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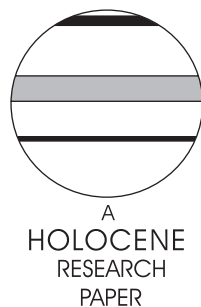
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Testing the influence of climate, human impact and fire on the Holocene population expansion of *Fagus sylvatica* in the southern Prealps (Italy)

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Abstract: This study addresses the timing and causes of the Holocene population expansion of *Fagus sylvatica* at two sites in the southern Prealps (Italy): Lago di Fimon and Lago Piccolo di Avigliana. At both sites pollen and microcharcoal have been analysed at high temporal resolution. The impact of humans and of fire on the forest dynamics is tested by means of time-series analysis and the influence of climatic change has been inferred from summer temperature and precipitation reconstructions in the Alps. The time intervals during which the population expansion of *F. sylvatica* occurred (ie, phases during which population doubling times were shortest) is determined by fitting linear regressions through the ln-transformed *Fagus* pollen-accumulation rate (ln(PAR)). At Lago di Fimon, the population expansion of *F. sylvatica* occurred at 7300–6400 cal. yr BP (FIM I). After a marked decline the population re-expanded at 5500–4700 cal. yr BP (FIM II). At Lago Piccolo di Avigliana *F. sylvatica* expanded c. 5300–4600 cal. yr BP (AVP I). Time-series analyses show that *Fagus* expanded after forest fires decreased during FIM I, and human impact likely contributed to the *F. sylvatica* population expansions at the two sites during FIM II and AVP I. The comparison with independent climatic records suggests that favourable climatic conditions (eg, cool and wet) were a determining factor. Our study suggests that the expansion of *F. sylvatica* populations has been triggered by more than one single factor alone.

Key words: *Fagus sylvatica*, pollen, microcharcoal, climate, vegetation history, human impact, fire, plant populations, Holocene, Italy.

Introduction

It seems likely that future distributions of species ranges will change in response to current climatic changes (Intergovernmental Panel on Climate Change (IPCC), 2001; Thuiller *et al.*, 2005; Overpeck and Cole, 2006), but predicting the rate and direction of species ranges is complex, because environmental interactions and disturbance may influence biotic responses to climatic change (Overpeck and Cole, 2006). Therefore understanding what has been driving changes in population abundances and species ranges in the past may lead to better predictions of future biotic responses to climatic change (Peteet, 2000).

Fagus sylvatica today is widely distributed in Europe and is apparently still expanding its range (Björkman and Bradshaw, 1996). Palaeoecological attempts to analyse its postglacial extent and population expansion have been numerous, providing insight into vegetation dynamics at different times and spatial scales, and in different geographical and climatic regions. The spreading history and the population expansion of *F. sylvatica* has been interpreted as reflecting: distance of glacial refugia, ie, migrational lag (eg, Birks, 1989; Lang, 1994), climatic changes (Rudolph, 1930; Welten, 1944; Firbas, 1949/1952; Huntley *et al.*, 1989; Tinner and Lotter, 2006) and disturbance on vegetation (ie, natural/anthropogenic fires or increases of pollen related to human activities; Godwin, 1956; Iversen, 1973; Björkman, 1997; Küster, 1997; Ralska-Jasiewiczowa *et al.*, 2003).

Tinner and Lotter (2006) reviewed the existing hypotheses and concluded that climatic change was probably the main determinant

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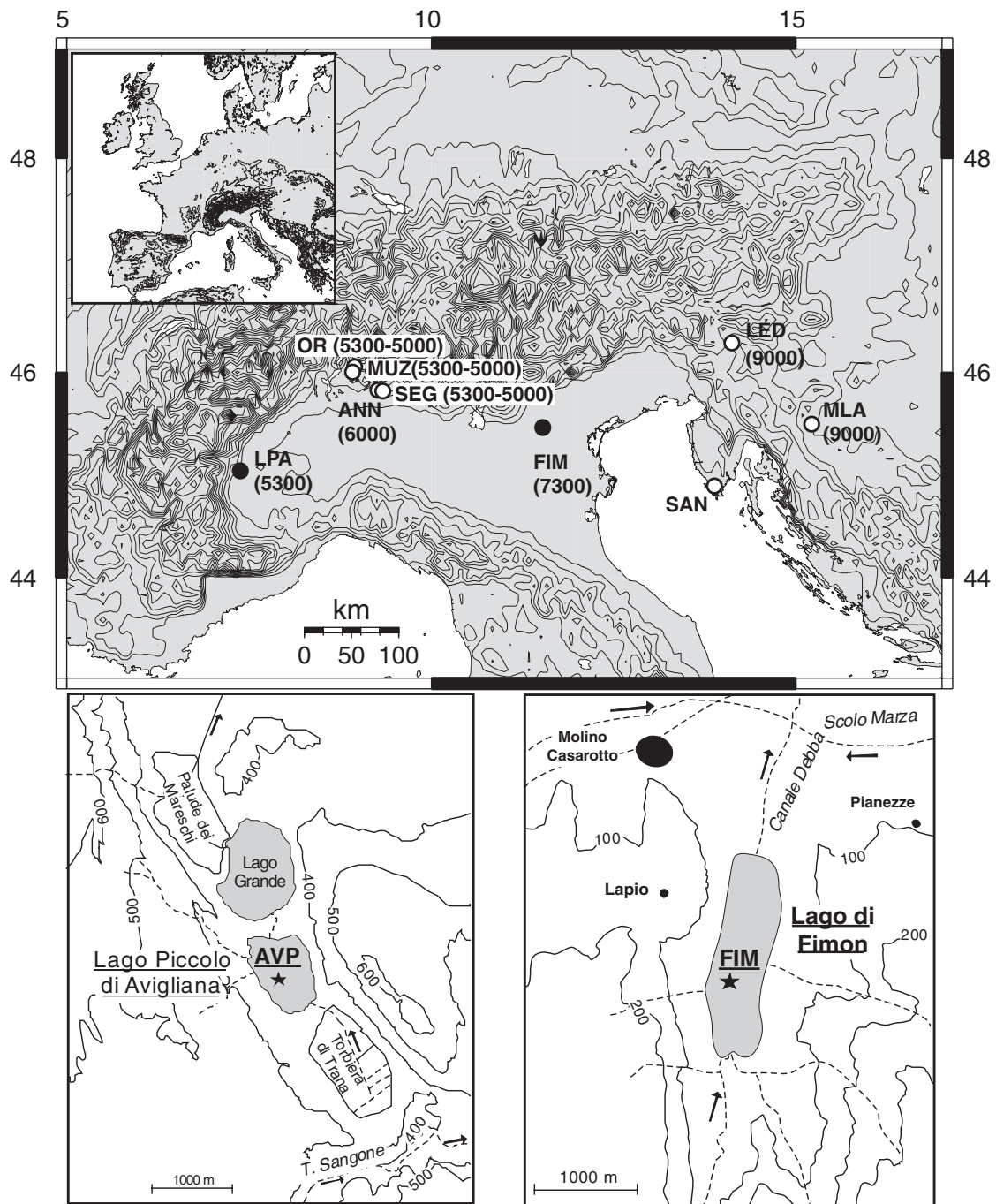


Figure 1 Top panel: location of sites: Lago Piccolo di Avigliana (LPA, 356 m a.s.l., this study), Lago di Fimon (FIM, 23 m a.s.l., this study), Šandalja II – *Fagus* macrofossils charcoal evidence dated at $25\,260 \pm 240$ cal. yr BP (SAN, 60 m a.s.l., Willis and van Andel, 2004); Mlaka (MLA, 140 m a.s.l., Andrić and Willis, 2003); Ledine (LED, 1100 m a.s.l., Culiberg and Serceļ, 1996); Lago di Annone (ANN, 224 m a.s.l., Wick and Möhl, 2006) and Lago del Segrino (SEG, 374 m a.s.l., Gobet *et al.*, 2000); Lago di Origlio (OR, 416 m a.s.l., Tinner *et al.*, 1999), and Lago di Muzzano (MUZ, 337 m a.s.l., Gobet *et al.*, 2000); number in brackets: timing of expansion of *Fagus sylvatica* in cal. yr BP. Bottom left: sketch map of Lago Piccolo di Avigliana with coring location marked by an asterisk. Bottom right: sketch map of Lago di Fimon and location of the Neolithic settlement of Molino Casarotto (solid circle); asterisk: coring locations

in driving the population expansions of *F. sylvatica* across Central Europe and that other factors were of secondary importance. Similarly, Giesecke *et al.* (2007) concluded that climatic control cannot be rejected as an explanation for Holocene changes in distribution and abundance of *F. sylvatica*. On the other hand, they emphasized that non-climatic factors may also help explain the pattern of population expansion in the lowlands of Central Europe.

