ORIGINAL ARTICLE

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The mid-Holocene extinction of silver fir (*Abies alba*) in the Southern Alps: a consequence of forest fires? Palaeobotanical records and forest simulations

Abstract   Pollen records suggest that *Abies alba* played a dominating role in both the montane and lowland forests at the border of the Southern Alps between ca. 8500 and 5700 years ago. Two major declines in fir, at about 7300–7000 cal B.P. and at ca. 6000 cal B.P., followed by the local extinction of the species are characteristic of the area below ca. 1000 m a.s.l. In order to test the impact of fire on the population dynamics of silver fir, a dynamic model (DisC-Form) with a fire module was applied to simulate the early- and mid-Holocene forest development. Simulation outputs based on different fire scenarios were compared with the pollen record from Lago di Annone (226 m a.s.l.). The marked *Abies* decreases shown in the pollen record can be simulated with very intensive fire scenarios, but they do not result in an extinction of silver fir in the model. Low charcoal influx values related to the *Abies* declines in the palaeobotanical record suggest that fire was not the only reason for the extinction of silver fir. Human impact, as well as Holocene climatic changes leading to temporary moisture deficits and reduced adaptability due to low genetic variation may have had a significant impact on the *Abies* forests.

Keywords   Northern Italy · Abies alba · Pollen analysis · Charcoal · Fire history · Dynamic forest model

Introduction

Silver fir (*Abies alba* MILL.) in the Southern Alps has had a rather dramatic history, which may be attributed to natural and/or anthropogenic causes. Pollen records suggest that *Abies alba* was a major constituent of the forests on the

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southern slopes of the Alps down to the Po Plain between about 9000 and 6000 cal B.P. (Schneider 1978; Schneider and Tobolski 1985; Wick 1989; Tinner et al. 1999). Natural stands of silver fir today are restricted to the upper montane zone, i.e. to the belt between 1000 and 1700 m a.s.l. (Brändli 1998). The species is considered to be sensitive to atmospheric or soil drought during the growing season and to be less competitive on calcareous soils (Lévy and Becker 1987; Becker 1989; Guicherd 1994). While the reason for the silver fir decline is not clear, all data suggest that the species disappeared as a response to unfavourable environmental conditions, which caused more or less simultaneous *Abies* decreases at about 7000 and 6000 cal B.P. (Zoller 1960; Schneider 1978; Schneider and Tobolski 1985; Wick 1989, 1996a; Tinner et al. 1999; Gobet et al. 2000). Reasons suggested for the extinction of *Abies* include fire, climatic change, and increasing anthropogenic pressure (Schneider and Tobolski 1985; Wick 1989; Tinner et al. 1999).

The influence of various biotic and abiotic factors on the vegetation has been determined by comparing pollen records with forest development scenarios generated with dynamic models (Lotter and Kienast 1990; Lischke et al. 2000; Keller et al. 2002). Whereas Keller et al. (2002) used the dynamic model DisCForm to simulate Holocene vegetation development at Lago di Annone (226 m a.s.l.) with respect to climate and migrational processes, the emphasis of our study is placed on the population dynamics of silver fir and the role of fire. With the aim of assessing the importance of fire as a cause for the mid-Holocene silver fir decline, the DisCForm model was extended by fire scenarios based on subfossil charcoal records from nearby lakes (Tinner et al. 1999) and the simulation outputs were compared with the pollen record from Lago di Annone.

The study site

Lago di Annone (226 m a.s.l., Fig. 1) is one of several lakes situated near the southern end of Lago di Como (Northern Italy), in the transitional zone between the southern slope
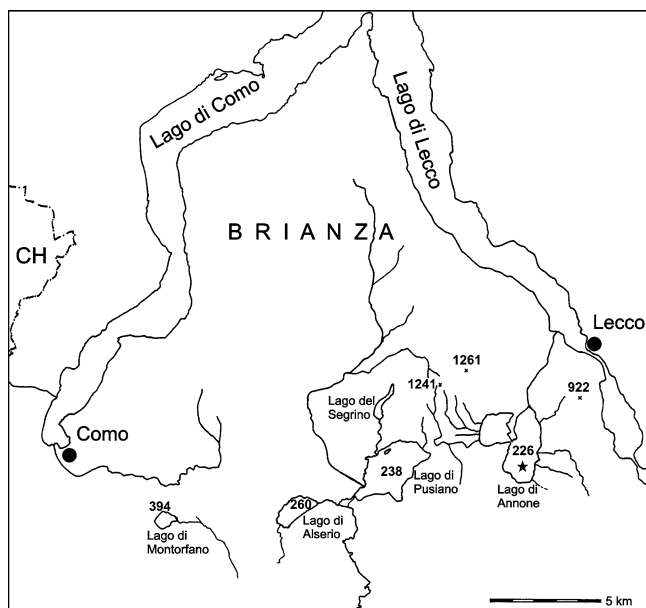
Fig. 1 Study area; the location of the sediment core AN-2 is marked by an asterisk

of the Alps and the Po plain. The lake has a water surface of 5.5 km^2, a maximum water depth of about 14 m, and a catchment area of 22.5 km^2. The two-part basin is close to Monte Barro (922 m a.s.l.) to the north-east and Monte Rai (1261 m a.s.l.) and Monte Cornizzolo (1241 m a.s.l.) to the north and north-west.

