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Species responses to fire, climate and human impact at tree line in the Alps as evidenced by palaeo-environmental records and a dynamic simulation model

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Summary

1. We use high-resolution records of macroscopic charcoal and plant remains from sediments of a lake in the Swiss Alps (Gouillé Rion, 2343 m a.s.l.) to reconstruct local fire variability and vegetation dynamics over the last 12 000 years.

2. Species response to fire variability and to summer temperature was obtained by combining regression analyses between contiguous series of plant macrofossils, macroscopic charcoal and an available reconstruction of past summer temperature.

3. With a dynamic landscape vegetation model (LandClim), we simulated fire regimes using two levels of ignition frequency and moisture availability to disentangle the role of climate vs. humans on fire occurrence. The simulation results show that human disturbance was relevant in controlling the fire variability and are in agreement with pollen evidence of human impact from previous studies from Gouillé Rion.

4. Our results show that fire is a natural disturbance agent in the tree line ecotone. Biomass availability controlled the fire regime until increased land use and anthropogenic fire during the past 4000 years changed species composition and vegetation structure close to the tree line.

5. Important species at the tree line ecotone such as *Pinus cembra* greatly benefitted from periods with temperature above the modern mean July temperature, if anthropogenic fire disturbance was not too severe, such as during the Bronze Age (*c.* 4000 cal. years BP).

6. When mean July temperatures were lower than modern mean July values, *Juniperus nana* and *Larix decidua* were at an advantage over *P. cembra*. With increasing anthropogenic fire, open lands with *J. nana* replaced *L. decidua* and *P. cembra* forest stands.

7. *Synthesis*. Fire activity was low to moderate during the early and mid-Holocene. Intensified land use coupled with fire occurrence since the Bronze Age (*c.* 4000 cal. years BP) had a larger impact on species composition near the tree line than climate change. Although climate change will alter vegetation composition, future dynamics of mountain forests will be co-determined by anthropogenic fire. For example, high fire variability may impede upslope establishment of forests in response to climatic warming as expected for this century, with serious implications for forest diversity.

Key-words: Alps, Bronze Age, dynamic vegetation model, fire history, human impact, LandClim model, macroscopic charcoal, palaeoecology and land-use history, regression analyses, tree line ecotone

Introduction

Fire is a prominent factor driving vegetational pathways in many mountain ecosystems (Carcaillet 1998; Gobet *et al.* 2003; Stähli *et al.* 2006). For instance, at low altitude, forest

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fires promote dominance by fire-prone or early successional species, whereas at higher altitude, where conditions are moister, infrequent fires allow the establishment of fire-sensitive or late-successional species (e.g. the Pacific Northwest, Agee 1993). Under natural conditions, fire occurrence is generally controlled by ignition frequency and fuel dryness, although in the Alpine region humans have intentionally altered fire regimes since the Neolithic and perhaps earlier (Gobet *et al.* 2003; Carcaillet *et al.* 2009). However, with the exception of particularly fire-prone areas, fire frequency in the Alps is generally low under present climatic conditions and land-use patterns. Most historical fires occurred in drier south-slope (Conedera *et al.* 2004) or in submontane forests of continental, rain-sheltered valleys (e.g. the Swiss Rhone valley; Zumbrunnen *et al.* 2009) and were of anthropogenic origin. Fire is less frequent in higher-elevation forests, where high-elevation livestock grazing has kept biomass low for millennia and the climate is cooler and moister. However, the tree line ecotone is also highly sensitive to climatic and land-use changes that may alter the susceptibility to fire occurrence. For example, ongoing agricultural abandonment favours afforestation and increases fuel loads in former high-elevation pastures (Rutherford *et al.* 2008). Furthermore, rising temperatures induce upslope migration of individual species and allow rapid (i.e. decadal-scale) upslope tree line expansion into unforested landscapes (e.g. Harsch, Hulme & McGlone 2009). Climatic change may also increase the incidence of hot, dry weather conditions that favour fire occurrence in previously moist ecosystems. In agreement, recent studies concluded that fire frequency and intensity are likely to increase in the future as average temperatures rise and summer precipitation declines (IPCC 2007; Marlon *et al.* 2009).

Two approaches, palaeo-environmental reconstructions (e.g. sedimentary analyses) and dynamic modelling are commonly used to study the interactions among climate, fire occurrence, land use and vegetation beyond the annual to decadal scale of observations and experiments (Keller *et al.* 2002; Tinner *et al.* 2005; Schumacher & Bugmann 2006; Brubaker *et al.* 2009; Conedera *et al.* 2009). Retrospective studies using lake-sediment charcoal as a proxy for past fire regimes provide valuable long-term fire-regime records, but are still rare in the Alps. When paired with high temporal-resolution and contiguous palaeobotanical reconstructions, charcoal records can be used to infer the ecological impacts of changing fire regimes over millennia (Tinner *et al.* 1999; Whitlock & Millspaugh 2001). This approach is extremely time-consuming and thus even more rare (Conedera *et al.* 2009). Dynamic vegetation models can bolster interpretations of sedimentary series by testing competing hypotheses, because the underlying factors of environmental change can be isolated in mechanistic model experiments (Keller *et al.* 2002; Anderson *et al.* 2006; Heiri *et al.* 2006). In addition, models can simulate competing scenarios to examine vegetational responses at spatial and temporal resolutions unobtainable from sedimentary series. Furthermore, dynamic landscape models that are validated using long-term palaeoecological reconstructions may be confidently employed to simulate future vegetation outcomes.

In this paper, we use a Holocene macroscopic charcoal and macrofossil lake-sediment record from the Swiss Central Alps that has been previously published (Kaltenrieder, Tinner & Ammann 2005). The well-dated contiguous macroscopic charcoal and plant macrofossil records are used for the first time to reconstruct local fire history and to derive responses of tree line vegetation to fire occurrence. Then, we statistically compare our local records with quantitative climate reconstructions from another site in the Alps (i.e. Hinterburgsee, Heiri *et al.* 2003) to gain insights into vegetation responses to Holocene climatic change. We compare our fire reconstruction with fire events simulated by the LandClim dynamic landscape vegetation model to examine with high spatial and temporal precision potential forcing mechanisms of fire-regime change. The model simulation allows us to better understand whether climate and/or human impact better explain the observed Holocene fire regime changes. Our results might be relevant to better direct future environmental development under global change scenarios, such as the response of the tree line ecotone to warming temperature and increasing anthropogenic fire.