The aim of this study is to address the timing and causes of the Holocene population expansion of *F. sylvatica* in the southern Prealps, a topic that has not often been addressed in previous studies.

We use two well-dated lake-sediment archives with pollen and microcharcoal analyses of high-temporal resolution: Lago di Fimon and Lago Piccolo di Avigliana (southern Prealps, Italy; Figure 1). The Forest fires and human impact hypothesis predicts that populations of *F. sylvatica* expanded in response to human-induced forest openings by deforestation and/or anthropogenic/natural forest fires (Godwin, 1956; Iversen, 1973; Björkman, 1997; Küster, 1997; Ralska-Jasiewiczowa *et al.*, 2003). We test this hypothesis using cross-correlations among time-series at these two sites. In particular, we expect that anthropogenic-pollen indicators and/or microcharcoal

are positively correlated at positive time lags with *Fagus* pollen. We analysed the influence of climatic change at times of population expansions by means of a comparison between our pollen records and palaeoclimatic reconstructions from central Europe and the Alps (Haas *et al.*, 1998). The climate change hypothesis proposes that climatic change involving increasing summer precipitations and decreasing (spring) frost occurrence (Rudolph, 1930; Welten, 1944; Firbas, 1949/1952; Huntley *et al.*, 1989; Tinner and Lotter, 2006) favoured the population expansion of *F. sylvatica*.

Study sites

Lago di Fimon (23 m a.s.l.; 45°28'N, 11°32'E; 67 ha surface area; max. water depth 3.9 m) is located in a broad depression on the northern side of the Berici Hills (Figure 1). The bedrock of these hills, which were outside the area of glacier extension during the last glacial maximum, consists of Cretaceous–Miocene carbonates and of volcanic rocks (Castiglioni and Pellegrini, 2001). The outlet of the lake is dammed by alluvial sediments deposited by the Bacchiglione River. The lake is fed by several minor inlets and drained by one artificial outlet (Canale Debba, Figure 1). Mean annual, mean January and mean July temperatures are at present around 11°C, 0°C, and 22°C, respectively, and average annual precipitation is 1105 mm/yr (Cerato, 1997). The present climatic regime is temperate and humid, with no dry season. A forest with *Quercus pubescens*, *Ostrya carpinifolia*, *Fraxinus ornus* and *Celtis australis* covers the slopes of carbonate-rich soils. Where more silty soils occur, *Castanea sativa*, *Quercus petraea* and *Acer pseudo-platanus* occur. The presence of *C. sativa* is favoured by selective plantations.

In the vicinity of the lake (Molino Casarotto, Figure 1) a pile-dwelling settlement consisting of three houses with a hearth in the central part of each house has been excavated (Bartolomei *et al.*, 1986). The posts consist of *Alnus glutinosa*, *Fraxinus ornus*, *Acer platanoides*, *F. sylvatica* and *Corylus avellana* wood (Corona *et al.*, 1974). The stone and pottery assemblages belong to the first phase of the Vasi a Bocca Quadrata Culture (Bartolomei *et al.*, 1986). The age of the settlement was estimated by re-calibrating ¹⁴C dates (Bagolini and Biagi, 1990) using CALIB 5.1 (Stuiver and Reimer, 1993) and the INTCAL04 (Reimer *et al.*, 2004). Although a wide time span was obtained (7150–5750 cal. yr BP), calibrated ages from the main hearth in the first and second houses and on the peripheral hearth of the first house clustered into a much shorter time interval (ie, 6400 ± 200 (2σ) cal. yr BP).

Lago Piccolo di Avigliana (referred in the text as LPA; 356 m a.s.l.; 45°03'N, 07°23'E; 60 ha surface area; max. water depth 12.5 m) is confined by glacial moraines and by hills where crystalline

rocks outcrop (Figure 1; Petrucci *et al.*, 1970). The climate is temperate-humid, without summer drought. Average annual precipitation is ~880 mm/yr, and mean annual, mean January and mean July temperatures are 13°C, 2°C, and 24°C, respectively (Biancotti *et al.*, 1998). Vegetation is dominated by *A. glutinosa*, *Salix* sp., *Populus* sp. and *Robinia pseudoacacia*. Surrounding hills are dominated by *C. sativa* plantations and by *Q. petraea*, *Q. pubescens*, *Corylus avellana* and *Fraxinus excelsior*. *F. sylvatica* and *Abies alba* are absent in the hydrological catchment. Piles of *Q. robur* and *Ulmus campestris*, lithic remains and bronze objects in a peat bog close to the lake all attest to the presence of pile-dwellings during the Middle to Late Bronze Age (ie, 3550–3250 cal. yr BP; Volta, 1955).

Material and methods

Lake sediments were obtained with a Streif modified Livingstone piston corer (8 cm in diameter; Merkt and Streif, 1970) from Lago di Fimon (at 2.38 m water depth) and from Lago Piccolo di Avigliana (at 12 m water depth) from a floating platform. Cores were wrapped in plastic foil and stored at 4°C.

The sediments at Lago di Fimon (core FIM A) consist of calcareous marl from the top to about 32 cm depth. Below this level to about 200 cm depth the silt and clay contents are higher (calcareous silty clay), and are again lower between 200 and 250 cm (calcareous marl). Below 250 cm depth the deposit is more organic (calcareous silty gyttja) until 600 cm depth and is followed by a calcareous gyttja down to 800 cm.

At Lago Piccolo di Avigliana the sediment consists of homogeneous fine-detritus gyttja (FDG) from the top to c. 280 cm depth. This is followed by a FDG, with distinct but discontinuous laminations until c. 650 cm depth, which is in turn followed by a homogeneous FDG (Finsinger and Tinner, 2006).

