

Spatial gradient of temperature and potential vegetation feedback across Europe during the late Quaternary

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Received: 3 September 2007 / Accepted: 31 March 2008 / Published online: 17 June 2008
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Abstract After the last glacial maximum (LGM; 18,000 years BP) plants migrated onto areas made free by the retreating ice sheets. Pollen records document changes in ecosystems and are an important proxy for the reconstruction of climate parameters. Here, we quantify changes in January temperature (T_{jan}) over the past 14,000 years using 216 European pollen records. We used functional principal component analysis to evaluate the patterns of change over this period of time. Between 14 and 12 ka, T_{jan} records show comparable changes across Europe. After this time period, northwest and southeast Europe experienced differing trends in T_{jan} , trends that became pronounced by 9 ka. The spatial gradient of T_{jan} records is well-correlated with the overall change from steppe to increasingly diverse forest ecosystems. In particular, differential incorporation of conifer vs. deciduous species into forest ecosystems, based on differential colonization out of refugia, likely resulted in albedo gradients over Europe that affected regional T_{jan} .

Keywords Climate · Vegetation dynamics · Pollen · Europe · Last glacial maximum · Holocene · Albedo

1 Introduction

The geographical ranges of plant taxa and biomes have changed substantially since the last glacial maximum

(LGM), primarily in response to climate changes induced by variations in the Earth's orbit. Sensitivity experiments using coupled vegetation-atmosphere models (Broström et al. 1998; Foley et al. 1994; Kutzbach et al. 1996) suggest that past land-cover changes are likely to have had an impact on late-Quaternary climates (de Noblet et al. 1996; Texier et al. 1997; Ganopolski et al. 1998a, b; Kubatzki and Claussen 1998). Evaluating past vegetational changes and their potential impacts requires extended datasets of a proxy that provides reliable reconstructions of past surface conditions (Prentice and Webb III 1998).

Quaternary pollen records, which integrate vegetation over broad areas, lend themselves to numerical approaches. Pollen assemblages record vegetational composition and pattern that are in equilibrium with climate (Webb 1986). This relationship has been a major focus of research in Quaternary palynology for several decades and has led to the development of tools to reconstruct past climates (Guiot 1990; Overpeck 1985) and vegetation types (Prentice et al. 1996) from fossil pollen assemblages.

Davis et al. (2003) used composite pollen records to provide quantitative estimates of temperature fluctuation from 11,500 years BP (11.5 ka) to the present for Europe. They averaged climate data over six main regions to synthesize winter vs. summer temperature change during post-glacial warming. The six regions were delineated based on the expectation that they would yield a climate change "continuum over Europe." Davis et al. (2003) showed that summer and winter temperatures exhibited different trends over time, both within and between the six regions. They attributed the Holocene temperature variability primarily to changes in winter insolation. However, temperature changes and climate variability over the continents are also a consequence of complex interactions between the geosphere, hydrosphere, cryosphere and biosphere. Among

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these interactions, there are feedbacks with the extent of the ice sheets (Clark et al. 1999), the northern Atlantic Ocean (Khodri et al. 2005) and its thermohaline circulation (Broecker 2000; Bryden et al. 2005), soil composition (Powelson 2005) and type of vegetation cover (Foley et al. 1994; Gallimore and Kutzbach 1996; Chapin III et al. 2005; Foley 2005).

Here we focused on the relationship between one climate variable, January temperature (Tjan) and biome changes during the past 14,000 years. Land cover type is an important modulator of regional climate and atmospheric composition (Pielke et al. 1998). Ecosystems have an impact on the physical properties of the land surface such as albedo and roughness length, water and carbon fluxes and energy between the vegetation and atmosphere (Rind 1984; Sellers et al. 1997; Pielke et al. 1998). In this study, we investigated the potential feedback of vegetation dynamics on Tjan over Europe.

Based on the decomposition of reconstructed Tjan on a Fourier basis, we performed a functional principal component analysis (Ramsay and Silverman 2005) to characterize the pattern of changes over Europe. We then determined the correlation between broadleaf and conifer biome geographical ranges with Tjan. To do this, we used an extensive network of palynological time series on local and/or regional scales. We used this dataset to reconstruct unaveraged Tjan, as well as to characterize vegetation biomes throughout Europe for the last 14 ka.