Lago di Annone is situated in the warm-temperate Insubrian climate, characterised by mild and fairly dry winters and high summer precipitation. The bedrock geology around the lake is mainly formed by Mesozoic carbonates, i.e. Cretaceous flysch. Little is left of the natural vegetation in this area; the forests on the slopes of Monte Barro and Monte Rai mainly consist of *Castanea sativa*, *Quercus pubescens* and *Alnus glutinosa*. *Fraxinus ornus* and *Ostrya carpinifolia*, two characteristic taxa of this submediterranean vegetation complex (Oberdorfer 1964), usually occur in successional forests on abandoned meadows and pastures. The forests above 800–1000 m a.s.l. are dominated by *Fagus sylvatica*.

Methods

Pollen and charcoal analysis

The palaeobotanical investigations were made on a sediment core taken with a modified Livingstone piston sampler in about 6 m of water depth (Fig. 1). For pollen analysis the core was sampled every 2.5 cm and the material (1 cm^3) was treated using standard methods. Tablets with a constant concentration of *Lycopodium* spores added to each sample facilitated the calculation of pollen influx (Stockmarr 1971). For the analysis of macroscopic charcoal, the sediment core was cut into slices of 2.5 cm thickness with an average volume of about 70 cm^3 and sieved through

a 0.2 mm mesh. Spreadsheet calculations and pollen diagrams were made with the programs Tilia and Tilia × graph (Grimm 1992). Pollen percentage values are based on the total pollen sum of terrestrial taxa in the pollen diagrams and on the pollen sum of the tree taxa included in the forest model for comparison with the simulation outputs. The time scale attached to the pollen and charcoal record is based on 19 calibrated radiocarbon dates made on terrestrial plant macrofossils (Wick, in prep.). All the dates mentioned in the text are calibrated years B.P. Sampling resolution in the period of interest is about 50 years and therefore lower than in the study of Lago di Origlio (11 years) and also lower than that suggested for long-term fire-ecological studies by means of pollen and charcoal (5–10 years, Birks 1997). However, since the sediment core was continuously sampled for charcoal, we assume that our sampling resolution is sufficient to detect the main fire effects on vegetation around Lago di Annone.

The vegetation model

The forest model we used is an extended version of the DisCForm model (Lischke et al. 1998; Löffler and Lischke 2001) that was derived from the forest gap model ForClim (Bugmann 1994, 1996). Whereas the traditional gap-model approach focuses on single trees, DisCForm is a distribution-based model, i.e. it summarises the tree-population densities in several height classes, and represents spatial variability by theoretical descriptions of the tree density distribution (Poisson distribution) in each height class. From the tree population densities in the different height classes the biomass per species in tons per hectare (t/ha) is estimated.

As model input data, site-specific data for bioclimatic variables, immigration dates, regional fire history and human impact were used. To avoid any kind of circularity, the model input is not based on palaeoecological data from Lago di Annone. Details of the model as well as of the climate and the immigration input are given by Keller et al. (2002).

The fire and human impact modules

In order to simulate the impact of fire and human activity in the catchment of Lago di Annone, two sub-models (modules) were added to DisCForm. The fire module includes a fire-history scenario based on the charcoal influx data from Lago di Origlio, a small lake situated about 40 km west of Lago di Annone (Tinner and Conedera 1995; Tinner et al. 1999). Following the suggestion that charcoal records in lake sediments represent fire events within a radius of 20–50 km (Clark 1990; Tinner et al. 1998), the fire scenario from Origlio can be assumed to reflect major trends in the fire history at Lago di Annone as well.

The charcoal influx values from Lago di Origlio (Tinner et al. 1999) were grouped into four classes (1 to 4, Fig. 2) characterising the fire regime of each 20-year simulation
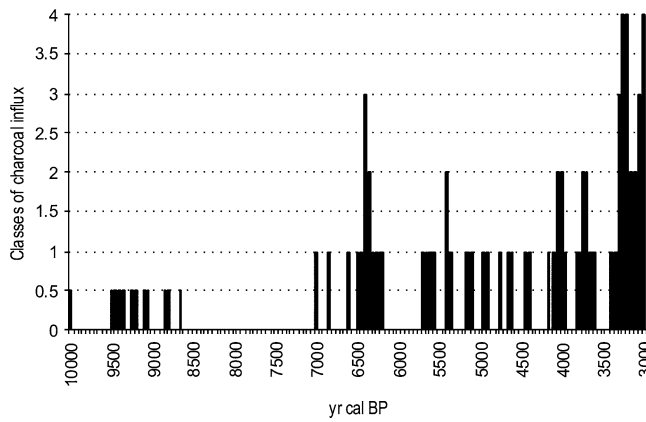
Fig. 2 The fire-history model input based on the charcoal influx values from Lago di Origlio (Tinner et al. 1999); class 0 represents very low fire frequency and intensity, class 4 high fire frequency and/or very hot fires

interval. It is not possible to differentiate between fire frequency and fire intensity from charcoal data. The variable combines the intensity of single fire events and the distance between the area burnt and the lake. Based on these fire values, the mortality rates of the different tree taxa were

Table 1 Fire-sensitivity factors of forest trees as used in the fire module

Fire-sensitivity factor	Definition of fire-sensitivity factor	Taxa representing the fire-sensitivity factor
0	Fire-tolerant: high fire frequency favours abundance	*Corylus*
1	Fire-tolerant: indifferent or favoured by moderate to high fire frequency	*Quercus*
2	Fire-tolerant: high fire frequency leads to decreases	*Fagus*
3	Fire-intolerant: fire strongly affects the taxa, may lead to local extinction	*Ulmus, Tilia*
4	Fire-intolerant: fire rapidly leads to local extinction	*Abies*

After Delarze et al. (1992) and Tinner et al. (2000)

Table 2 Similarity indices comparing the simulation outputs of different fire and human impact scenarios and the pollen record, with correlation values of simulated and subfossil *Abies* pollen percentages calculated for the time windows 9000–2000 cal B.P. (I) and 8000–5000 cal B.P. (II)

modified in the model. In the Southern Alps, Delarze et al. (1992) and Tinner et al. (2000) classified the major tree species with respect to their specific reaction to forest-fire frequencies. Referring to Tinner et al. (2000), we defined fire-sensitivity factors as shown in Table 1.