Samples of 1 cm³ (thickness = 1 cm) were prepared with standard physical (500 μm sieving and decanting) and chemical (HCl, KOH, HF and acetolysis) methods (Moore *et al.*, 1991). *Lycopodium* tablets were added to estimate pollen concentration, following Stockmarr (1971). A minimum pollen sum of 300 grains (excluding aquatic plants and ferns) was counted at a magnification of ×400 under a light microscope and identified with keys, pollen atlases (Punt *et al.*, 1976–1996; Moore *et al.*, 1991; Reille, 1992–1998), and the reference collection of the Institute of Plant Sciences of Bern. Microcharcoal particles were identified as black, completely opaque, angular fragments that occurred in the pollen slides (Clark, 1988). Only charcoal particles >75 μm² (or longer than 10 μm) were counted under a light microscope at ×200

Table 1 AMS-radiocarbon dates from Lago di Fimon (FIM A; this study) and Lago Piccolo di Avigliana (AVP 1; Finsinger and Tinner, 2006)

Lab. number	Depth (cm)	¹⁴ C age BP	Cal. age BP (2σ range)	Mean cal. age BP
<i>Lago di Fimon</i>				
Erl-5579	284.5	1346 ± 56	1370–1145	1255
Erl-5580	407.5	3160 ± 58	3555–32005	3390
Poz-5305	512	4840 ± 40	5650–5475	5560
Poz-5306	551	5860 ± 35	6775–6570	6670
Erl-5581	578.5	6261 ± 61	7310–7000	7160
Erl-5582	697	8707 ± 75	10 115–9530	9820
Erl-5583	746.5	9736 ± 79	11 270–10 780	11 030
<i>Lago Piccolo di Avigliana</i>				
Erl-4558	175	1565 ± 43	1260–1700	1480
Erl-4804	192	1741 ± 38	1450–1890	1670
Erl-4805	335	3175 ± 51	3300–3500	3400
Erl-4803	422	4460 ± 51	4860–5380	5120
Erl-4802	481	5230 ± 51	5860–6180	6020
Erl-4801	634	8723 ± 63	9480–10 000	9740

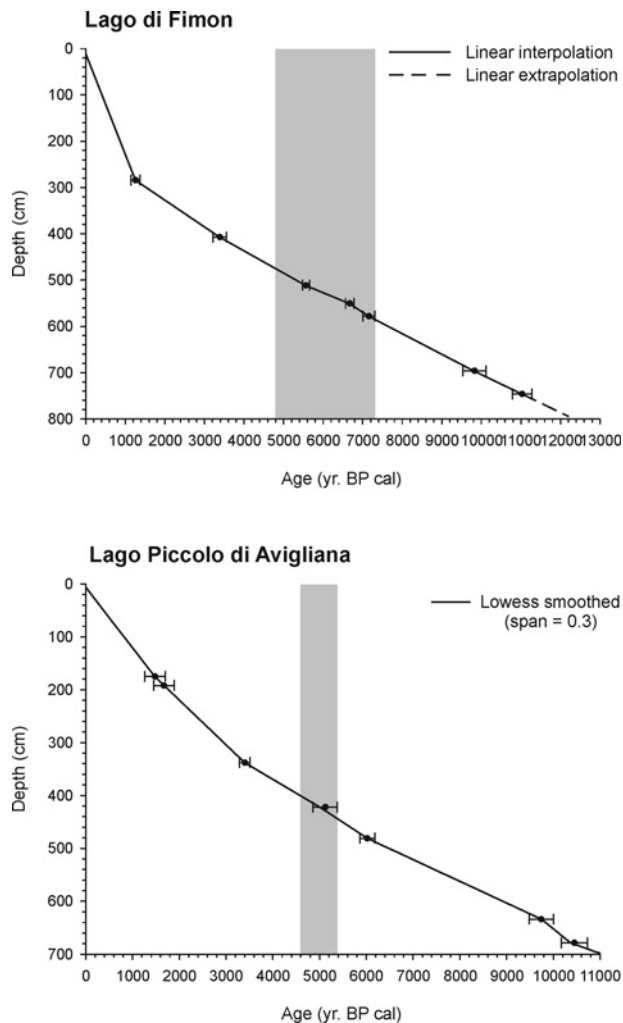


Figure 2 Depth–age models of Lago di Fimon and Lago Piccolo di Avigliana. Error bars indicate 95.4% confidence intervals; dots represent mean calibrated ^{14}C dates (Table 1), and shaded areas show the high-resolution analysis section

magnification, following Tinner and Hu (2003) and Finsinger and Tinner (2005). Changes in pollen composition were detected with the program ZONE 1.2 and optimal partition sum of squares (Birks and Gordon, 1985). The number of significant pollen zones was evaluated by comparison with the broken-stick model (Bennett, 1996).

Depth–age models of the sediment stratigraphies are based on AMS radiocarbon-dated terrestrial plant macrofossils. For the Fimon stratigraphy, seven radiocarbon dates were first converted to calibrated years BP (Table 1) with CALIB 5.1 (Stuiver and Reimer, 1993) and the INTCAL04 data set (Reimer *et al.*, 2004), and then their mean calibrated ages were linearly interpolated versus depth (Figure 2). The oldest date (746 cm depth) has an estimated age of $\sim 11\,030$ cal. yr BP. A constant sedimentation rate of 0.40 mm/yr was extrapolated below 746 cm, providing an age of 12 200 cal. yr BP at 800 cm depth. The Lago Piccolo di Avigliana depth–age model is based on nine calibrated dates and a Lowess interpolation (Figure 2; Finsinger and Tinner, 2006).

Detection of human impact on vegetation is based on the abundance of selected anthropogenic indicators following Behre (1981): *P. lanceolata*, *Rumex* type (including *R. acetosa* t. and *R. acetosella*), *Urtica*, *Potentilla* t., *Thalictrum* and *Humulus* type (*Humulus* and *Cannabis sativa*), which have been proven to be useful in our study area (eg. Valsecchi *et al.*, 2006).

Time-series analysis: cross-correlations

We used cross-correlations because this kind of time-series analysis allows the detection of relationships between independent variables for various time lags. The presence of statistically significant correlations and lags provides evidence for direction and rates of succession (Clark *et al.*, 1989). Cross-correlations were applied between microcharcoal accumulation rates (CHAR) and pollen percentages to analyse the influence of fires on vegetation, and between pollen pairs to analyse vegetation response to human impact.

The analysis of time series is based on the following basic assumptions: (1) all time intervals between adjacent samples are equal; and (2) the data are stationary and thus have no trends in mean or variance in the series (Green, 1983; Clark *et al.*, 1989). The sediment accumulation rate for time intervals during which pollen-inferred *F. sylvatica* population expansions occurred is nearly constant (Figure 2). Therefore, a contiguous sampling was applied to the sediment archives in order to fulfil assumption (1) and to obtain charcoal records without gaps, thus allowing the reconstruction of an uninterrupted fire record. Cross-correlations were subsequently calculated for time-intervals during which pollen-inferred *F. sylvatica* population expansions occurred, ie, for two time-intervals at Lago di Fimon (FIM I: 7300–6400 cal. yr BP, and FIM II: 5600–4800 cal. yr BP), and for one time-interval at LPA (AVP I: 5300–4600 cal. yr BP). Within these three time-intervals the estimated time resolution of sediment samples is almost constant: 21 ± 4 and 23 ± 5 calibrated years for phases FIM I and FIM II, and 18 ± 1 calibrated years for phase AVP I, respectively.

Changes in pollen percentages, concentrations and pollen accumulation rates are generally in good agreement (Figure 3). Hence, in order to avoid the possibility that common trend (eg. changes in sedimentation rate) might control the correlations, pollen percentages were chosen for statistical comparison with CHAR (Clark *et al.*, 1989). Because in our time series some variables contain a marked trend, they were linearly de-trended prior to analysis and marked with an asterisk (eg. *Fagus**) to avoid spurious correlations. The span of the cross-correlations was restricted at ± 10 lags for phase FIM I and at ± 9 lags for phases FIM II and AVP I, resulting in a maximum time lag of $c. \pm 220$ years for both lakes, following Green (1983). The 0.05 level of significance was estimated by computing ± 1.96 standard errors of the correlation coefficients (test two-sided, null hypothesis $H_0: r = 0$).