Materials and methods

STUDY SITE

Gouillé Rion (46°09′25″ N, 07°21′45″ E) is a small lake (0.5 ha) with a catchment area of *c.* 80 ha, located at 2343 m a.s.l. in the Rhone Valley of the Swiss central Alps (Fig. 1). The valley is relatively dry, with precipitation (mean: *c.* 1100 mm year^{-1}) most abundant during winter and temperatures (annual mean: *c.* 1 °C) with maximum values in July (*c.* 8 °C, Thornton, Running & White 1997). Fires in the region are mostly concentrated in the late summer when climatic conditions are warm and dry. However, historical records indicate human activities during the last 100 years were more important than climate in controlling fire occurrence (Zumbrunnen *et al.* 2009).

The lake is situated within the modern tree line ecotone, which represents the transition zone between the closed forest (i.e. the timberline, 2100 m a.s.l.) and upper limit of individual tree species (i.e. the tree line limit, *c.* 2350 m a.s.l., with single trees > 2 m, Arno & Hammerly 1993; Körner 1999). Today, the tree line ecotone is mostly composed of *Pinus cembra* L., *Larix decidua* Mill., together with *Vaccinium* and *Rhododendron* species in the understorey (Kaltenrieder, Tinner & Ammann 2005). Although *L. decidua* and *P. cembra* are not under their optimal growing conditions at tree line, they are the only trees that can survive and reproduce under these harsh continental climatic conditions (Ozenda 1988; Ellenberg 1996). Open woody vegetation around Gouillé Rion established during the Bronze Age with dwarf shrubs *Juniperus nana* Willd. and *Alnus viridis* Dc. (Tinner, Ammann & Germann 1996; Kaltenrieder, Tinner & Ammann 2005). *Picea abies* L. dominates nearby forests at lower altitudes (800 to about 1700 m a.s.l.).

CHRONOLOGY, PLANT MACROFOSSILS AND STATISTICAL TREATMENT OF CHARCOAL DATA

Continuous macrofossil records including charcoal area concentrations (mm^2 cm^{-3}) were available from previous studies and full methodological descriptions are provided elsewhere (Tinner, Ammann & Germann 1996; Kaltenrieder, Tinner & Ammann 2005; Tinner &

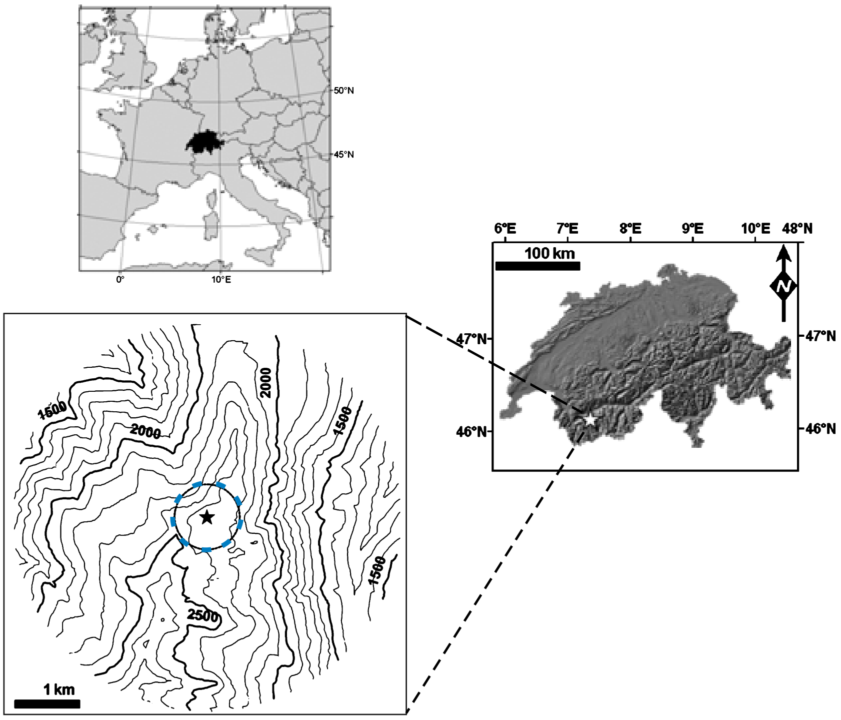


Fig. 1. Location of the investigated site in the Central Swiss Alps. The catchment area (500 m radius, dashed circle) corresponds to *c.* 80 ha and to the simulated area burned. The position of the site allows fire to spread just from the north-facing slope, decreasing the probability for fire to spread from the drier south-facing slope.

Kaltenrieder 2005). We used *c.* 22–25 cm^3 of sediment and sieved through a 0.2-mm mesh screen to gain all macrofossils, including charcoal particles. We amalgamated three records (GR1, GR2 and GR 6–7) according to their independent accelerator mass spectrometry radiocarbon chronologies (see Appendix S1 in Supporting Information). The period 12 000–2600 cal. years BP (GR 6/7) is covered by the macrofossil (and charcoal) record published in Kaltenrieder, Tinner & Ammann (2005) and reaches a continuous sampling resolution of 0.5 cm (44 ± 19 years per sample, total of 212 samples). The last 2600 years (GR1 and 2) are presented in Tinner, Ammann & Germann (1996) and reach a sample resolution of 3 cm (62 ± 11 years per sample, total of 39 samples). Only terrestrial plant macrofossils were used for dating (Tinner, Ammann & Germann 1996; Kaltenrieder, Tinner & Ammann 2005). The chronology of the new synthesis macrofossil record (total of 39 radiocarbon dates) spanning the entire Holocene is described in detail in Appendix S1.

Charcoal area concentrations were not statistically analysed in previous studies of Gouillé Rion. We interpolated all charcoal area concentrations to the median sample resolution (51 years) and converted to charcoal accumulation rates (CHAR, $\mu m^2\ cm^{-2}\ year^{-1}$). We smoothed CHAR values with a standard Locally Weighted Scatterplot Smoothing (LOWESS, 800-year window) to identify background charcoal (BCHAR, which might be secondary deposited charcoal or reflect regional fire activity, Whitlock & Larsen 2001). Smoothing using a robust LOWESS resulted in the same number of fire events. Residuals were obtained by subtracting (untransformed) raw CHAR from the BCHAR values. To reconstruct inferred fire frequency (IFF, fire episodes per 500 and 1000 years), we compared two different approaches to identify thresholds values, i.e. the values above which local fire episodes are identified from residual peaks. We first considered a locally defined threshold (Higuera *et al.* 2008) based on the 90th percentile of the noise distribution, as defined by a Gaussian mixture model (Gavin, Brubaker & Lertzman 2003a). The local threshold method is appropriate in our case because long-term changes in fuel availability and species composition may have affected charcoal production around the site (Tinner *et al.* 2005). In this analysis we did not perform a minimum-count screening, because CHAR values are based on area rather than number. We also considered a more conservative approach, using a globally defined threshold value based on the 99th percentile of the noise distribution. In a final step, we smoothed the IFF over 500- and 1000-year windows to evaluate trends in biomass burning over time. For the analyses, we used the Charanalysis software by Higuera *et al.* (2008).

