. The APFT% of the northern zone exceeds that of the middle zone throughout the Holocene, except in phases 5 and 4.

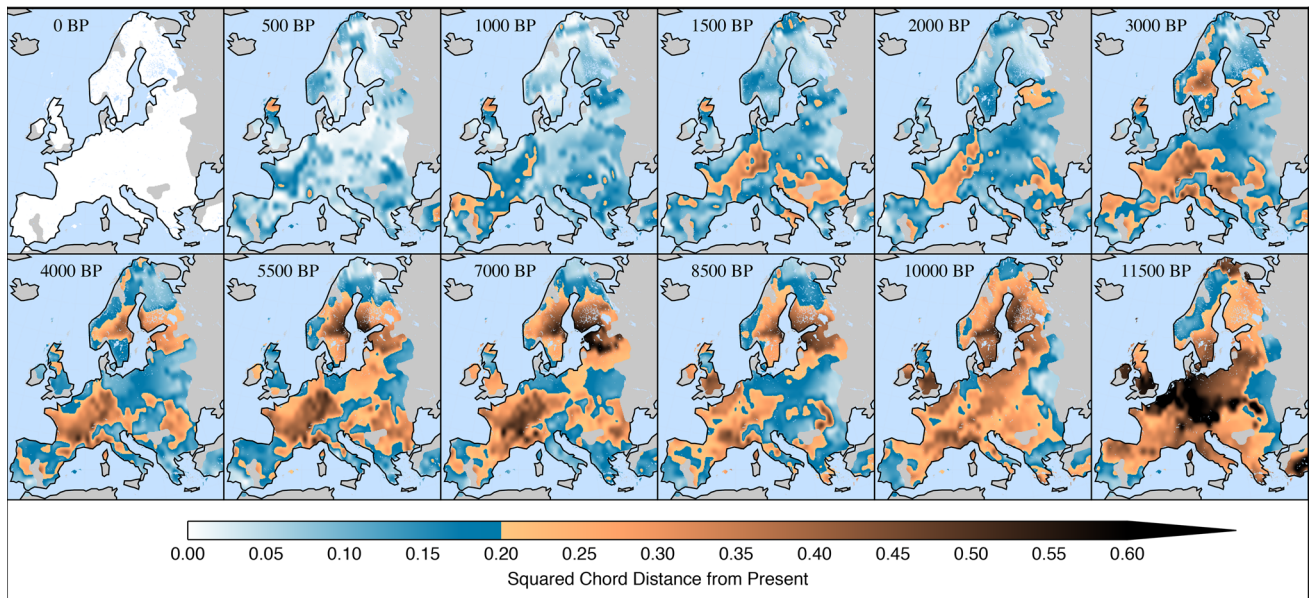


Fig. 5 Difference (SCD score) between modern and Holocene PFT assemblages. Larger score means greater difference. Threshold dividing “same as modern” from “different from modern” vegetation

is 0.2 (Fig. 2). Calculations based on 4-D interpolated PFT scores, derived from fossil pollen data