Results and interpretation

Lateglacial and Holocene vegetation dynamics at Lago di Fimon

At the base of the sequence (Figure 4), *c.* 12 000 cal. yr BP, tree pollen (*Betula*, *Pinus sylvestris* t., *Quercus* deciduous t. and *Ulmus*), and herb pollen (eg. *Artemisia* and Poaceae) were abundant. The woodlands were thus dominated by thermophilous deciduous trees along with pine. The marked decrease of *Quercus* deciduous t. and *Ulmus* and the increase of *Betula*, *Juniperus*, *Artemisia* and Chenopodiaceae pollen between $\sim 11\,800$ and $\sim 11\,200$ cal. yr BP indicates the vegetation change in response to the Younger Dryas climatic shift, which has been detected in pollen records at most sites in the southern Prealps (eg. Tinner *et al.*, 1999; Gobet *et al.*, 2000; Finsinger and Tinner, 2006; Wick and Möhl, 2006). The subsequent gradual increase of *Quercus* deciduous t., *Ulmus* and *Corylus* and the decrease of *Betula* and *Pinus sylvestris* t. pollen starting from $\sim 11\,200$ cal. yr BP (zone FIM 2) mark the pollen-inferred vegetation response at the onset of the Holocene. The pollen data suggest the presence of deciduous

LAGO DI FIMON (Vicenza, 23 m a.s.l.)
 Pollen percentage diagram
 Selected taxa
 Analyst: V. Valsecchi

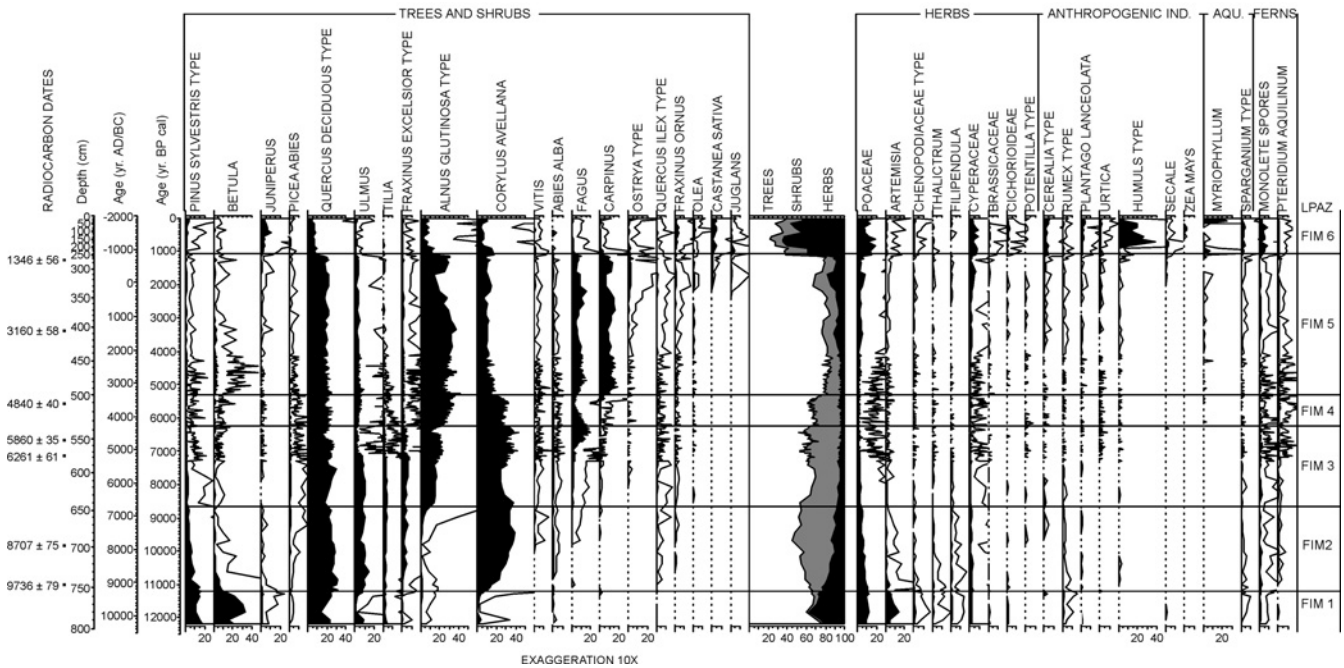


Figure 4 Lateglacial and Holocene pollen stratigraphy of Lago di Fimon. Only selected pollen types are shown

forests dominated by hazel, oak and thermophilous trees near the lake. At Lago di Fimon the continuous curve of spores of the fire-favoured and fire-prone *Pteridium aquilinum* (Moore *et al.*, 1991; Tinner *et al.*, 1999) points to disturbances starting at ~11 000 cal. yr BP. Low pollen percentages (<1%) of *Fagus* are continuously recorded after ~9600 cal. yr BP. At *c.* 8500 cal. yr BP (onset of zone FIM 3) a marked increase of *Alnus glutinosa* t. pollen and a subsequent slight decline of *Corylus* pollen probably indicates a shift to more humid conditions, as suggested for similar vegetation changes in the southern Prealps (Tinner *et al.*, 1999; Gobet *et al.*, 2000; Finsinger *et al.*, 2006). Between 7300 and 6400 cal. yr BP, *Fagus* pollen gradually increased (up to 20%; Figures 3 and 4). During this time-interval a more intense disturbance regime is inferred from the sudden increase of *Pteridium aquilinum* spores and the continuous presence of *Urtica* pollen. This evidence coincides with the ages of ¹⁴C dates obtained from the pile-dwelling settlement in Molino Casarotto (Figure 1). Other anthropogenic indicators (eg, *Plantago lanceolata*), however, do not show significant changes in abundance. *Fagus* pollen abundance decreased between ~6200 and 5300 cal. yr BP (zone FIM 4) and increased again at ~5300 cal. yr BP (Figures 3 and 4). This second *Fagus* wave was paralleled by the increase of *Carpinus* (up to 18%) and of *Betula* pollen (onset of zone FIM 5). After 5300 cal. yr BP two phases characterized by increases of herb pollen occurred. The first phase is dated between ~3900 and 3100 cal. yr BP and was likely related to human activity during the Bronze Age, while the second phase likely occurred during the Late Iron Age (~2400–1350 cal. yr BP). A further change in the vegetation cover is marked by the appearance of *Castanea sativa* and *Juglans* pollen grains after ~2200 cal. yr BP (270 yr BC), which indicates the presence of sweet chestnut and walnut during the Iron Age in the southern forelands of the Alps (Conedera *et al.*, 2004; Finsinger and Tinner, 2006). After ~AD 850 (1100 cal. yr BP) herb pollen and several anthropogenic indicators (eg, *Humulus* t., *Cerealia*, *Secale*, *Plantago lanceolata* and *Urtica*) markedly increased. Pollen-inferred vegetation indicates that the mixed-oak

forest was displaced by more open vegetation as a result of more intensive land use.

Holocene vegetation dynamics at Lago Piccolo di Avigliana (LPA)

Since Holocene vegetation dynamics at this site have already been discussed in a previous publication (Finsinger and Tinner, 2006), only the vegetational changes that occurred during the *F. sylvatica* population increase are presented (Figure 3). Vegetation was dominated by deciduous *Quercus deciduous* t., *Corylus* and *Alnus glutinosa* t., with *Fraxinus excelsior* t., *Ulmus* and *Tilia* being present at lower densities until ~5100 cal. yr BP (Figure 3). The forest was likely closed with some open patches, as inferred from constantly low herb pollen values. However, discontinuous and faint disturbances by fire can be inferred from the charcoal record and from short-term increases of *Pteridium* spores (*c.* <200 years). Between *c.* 5200 and 4900 cal. yr BP higher *Corylus* pollen values likely point to a vegetation response to openings in the forests. During the time interval when *Fagus* pollen percentages increase (ie, ~5100–4700 cal. yr BP), *Corylus* pollen values decrease, the amplitude and frequency of changes in *Pteridium* spore abundance decrease, and herb pollen values are comparable with the period before the *F. sylvatica* population expansion. Overall, the tree pollen curve has a saw-tooth shape: a sharper decrease 5150–5050 cal. yr BP and a more gradual increase 5050–4700 cal. yr BP, possibly indicating a disturbance followed by a gradual population growth.