2 Data and approach

The fossil pollen dataset consisted of 216 records with reliable timescales selected from the European Pollen Database (EPD). Tjan was inferred for each fossil pollen assemblage using a statistical method based on the probability density function (Kühl et al. 2002) of each plant species identified in the pollen spectrum. The method requires a dataset of modern geographical ranges and related climate variables for those taxa identified in the fossil samples. Pollen grains are often not identified to the species level. Laurent et al. (2004) georeferenced plant distributions obtained from two major sources: Atlas *Florae Europaeae* (Jalas and Suominen 1972; Jalas et al. 1996, 1999) and Atlas of North European Vascular Plants (Hultén and Fries 1986) and assigned pollen taxa to each plant taxon. We used that modern dataset, which consists of 146 taxa and interpolated values of Tjan obtained from the Climate Research Unit, UK (New et al. 1999).

The reconstructed Tjan for each fossil sample is the median value of the distribution and the standard error corresponds to the extent of the intersect value. The range of the standard error depends on the number of taxa

identified and the accuracy of the pollen identification within each fossil sample. We focused on Tjan because it has a strong impact on temperate plant species (both conifers and deciduous trees) in Europe in terms of the timing of bud burst, growth, flowering and plant survival.

The average sampling resolution of the pollen records extracted from the EPD is around ± 250 years. To perform a spatial comparison of all records we sub-sampled each record at 1,000-year intervals, which revealed coherent patterns over the network of data.

To describe Tjan variability at the European scale using a reduced number of variables we applied a Functional Principal Component Analysis (FPCA), which is an extension of Principal Component Analysis (PCA) to functional data (Ramsay and Silverman 2005). FPCA makes it possible to use information on the rates of change, i.e., the derivatives of the curves, of Tjan. Since the curves are intrinsically smooth, we can describe each curve as a linear combination of a small number of basis functions. A site i ($i = 1, \dots, N$) is described by a Tjan curve $X_i(t)$. This Tjan curve is observed (with noise) at time t_j ($j = 1, \dots, n_i$). The noise ε_{ij} of observation X_{ij} is assumed to be an independent, centered, normal variable with constant variance σ^2 . The $X_i(t)$ are modeled as independent realizations of a stochastic process $X(t)$ that has mean $E(X(t)) = \mu(t)$ and a covariance function $\text{cov}(X(s), X(t)) = G(s, t)$. We assume that there is an orthogonal expansion (in L^2 sense) of G in terms of eigenfunctions (EF) $\varphi_k(\cdot)$ and hierarchically ordered eigenvalues λ_k : $G(s, t) = \sum_k \lambda_k \varphi_k(s) \varphi_k(t)$ where s and t lie in the time range of measurements. The FPCA allows us to represent observation X_{ij} as:

$$X_{ij} = \mu(t_j) + \sum_{k > 0} \zeta_{ik} \varphi_k(t_j) + \varepsilon_{ij}$$

$\mu(t)$ and $G(s, t)$ are estimated using a Fourier transform with observation points at every 1,000 years (Fig. 1). λ_k and $\varphi_k(\cdot)$ are the eigenvalues and eigenvectors of $G(s, t)$ and have the same interpretation as classical PCA. This means that every observation curve can be represented as a linear combination of eigenvalue functions.

We assume that $G(s, t)$ does not depend on the spatial dimension and is identical for all records. Therefore, the temporal (co)variance is based on the same underlying statistics for all fossil records. Space–time interaction models are difficult to specify and generally rely on assumptions such as stationarity that are not assumed here. Moreover to estimate this kind of interaction, it is necessary to assume a spatial correlation structure. This assumption is reasonable since a major aim of FPCA is to describe the empirical spatial variability.

The principal components are the eigenvalues of $G(s, t)$, the empirical covariance operator, and they characterize the variability of the sample of random curves, Tjan. Thus,

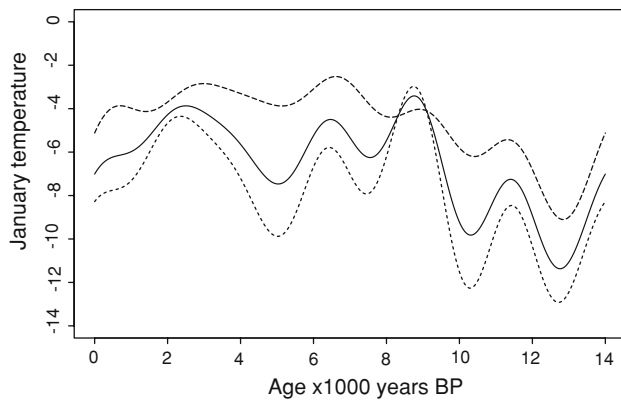


Fig. 1 January temperature during the past 14,000 years. The *solid line* is the Tjan average over the 216 sites used in this study. The *short-dashed* and the *long-dashed* lines are the averages of Tjan over those sites with coefficients of the functional principal component greater (SW Europe) and smaller (NW Europe) than zero, respectively (see Fig. 3)