Since forest fires affect the mortality of trees as well as the establishment of seedlings (e.g. Bond and van Wilgen 1996), the fire module interacts directly with the mortality rate and indirectly with tree establishment and competition. The model was run with different impact factors, i.e. different levels of fire intensity (fire index i), ranging from 0.666 to 4 (see Table 2), where a fire scenario of 0.666 indicates a fire that passes very quickly as a ground fire without causing much damage, whereas an index of 4 represents a strong, hot crown fire. Together with the species-specific sensitivity (s_s), the fire index affects the mortality coefficient of the DisCForm model. This mortality coefficient is multiplied by the fire intensity class derived from the charcoal data from Lago di Origlio. The fire module may be summarised as follows:

$$\Phi = v_t \times i \times s_s$$

where Φ is the resulting mortality coefficient, v_t is the given fire intensity at a certain period (based on charcoal data from Lago di Origlio), i is the fire index and s_s is the specific reaction of a tree to fire (species-specific fire sensitivity factor, ranging from 0 to 4).

As shown by increasing values for cereals, *Plantago lanceolata*, and Gramineae in the pollen records, Neolithic human impact in the Southern Alps became important at around 7000 cal B.P. (Tinner et al. 1999, 2000; Gobet et al. 2000; Mathis et al. 2001). In the model, this is taken into account in two different ways, by increased fire frequency and by the impact of browsing by domestic animals. We call the first scenario with increased fire frequency "human fire" and the second "additional browsing". The latter is based on the assumption that during periods of increased human impact as shown by charcoal and other indicators of human activity regeneration of trees is affected by grazing cattle (Mathis et al. 2001).

Validation of the model outputs with pollen data

The simulations were run for the period from 12,000 cal B.P. to today and included the immigration and

Fire index	Human fire	Browsing pressure	Similarity index	Correlation value I	Correlation value II	Graph (Fig. 5)
0.666	+		0.615	0.37	0.64	C
0.666		+	0.645	0.42	0.66	B
1	+		0.634	0.42	0.67	–
1		+	0.662	0.46	0.69	D
2		+	0.642	0.47	0.70	–
3		+	0.642	0.48	0.71	E
4	+		0.641	0.51	0.72	G
4		+	0.682	0.54	0.73	F

establishment processes of the different tree species. The validation however was limited to the time span between 10,000 and 3000 cal B.P. in order to avoid time periods that turned out to be difficult to simulate (Keller et al. 2002).

For the validation with pollen records, the DisCForm outputs, given as biomass per species, have to be transformed into pollen percentages. Following previous publications (Lotter and Kienast 1990; Lischke 1998; Lischke et al. 2000; Keller et al. 2002) we used the conversion factors of Faegri and Iversen (1975) and Andersen (1970). They estimate the ratio between the representation $p_i \times P^{-1}$ of a taxon i in the pollen record P and its representation $v_i \times V^{-1}$ in the vegetation V. The total basal area of each tree-height class was determined using the empirical height-dbh (diameter at breast height) relationship of Bugmann (1994) and then summed to the total basal area of the species (Lischke et al. 2000).

In a first step, a visual comparison was used to choose the most accurate simulations. In order to have a more objective and quantitative tool, similarity indices were calculated. Pollen data as well as the simulation outputs were first filtered using a Gaussian Low Pass Filter with a smoothing effect on a 400-year period. The similarity index according to Cormack (1971) and Wolda (1981) was calculated as follows:

$$\text{similarity} = 1 - \frac{\sum_{i=1}^{n_{\text{taxa}}} \sum_{j=1}^{n_{\text{times}}} \left|\text{pollen}_{i,j} - \text{simulation}_{i,j}\right|}{\sum_{i=1}^{n_{\text{taxa}}} \sum_{j=1}^{n_{\text{times}}} \text{pollen}_{i,j} + \text{simulation}_{i,j}}$$

where the difference of the pollen value from the simulation output is summed for each period (n_{times}) and each species (n_{taxa}). The similarity index expresses the fraction of values that are common to both data sets. It shows the differences in the relative distribution of the simulation output and the pollen record as well as the importance of these differences (Bugmann 1994). In addition we calculated a correlation between the *Abies* biomass simulations and the *Abies* pollen percentage record.

Regression analyses

The significance of fire for the silver-fir declines was tested using regression analyses between *Abies alba* (pollen percentages) and the fire indicators charcoal (influx of macroscopic particles) and *Pteridium* (spore percentages, excluded from pollen sum) in the data from Lago di Annone. In order to exclude successional trends, such as expansion and extinction, the data set for the regressions was restricted to 37 data points between 5500 and 7450 cal B.P. (corresponding to 550–460 cm sediment depth). Interdependencies between the taxa caused by percentage calculations were avoided by using influx values (charcoal fragments, pollen, and spores cm^{-2} year^{-1}). Because of non-linear relationships, all data were log-transformed.