Discussion

Defining the timing of the population expansions of *Fagus sylvatica*

The 'empirical limit' is defined as the point at which pollen of a taxon becomes consistently present in consecutive samples while the 'rational limit' is defined as the point at which the pollen curve begins to rise to sustained high values (eg, Watts, 1973). Conventionally,

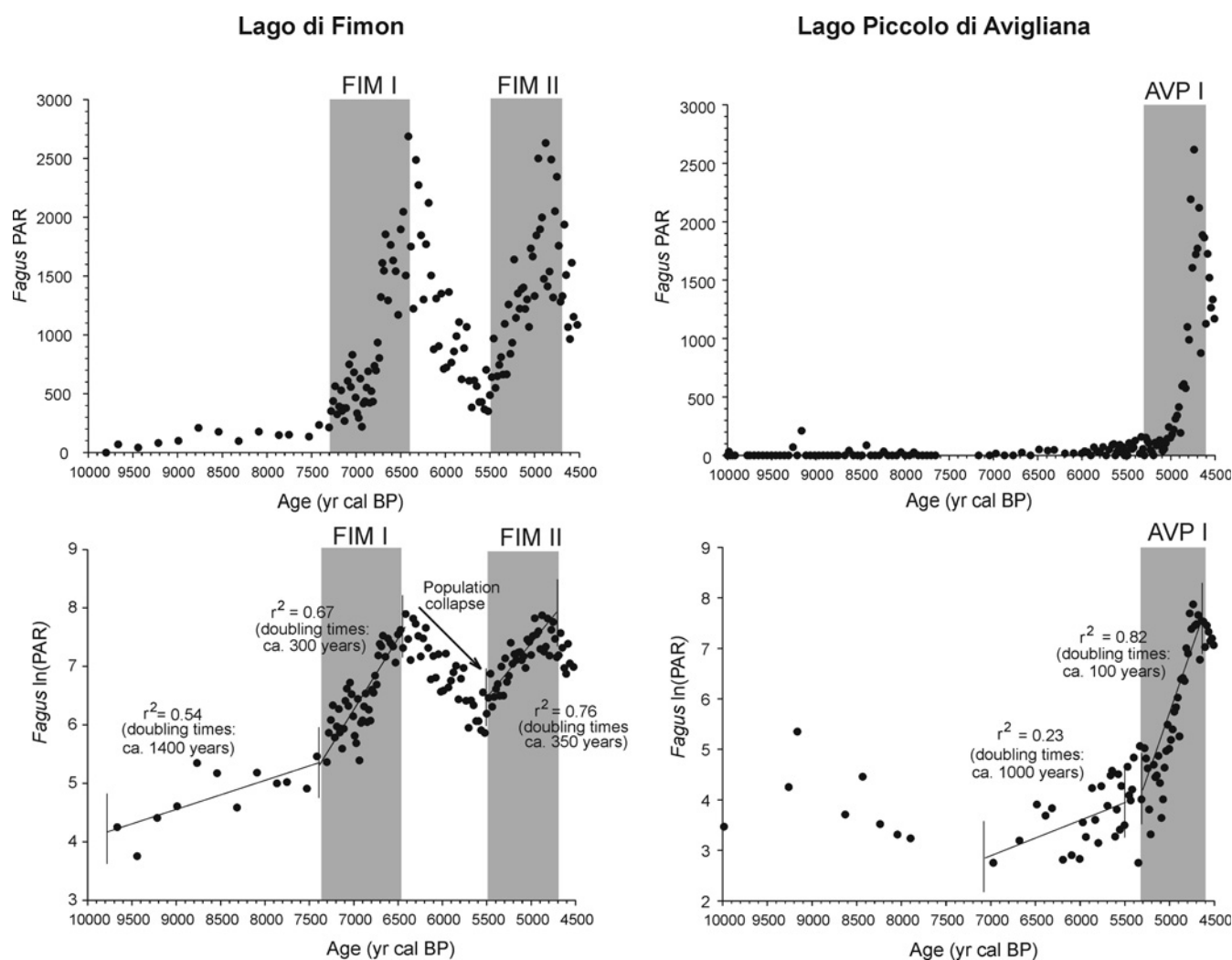


Figure 5 Scatter plots illustrating pollen accumulation rate (PAR) of *Fagus* pollen (top panel) and ln-transformed PAR (*Fagus* ln(PAR); bottom panel) for Lago di Fimon (left) and for Lago Piccolo di Avigliana (right). Continuous lines in the bottom panel are linear regression of *Fagus* ln(PAR) versus age, indicating the rise in PAR best-fit exponential models. The increase of *Fagus* ln(PAR) can be split into two stages characterized by different population doubling times. Grey boxes indicate main population expansion phases of *F. sylvatica*

these limits or threshold values (eg, 0.5%, 1%) are used to infer past plant dynamics such as, eg, tree arrival, establishment and population expansions (eg, Watts, 1973; Birks, 1989; Lang, 1994; Magri *et al.*, 2006). Population mass expansions have been conventionally associated with the rational limit of the pollen curve (Lang, 1994), while the empirical limit of the pollen curve was used to estimate the first local presence of *F. sylvatica* populations (eg, Birks, 1989).

Bennett (1985) suggested that the exponential increase of pollen-accumulation rates (PAR) more than pollen percentages reflects the abundance of past plant populations because such values are not interdependent on relative abundances of other pollen types. The exponential increase of a plant population can then also be expressed by means of its population doubling times (eg, Bennett, 1983). Following this approach, we define the time intervals during which the main population expansion occurred (ie, phases during which population doubling times were shortest) by fitting linear regressions through the ln-transformed *Fagus* PAR (*Fagus* ln(PAR); Bennett, 1983) versus time, and selecting the time-interval that explained the highest variance (r^2 ; Figure 5). The doubling times of *F. sylvatica* populations at Lago di Fimon and at LPA, as inferred from pollen PAR, appear to be very different (Figure 5). During phases FIM I and FIM II, *F. sylvatica* expansions had slower doubling times (eg, ~300–350 years) than the population expanding at LPA (~100 years). We exclude the

possibility that the differences in doubling times are due to uncertainties in the depth–age models of the two sediment cores, because trends in percentages and PAR values are comparable (see Figure 8).

At Lago di Fimon, the main population expansion identified by means of this procedure has an age of 7300–6400 cal. yr BP and yielded an r^2 value of 0.67 (phase FIM I). We identified a second expansion phase at 5500–4700, where *F. sylvatica* re-expanded after a marked decline, by calculating a second regression equation that yielded a r^2 value of 0.76 (phase FIM II, Figure 5). At LPA, the main population expansion of *F. sylvatica* occurred at 5300–4600 cal. yr BP ($r^2 = 0.82$; AVP I, Figure 5). Since population growth rates before the main expansion phases (ie, FIM I and AVP I, see Figure 5) were much lower (population doubling times *c.* 1400–1000 yr), we infer a break in rates of population increase at the onset of the main expansion phases. Such changes in doubling times could have many explanations, including a climatic shift or increased disturbance by forest fires (either natural or anthropogenic). In addition to the effects of these factors, we also discuss the influence of intrinsic biotic factors such as migrational lags or genetic adaptation on the timing of the population expansions at the two sites, because these factors may also have had an influence on the spreading history and the population expansion of *F. sylvatica* (eg, Birks, 1989; Lang, 1994).