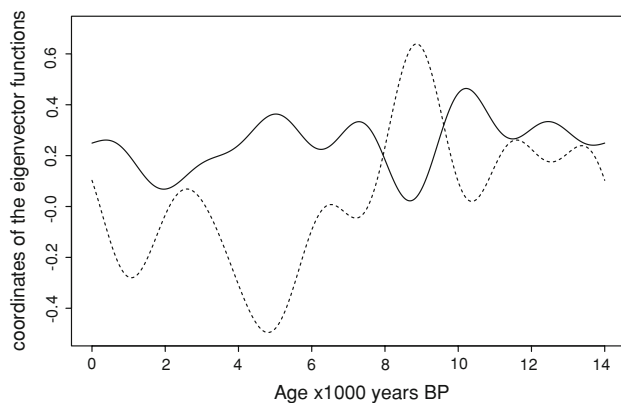


Fig. 2 The first two eigenfunctions of the functional principal component analysis represent 74.7% (*solid line*) and 22.7% (*dashed line*) of the variance, respectively. The moderate opposition between 14 and 12 ka of the two *curves* reflects mostly the variability among the eigenfunctions and not two different trends

the first few principal components quantify the most important structural differences between curves. This model stipulates that each sample random curve Tjan can be approximated by a transformation comprising common principal components with varying strengths, as captured in the coefficient “score”. The quality of the approximation corresponds to the percentage of the variability explained by the principal components. This is measured by the eigenvalue of $G(s, t)$. Each coefficient score expresses the variability within each Tjan time series (Fig. 3).

To differentiate vegetation types at each site we used the sum of pollen percentages of broadleaf tree taxa (*Acer*, *Alnus*, *Betula*, *Carpinus*, *Corylus*, *Fagus*, *Fraxinus*, *Ostrya*, *Populus*, *Quercus*, *Salix*, *Tilia*, *Ulmus*) and conifers (*Abies*, *Cupressaceae*, *Larix*, *Picea*, *Pinus*) at 13, 9 and 5 ka. To synthesize these results we interpolated the pollen

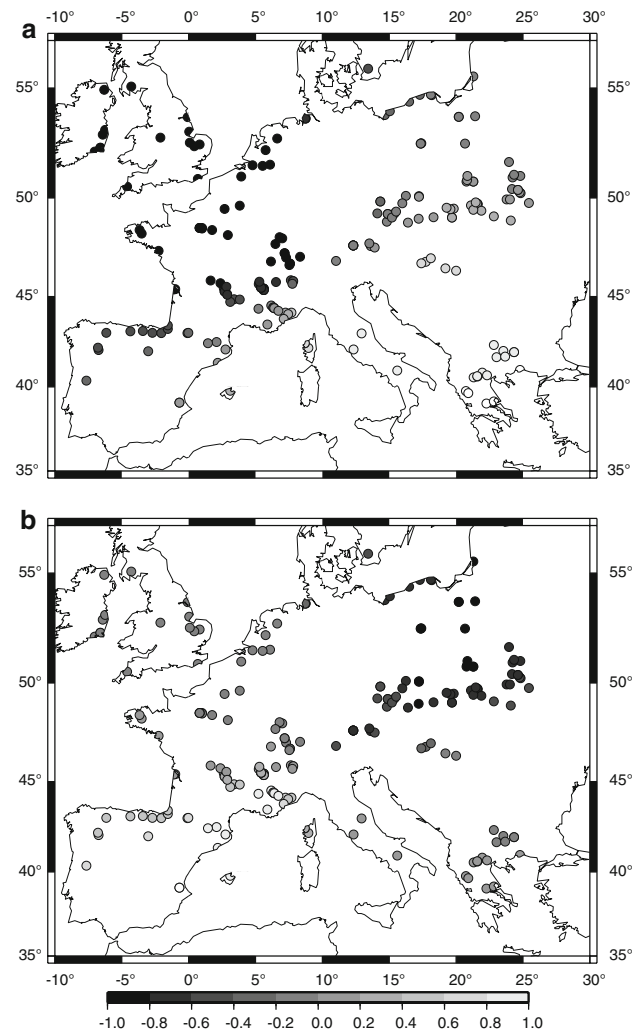


Fig. 3 Coefficient values from -1 (*black circles*) to $+1$ (*white circles*) of the eigenvector functions. **a** Map represents the coefficients of the first FPCA, **b** those of the second FPCA