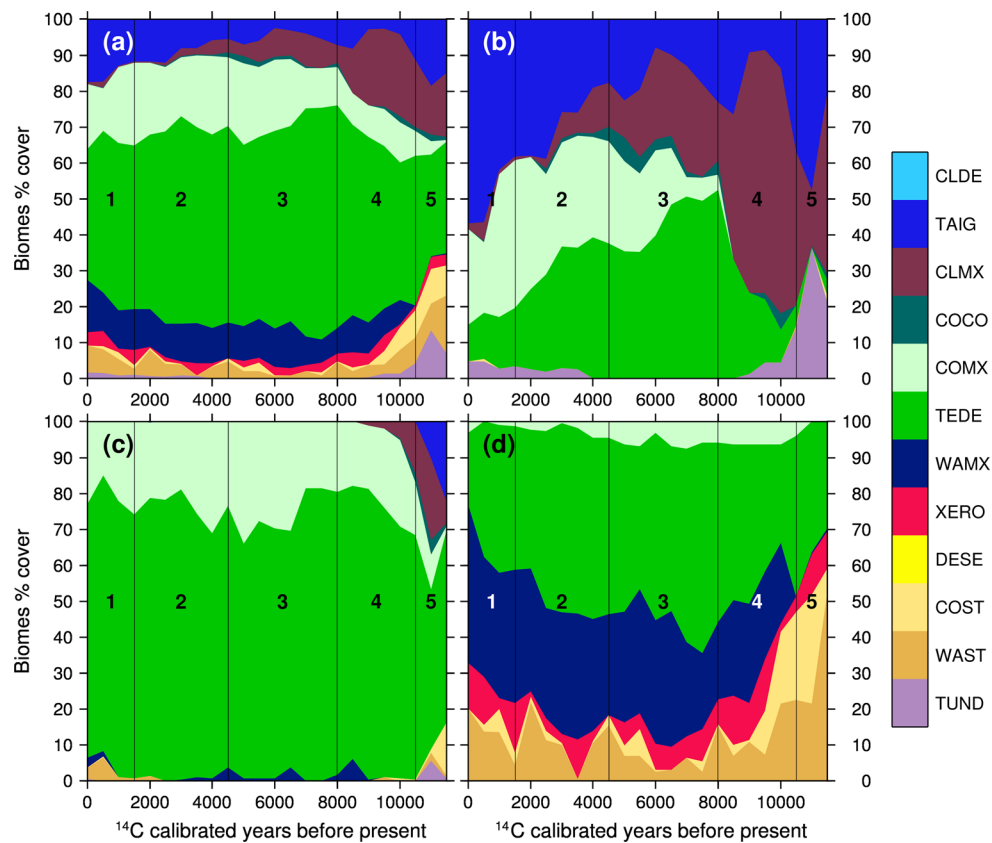


Fig. 6 Area-weighted average percent cover of biomes at 500-year intervals throughout the Holocene for all of Europe (a), and for the northern (b), middle (c) and southern (d) zones (Fig. 3). Biomes as in Peyron et al. 1998 (CLDE is cold deciduous forest, TAIG is taiga, CLMX is cold mixed forest, COCO is cool conifer forest, TEDE is

temperate deciduous forest, COMX is cool mixed forest, WAMX is warm mixed forest, XERO is xerophytic woods/scrub, DESE is desert, COST is cool steppe, WAST is warm steppe and TUND is tundra)

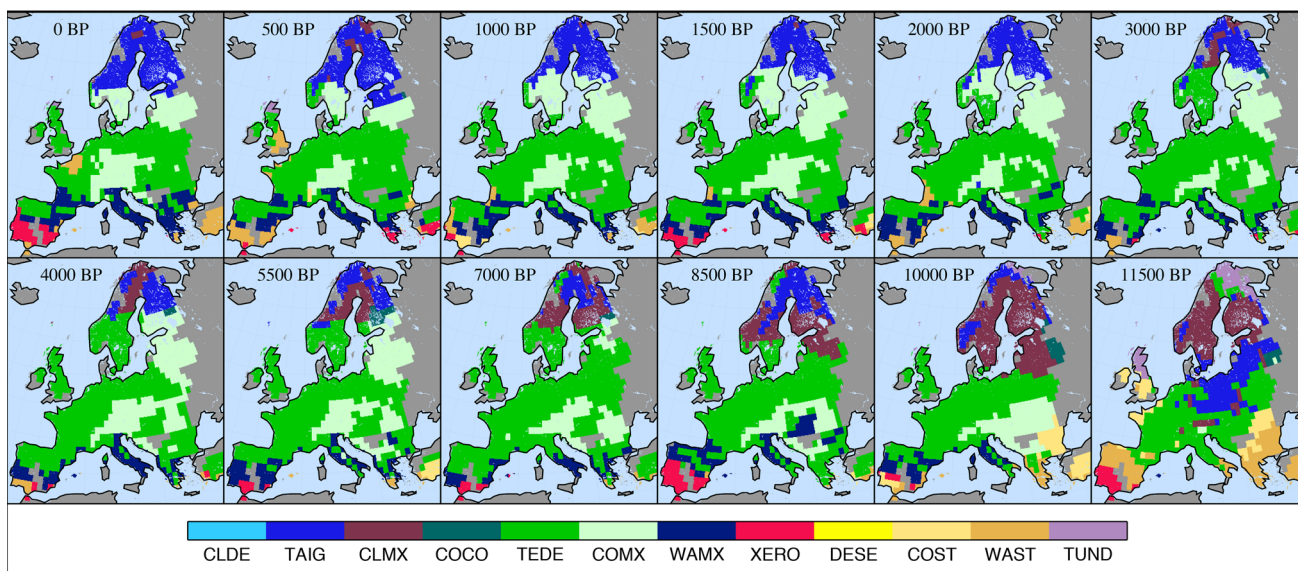


Fig. 7 Distribution of biomes throughout the Holocene. Calculations based on 4D interpolated PFT scores, derived from fossil pollen data, following the methodology of Peyron et al. (1998)