Results

Holocene vegetation development and fire history at Lago di Annone

In northern Italy mesophilous tree taxa such as *Quercus*, *Ulmus*, *Tilia* and *Alnus* immigrated during the Late-glacial and therefore were able to expand quickly when the climate became more favourable at the onset of the Holocene (Wick 1996b). The early-Holocene forests at Lago di Annone were dominated by *Quercus*, but *Ulmus*, *Tilia* and *Fraxinus* were common as well (Fig. 3). *Corylus* had an optimum between ca. 10,000 and 9000 cal B.P. and *Alnus* spread at about 9200 cal B.P. Although present in the area since the early Holocene, *Abies* was not able to compete with the deciduous trees until about 9000 cal B.P., when it started to expand continuously. High pollen percentages, stomata on the pollen slides and needles in the macrofossil record suggest that between about 8300 and 5700 cal B.P. silver fir played a major role both in the montane areas as well as in the lowlands. At 7300–7000 cal B.P. a strong decrease in *Abies* was followed by decreases in *Ulmus* and *Tilia*, while *Corylus* and *Alnus* expanded. *Abies* was able to recover and again became a dominant tree for a few centuries before it finally declined between 5900 and 5500 B.P. Subsequently, the habitats of silver fir in the montane area were occupied by *Fagus sylvatica*, whereas in the surroundings of Lago di Annone *Quercus* and *Alnus* became more frequent. After ca. 5300 cal B.P. silver fir definitely disappeared from the catchment of Lago di Annone.

As shown by the low charcoal influx values (Fig. 4) forest fires occurred regularly, but with relatively low frequencies in the early Holocene and during the two periods rich in *Abies*. After the first *Abies* decline, frequency and probably also intensity of fires increased. At the same time, increases in *Pteridium aquilinum*, grasses and human indicators such as Cerealia and *Plantago lanceolata*, together with marked declines in *Ulmus* and *Tilia*, point to forest clearances by Neolithic man. Also the second *Abies* decrease is followed by increases in *Pteridium* and human indicators along with a continuously increasing charcoal curve, suggesting a relationship between Neolithic settlement and the extinction of silver fir. However, notable lags of 200–300 years occurred between the beginning of the *Abies* decreases and the increases in *Pteridium* and human indicators (Fig. 4). The charcoal curve provides little evidence for natural or man-made forest fires that could have destroyed the *Abies* forests. Especially during the second *Abies* decline charcoal influx is very low. The high charcoal influx at the beginning of the first *Abies* decline can at least partly be attributed to a methodological effect: high concentration and influx values of all the major taxa point to temporarily lower sediment accumulation rates, which were not fully taken into account by the depth-age model used as a basis for influx calculations.

The result of the regression analysis of *Abies* pollen influx and charcoal influx shows a significant negative relationship ($p = 0.01$) between the two variables. An R-squared

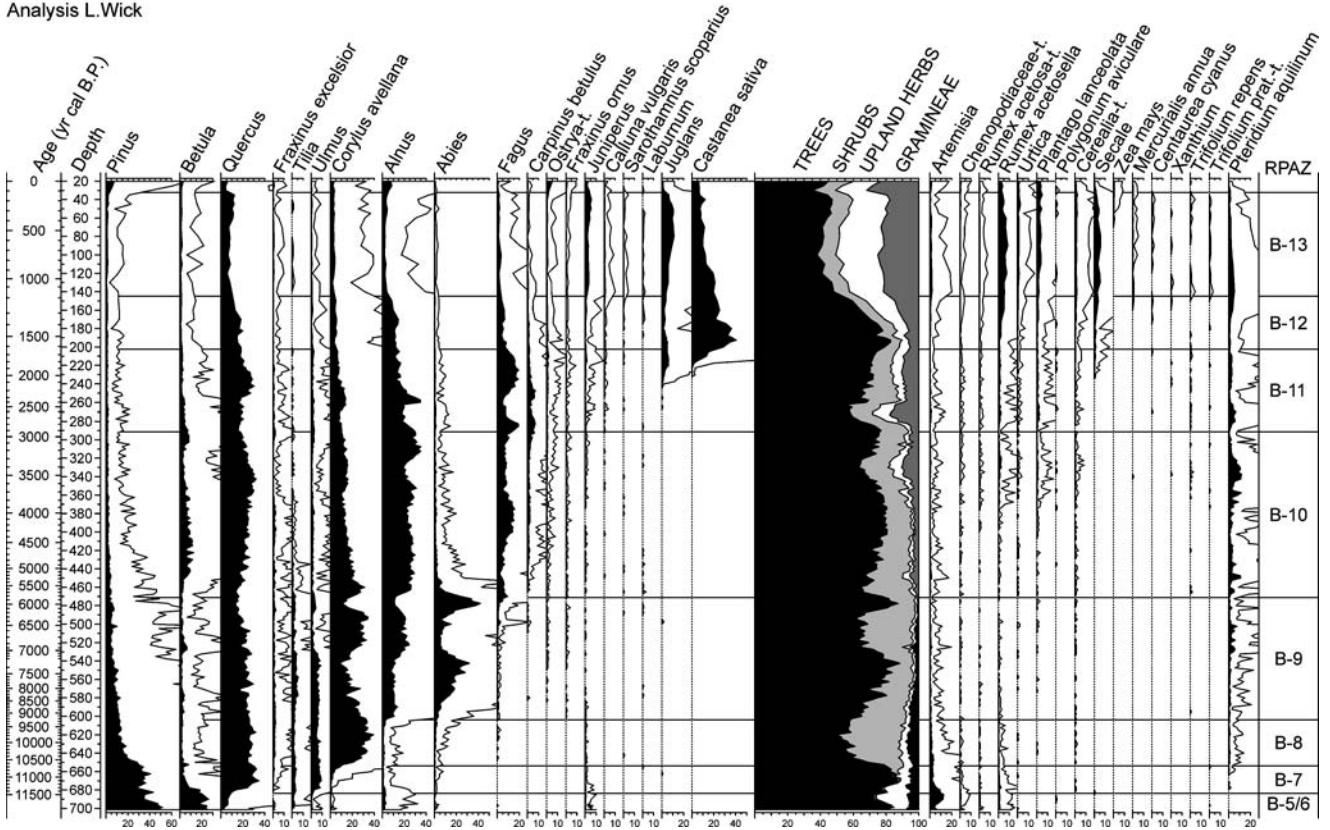LAGO DI ANNONE   226 m asl
Analysis L.Wick