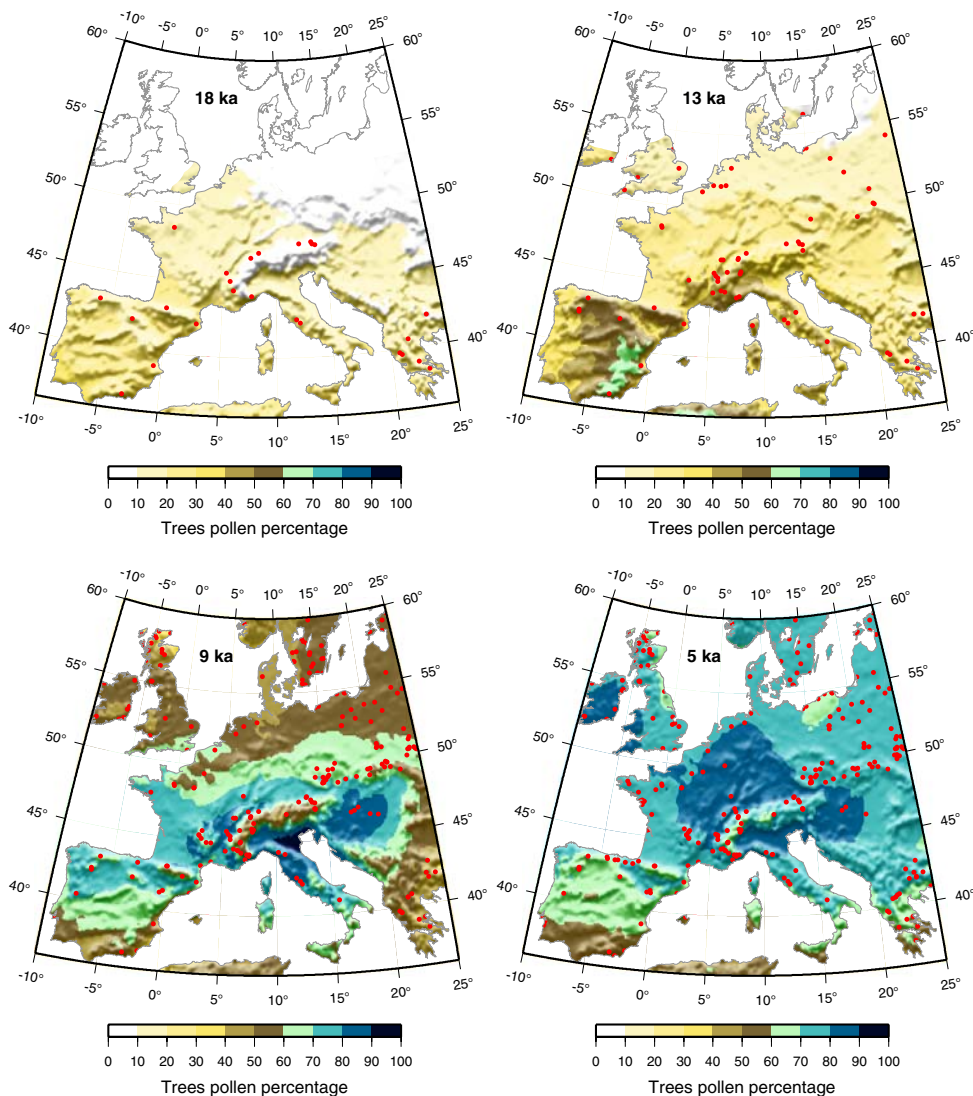
percentages of the broadleaf taxa and conifers to a 50-km grid and mapped the gridded data using a UTM projection. Pollen percentages were interpolated from individual site locations to the grid points using a thin plate spline.

Finally, we computed correlation coefficients between the coefficient “scores” of the FPCA performed on Tjan and the pollen percentages of broadleaf taxa and conifers at each site and for each time period.

3 Results and interpretations

The first two principal curves φ_1 and φ_2 (Fig. 2) represent the two dominant patterns within the dataset (Fig. 3). Their eigenfunctions explain 97.4% of the variance ($\lambda_1 + \lambda_2 / \sum \zeta_{ik} = 0.974$) and summarize the major trend in Tjan over the past 14 ka in Europe. The scores ζ_{ik} ($i = 1, 2$) are the

Fig. 4 Interpolated distribution areas of trees from fossil pollen data dated between 20 and 16 ka (18 ka), between 14.5 and 13.5 ka (13 ka), between 10.5 and 9.5 ka (9 ka) and between 5.5 and 4.5 ka (5 ka)



coefficients of the first two EFs of the FPCA. The first EF (78% of the variability; Fig. 2) of the FPCA is smaller in amplitude than the second. This small first EF implies that Tjan was comparatively stable (i.e., variability was reduced) throughout Europe during the Holocene. The mapped scores ζ_{ik} of the decomposition of Tjan (Fig. 3a) show opposing values between SE and NW Europe.