TESTING RECONSTRUCTED FIRE REGIMES WITH A DYNAMIC LANDSCAPE MODEL

We tested competing scenarios explaining the observed dynamics among climate, fire occurrence, human impact and vegetation with the LANDCLIM model (Schumacher, Bugmann & Mladenoff 2004; Schumacher & Bugmann 2006). LANDCLIM is a spatially explicit stochastic model consisting of a local model simulating forest succession and a landscape model simulating disturbance processes such as fire, wind and harvest. LANDCLIM operates on long time scales (hundreds to thousands of years) at a spatial extent large enough to encompass landscape- to regional-scale disturbance events (i.e. up to *c.* 100 km^2), but at fine enough resolution to capture local physiographical variation (i.e. grid cells of 25 × 25 m). Fire events and vegetation composition are emergent properties of the model that dynamically respond to changing climatic conditions. Vegetation composition is simulated using competitive interactions based on species-specific tolerances for moisture availability, temperature, light, as well as growth rates and maximum size. Fire occurrence requires an ignition source, and the probability that a fire spreads is determined using an exponential relationship between a drought index calculated from climatic and edaphic conditions, and a fire-spread coefficient (Appendix S2.1; Schumacher *et al.* 2006). LANDCLIM has been previously used to simulate wildfire in mountain ecosystems in both the European Alps and North American Rocky Mountains (e.g. Schumacher *et al.* 2006). For complete documentation of LANDCLIM and the LANDCLIM fire routine see Schumacher, Bugmann & Mladenoff (2004), Schumacher & Bugmann (2006) and Appendix S2.1–S2.4.

We simulated vegetation and fire dynamics within a 500-m radius (*c.* 78 ha landscape) of Gouillé Rion. Because fires may also spread into our study landscape, we produced exploratory simulations with a larger landscape (i.e. within a 3-km radius of Gouillé Rion, Appendix S2.4). In any case, our chosen landscape radius (500 m) matches the local source area of macroscopic charcoal (0–500 m, e.g. Lynch *et al.* 2002) and of plant macrofossils (0–100 m, Birks 2001) and, most importantly, it encompasses the Gouillé Rion watershed. Climatic inputs to LandClim were estimated by overlaying a quantitative chironomid-inferred reconstruction of Holocene July average temperature anomaly from Hinterburgsee, a subalpine lake in the northern Swiss Alps, with modern temperature and precipitation data (Heiri *et al.* 2003, 2006). Modern climatic data were obtained from weather station data from the period 1960 to 2006 that was interpolated to a 1-ha resolution using the DAYMET model (Thornton, Running & White 1997; Swiss Federal Institute for Forest Snow and Landscape Research). Precipitation variation is determined using the distribution of precipitation abundance in the period 1960–2006 and the modern relationship between temperature and precipitation. All extant Central European trees were included in our simulations, with the exception of *Pinus mugo*, which is most competitive on carbonatic soils, does not grow in the region and is absent in the fossil record. We also expanded the species list used in previous LandClim studies by including *J. nana*, a shrub species that is abundant in the macrofossil record. *Juniperus nana* life-history parameters follow Ellenberg (1996).

We compared LandClim output from four scenarios (10-year time steps, each averaged over 25 replicates) to Gouillé Rion fire reconstructions. Each simulation represents a different combination of moisture availability and ignition frequency. Our first scenario (S-1), builds on previous modelling and palaeobotanical efforts at Gouillé Rion. P.D. Henne, C.M. Elkin, B. Reinekink, H. Bugmann and W. Tinner (unpublished data) demonstrated that the reconstructed vegetational dynamics during the early Holocene (i.e. before 8000 cal. years BP) could only occur with drier-than-present soil conditions. Thus, we simulated Holocene vegetation and fire occurrence using poorly developed soils, and precipitation 30% lower than at present (for details about parameters used in the simulations see Appendix S2.2). Because precipitation likely increased during the middle Holocene and soil depth increased with time, a second scenario (S-2) uses modern precipitation abundance and soil depths. We used an ignition coefficient for S-1 and S-2 (Appendix S2.1–S2.3) that is consistent with natural ignition frequencies for the central Alps (i.e. 0.002; Schumacher *et al.* 2006). Higher ignition frequency is a consistent consequence of increasing human land use worldwide. For example, increasing fire frequency and consequent vegetational change throughout the Alps *c.* 4000 cal. years BP coincided with intensified land use during the Bronze Age (Tinner *et al.* 2003). Therefore, scenarios three (S-3) and four (S-4) mimic intensifying land use during the late Holocene by increasing the ignition coefficient 10-fold (i.e. from 0.002 to 0.02, see Appendix S2.2). This degree of change is consistent with the findings of Zumbrunnen *et al.* (2009) when comparing areas with low vs. high population density and land use. We further justified this approach with a sensitivity test that varied the ignition coefficient from 0.001 to 0.2 and found that the area burned does not increase linearly with the number of ignitions (Appendix S2.3). We used modern precipitation abundance and soil conditions for S-3, and used 30% less precipitation than at present in S-4. Soil conditions and the percentage of modern precipitation abundance remain constant through time within each model run. To facilitate comparison of simulated and reconstructed fire regimes, we plotted total simulated burned cells at 10-cells bin intervals and surface area burned at 10-year intervals. Additionally, we plotted events that burned a large portion of the landscape (i.e. at least 10%) for comparison among simulations. Those events in any case cannot be compared to our reconstructed events from sediment charcoal since they were not statistically treated the same way.

REGRESSION ANALYSES

Unimodal or linear responses of species to environmental variables can be used to identify species environmental optima and disturbance tolerances. We examined the relationship between tree species abundance and Holocene summer temperature and fire frequency by fitting macrofossil percentage data with multiple regression models. We used a Generalized Additive Models (GAM; Hastie & Tibshirani 1990) to describe the dependence of the three important woody plant species *P. cembra*, *L. decidua* and *J. nana* to local fire impact and summer temperature. We used plant macrofossils (%) as a proxy for species abundance at a local scale (0–100 m, Birks 2001). Plant macrofossil concentrations show similar trends as percentages at Gouillé Rion (Kaltenrieder, Tinner & Ammann 2005). Also, we used positive macroscopic charcoal residuals (i.e. the fraction of sediment charcoal not including background; Clark, Royall & Chumbley 1996; Lynch *et al.* 2002; Gavin, Brubaker & Lertzman 2003b). Macroscopic CHAR influx (including the background component) is instead more appropriate when compared with extra-local to regional-scale vegetational proxies such as pollen (Colombaroli *et al.* 2008). The departure from mean Holocene July temperatures, as reconstructed from chironomid assemblages at Hinterburgsee (Heiri *et al.* 2003) was used as a quantitative proxy for Holocene temperature variation in the Alps. For the analyses, we considered a maximum of two degrees of freedom and a Poisson distribution of the data. Stepwise selection based on the degrees of freedom (i.e. the polynomial order of the function) was used to identify the optimum model complexity that is alternative to the null model (i.e. no changing of species values with the predictor). This is done by choosing the model with the lowest AIC value (Akaike Information Criterion), which allows estimation of the parsimony of a particular regression model based on the residual variance (i.e. the difference between the observed and the fitted value). Finally, we evaluated the outputs of distinct regression models by comparing the residual values of Generalized Linear Models vs. GAM. For all the analysis, we used Canoco 3.0.