Fig. 3 Pollen percentage diagram from Lago di Annone (226 m a.s.l.) including the major taxa
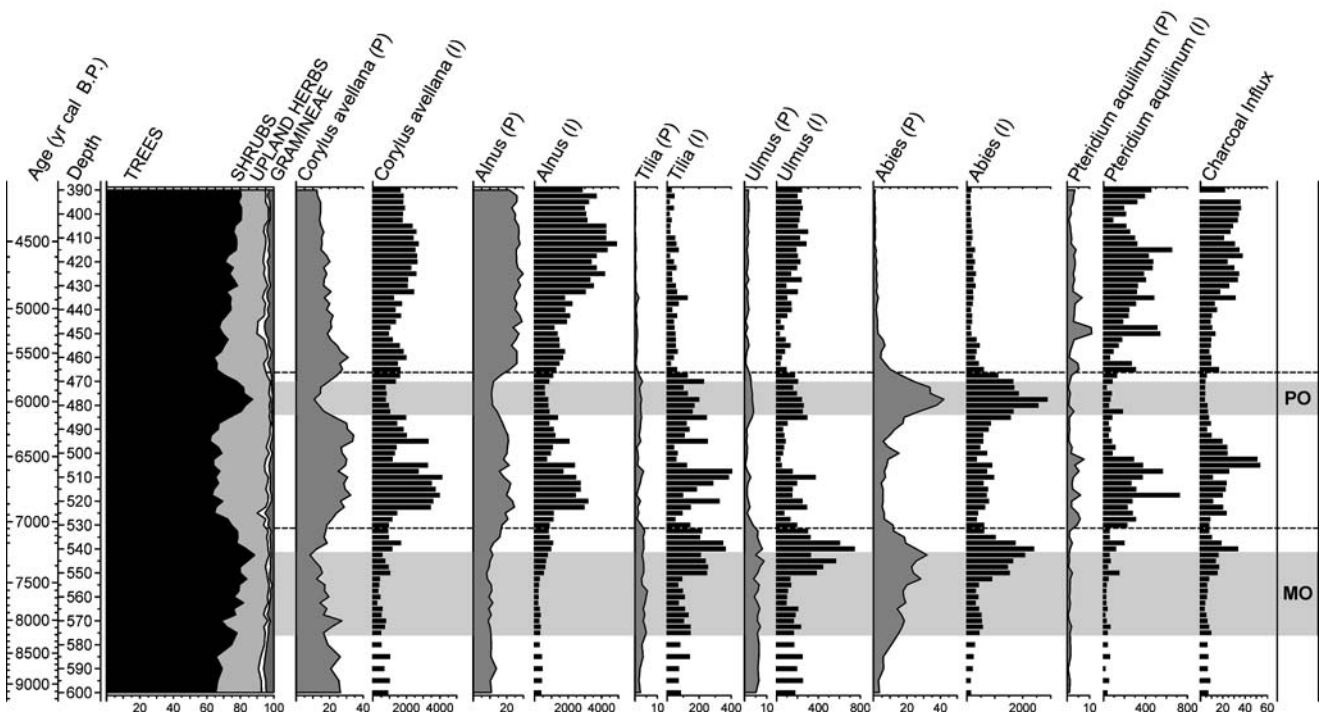
LAGO DI ANNONE AN-2

Fig. 4 Pollen percentages and influx (pollen grains cm^{-2} year^{-1}) of selected taxa and macroscopic (≥ 0.2 mm) charcoal influx given as charcoal fragments $\times$ 70 cm^{-2} year^{-1}. Shaded areas indicate periods of cooler climate recorded in the Southern Swiss Alps: MO, Misox oscillation, PO, Piora I oscillation (Zoller 1960, 1977), corresponding to the central-European climatic oscillations CE-3 and CE-5 respectively (Haas et al. 1998)

value of 0.173, however, suggests that forest fires were not the only factor responsible for the *Abies* fluctuations. The relationship between *Pteridium* and charcoal is positive and rather strong ($p<0.01$, R-squared $= 0.49$), indicating that bracken is clearly favoured by forest fires.