The second EF (Fig. 2) summarizes another trend (21% of the variability) in the Tjan time series. This axis shows more disparate values than the first EF, indicating that other areas besides SE and NW Europe have undergone pronounced Tjan change. Indeed, the mapped coefficients of the decomposition of Tjan (Fig. 3b) show the variability across an area that extends from NE towards SW Europe.

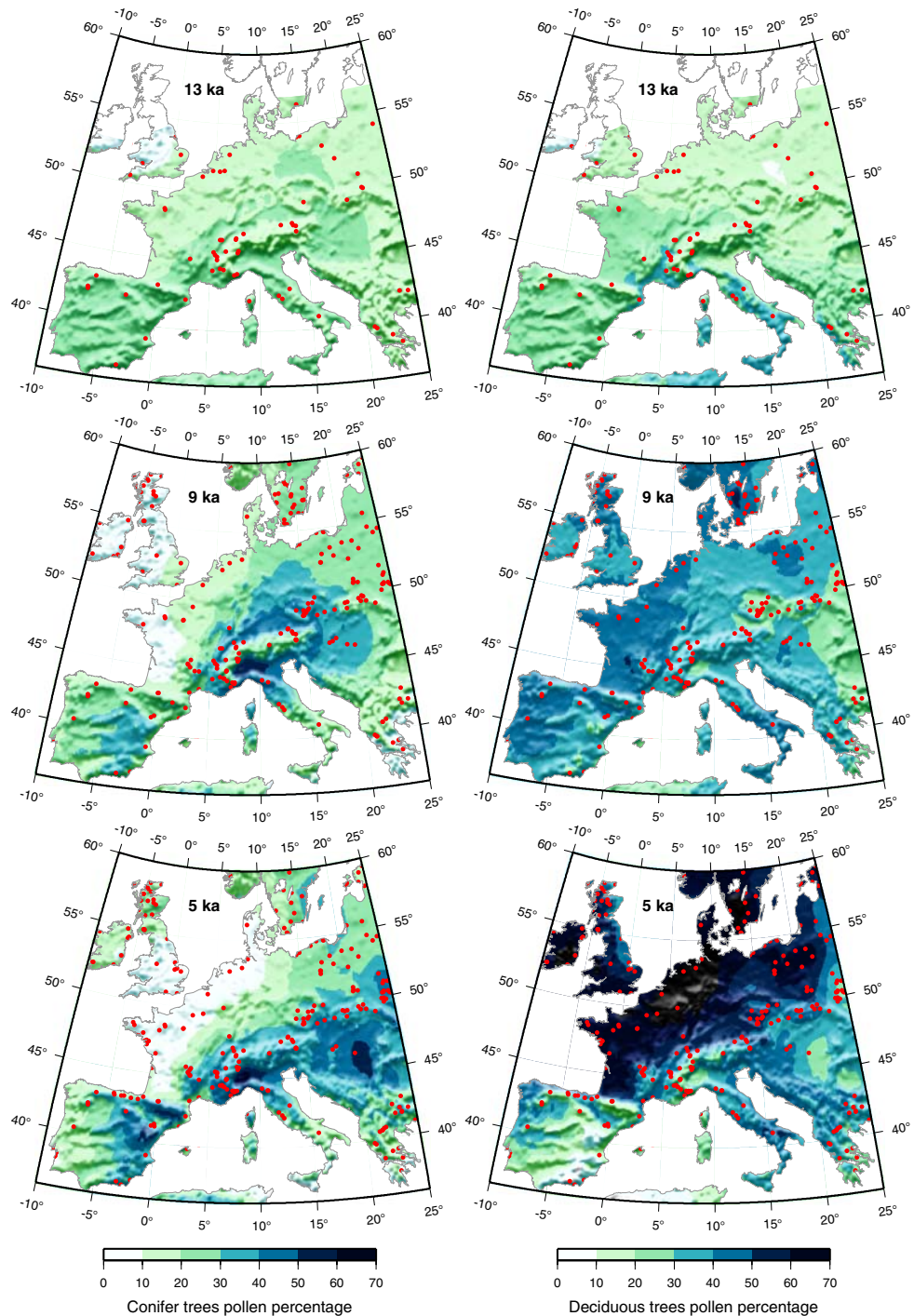
Between 14 and 12 ka both EFs show reduced variability (Fig. 2), indicating that Europe recorded relatively comparable Tjan changes during this time period. However, after 12 ka and throughout the Holocene the two EF

values show opposite trends, indicating the cessation of a unifying process behind Tjan change. The largest mismatch between NW and SE Europe occurred around 9 and 5 ka (an inversion of the trend at 9 ka and an amplitude spike at 5 ka).