Results

IDENTIFICATION OF CHARCOAL PEAKS, RECONSTRUCTED INFERRED FIRE FREQUENCY AND MEAN FIRE INTERVAL

We identified 23 local fire episodes during the last 12 000 years using a local threshold value (Higuera *et al.* 2008 and Fig. 2). The reconstructed fire events from sediment charcoal likely represent a cluster of fire events that cannot be captured at yearly scale because of the sample resolution (51 years in our case, see also Whitlock & Larsen 2001). Charcoal accumulation rates (CHAR) of particles > 200 μm average between 1000 and 3000 $\mu m^2\ cm^{-2}\ year^{-1}$, with maxima of 4000 $\mu m^2\ cm^{-2}\ year^{-1}$ around 3000 and 1000 cal. years BP,

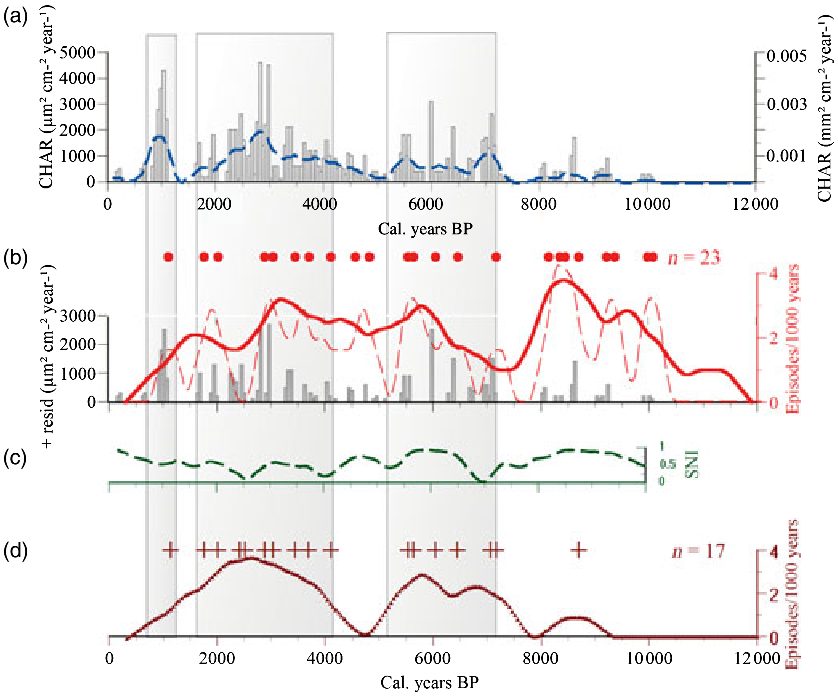


Fig. 2. The reconstructed local fire history around Gouillé Rion. (a) Raw CHAR (charcoal accumulation rates µm^2 cm^{-2} year^{-1}) and BCHAR (i.e. background charcoal, dashed line); (b) reconstructed fire episodes around the lake, inferred fire frequency (IFF; 1000 and 500 years windows, respectively) and positive residuals (bars); (c) signal-to-noise index 0-1 (Higuera *et al.* 2009); (d) a more conservative fire reconstruction, identifying peaks (crosses) with high absolute values of positive residuals and corresponding IFF (1000 years window). Shadowed areas show periods with increased values of total CHAR and BCHAR. Most of the analysis of this study is based on the interpretation in (b).

and minimum values before 7500 cal. years bp (Fig. 2a). Background component (BCHAR) increases after 7500 cal. years bp, reaching maximum values around 6000, 3000 and 1000 cal. years bp (Fig. 2a). The resolution of the charcoal record (51 years) defines the minimum detectable mean return interval, with the sample resolution ideally one-fifth of the fire return interval (Clark 1988; Higuera *et al.* 2007). Thus the minimum reliably detectable mean fire return interval for Gouillé Rion is *c.* 250 years. Overall, mean fire interval values (MFI) range between *c.* 250–900 years per fire, and corresponding IFF ranges between 1–4 fires episodes per 1000 cal. years bp with highest values registered around 8500, 6000 and 3000 cal. years bp (Fig. 2b). Signal-to-noise index, which is an indicator of how distinct peaks are from background (Higuera *et al.* 2009), show minimum values (i.e. maximum of noise) at *c.* 2500, 4000 and 7000 cal. years bp (Fig. 2c). The alternative, more conservative, reconstruction, which uses a globally defined threshold value (Fig. 2d), identifies a total of 17 fire episodes. Those events are mostly associated with the highest raw CHAR values and are grouped in two periods, between 7000–5000 cal. years bp and 4000–1000 cal. years bp (Fig. 2d).

The comparison between the plant macrofossil record and reconstructed fire frequency (Fig. 3) shows that the *P. cembra* expansion (*c.* 9000 cal. years bp) occurred when fire frequency values were highest in the record (i.e. *c.* 3 episodes per 1000 years). However, *P. cembra* decreased after 4000 cal. years bp, during a phase of increasing IFF values, which favoured *J. nana* and *L. decidua* (Fig. 3d). In contrast, the first expansion of *L. decidua* (*c.* 11 600 cal. years bp) started before the occurrence of charcoal-inferred local fires.