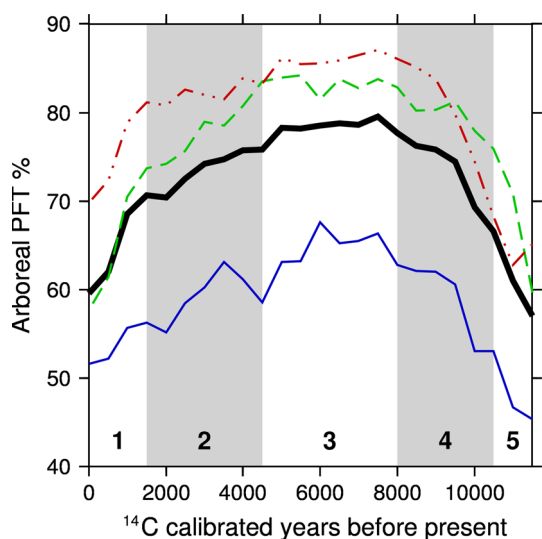


Fig. 8 Percentage forest cover (APFT%). Red, green, and blue curves represent the north, middle and southern zones respectively, while the black curve is for the whole of Europe (see Fig. 3). Each curve represents the area-weighted average percentage of all PFT scores belonging to arboreal PFTs at 500-year intervals throughout the Holocene

The spatial distribution of low-APFT% areas is similar, though not identical, at the beginning of the Holocene and modern times. In both time periods, western and south-eastern Europe experience the lowest APFT%, while APFT% remain higher in northern Europe. However, the low-APFT% areas extend farther northeast into the European Plain at modern times than they did at the beginning of the Holocene (Fig. 9).

Discussion

SCD temporal dynamics

Though magnitude and timing differ slightly between the continental and the zonal area-weighted averages (Fig. 3), the general story appears to be the same for all analyses of Holocene European vegetation dynamics. Between 11.5 and 10 ka (phase 5), each zone adjusted in its own way to deglaciation. Between 10 and roughly 8 ka (phase 4), the SCD scores trend downward for all zones, in the direction of modern conditions, likely as the climate settled into the warm Holocene interglacial. But then, at roughly 8 ka, something happened to disrupt this downward trend in SCD scores for all three zones, causing the trend to either plateau (in the case of the southern zone) or reverse and then plateau (in the case of the middle and northern zones) until approximately 4 ka (phase 3), when the decreasing trend towards modern conditions resumed. This synchronicity suggests a possible climatic cause.

The same could be said for the inflection point at ~4 ka, ending the plateau period (phase 3, 8 to 4 ka) and sending the SCD score trends back in the direction of modern conditions in phase 2. Though the phases that emerge from our analysis roughly correspond with the Blytt-Sernander Holocene climate classification system, by 4 ka Neolithic and/or Bronze Age societies had established themselves throughout almost all areas of Europe in ever-increasing populations (Harding 2000), so it is possible that human activity could have contributed significantly, either directly through vegetation clearance, or indirectly through