Lago di Fimon (FIM I)

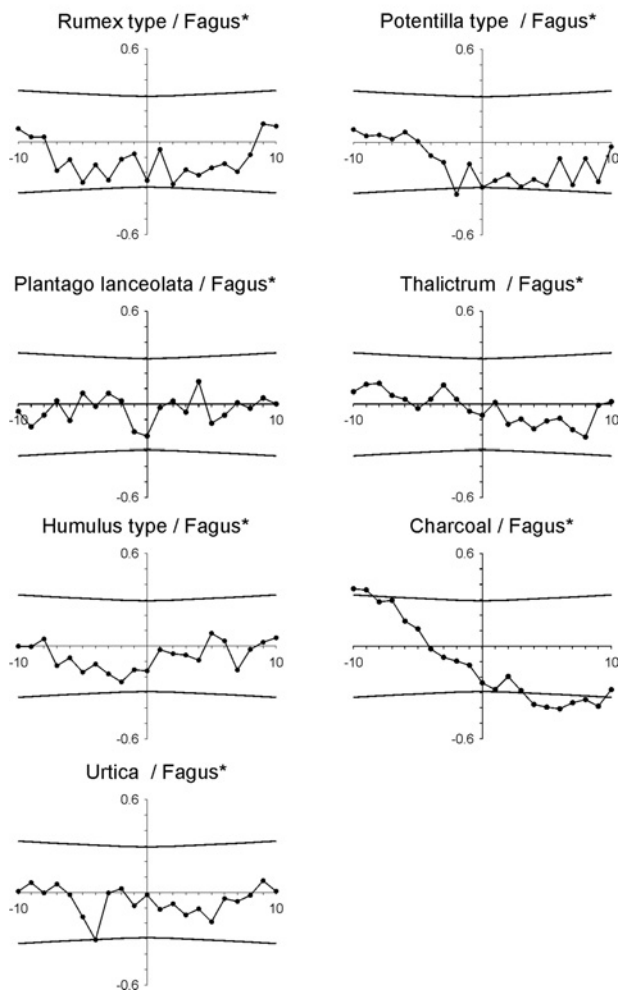


Figure 6 Selected cross-correlograms for Lago di Fimon (time period 7300–6400 cal. yr BP), pollen percentage versus *Fagus** (* is linearly detrended) percentage, and charcoal-accumulation rate versus pollen percentage. The x-axis indicates the lag (point) = ~ 23 yr (± 10 lags correspond to $\pm \sim 230$ yr); the y-axis is the coefficient of the correlation. Significance levels indicated by horizontal lines

Influence of intrinsic biotic factors

It has been suggested that the modern populations of *F. sylvatica* in the southern Prealps may originate from refugia (ie, regions where populations survived the glacial conditions) in Croatia and Slovenia (eg, Willis and van Andel, 2004; Magri *et al.*, 2006). These refugia also contributed to the recolonization of *F. sylvatica* in Central Europe. At present we do not know if the delayed population expansion in the southern Prealps was caused by genetic adaptation to the different climatic conditions (Davis and Shaw, 2001). Because immigration of a taxon into an area was the precondition for population growth, we first consider migrational lags between the two sites. Although in the southern Prealps a unidirectional spread from the east to the west occurred (eg, Magri *et al.*, 2006), at first glance the timing of population expansion is not dependent on the distance from the refugia. In Croatia and Slovenia, where full-glacial *Fagus* macrofossil charcoals have been identified (Šandalja; Willis and Van Andel, 2004), the pollen increase occurs at ~ 9000 cal. yr BP (Ledine and Mlaka; Culiberg and Sercelj, 1996; Andrić and Willis, 2003), while at Lago di

Fimon, which lies *c.* 250 km west of Slovenia, its population expansion took place ~ 2000 years later (~ 7300 cal. yr BP; Figure 1). As inferred from the rational limit in pollen records from sites in the central sector of the southern Prealps (~ 200 km away from Fimon, Figure 1), the population expansion is dated at Lago di Annone (Wick and Möhl, 2006) to ~ 6000 cal. yr BP, while at Lago del Segrino, Lago di Origlio and Lago di Muzzano (Figure 1) it is dated to ~ 5300 – 5000 cal. yr BP (Tinner *et al.*, 1999; Gobet *et al.*, 2000). The latter coincide with the age of the expansion at LPA, located in the western sector of the southern Prealps (~ 300 km from Fimon). If a migrating front moving from east to west is considered (Magri *et al.*, 2006), the population expansion of *F. sylvatica* should have crossed LPA later than the central sector of southern localities and not be almost simultaneous. In addition, the continuous pollen curve of *Fagus* prior to the population expansion (see Figure 4 for Lago di Fimon) likely points to the local presence of the tree at low population densities about 2000 years prior to its population expansions at many localities in the southern Prealps (this study and other sites, eg, Lago di Origlio and Lago di Annone, Figure 1; Tinner *et al.*, 1999; Wick and Möhl, 2006) as well as in Europe (Giesecke *et al.*, 2007).

Finally, the heavy seeds of *F. sylvatica* were unlikely at a disadvantage through its migration speed, because other trees producing heavy seeds expanded earlier in the Lateglacial and early Holocene (eg, *Corylus* and *Quercus*, Finsinger *et al.*, 2006) and because *F. sylvatica* is bird-dispersed, which makes rare but long dispersal-jumps highly probable (Bennett, 1988; Clark, 1998). We can therefore reject the hypothesis that migrational lag is a cause of differences in the timing of population expansion of *F. sylvatica* at the two sites.

Influence of human impact and of forest fires

The three intervals of fastest doubling-times (FIM I, FIM II and AVP I) obtained by fitting linear regressions through the *Fagus* ln(PAR) data were chosen for the cross-correlations, for they represent the phases during which the *F. sylvatica* populations were rapidly growing (Figure 5). We tested whether pollen-inferred human impact and microcharcoal-inferred fire disturbance influenced the population expansions of *F. sylvatica* at the two sites. Change in frequency of forest fires may be due to natural or anthropogenic factors. In the Alps natural ignition sources are lightning, and the fire frequency is controlled by moisture conditions and dependent on the flammability of species (Carcaillet, 1998).

At the onset of phase FIM I (7300–6400 cal. yr BP, Figures 3 and 5), *Ulmus*, *Tilia* and *F. excelsior* slightly declined before the first increase of *Fagus* pollen. During this phase, human–vegetation interactions likely occurred at Fimon because a well-dated Neolithic settlement had been present at ~ 2 km from the lake since 6900 cal. yr BP (Bartolomei *et al.*, 1986). In effect, human impact is depicted during this phase by *Urtica* pollen, which increased after the beginning of phase FIM I. The influence of human impact on the abundance of *Fagus* shows no statistically significant correlation for some anthropogenic indicators (ie, *Rumex* t., *Thalictrum* and *Plantago lanceolata*; Figure 6). *Urtica* and *Potentilla* t. pollen reveal weak significant negative correlation at negative lags. These correlograms may indicate that pollen-inferred human impact did not play an essential role in the expansion of *F. sylvatica*. On the other hand, we found a significant negative correlation between microcharcoal and *Fagus* at positive lags (lag 4, corresponding to ~ 80 yr). The latter indicates that a decrease in forest fires allowed the FIM I population expansion of *F. sylvatica*. The significant positive correlation at lag -9 between microcharcoal and *Fagus* seems too early (190 yr) to plausibly have any relation. Higher abundance of microcharcoal at the beginning of phase FIM I occurred when *Fagus* pollen percentages were low (Figure 3). We do observe that when charcoal values