SIMULATED FIRE REGIMES AT GOUILLÉ RION

Ignition frequency has a larger impact on simulated fire frequency and size than climatic conditions. For example, LandClim simulates comparable fire frequencies and fire sizes in scenario S-1 (dry, low ignition) and S-2 (wet, low ignition; Fig. 4). In both scenarios, most simulated fires are small ($<$ 1 ha), and the most severe events do not burn more than 10% of the total landscape (Fig. 4a,b). These values are consistent with Zumbrunnen *et al.* (2009), who found that 85% of fires in Valais from 1900 to 2000 were $<$ 1 ha, because landscape fragmentation is responsible for a patchy fire pattern. Thus, our basic unit of analysis (25 × 25 m grid cell) is consistent with the minimum patch size that is likely to burn in cultural landscapes. Overall, fire size distribution is also similar between the simulations with more frequent ignitions despite climatic and edaphic differences (S-3 and S4, Fig. 4c,d). Also, the number of fires simulated in the high ignition scenarios is well below the maximum number of fires that could burn with unlimited ignitions (Appendix S2.3). Average fire sizes are larger when ignition is high (*c.* 1–2 ha), and the frequency of large events (e.g. $>$ 10 ha) increases, but not proportionally, with the number of ignitions. Also, increased frequency of larger events following higher ignition coefficients can be

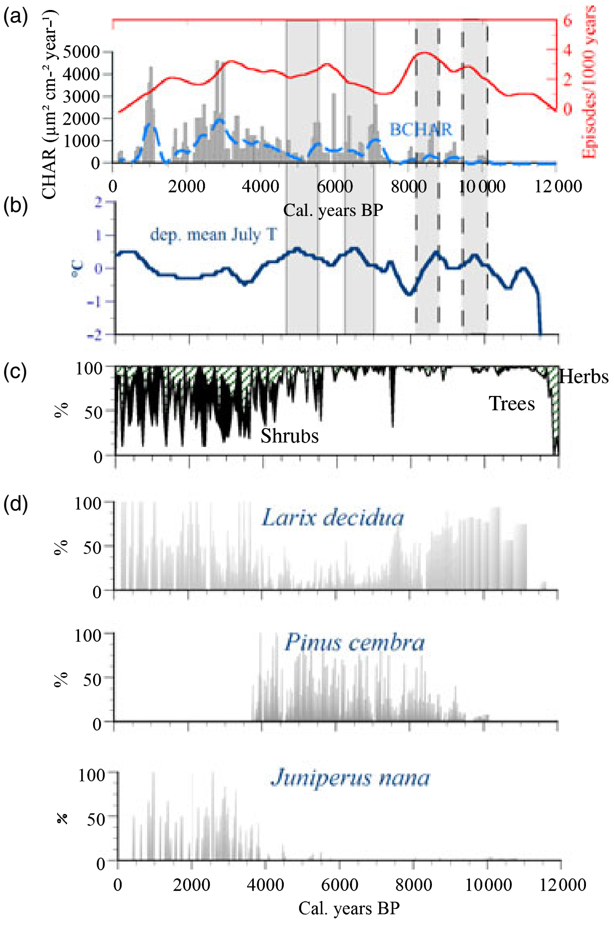


Fig. 3. Fire–vegetation relationship (a) inferred fire frequency (IFF continuous line), raw charcoal accumulation rates (CHAR) and trend in background charcoal (BCHAR, dashed line); (b) departure from mean July summer temperature (Heiri *et al.* 2003). Shadowed areas represent phases of concordance (shadowed area with dashed line) and discordance (shadowed area with continuous line) between summer temperature and charcoal data; (c) trend of afforestation at the tree line limit, with the expansion of the shrub ecotone around 4500 cal. years BP; (d) percentages of macrofossil for *L. decidua*, *P. cembra* and *J. nana* (modified from Kaltenrieder, Tinner & Ammann 2005).

partly related to a possible effect of proximity of ignitions (Appendix S2.3). Despite the dominant impact of ignition frequency on fire regimes, scenarios with dry climate do simulate larger fire sizes (i.e. up to 80% larger in the dry climate scenarios; Fig. 4d). Considering a larger landscape (total radius of 3 km, Appendix S2.4) did not increase fire frequency within the dominant charcoal source area (i.e. within 500 m of Gouillé Rion). However, infrequent very large fires that spread from the larger landscape did increase the maximum fire size for scenario S1 (Appendix S2.4).

SPECIES RESPONSE CURVES

Generalized Additive Models show species response to varying macrocharcoal residuals. For instance *J. nana* shows a positive linear response, whereas *L. decidua* exhibits a negative response (Fig. 5a). The decline of *P. cembra* with increasing positive charcoal residuals is more marked than in *L. decidua*. The response of *L. decidua* and *J. nana* to reconstructed summer July temperature shows an optimum 2 °C below the Holocene (and also the modern) mean July temperature of 8.1 °C (Fig. 5b). In contrast, *P. cembra* increases when average July temperature was above the Holocene mean.

Distinct responses of species to reconstructed summer temperature and to charcoal residuals show that these two variables are not correlated (Pearson correlation positive CHAR residuals and July summer temperature = 0.046). Visual correlation between fire frequency, July temperature and normalized CHAR show that charcoal and summer temperature are positively correlated before 7500 cal. years BP, and negatively correlated after *c.* 7500 cal. years BP (Fig. 3b).