We used pollen percentages to reconstruct trees and herbs (Fig. 4) and then broadleaf deciduous and conifer biomes (Fig. 5). The size of the dataset used for each time slice varied depending on the data available in the EPD.

We computed correlation coefficients between the first EF (78% of Tjan variability) and the reconstructed conifer and broadleaf biomes at 13, 9 and 5 ka (Fig. 6). We interpreted correlation coefficients between Tjan and biome distributions at each time slice to be a reflection of the relationship between the post-glacial spread of tree species and local changes in Tjan. Deciduous trees such as *Quercus* spread north and northeast from glacial refugia located near the Mediterranean (Brewer et al. 2002). By

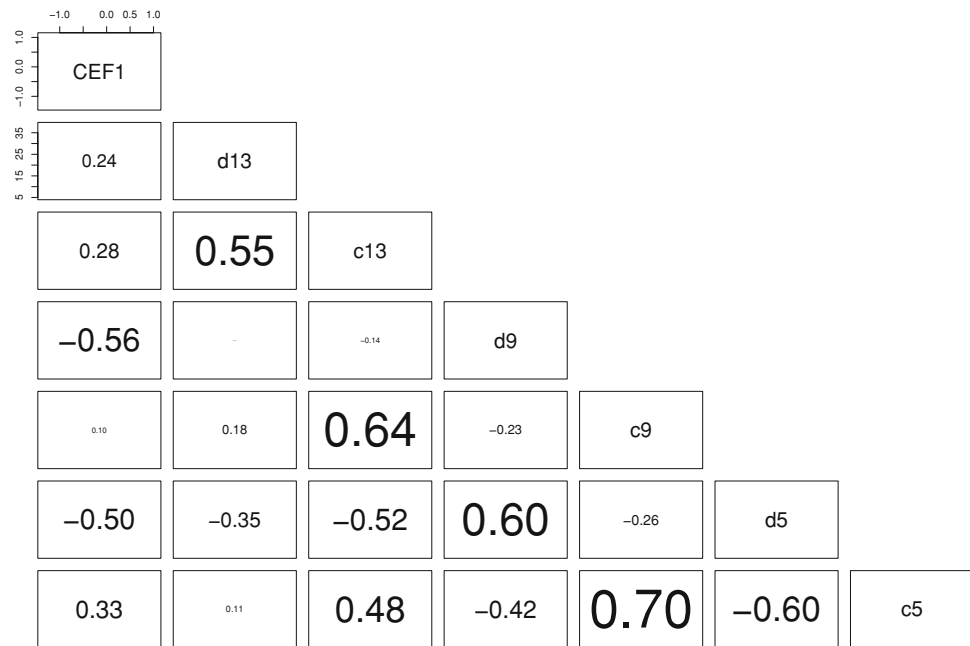
Fig. 5 Interpolated distribution areas of conifers (*Abies*, Cupressaceae, *Larix*, *Picea*, *Pinus*) and deciduous trees (*Acer*, *Alnus*, *Betula*, *Carpinus*, *Corylus*, *Fagus*, *Fraxinus*, *Ostrya*, *Populus*, *Quercus*, *Salix*, *Tilia*, *Ulmus*) from fossil pollen samples dated between 14.5 and 13.5 ka (13 ka), between 10.5 and 9.5 ka (9 ka) and between 5.5 and 4.5 ka (5 ka)



5 ka, all deciduous tree taxa were outside their glacial refugia, which explains the negative correlation coefficient between 13 and 5 ka ($R^2 = -0.35$; Fig. 6). In contrast, the conifer biome did not show opposing spatial distribution patterns between 13 and 9 ka ($R^2 = 0.64$), between 9 and 5 ka ($R^2 = 0.70$) or between 13 and 5 ka ($R^2 = 0.48$; Fig. 6). Today's dominant European conifers (e.g., *Pinus*, *Abies* and *Picea*) came from glacial refugia near the Alps, the Hungarian plain and the Carpathian Mountains

(Terhürne-Berson et al. 2004; Willis and van Andel 2004; Cheddadi et al. 2006); they expanded to dominate the landscape at 13, 9 and 5 ka (Fig. 5). The deciduous biome showed negative correlation with the first EF at 9 and 5 ka because of its strong opposing pattern of spatial distribution within NW Europe at the two time slices (Figs. 3, 5). Conversely, the conifer biome showed positive correlation with the first EF at 5 ka because conifers dominated SE Europe at this time (Figs. 3, 5).