Lago di Fimon (FIM II)

Lago Piccolo di Avigliana (AVP I)

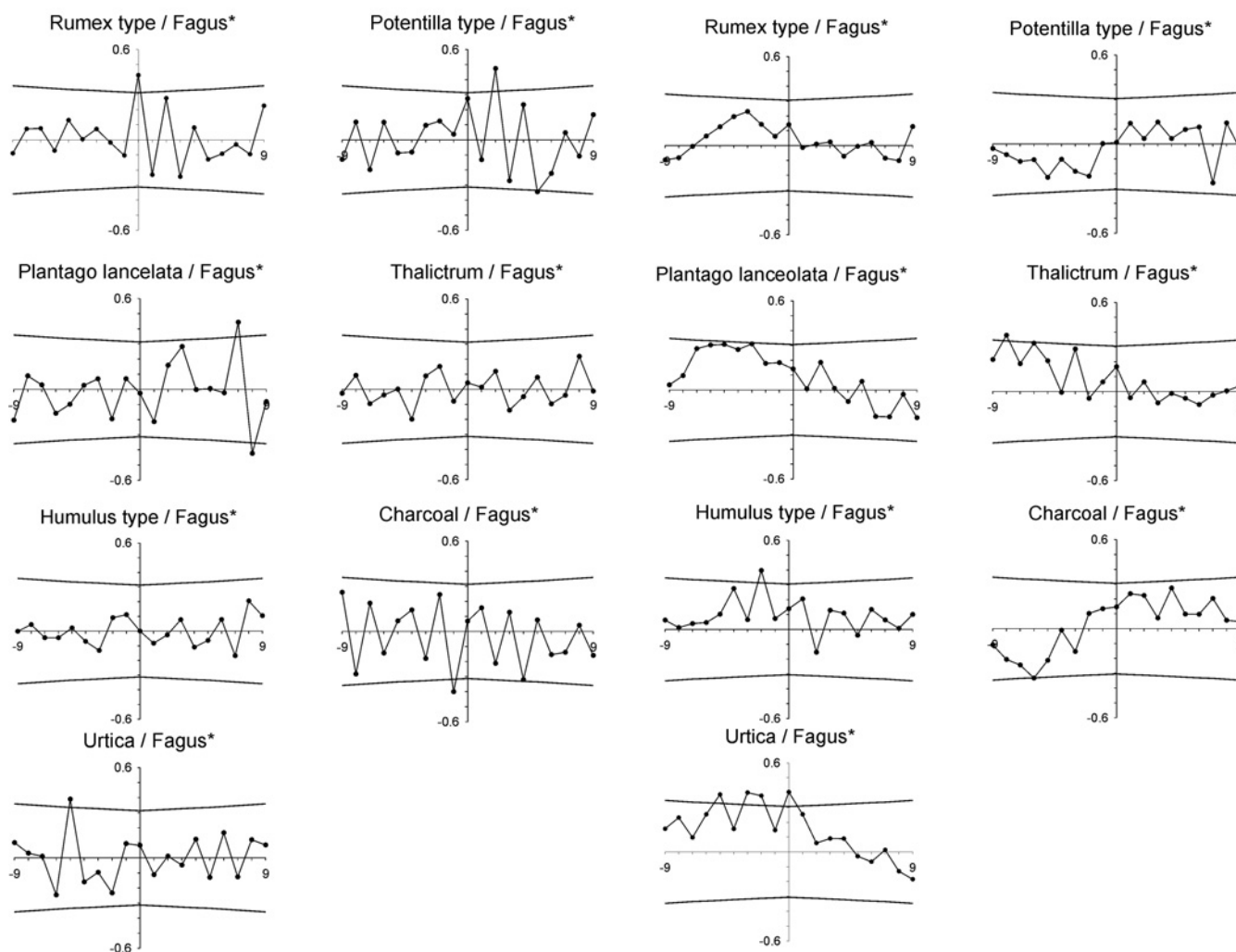


Figure 7 Selected cross-correlograms for phases FIM II (5500–4700 cal. yr BP) and AVP I (5300–4700 cal. yr BP), pollen percentage versus *Fagus** (* is linearly detrended) percentage and charcoal accumulation rate versus pollen percentage. The x-axis indicates the lag (point) (~18 yr for LPA, ~23 yr for FIM II), the y-axis is the coefficient of correlation. Significance levels indicated by horizontal lines

decreased to background values (about 6800 cal. yr BP) *Fagus* pollen percentages increased. It is, however, unlikely that the population expansion of *F. sylvatica* was caused by a reduction of forest fires because previous to its expansion charcoal-inferred fires were as low as during FIM I. It seems more likely that decreased forest fires during the phase FIM I may have facilitated but not triggered the expansion of *Fagus*.

Between the phase FIM I and FIM II (ie, 6400–5500 cal. yr BP) *Fagus* pollen gradually declined to extremely low values (~2%), indicating a slow collapse of its population within a millennium (Figures 3 and 5). The tree-pollen sum also decreases, and the increase of pollen of the light-demanding shrub *Corylus* (zone FIM 4; Figure 4) sustains the interpretation of a collapse of the shade-tolerant *Fagus* forest. Charcoal concentration, CHAR and *Pteridium* spores also increase, indicating an increase in forest fires and a response of terrestrial vegetation to this disturbance during this phase characterized by low *Fagus* percentages and PARs (Figure 3).

During phases FIM II (5500–4700 cal. yr BP; Figure 3) and AVP I (5300–4700 cal. yr BP; Figures 3 and 5), the light-demanding *Corylus* was replaced by the shade-tolerant *F. sylvatica*. At Lago di Fimon, correlograms of *Rumex* t., *Potentilla* t. and

P. lanceolata for FIM II show significant positive correlation with *Fagus* at time lags 0, 2 and 7, respectively (Figure 7), suggesting that human impact favoured the expansion of *F. sylvatica*. On the other hand, the cross-correlogram between *Urtica* and *Fagus* indicates that human impact as inferred from this pollen-type did not significantly favour the expansion of *F. sylvatica*. The correlogram between microcharcoal and *Fagus* shows a significant negative correlation at lag -2, suggesting that *F. sylvatica* was not favoured by fire events during this phase.

During the *F. sylvatica* population expansion at LPA, the correlogram of *Urtica* shows a positive correlation with *Fagus* at 0 lags, suggesting occurrence of peaks of *Urtica* and *Fagus* pollen at the same time. This suggests that a slight human disturbance occurred during the time of the *F. sylvatica* expansion (Figure 7). The correlogram of microcharcoal versus *Fagus* shows no significant correlation, thus revealing that forest fires possibly had a marginal, if any, influence on the *F. sylvatica* population expansion.