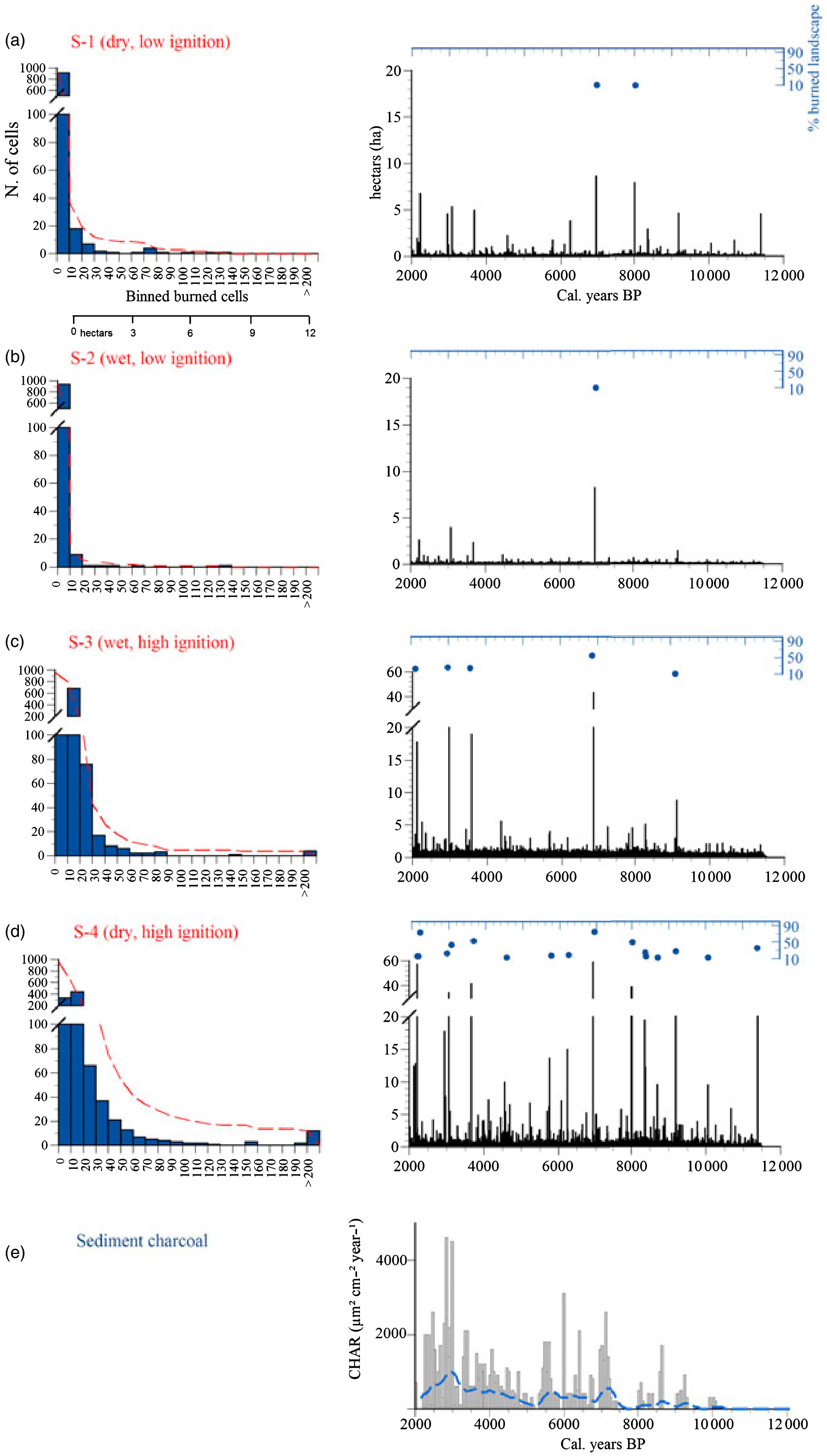
Discussion

FIRE VARIABILITY AT GOUILLÉ RION OVER THE LAST 12 000 YEARS

Reconstructed local fire episodes show that the trend in local biomass burning changed over time (Fig. 2). The causes of fire regime changes in terms of frequency and size are often ambiguous, because fire occurrence reflects the integrated effects of (i) climatic variability at a decadal-to-centennial scale (affecting vegetation composition) and at an interannual scale (i.e. changes in temperature and moisture that control fuel flammability and ignition probability); (ii) changes in species composition, e.g. through the immigration of more fire-prone species and (iii) human-related activities such as grazing and land clearance, which limit the availability of fuel or directly increase fire occurrence by ignition. On the basis of the palaeo-environmental record (e.g. pollen, macrofossils), we discuss how the observed variability in fire occurrence might be related to the above factors over a long time scale (last 12 000 years).

During the transition between the Late Glacial and early Holocene (*c.* 12 000–10 000 cal. years BP) local fire activity was negligible near Gouillé Rion (Fig. 2b). Around 11 350 cal. years BP, only *c.* 200 years after temperature had abruptly increased by about 3–4 °C, the tree line moved upward by about 800 m and reached Gouillé Rion elevation (2343 a.s.l., Tinner & Kaltenrieder 2005). However, the presence of

Fig. 4. The four scenarios of fire simulations on a total area of *c.* 78 ha around Gouillé Rion, Switzerland, corresponding to a radius of 500 m around the lake. Histograms (left side) represent binned numbers of cells at 10-cell intervals. Cumulative ogive curves are shown (dashed lines increasing right to left). Diagrams (right side) are 10-year averages of burned cells with corresponding events > 10% of landscape (dots). (a) S-1: scenario with dry and low number of ignitions; (b) S-2: scenario with wet and low ignitions; (c) S-3: scenario with wet and high ignitions; (d) S-4: scenario with dry and high ignitions; (e) raw charcoal accumulation rates (CHAR, histograms, exaggeration 2x) and background charcoal (BCHAR, dashed line). Wet conditions in S-2 and S-3 correspond to present mean values.


(a)
S-1 (dry, low ignition)
N. of cells
1000
800
600
100
80
60
40
20
0
0 10 20 30 40 50 60 70 80 90 100 110 120 130 140 150 160 170 180 190 >200
Binned burned cells
0 hectars 3 6 9 12
hectars (ha)
20
15
10
5
0
2000 4000 6000 8000 10 000 12 000
Cal. years BP
% burned landscape
90
50
10
(b)
S-2 (wet, low ignition)
(c)
S-3 (wet, high ignition)
1000
800
600
400
200
60
40
(d)
S-4 (dry, high ignition)
(e)
Sediment charcoal
CHAR (µm² cm⁻² year⁻¹)
4000
2000
2000 4000 6000 8000 10 000 12 000
Cal. years BP

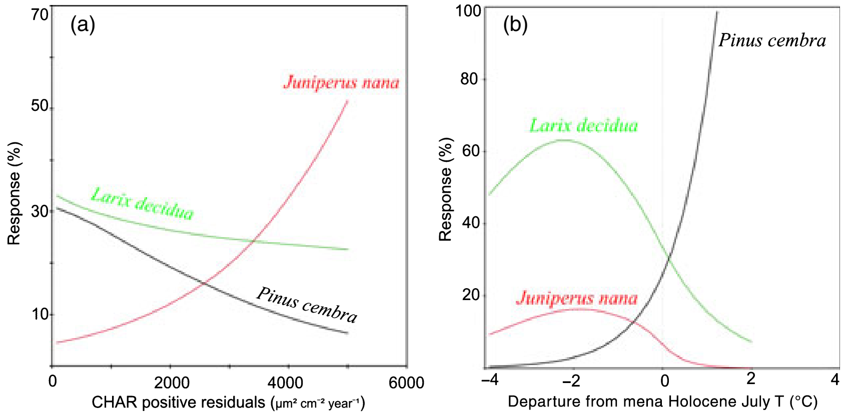


Fig. 5. (a) Species response curves to CHAR (charcoal accumulation rates) positive residuals; (b) response curves to Holocene mean summer temperature, which is approximately equal to the present mean July temperature (8.1 °C).

heliophilous *J. nana*, *Dryas octopetala* L., *Rumex*, and *Salix* macrofossils at this time (Tinner & Kaltenrieder 2005; Fig. 3d) indicates that *L. decidua* grew in an open environment and biomass was probably too low to support fire occurrence (Tinner, Ammann & Germann 1996). At lower altitudes (e.g. Upper Engadine, Gobet *et al.* 2003), where conditions were probably drier, fire occurred in parkland environments dominated by *Pinus* species.