Simulation outputs and validation

The simulation outputs (Fig. 5B–G) show distinct decreases in *Abies alba* at around 7000 cal B.P. as a response to increased fire intensity in the model input. However, only the scenario with the highest fire intensity 4, combined with additional browsing pressure and/or human activity (Fig. 5F and G) causes a displacement of silver fir after 6000 cal B.P. that is comparable with the pollen record. The two characteristic peaks of *Abies* (around 7500 and 6000 cal B.P.), its low abundance between 7000 and 6500 cal B.P. and the virtual absence of silver fir after about 5400 cal B.P. could not be simulated. The similarity values, ranging between 0.615 and 0.682 (Table 1), suggest no clear preference for any of the fire scenarios.

For the mono-specific correlation between simulated *Abies* values and pollen data (Table 1), time intervals of 7000 years (9000–2000 cal B.P.) and 3000 years (8000–5000 cal B.P.) respectively were considered. For both periods the best value resulted with fire intensity 4 (i.e. the highest mortality coefficient) and additional browsing pressure starting at 6000 cal B.P. The correlation over the 7000-year sequence is considerably better than that for the 3000-year time interval spanning the period with the two *Abies* peaks.

Discussion

In their forest simulations, Keller et al. (2002) showed that factors other than fire, such as climate and immigration patterns, are only important during the early Holocene. However more detailed simulations with fire were not done in that study. A comparison with the simulation outputs of Keller et al. (2002) shows that extending the DisCForm model by a fire module has a significant impact on the similarity index. However, the similarity index cannot be
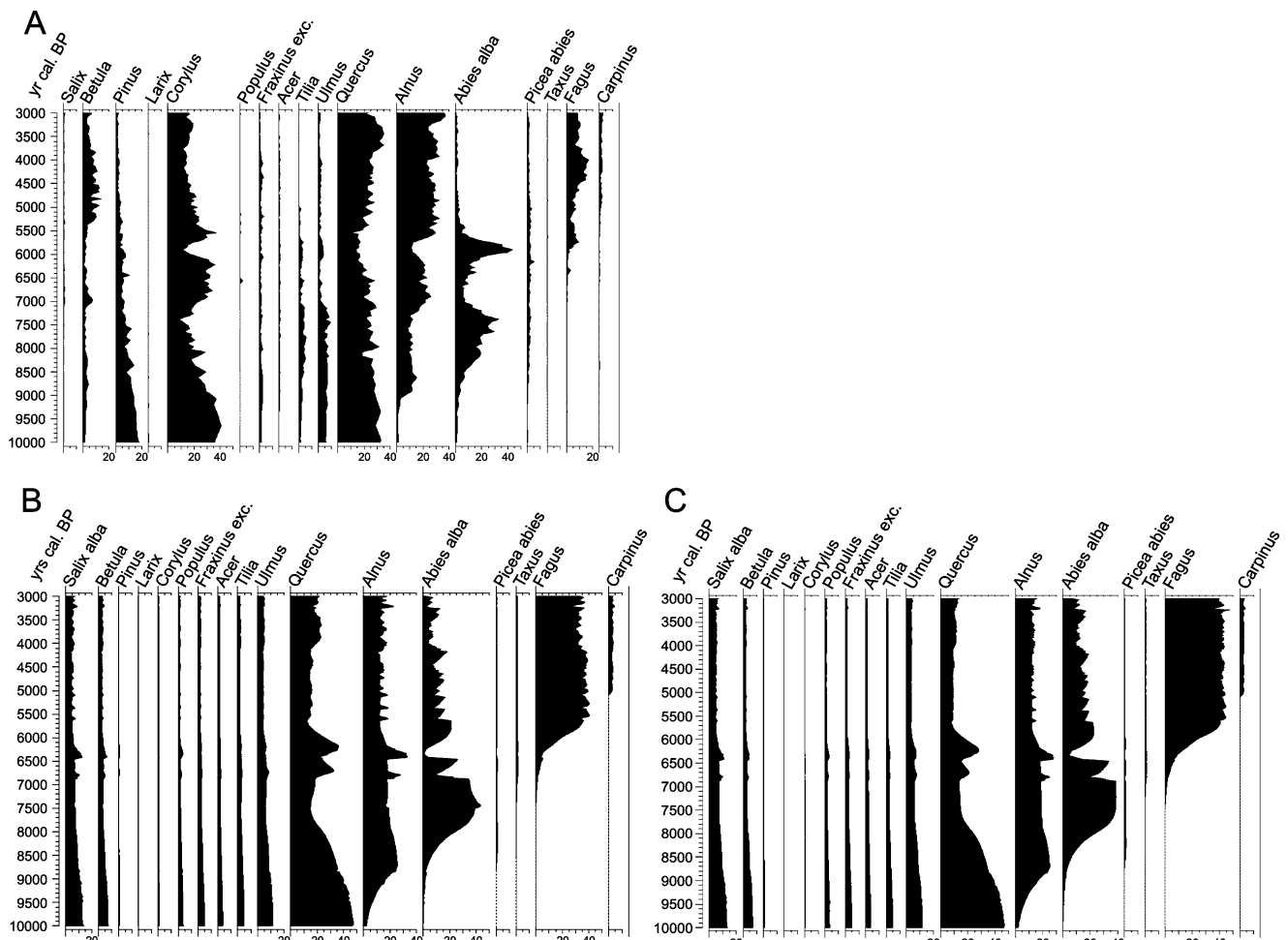