We could hypothesize that a decrease in forest fires (phase FIM I) and the occurrence of human impact (FIM II and LPA) favoured the expansion of *F. sylvatica*. These results are partly in agreement with those of palaeoecological analyses in northern Europe, where a close connection between *F. sylvatica* establishment and

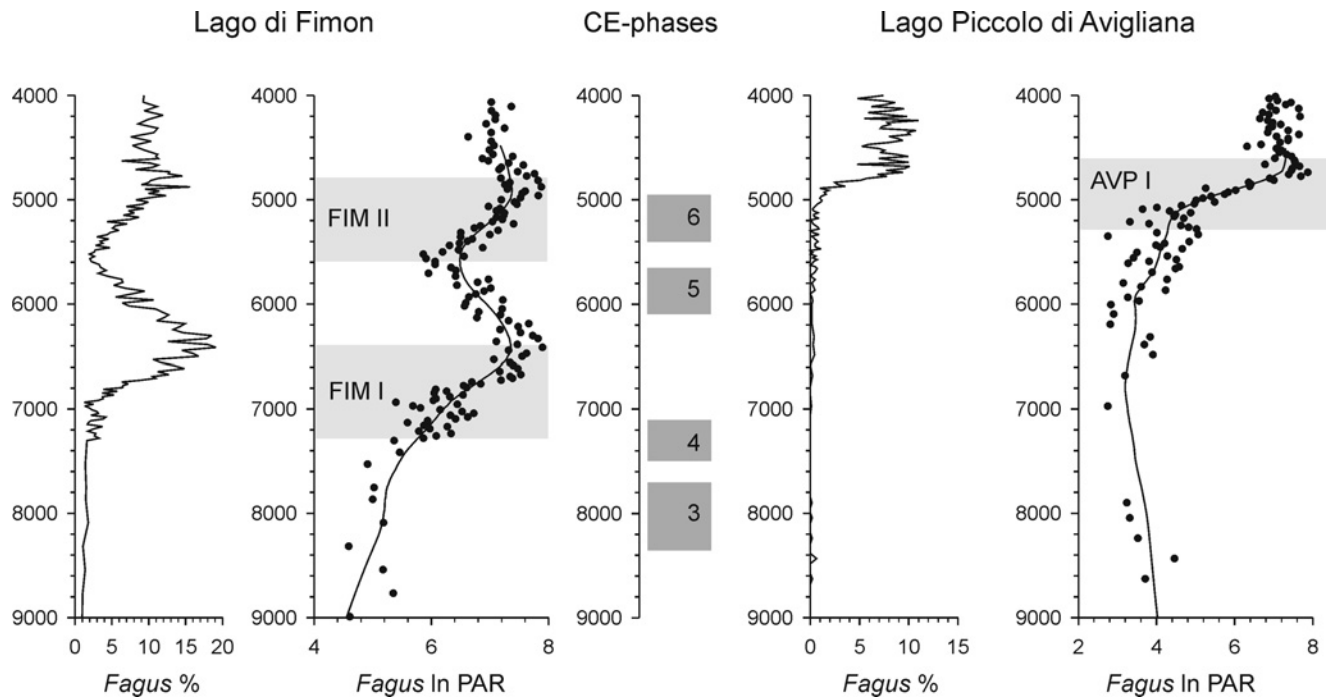


Figure 8 Comparison between changes in *Fagus* pollen abundances in the southern Prealps (Lago di Fimon and Lago Piccolo di Avigliana) and climatic proxies: CE-phases (cold and wet phases after, Haas *et al.*, 1998, labelled with numbers). FIM I, FIM II and AVP I indicate main population expansion phases of *F. sylvatica* (see Figure 5 and text for details)

disturbance factors such as fire episodes and human clearing was indicated by palaeoecological investigations (Björkman and Bradshaw, 1996; Ralska-Jasiewiczowa *et al.*, 2003; Bradshaw and Lindbladh, 2005).

Influence of climate change

As shown by multiproxy reconstructions from the Alps and their northern forelands (CE-Events, ie, cold and wet phases in Central Europe, Haas *et al.*, 1998), summer climatic conditions changed in the Alpine region during the periods when the *F. sylvatica* populations expanded at Lago di Fimon and at LPA (Figure 8). Since the frequency of forest fires is also influenced by moisture conditions, it is likely that during cool and wet phases a general decrease of forest fires occurred.

We assume a dynamic equilibrium between biotic responses of *F. sylvatica* and climate (Webb, 1986) and, therefore, allow a time lag of at least a few hundred years, as has been also suggested for eastern North America (Prentice *et al.*, 1991). Moreover, the accuracy of the chronologies of our data and of the palaeoclimatic reconstructions is restricted to the limits of the radiocarbon-dating approach, resulting in age uncertainties (95% confidence intervals) of *c.* ± 100 –300 years, if the errors of radiocarbon measurement, radiocarbon calibration and the calculated age–depth relationships are taken into account.

A climatic influence on the abundance of *F. sylvatica* populations has been shown by numerous previous studies. On a continental scale, climatic variables and their changes in time seem to have an influence on the present distribution as well as the Holocene history of *F. sylvatica* and *F. grandifolia* (the European and North American species, respectively, Huntley *et al.*, 1989; Prentice *et al.*, 1991; Sykes *et al.*, 1996). At the single-tree scale, evidence from tree-ring studies showed that growth at its southern range is reduced in response to dry summer climate (Piovesan and Schirone, 2000; Jump *et al.*, 2006). In addition, at its northern range (or at higher altitude) it is limited by growing-season length because of its sensitivity to late (spring) frosts (Lang, 1994).

Without taking into account the dating uncertainties, the population expansions (ie, 7300 cal. yr BP at Fimon and 5250 cal. yr BP at AVP, Figure 8) fall into CE-4 and CE-6, respectively (Haas *et al.*, 1998). However, local presence of the tree at low population densities about 2000 years prior to its population expansions is shown by the continuous pollen curve at both sites (Figure 8). This indicates that the population expansions have not been favoured by previous cold and wet phases (ie, CE-3 at Fimon and CE-5 at LPA). We therefore conclude that favourable climatic conditions (as inferred from the CE-event records) were a determinant but not the only factor for the population expansion of *F. sylvatica*.

On the other hand, climatic conditions might have been crucial for the difference in timing of the first population expansion of *F. sylvatica* at LPA and at Lago di Fimon. At present there is a difference of *c.* 300 mm/yr mean annual precipitation between the two sites. If this difference persisted throughout the study period, it may explain why *F. sylvatica* expanded later at LPA and at the time of the second population expansion at Fimon.

Conclusions

Pollen and microcharcoal records from two sites located in the southern Prealps (Lago di Fimon and Lago Piccolo di Avigliana) were analysed at high temporal resolution to study the response of *F. sylvatica* to human impact, forest fires and climate change. The timing and duration of the main population expansions were determined by means of changes in population doubling times, while the influence of human impact and forest fires were estimated by time-series analyses. The influence of climatic change is addressed by comparison with climatic proxies. At Lago di Fimon the mass expansion of *Fagus* (FIM I: 7300–6400 cal. yr BP) was followed by a collapse and a subsequent re-expansion (FIM II: 5500–4700 cal. yr BP), while at Lago Piccolo di Avigliana the mass expansion occurred later and was not followed by a drastic collapse of the species (AVP I: 5300–4700 cal. yr BP).

It is likely that population expansion of *F. sylvatica* was favoured by climatic change, because we observed that *F. sylvatica* expanded at both sites during cold and wet climatic phases (CE-events). Results of cross-correlations indicate that *Fagus* expanded at Lago di Fimon after forest fires decreased (FIM I), while fires had no statistically significant influence during its mass expansion during FIM II and AVP I. Human impact, instead, as inferred from anthropogenic pollen indicators, seems to have increased prior to or at the same time as the *Fagus* increases during FIM II and AVP I, respectively. We could therefore hypothesize that disturbance of the forest created small openings that were first rapidly colonized by light-demanding plants (eg. *Corylus* and *Pteridium*), later replaced by the more shade-tolerant *F. sylvatica*. These results are partly in agreement with results of palaeoecological analyses in northern Europe, where a close connection between *F. sylvatica* establishment and disturbance factors was indicated by palaeoecological investigations.

Taken together our study suggests that at some sites in Europe the expansion of *F. sylvatica* populations has been triggered by more than one single factor alone. In particular, it provides evidence that combined effects of climatic change and human impact might have been decisive in our region, the southern Prealps. The role of human impact documented in our records underscores the need to consider future land-use changes and disturbance when forecasting the response of *F. sylvatica* to climatic change scenarios.

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