Fig. 6 Pairwise correlation coefficients between the first eigenfunction (CEF1) and percentages of deciduous trees at 13 (d13), 9 (d9) and 5 ka (d5) and percentages of conifers at 13 (c13), 9 (c9) and 5 ka (c5). The character size of the correlation coefficients was made proportional to their values, to accentuate their significance



4 Discussion

The main feature of the Quaternary climate record is abrupt and widespread temperature change at each glacial–interglacial transition (Jouzel et al. 1993; Petit et al. 1999; Cheddadi et al. 2005). Furthermore, reconstructions have shown that temperature fluctuates less during interglacial than glacial periods (Bond et al. 1992, 1993). Based on a high-resolution ice core from Greenland, Alley et al. (1997) calculated a relatively stable 5°C temperature range for the Holocene. In contrast, the most recent glacial period recorded several abrupt temperature reversals with temperature gradients two to three times higher than those observed during the subsequent interglacial (NGRIP members 2004).

The global warming that occurs during glacial–interglacial transitions is triggered by a steady increase in summer insolation (Berger 1978). However, temperature changes recorded by Quaternary continental and marine paleosubstrates are not linearly correlated to insolation forcing (King 1996) since there are biosphere–geosphere–atmosphere interactions that induce additional climate variability.

The results we presented here help to explain the spatial and temporal variability of January temperature over the European continent during the past 14 ka. The overall climate reconstruction (Fig. 1) was consistent with previous studies (Davis et al. 2003). The new insight derived from these results originated first from our statistical approach, which depicts opposite trends in Eastern and Western Europe during the Holocene (Fig. 3a) and a similar, albeit less pronounced, pattern for areas between

the Baltic Sea and the Iberian Peninsula (Fig. 3b) and second, from the interpretation of the causes driving these changes. The most extreme changes in the Tjan values of Europe clearly occurred at 9 and 5 ka (Fig. 2).

It is intriguing that Tjan changes in Europe were spatially more uniform during the warming at the end of the last glaciation (between 14 and 12 ka) than during the Holocene, which was characterized by strong differences between NW and SE Europe. One possible explanation is that the warming from a glaciated environment immediately resulted in areas available for plant colonization. As different species expanded out of their respective refugia, the resulting diverse ecosystems gave rise to varied climate feedbacks, thus resulting in a climatically and biologically heterogeneous late-Holocene landscape.

Changing distributions of vegetation over the last 18 ka in Europe have been extensively documented from fossil pollen records (e.g., Berglund et al. 1996). Spatial reconstruction of vegetation patterns have shown that during the last glacial maximum (Fig. 4, 18 ka) herbaceous taxa comprised more than 80% of the pollen taxa. Between 18 and 13 ka, tree-cover was minimal in areas north of 45° latitude in Europe (Fig. 4). After 13 ka, Europe experienced successive waves of migration of several tree species. The late glacial and the early Holocene were dominated by coniferous taxa (Fig. 5) such as *Pinus* and *Juniperus*. After this time, broadleaf deciduous trees (*Quercus* and *Corylus* and then *Fagus*, *Alnus*, *Ulmus* and *Carpinus*) progressively replaced conifers. By 5 ka, forest biomes had replaced steppe throughout Europe: tree ecosystems constituted more than 50% of the land area (Fig. 4). This sequence is broadly similar to that

reconstructed by Williams (2002) for North America since the last glacial maximum. Our data revealed a spatial coherency in the reconstructed ranges of deciduous trees and conifers (Fig. 5) for most of the Holocene. This corroborates a genetic survey of 22 temperate plant species that indicated diversity patterns across Europe were established during several thousands of years (Petit et al. 2005).

Humans increasingly impacted that landscape through clearance of woodlands, cultivation and grazing after the mid-Holocene (Zohary and Hopf 1993), however, many studies argue that the human impact was not widespread until after 5 ka (see Ruddiman 2003). The main vegetation transitions over Europe are synchronous with those identified in North America during the Holocene and Late Glacial which suggests that they were primarily driven by large-scale atmospheric circulation (Gajewski et al. 2006) and that human impact became more detectable after 5 ka.

Broad-scale changes in forest ecosystems were constrained by migrational routes and rates from the glacial refugia, as well as by competition between species. Broadleaf deciduous trees such as *Quercus*, *Corylus*, *Carpinus*, *Ulmus*, *Fagus* and conifers such as *Pinus*, *Abies*, *Picea*, did not colonize Eastern and Western Europe simultaneously. All of these taxa spread from different glacial refugia (Bennett et al. 1991; Brewer et al. 2002; Willis and van Andel 2004; Cheddadi et al. 2006), following different migrational routes with different rates of spread. Such vegetation dynamics would create geographically diverse ecosystems, with diverse attributes of albedo, surface roughness and leaf area, all parameters having a strong influence on climate. Variation in vegetational albedo induces important regional temperature gradients (Foley et al. 1994; Chapin III et al. 2005; Foley 2005). Specifically, the replacement of snow cover by a vegetation cover gives rise to a projected temperature increase of ca. 2°C (Foley et al. 1994; Crucifix et al. 2002). Forest biomes have a lower albedo (0.05–0.2) than grassland biomes (0.16–0.26) and conifer forests have a lower albedo (0.05–0.15) than deciduous forests (0.15–0.20) (Oke 1987).