Fig. 5 Comparison of pollen data and simulation outputs. **A** Pollen record from Lago di Annone; percentage calculations are based on the total pollen sum of taxa included in the simulations. **B–G** simulation outputs with different scenarios of fire intensity (fi), human fire and browsing pressure; (**B**) fi = 0.666, browsing; (**C**) fi = 0.666, human fire; (**D**) fi = 1, browsing; (**E**) fi = 3, browsing; (**F**) fi = 4, browsing; (**G**) fi = 4, human fire

improved substantially by applying different fire scenarios (Table 2). On the other hand, the simulation outputs (Fig. 5) suggest that the patterns of individual tree taxa change with fire intensity. Thus, if calculated over a long period, major vegetation patterns and trends contribute to a high similarity index, whereas short-term changes and responses of single tree taxa seem to have little influence on the similarity index. For changes within short periods and with respect to specific taxa, correlation calculations or a visual comparison of pollen records and model outputs may be more useful.

Although *Abies alba* is considered to be highly sensitive to crown fires (Buffi 1987), its rapid declines and the subsequent extinction can only be simulated with a very hot fire scenario and a high mortality coefficient. However, no evidence exists in the pollen and charcoal records for such strong and frequent fires, and archaeological findings indicating Neolithic human activity in the catchment of Lago di Annone are very sparse. The DisCForm model produces quite abrupt declines of *Abies* as a response to fire events, whereas the pollen record (Figs. 3 and 4) suggests

continuous decreases within about 200–300 years that may be due to a continuing impact of unfavourable biotic or abiotic factors. This shortcoming of the model might be improved by using a more complex fire module including the effects of repeated fires and the impact of fire on seeds and seedlings.

The results of the model simulations point to a strong relationship between fire and the abundance of silver fir, as has been shown by fossil pollen and charcoal at Lago di Origlio (Tinner et al. 1999). However, there are major differences between the simulations and the pollen record from Lago di Annone that may partly be due to the model and its inputs. The ecological requirements of silver fir used in the model refer to its modern distribution at altitudes between ca. 650 and 1600 m a.s.l. However, there is palaeobotanical evidence that during the early and middle Holocene *Abies alba* was growing on habitats outside its modern range (e.g. Wick et al. 2003; Carcaillet and Muller 2005), suggesting that its ecological potential is not fully taken into account in the model. Nevertheless, both the pollen record from Lago di Origlio and our model outputs
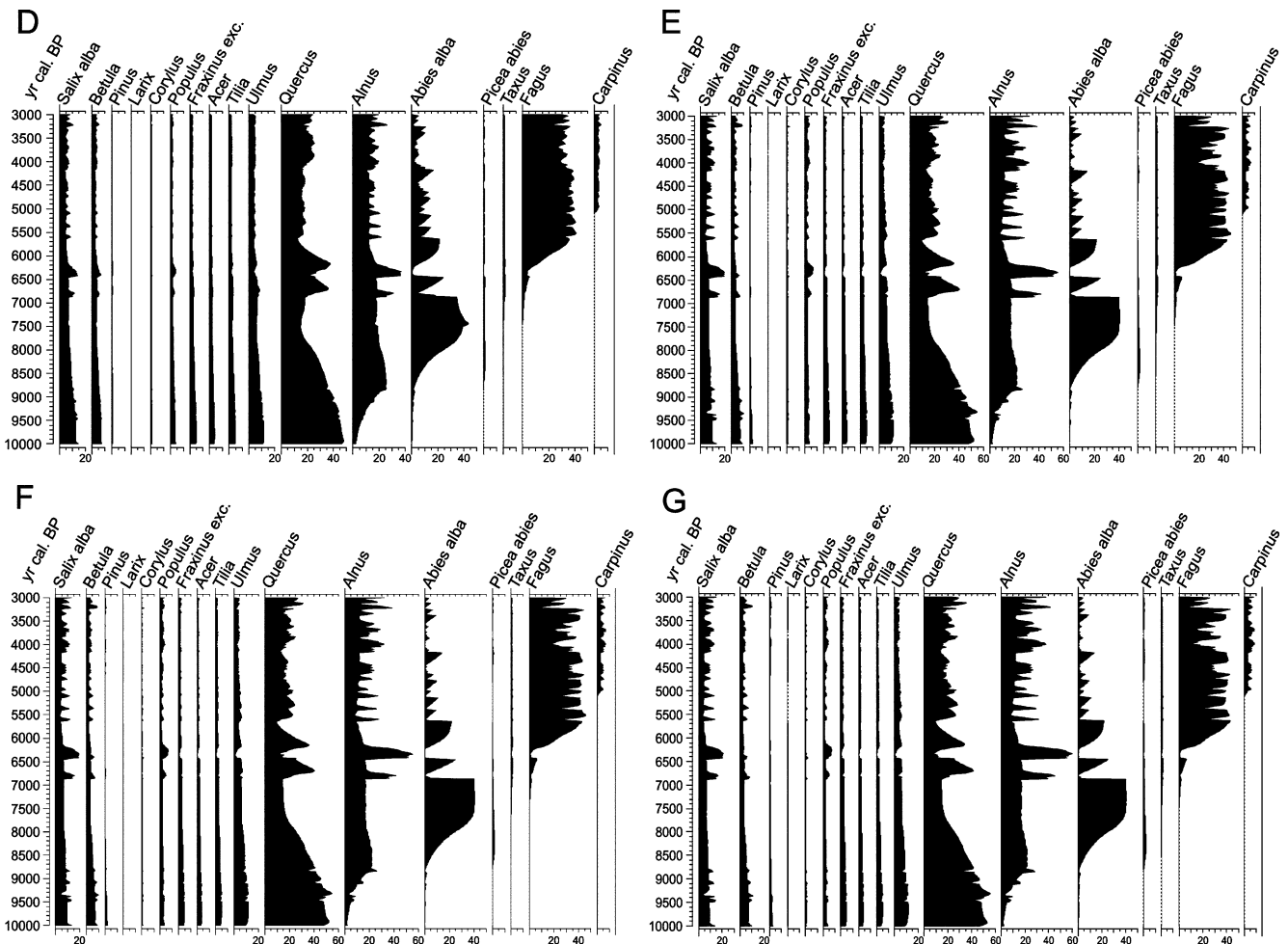