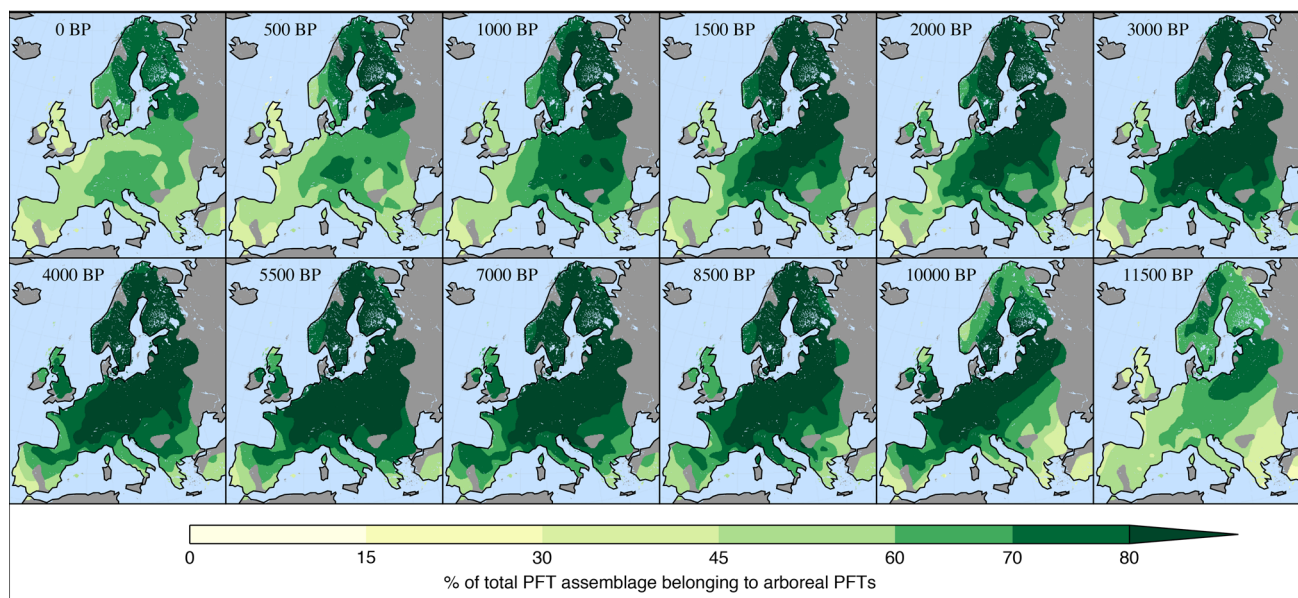


Fig. 9 Estimated forest cover throughout the Holocene (APFT%), calculated as percent of sum of all PFT scores belonging to arboreal PFTs (as in Fig. 8). Calculations based on 4D interpolated PFT scores, derived from fossil pollen data

the impacts of vegetation clearance on climate (e.g. Reale and Shukla 2001). The final rapid drop in SCD scores between 1.5 ka and modern times (phase 1) is likely due to human activity, given that human populations (and associated land use) increased rapidly over this period (Kaplan et al. 2009, 2011).

As Gaillard et al. (2010) point out, changes in the pollen record often underestimate changes in the actual vegetation cover, and so it is possible that the magnitude of the dynamics observed here might be an underestimate of the actual magnitude of vegetation changes over the Holocene.

Age of the modern landscape

On average, the modern European landscape came into being around ~4 ka, with slight differences in timing when the northern, middle and southern zones are analysed separately. This timing corresponds well with the conclusions drawn by various authors for diverse regions across Europe, who suggest that human activity (land clearing for agriculture, metallurgy, etc.) by Neolithic or Bronze Age societies created the “cultural landscapes” that were still widespread throughout Europe before the Industrial Revolution (e.g. Odgaard and Rasmussen 2000; Andric and Willis 2003; Bradshaw 2004). For southern/Mediterranean Europe, however, this timing also matches well with a late-Holocene aridification trend beginning around 5.5 ka (Harrison and Digerfeldt 1993; Jalut et al. 2009). Grove and Rackham (2003) also argue that the vegetation of southern/Mediterranean Europe was established early due to climatic causes and that human influence played a

secondary role. The modelling simulations performed by Reale and Shukla (2001) suggest that anthropogenic removal of vegetation in the southern/Mediterranean part of Europe during the Roman Classical Period (~2 ka) could have had a significant impact on the hydrological cycle (and thus climate) of the region, though Dermody et al. (2012) find the opposite. De Beaulieu et al. (2005) conclude that the debate is still open on the relative agency of humans and climate in the development of the vegetation of Mediterranean Europe.

In any case, the spatial distribution of landscape age is far from homogeneous (Fig. 5). Indeed, some of the youngest as well as oldest landscapes can be found in the southern, middle and northern zones of this analysis. There do not appear to be clear trends according to climatic gradients or history of spread of human societies. As both the calculation of SCD scores from PFT assemblages and the calculation of PFT scores from pollen assemblages are non-linear processes, it is not possible to deconstruct the causation underlying the patterns of landscape age in space from the SCD analysis. However, given the location of the three oldest areas (northern Scandinavia, southwestern Spain and eastern Europe), one could speculate that the combined impact of human activity and changing climate would have been small in these places, as well as being distant from ecotones and other thresholds for PFT change. The consistently cold climate of the extreme northern latitudes of northern Scandinavia precludes almost any significant human modification of the vegetated landscape (other than perhaps reindeer herding). The stability of vegetation in south-western Spain suggests that the region

remained warm and dry throughout the Holocene. And in eastern Europe poor land conditions probably acted to limit farming, such as the swampy ground of the Pripet marshes and the Białowieża Forest region that remains one of the last remaining stands of old growth forest in Europe.