At present, there is no method to quantitatively evaluate interactions between climate and biome dynamics over several thousands of years. The importance of albedo on climate dynamics has been demonstrated in model simulations, although most work has been based on interactions across shorter time-scales. Wang et al. (2004) asserted that the extent of the dryness in the Sahel during the past decades can only be fully explained by taking into account vegetation feedback. Delire et al. (2004) modeled vegetation dynamics over periods up to a century and showed a clear influence on precipitation.

In Europe during the last glacial period, tree-cover was minimal until ~14 ka, when the first conifers, such as pine, began to spread (Cheddadi et al. 2006). Thus, prior to 14 ka the landscape was covered by mostly treeless vegetation and the albedo of its surface was homogeneous. The reduced spatial variability in the Tjan record over the continent that we observe until 12 ka (Fig. 2) may be related to such a homogeneous, treeless landscape. Our results lead us to visualize a European landscape in which regional variability of Tjan occurs only after forest species began to expand out of their glacial refugia. The reconstructed distribution of forest biomes at 13, 9 and 5 ka (Fig. 5) shows that the broadleaf deciduous trees propagated from the Mediterranean borderlands towards the Atlantic coast. The conifer forests spread mainly from the mountainous areas around the Alps and the Carpathians and from the Hungarian plain (Willis and van Andel 2004) towards eastern and southern Europe (Fig. 5). Throughout the last 14 ka, conifer forests comprised not more than 20% of the ecosystems along the Atlantic coast (Fig. 5). Thus, there were significant differences between northwestern and southeastern Europe, in terms of the potential influence of different biomes on the environment, which may explain the dissimilarity in Tjan records between these regions during the Holocene (Fig. 3).

To quantify and illustrate this hypothesis, we computed correlation coefficients between the first eigenfunction and the percentages of each biome type at 13, 9 and 5 ka (Fig. 6). Results revealed a significant relationship between vegetation types and Tjan records. Deciduous and coniferous biomes were, respectively, negatively and positively correlated with Tjan variability (that is expressed through the coefficient scores, Fig. 3a). In other words, the deciduous biome was located in areas (Fig. 5) where Tjan had a lower variability during the Holocene (Fig. 3a) and a higher temperature than the European average (Fig. 1). Conversely, the conifers occurred in areas (Fig. 5) where Tjan recorded a higher variability (Fig. 3a) but a lower temperature than the European average (Fig. 1).

These spatial correlations strongly suggest that the warming during the postglacial period caused the tree migrations and triggered the resulting forests dynamics and that the biome composition and distribution may have also had a feedback impact on climate. These data serve to further complicate discussions of anthropogenic climate and land-use change mechanisms.

5 Conclusions

During the postglacial period, temperate tree species recolonized Europe from their various glacial refugia leading to different biome distributions over Europe. The

reconstructed distributions of vegetation during the past 14 ka show that in northwestern Europe, temperate deciduous forests expanded during the Holocene while conifers colonized central, eastern and southeastern Europe.

The reconstructed January temperature shows significant climate differences between NW and SE and then SW and NE Europe during the Holocene. We suggest that the vegetation dynamics over Europe during the last 14 ka had a feedback on the regional records of Tjan.

In future we intend to test the impact of broadleaf and needle-leaf biomes on January temperature using a coupled vegetation–climate model. This will provide a basis for evaluating the role of different types of vegetation on temperature and allow a statistical assessment of their impacts.

Acknowledgments This work was supported by and is a contribution to the European Science Foundation Euroclimate project DECVeG: “Dynamic European Climate–VEgetation Impacts and Interactions”. We thank Liliane Bel, Christine Delire and Hope Jahren for stimulating discussions and valuable comments. We also thank three anonymous reviewers who helped substantially improve the manuscript. John Keltner assisted with English phrasing. The European Pollen Database contributors (<http://www.europeanpollendatabase.net>) are gratefully acknowledged for making their datasets publicly available to the scientific community. We are also very grateful to the *Free Software Foundation* for the software we used under the GNU/Linux General Public License, the R language (<http://www.r-project.org>) and the Generic Mapping Tools (<http://gmt.soest.hawaii.edu>). This is an ISEM-contribution number 2008-020.

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