Fires first occurred between 10 000 and 8000 cal. years BP (four episodes per 1000 years, MFI = 250 years), when *P. cembra* formed closed forests with higher biomass (Tinner & Kaltenrieder 2005). Increasing fire occurrence was probably promoted by higher fuel availability as well as the generally warm and dry conditions during the early Holocene. Around 8400 cal. years BP *L. decidua* forests collapsed, probably in response to strong climatic changes (see discussion in Tinner & Kaltenrieder 2005). Subsequently climatic conditions became less continental and moister, probably resulting in a decrease of fire frequency (8000–7000 cal. years BP).

After 7500 cal. years BP, it is difficult to assess whether the observed fire variability was mostly human- or climatically driven, since in nearby Sion (*c.* 8 km away) rather intense early Neolithic farming had established by 7300 cal. years BP (Curdy, Leuzinger & Leuzinger-Piccand 2003). Between 7500 and 3000 cal. years BP, a total of 12 local fire episodes occurred, with a period of higher IFF and raw CHAR values from 7500 to 5500 and a period of increasing IFF from 4500 to 2000 cal. years BP (Fig. 2b). These periods cover the Neolithic (*c.* 7500–4200 cal. years BP) and the Bronze Age (*c.* 4200–2800 cal. years BP) and may relate to human-induced fire activity around the site. Indeed, an increase of human impact during the Neolithic and especially during the Bronze Age is documented in the Gouillé Rion pollen record (Tinner, Ammann & Germann 1996).

After 3000 cal. years BP, a general decrease in fire activity occurred, with the exception of the Medieval period. Again, it is likely that the Medieval peak in fire activity relates to land use. Drier conditions during the Medieval Climate Anomaly may have promoted agricultural activity and thus fire use, or directly contributed to more fires because of generally drier conditions. In any case the establishment of today's open pastoral landscape with krummholz and dwarf shrubs (e.g. *L. decidua, Betula pubescens*, *P. abies*, *J. nana*, *D. octopetala, Vaccinium gaultherioides, Empetrum hermaphroditum, Rhododendron ferrugineum* and *Salix*) and herbs (e.g. *Potentilla, Saxifraga* and *Carex*) occurred at *c.* 1700 cal. years BP (Tinner, Ammann & Germann 1996; Kaltenrieder, Tinner & Ammann 2005). Inferred fire frequency decreased to 1–2 episodes per 1000 years (MFI: 500–1000 years), following a general decrease in biomass availability. Landscape openness reached a maximum at the end of the Medieval period (500 cal. years BP) and reforestation occurred regionally during the last century, following land abandonment and forest conservation policy (Rutherford *et al.* 2008).

Overall, our fire reconstruction shows that MFI values (*c.* 250–1000 years per fire, with *c.* 250 corresponding to the minimum reliably detectable return interval, Clark 1988) are comparable to the lower values found in a similar study from the central Alps, where *P. mugo* forests burned with a MFI of 230 years and *P. abies* forests with value of *c.* 600 years (Stähli *et al.* 2006; Genries *et al.* 2009), but are also highly variable if compared to historical data in the region (Zumbrunnen *et al.* 2009).

DISENTANGLING CLIMATIC AND HUMAN INFLUENCES ON FIRE VARIABILITY

Climatic and anthropogenic causes of fire-regime changes are difficult to disentangle using sedimentary records alone. For example, increasing CHAR and BCHAR values after 7200 cal. years BP indicate a change in fire regime while the vegetation type remained constant (*P. cembra* forest with *L. decidua*, Fig. 3d). Regional archaeological and pollen data (Welten 1982; Curdy, Leuzinger & Leuzinger-Piccand 2003; Harrison & Heyd 2007) as well as the absence of climatic evidence for a marked change at 7200 cal. years BP (Reasoner & Tinner 2008) suggest that humans caused this fire-regime shift. However, the lack of local evidence at Gouillé Rion makes it difficult to definitively assign a human cause. Nonetheless, our LandClim simulation allows us to examine independently the effect of climatic (i.e. moisture availability) and anthropogenic (i.e. number of ignitions) conditions on the extent of area burned around the lake.

In scenarios with low ignition (Fig. 4a,b), changing the degree of moisture availability in the landscape has a negligible effect on the area burned. Most of the fires in the landscape are very small for both simulations (< 1 ha, Fig. 4, histograms), and drier conditions also trigger fire episodes of limited extent (< 5 ha). The competing scenarios under modern precipitation abundance (Fig. 4c,d) show that changing the number of ignitions greatly increases the total area burned. Most of the fire episodes burned areas covering up to 2 ha (Fig. 4, histograms), and several events cover 10–50% of the simulated landscape (Fig. 4, diagrams). When coupled to drier conditions (Fig. 4d) the increased number of ignitions results in fires burning a greater portion of the landscape, although the number of smaller fire episodes remains comparable (Fig. 4c,d, histograms). Thus, our simulations show that ignition frequency has a larger impact than climatic conditions on the fire regime. Also, number of ignitions may greatly affect the size of area burned, when exacerbated by drier conditions.

Simulation results indicate that the CHAR increase after 7200 cal. years BP, probably relates to increased human impact during the Neolithic, which promoted fire occurrence through more frequent ignitions. Charcoal data also provide evidence that human disturbance overrode climatic control of local fires after the Neolithic. For example, the slight IFF increase between *c.* 8500 and 9500 cal. years BP (i.e. 3–4 episodes per 1000 years) matches the quantitative reconstruction of mean July temperature (Fig. 3b and Heiri *et al.* 2003). Thus the likelihood that hot, dry conditions conducive to fire occurrence occurred in any single year probably also increased during this interval. Summer temperature is in fact a major controlling factor for fire regime in subalpine areas in the modern landscape (Zumbrunnen *et al.* 2009). Conversely, around 6500 and 4500 cal. years BP, despite July temperature below the average, IFF increases (Fig. 3b).