It is important to note that landscape “age” merely refers to the most recent date at which the SCD score relative to modern times is greater than the SCD analogue threshold of 0.2. As the range of SCD scores in time is a continuum, so usage of a threshold is somewhat arbitrary. This threshold was statistically derived from the distribution of the calculated SCD values for each pixel pair having the same biome compared to the calculated SCD values for each pixel pair having different biomes (Fig. 2), with a success rate (true positive vs. true negative, e.g. Gavin et al. 2003) of one standard deviation (or ~66 %). This means that, ~33 % of the time, a pixel pair having different biomes could have an SCD score greater than 0.2, or a pixel pair having the same biomes could have an SCD score less than 0.2, yielding either a false positive or false negative, respectively. Furthermore, much vegetation change can occur within a pixel without the biome changing (Williams et al. 2004; Huntley 1990c), so comparing SCD scores to the case of matching or non-matching biomes may not be the ideal solution. Despite these drawbacks, statistical derivation and usage of a threshold in difference analysis is a common and accepted practice in vegetation reconstructions (Overpeck et al. 1985; Huntley 1990b; Williams et al. 2001; Odgaard and Rasmussen 2000) although there remains no generally applicable method for determining thresholds (Simpson 2012).

Biomes and APFT %

Biomes

Between 11.5 and 10 ka, both Europe as a whole, and the northern, middle and southern zones individually, exhibit significant dynamism in terms of changing biomes, as the continent made the transition from glacial to Holocene climatic conditions (Figs. 6, 7). However, the biome distributions established by 10 ka remained generally stable right through to the modern day, for the continent as a whole (Figs. 6a, 7) and for the middle zone (Figs. 6c, 7). As biomes are intended to represent potential natural vegetation in equilibrium with climate conditions, this suggests that Holocene climatic influence on vegetation remained more or less constant between 10 ka and modern times, at least for the middle zone. This is puzzling, considering the early Holocene dynamics of the middle zone SCD curve in Fig. 4. However, due to the way biomes are calculated based on ‘highest score wins’, it is possible to have a large change in PFT scores that does not bring about

a biome change, for instance where a single biome has a much larger score than other alternative biomes. Conversely, only a small change in PFT scores between multiple alternative biomes with similar scores can be sufficient to result in a biome change.

Thus, we agree with Williams et al. (2004) and Huntley (1990c) that a lack of changing biomes does not necessarily mean stable vegetation. Nevertheless, lack of significant changes in distribution and abundance of biomes in the middle zone does suggest stability of Holocene climate for that zone for most of the Holocene, in agreement with the findings of Davis et al. (2003). Indeed, Huntley (1990a) also concluded that the biomes of north-western Europe (within our middle zone) reached modern distribution around 8 ka, but the internal floristic composition of those biomes continued to change throughout the Holocene. It is these internal changes, invisible on the biome level, that drive the SCD dynamics we see in the green curve of Fig. 3.

The story is different for the northern and southern zones (Figs. 6b, d, respectively), which both show important changes in relative abundance of biomes throughout the Holocene and drive the biome dynamics of the European continent as a whole.

In the north, these changes consist of a reorganization of biomes, with *cold mixed forest* dominating early in the Holocene, *temperate deciduous forest* dominating in the middle Holocene, and *cool mixed forest* and *taiga* replacing them both in the late Holocene (Figs. 6b, 7). Such dynamics reflect a trend in climate to a mid-Holocene optimum, followed by late Holocene cooling, as described by Davis et al. (2003). The timing of the northwestward migration of Norway spruce (*Picea abies*) from the Urals region into Fennoscandia as documented by Giesecke and Bennett (2004) and Seppä et al. (2009) also matches the timing of the rise in dominance of *taiga* and *cool mixed forest*, both of which contain the PFT to which this taxon belongs, at the expense of the *cold mixed* and *temperate deciduous forests*, neither of which contain this taxon.