Fig. 5 Continued

show that silver fir declines as an immediate response to increases in fire frequency, whereas at Lago di Annone the correlation between charcoal and *Abies* is less obvious. Here, Neolithic forest clearances as indicated by increases in non-arboreal pollen, *Pteridium* spores and charcoal occur with a distinct lag after the beginning of the decreases in *Abies*. Furthermore, the pollen curves of *Tilia* and *Ulmus*, both taxa considered to be very sensitive to fire (Delarze et al. 1992), seem to be related more closely to charcoal and other human indicators and to the expansion of *Pteridium* than to *Abies*. The immediate responses of *Tilia* and *Ulmus* to fire and other human impact starting after the onset of the two *Abies* declines may indirectly indicate that fire was not the only factor triggering the fir declines at Lago di Annone; however increasing human pressure since the Neolithic was probably the major reason for the failure of *Abies* to recover after its second decline. The regeneration of silver fir after the impact of fire is severely hampered, because during the winter, the young trees are the preferred fodder for wild and domestic animals. There is strong evidence from studies on coproliths that in the Neolithic evergreen plants such as *Abies* and *Rubus* were used intensively as winter fodder for domestic animals (e.g. Akeret et al. 1999).

As a montane species with a demand for sufficient humidity (Lévy and Becker 1987; Desplanque et al. 1998), silver fir was probably growing at the lower end of its ecological range in the surroundings of Lago di Annone (226 m a.s.l.), and therefore sensitive to environmental changes. Palynological investigations in southern Switzerland revealed several cool periods in the Holocene (Zoller 1960, 1977), which occurred simultaneously with timberline depressions in the Central and Southern Alps (Wick and Tinner 1997; Haas et al. 1998). The two *Abies* phases in the pollen record of Lago di Annone coincide with cooler climatic conditions at 8200–7400 cal B.P. (Misox oscillation, Zoller 1960, 1977), corresponding to CE-3 (Haas et al. 1998) and at 6100–5800 cal B.P. (Piora I oscillation, corresponding to CE-5), indicated as shaded areas in Fig. 4. Even if the climate scenario used with the DisCForm model did not seriously affect silver fir (Keller et al. 2002), climatic warming combined with lower relative humidity between these cold phases could have led to additional stress on *Abies*. The differences in the behaviour of *Abies* at Lago di Origlio and at Lago di Annone may partly be explained by the bedrock geology of the two regions. At Lago di Origlio, where the well-developed soils on siliceous bedrock have a high water capacity, the silver fir fluctuations are a clear response to increased fire frequency (Tinner et al. 1999); however, on the poor calcareous soils in the catchment of Lago di Annone moisture deficits may have affected the *Abies* populations prior to the onset of Neolithic forest clearances. Zoller (1960) discussed some additional reasons for the fir declines, such as diseases or soil characteristics and considered a combination of different biotic and abiotic factors leading to the extinction of *Abies alba*.

Recent genetic studies on European *Abies* populations related to modern *Abies* declines in central Europe have revealed an additional aspect of the mid-Holocene fir decline.

Konnert and Bergmann (1995) studied geographical differentiation among silver fir populations using isozyme gene markers and concluded that the postglacial re-colonisation of Europe by *Abies* occurred from three refugia in France, central Italy and the Balkans, whereas the refugial populations in Calabria and in the Pyrenees remained isolated. Referring to their studies of maternally inherited gene markers, Liepelt et al. (2002) postulate an eastern and a western Mediterranean *Abies* refugium. As shown by palaeobotanical investigations, northern Italy and large areas in central Europe were probably re-colonised by fir populations from the Apennine mountains (Zoller and Kleiber 1971; Schneider 1985; Huntley and Birks 1983; Lang 1994); Terhürne-Berson et al. (2004) suggest further refugial areas in the Pyrenees and potential ones in south-east France and north-west Italy. According to Larsen (1981, 1986) and Bergmann et al. (1990), the central-European fir has considerably lower genetic variation and vitality than populations with a provenance in Calabria or on the Balkans. Larsen (1986) relates the lack in genetic variation of silver fir to extreme climatic conditions (e.g. drought) affecting the refugial populations before or during their Lateglacial migration through the Apennines to central Europe. According to Larsen (1986), the modern decline of silver fir in Europe since the early 19th century is a consequence of reduced genetic variation resulting in a lack of adaptability.

With regard to its genetic pre-disposition, the extinction of *Abies alba* in our study area becomes more understandable. Low adaptability due to insufficient genetic variation and a coincidence of several unfavourable factors such as reduced moisture availability, soil characteristics, forest fires, human activity and other biotic and abiotic factors may have imposed a permanent stress on the fir populations that led to their extinction.

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