RESPONSE OF THE TREE LINE ECOTONE TO FIRE VARIABILITY

Our data provide clear evidence that occurrence of natural fires decisively influenced vegetational dynamics when human impact was negligible prior to 7200 cal. years BP. During the early Neolithic, control over the fire regime shifted from natural to human-driven, but tree line persisted at a higher elevation than at present (Tinner & Theurillat 2003; Heiri *et al.* 2006). Only after 4500 cal. years BP (onset of Bronze Age Alpine farming; Kaltenrieder, Tinner & Ammann 2005; Reasoner & Tinner 2008), did timberline (but not tree line) descend by several hundred metres. This shift was coupled with the establishment of a larger tree line ecotone, similarly to present-day *J. nana* subalpine dwarf shrublands (Tinner 2006). Palaeo data suggest that this was probably caused by burning, grazing and clear-cutting during the Bronze Age (Tinner & Theurillat 2003). Accordingly, modelling efforts also simulate the timberline above the elevation of Gouillé Rion after 4500 cal. years BP despite palaeobotanical evidence to the contrary (Kaltenrieder, Tinner & Ammann 2005; Tinner & Kaltenrieder 2005; Heiri *et al.* 2006). Our new data show that the enlargement of the tree line ecotone occurred together with an increase of IFF (three fire episodes in 1000 years). However, because neither fire frequency nor raw CHAR values exceeded values registered before (i.e. at 6000 and 8000 cal. years BP; Fig. 2b), fire impact alone was probably not the only factor promoting *J. nana* shrublands around 4500 cal. years BP. Instead, it is likely that open environments were maintained by fire occurrence and increasing grazing activity at higher altitudes during the Bronze Age, when Alpine summer farming started (Tinner, Ammann & Germann 1996; Reasoner & Tinner 2008). Thus, fast natural up-slope movement of the tree line ecotone following rapid climate changes (Tinner & Kaltenrieder 2005) is likely to be counter-balanced by anthropogenic fires, which can strongly constrain upslope migration of trees.

RESPONSE OF SPECIES TO FIRE IMPACT AND SUMMER TEMPERATURE

Fire occurrence and summer temperature are likely to be correlated at our location under natural conditions. Drier conditions that accompany higher temperatures should promote fire occurrence. Therefore, species response curves should respond in the same way to these co-varying variables. Our data instead show distinct responses of species to fire impact and summer temperature (Fig. 5), supporting our conclusion that the fire regime reflects human disturbances more strongly than climate variability, at least since the Bronze Age (*c.* 4000 cal. years BP). Specifically, response curves suggest that temperatures above the Holocene mean favour *P. cembra* over *L. decidua* and *J. nana,* whereas cooler temperatures (1–3 °C below the Holocene mean) favour *L. decidua* and *J. nana*. Accordingly, data from previous investigations also show that *L. decidua* expanded when *P. cembra* forest declined during cold phases; instead *P. cembra* was advantaged during stable periods with higher temperature (Wick & Tinner 1997). In contrast, *P. cembra*, the species most favoured by higher temperature, responds most negatively to increasing fire impact. *Larix decidua* also declines with increasing fire impact but is not as strongly affected as *P. cembra*, and *J. nana* is most abundant when fire frequency is highest in the record.

Our results can be explained by the ecological preference of pioneer and heliophilous *L. decidua* and *J. nana,* which today are outcompeted by shade-tolerant *P. cembra* under undisturbed conditions (Ellenberg 1996). The re-expansion of *L. decidua* at the beginning of the Bronze Age (*c.* 4000 cal. years BP, Fig. 3d) occurred as fire and grazing activity increased. This is in agreement with previous studies showing that agri-pastoral activities promoted *L. decidua* and *Alnus viridis* D.C. (Gobet *et al.* 2003). Timber exploitation may have also favoured *L. decidua* by eliminating late-successional trees such as *P. cembra* (Tinner, Ammann & Germann 1996; Zoller, Erny-Rodman & Punchakunnel 1996). Regression curves together with time series analysis show that *P. cembra* is more sensitive to burning (60 years after fires, cross correlograms in Appendix S3) than *L. decidua,* which is rather fire resilient because of its resprouting capacity and rapid establishment on mineral soils (Tranquillini 1979).

Accordingly, palaeoecological data show that distribution of *P. cembra* was wider in the past when fire was less frequent (Carcaillet 1998; Genries *et al.* 2009). Open conditions created by fire around 4500 cal. years BP that favoured *J. nana* (200 years after fires, Appendix S3) are in accordance with its ecological requirements (i.e. very shade-intolerant, Ellenberg 1996). Moreover, cattle refrain from grazing the pointed needles of *J. nana*.

Overall, the dominant tree line species (i.e. *P. cembra* and *L. decidua*) show different optima in respect to July summer temperature, and the presence of *P. cembra* is highly limited by fire occurrence. Under a more severe fire regime, which in the Late Holocene was mainly controlled by systematic burning, heliophilous species such as *J. nana* and *L. decidua* are at an advantage. Also, values of the threshold above which *L. decidua*–*P. cembra* forests switched to *Juniperus* shrublands, with isolated *L. decidua* (*c.* 3000 μm cm^{-2} year^{-1}, Fig. 5a) occurred when fire regime mostly switched from natural to anthropogenic (Fig. 2a). It is likely that without human disturbance, the tree line would raise. Rising temperatures could lead to further upslope tree line expansion, especially by *P. cembra,* which reaches the highest elevations of all European trees, especially on acidic soils (Brändli 1998). However, this conclusion is entirely dependent on future disturbance. Increasing fire activity and/or grazing would favour continued dominance by *J. nana* and *L. decidua*.

Conclusion

Our new quantitative reconstruction of fire regime and environmental response of species, combined with model simulations, allows us to better determine the nature of the observed variability of fire and to understand species response to important ecological factors such as fire impact and summer temperature. Our results support the hypothesis that local disturbance (such as fire occurrence and grazing) will be decisive in whether the timberline reaches its potential altitudinal limit (Shankman 1984; Stueve *et al.* 2009) under future global warming conditions, as was the case during the past four millennia.

Our data suggest that in the future anthropogenic fire occurrence will heavily affect ecosystems at the tree line ecotone. If climate should change towards warmer and/or drier conditions in the next decades (as anticipated for the Alps, IPCC 2007), environmental effects are likely to be exacerbated by anthropogenic fires, which today represent 90% of the total number of fire in the Alpine area (Zumbrunnen *et al.* 2009). The future of forest-management practices in the Alps (e.g. fire exclusion) may gain attention in the next decade as in the Pacific Northwest of the U.S., where it is debated whether increased fuel loads following policy of fire suppression led to greatly increased risk of high severity fire compared to pre-settlement forests (e.g. Taylor & Skinner 1998; Donato *et al.* 2009). Anthropogenic suppression of various disturbances (grazing, fire occurrence) may alter forest composition and structure at the timberline, stimulating the discussion over timberline restoration and nature conservation in the Alps. Allowing natural fire disturbance is relevant for keeping important ecosystem functions such as forest regeneration, biodiversity and also biomass control (Stähli *et al.* 2006). It has been suggested that rapid upslope migration of trees in response to climatic warming is important for maintaining forest diversity under rapid warming conditions (Tinner & Kaltenrieder 2005). Our study shows that increased fire impact is a decisive factor in creating open lands and impeding the recovery or establishment of forests. Thus, only control of fire impact close to the tree line may allow subalpine trees to expand to higher areas under global climate change conditions and help to maintain forest diversity in the Alps.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Radiocarbon dates and chronology.

Appendix S2. The LandClim model.

Appendix S3. Time series analysis.