In the south, these changes consist of an expansion of *temperate deciduous forest* in the middle Holocene (Figs. 6d, 7), then its replacement by *warm mixed forest*, *xerophytic wood/scrub*, and *warm* and *cool steppe* in the late Holocene, in agreement with the findings of Collins et al. (2012). It is difficult to say whether these dynamics were more driven by human activity (see subheading “Age of the modern landscape” above, this section) or more by the mid-to-late Holocene aridification (Magny et al. 2002) or warming (Davis et al. 2003) trends. Mostly likely, all processes interacted.

It is noteworthy that the xerophytic wood/scrub and steppe biomes maintained fairly consistent abundance throughout the Holocene as well. This contradicts the

conventional wisdom that there was a widespread expansion of xeric vegetation in the Mediterranean in the mid-late Holocene, but is nevertheless in agreement with the findings of Collins et al. (2012). In addition, the mid-Holocene expansion of *temperate deciduous forest* into the northern and southern zones, followed by its late-Holocene retreat back to the middle zone, is in line with climatic reconstructions showing a mid-Holocene climate “optimum” in the north (Davis et al. 2003) and relatively more humid (Magny et al. 2002) and cooler (Davis et al. 2003) conditions in the south.

APFT%

While biomes are designed to reconstruct potential natural vegetation and thus to filter out human activity (Prentice et al. 1996), reconstructing APFT% has no such bias. In fact, since the main activity of humans on the landscape is to preferentially clear forests in favour of non-forest vegetation, assessing APFT% can be considered as a proxy for assessing overall human impact on the landscape in regions where forest is the natural climax vegetation, as in most of temperate Europe.

On average, the development of European APFT% occurred in four phases (Fig. 8): an increase in percentage cover from 11.5 to 8 ka (marked phases 5 and 4 on Fig. 8 to match with previous figures), a relatively stable period between 8 and 5 ka, a gradual decrease from 5 to 1.5 ka, and then an abrupt drop between 1.5 ka and the modern day. When the north, middle and southern zones are analysed separately, the responses differ in magnitude but not in timing. Considering that different climatic processes occurred during the Holocene in the north (mid-Holocene warmer than present), middle (stable climate through to present) and south (mid-Holocene cooler/wetter than present) (Davis et al. 2003; Magny et al. 2002), it is notable that the dynamics of APFT% are synchronized between all three zones.

The decline in APFT% after the mid-Holocene can be attributable to a cooler and/or drier climate that would be less suitable for trees, and/or the impact of anthropogenic deforestation. Reconstructed biomes (Figs. 6, 7) indicate that the potential natural vegetation remained largely forest from the mid to late Holocene over central and northern Europe. This suggests that in these regions the decrease in forest cover shown by the decrease in APFT % (Fig. 8) was more likely the result of anthropogenic clearance and not climate. This contrasts with the southern region of Europe, where reconstructed biomes indicate an increase in non-forest biomes from the mid to late Holocene (Figs. 6, 7) at the same time as forest cover (APFT%) also declined (Fig. 8). This suggests that climate may have played a greater role in the decline in forest cover in this region, an

interpretation that is supported by independent evidence from lake level and isotope proxies for a decline in precipitation in southern Europe in the late Holocene (Collins et al. 2012). Overall, the decline in APFT% after the mid-Holocene across all areas of Europe (Fig. 8) is consistent with Bradshaw (2004) who suggested anthropogenic deforestation was the dominant disturbance factor in Europe after 5 ka with the establishment of Neolithic cultures. These cultures are considered to have spread from south-east Europe in the early Holocene (Turney and Brown 2007), and the earlier start to the mid-late Holocene decline in APFT% over Southern Europe compared to further north may reflect this earlier start in the region.

Though APFT% is similarly low at the beginning of the Holocene and modern times (Fig. 8), SCD scores at the beginning of the Holocene differ significantly from modern times (Fig. 3), and so does biome cover (Figs. 6, 7). Thus, the open landscapes of the early Holocene must have been very different in PFT composition from the open landscapes of modern times. The inflection point in the SCD trends (Fig. 3) around 8 ka, possibly associated with the final disappearance of the North American ice sheet, may be related to the inflection point at 8 ka in the APFT% curves (Fig. 8), when the trend of increasing APFT % plateaus. This could suggest that a change in PFT assemblages, possibly associated with climatic changes, might have been associated with the levelling off of the APFT% curves. The second inflection point in the SCD curves (Fig. 3, at ~4.5 ka, when the plateau period ends and the SCD scores begin to decrease again), also appears to correspond to the point in the APFT% curves where the plateau period ends and the gradual decline begins. Though no known climatic event is thought to have occurred at this point in time, it does roughly correspond with the establishment of agricultural and/or metalworking societies in central and northern Europe (they were already established much earlier in southern Europe), suggesting that perhaps anthropogenic land clearance might have been a primary forcing here. In any case, it seems reasonably clear that the final abrupt drop in APFT% between 1.5 ka and modern times, which matches the final abrupt drop in SCD scores for the same time period, was most likely a response to accelerating human land use in that period.

Interestingly, we do not see the increase in APFT% between 9 and 5 ka observed by Cheddadi and Bar-Hen (2009); in our study, APFT % is similarly high at both time periods. However, their forest cover reconstructions were based on the ratio of arboreal to non-arboreal taxa (rather than PFTs, as we have done here), their input dataset is different from ours, and their interpolation methods are unclear. We are aware of no other studies offering quantitative interpolated reconstructions of Holocene European forest cover based on pollen data. However, much work

has been done on the topic of the “natural” state (more open or more closed) of the European forest cover (Vera 2000; Svenning 2002; Bradshaw et al. 2003; Bradshaw 2004; Mitchell 2005; Birks 2005). Overall, the conclusion of that debate seems to be that the “natural” state of the European forests would be more closed cover. The results of our analysis appear to support that conclusion, with forest cover percentage increasing from the end of the last glaciation and stabilizing at fairly high levels until around 5 ka, when the decline sets in.

Conclusions

In this study, we have used plant functional types classified from pollen data to map and analyse the post-glacial development of the modern (AD 1750 to present) European vegetation in terms of squared chord distance from modern conditions, in terms of biomes, and in terms of landscape openness (APFT%). We have shown that the vegetated landscape of Europe was already similar to modern conditions approximately 4,000–5,000 years ago, around the same time that Neolithic and Bronze Age societies established themselves and began clearing the land (slightly earlier in southern Europe). Though correlation is not necessarily causation, this timing, combined with the subsequent clear deforestation trend lasting until modern times suggests that human land use may already have been the dominant factor driving changes in vegetation cover over much of Europe from the mid-Holocene. Vegetation dynamics during the first half of the Holocene, by contrast, appear to have been driven mainly by climate, as evidenced by the rapid post-glacial increase in forest cover between 11.5 and 8 ka, and by the abrupt reversal in SCD scores at 8 ka, possibly corresponding with the final disappearance of the North American ice sheet and the associated reorganization of atmospheric circulation.

These findings are not completely new; rather, they reinforce earlier conclusions that anthropogenic cultural landscapes similar to those of modern times were already established throughout Europe by Neolithic times (e.g. Bradshaw 2004; Odgaard and Rasmussen 2000). However, the types of reconstructions that we show, in the form of maps and area-average time series, have never before been produced for Europe using such a complete dataset or objective methodologies.

Huntley (1990c) points out that the utility of seeking evidence of human activity on such large spatial, temporal and taxonomic scales is questionable. However, we would argue that, though definitive conclusions cannot be drawn, it is possible to inquire into the intertwining roles of human activity and climate change in shaping the vegetated

landscape of Europe by looking at the same dataset in multiple ways, as we have done.

Finally, we note that the concept of landscape “age” is relative and must be interpreted with caution. Nevertheless, for those interested in understanding the history of European vegetation dynamics, maps such as Figs. 4 and 5 offer a valuable starting point. In particular, Fig. 4 could be useful for projects such as the Natura 2000 network, for example in helping to identify regions with the oldest vegetation in Europe that might be of particularly high conservation value.

This study contributes to the understanding of European vegetation history from the palaeoecological, macroecological and biogeographical perspectives by presenting a palaeoecological narrative that is quantitatively explicit in space, time and vegetation type and that allows speculation on the relative agencies of climate versus human activity. The results of this work may interest the earth system modelling community, as it offers potential benchmarking materials at appropriate spatial, temporal and taxonomic scales for comparison to model output. Mapping the age of the modern landscape should be of interest to the conservation community, as it can help to target conservation efforts to the “oldest” landscapes that might be of higher conservation priority, although such questions are often asked at smaller spatial scales than we present here (Birks 2012). Finally, studies such as this can contribute to the debate on “what is natural?”, and understanding the past development of the European landscape is crucial to understanding both its modern state and its possible future evolution under changing climate and land use patterns.

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