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ORIGINAL ARTICLE

# Human and climatic impact on mires: a case study of Les Amburnex mire, Swiss Jura Mountains

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**Abstract** Modern period long-term human and climatic impacts on a small mire in the Jura Mountains were assessed using testate amoebae, macrofossils and pollen. This multiproxy data analysis permitted detailed interpretations of local and regional environmental change and thus a partial disentanglement of the different variables that influence long-term mire development. From the Middle Ages until A.D. 1700 the mire vegetation was characterised by ferns, *Caltha* and *Vaccinium*, but then abruptly changed into the modern vegetation characterised by Cyperaceae, *Potentilla* and *Sphagnum*. The cause for this change was most probably deforestation, possibly enhanced by climatic cooling. A decrease in trampling intensity by domestic animals from A.D. 1950 onwards allowed *Sphagnum* growth and climatic warming in the A.D. 1980s and 1990s may have been responsible for considerable changes in the species composition. The mire investigated is an example of the rapid changes in mire vegetation and peat development that occurred throughout the central European mountain region during the past centuries as a result of changing climate

and land-use practice. These processes are still active today and will determine the future development of high-altitude mires.

**Keywords** Testate amoebae · Macrofossils · Pollen analysis · Human impact · Climate change · Jura Mountains

## Introduction

Mire ecosystems will respond individually to climate and land-use changes according to local conditions such as hydrology, bedrock and altitude. In order to understand the long-term development of mire ecosystems, detailed investigations of mires of different types and from different regions are required. Palaeoecological investigations capable of capturing long-term changes have been concentrated on relatively undisturbed ombrotrophic bogs, as these provide the best archives for past environmental change. However, the current investigation is made on a site impacted by human activities—a small (0.2 ha) mire located in the middle of a traditional pasture woodland in the Jura Mountains.

Mountain mires constitute a small but important landscape element, both as important ecological components in themselves and as natural archives for environmental change. Many such high-altitude central European mires show strong decomposition and/or disturbance in the upper peat stratigraphy (e.g. van der Knaap et al. 2000; Shotyk 2002; Roos-Barraclough et al. 2004; Sjögren et al. 2005), suggesting major environmental changes in the past centuries. It is the upper part of the peat that is of interest here, and the

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present investigation can be seen as a case study of the long-term effect of environmental change on mire ecosystems and peat development in general, and on grazed mountain mires in particular.

The effects of climate and land-use change on mires during the last millennium can seldom be clearly separated because of interaction, both directly in how the mire vegetation responds to another type of environmental change, and indirectly as climate change affects land-use practices (and to some extent vice versa). Still it is possible to determine to some degree which parameter is the most important for a given change in the environment, and how this may interact with other important changes (Hausmann et al. 2002). Multiproxy approaches have been shown to be the best method for the interpretation of complex environmental change (Ammann et al. 2000; Birks et al. 2000; Birks and Birks 2006). In this paper, testate amoebae, macrofossils, wetland pollen, upland pollen and peat characteristics have been analysed in order to study human and climatic impacts on the mire development.

#### Site description

The landscape in the higher part of the Jura Mountains along the border between France and Switzerland (Fig. 1) is a mosaic of approximately equal parts of conifer forests, open and wooded pastures. The wooded pastures are dominated by *Picea abies*, while *Abies alba*, *Fagus sylvatica* and scattered *Acer pseudoplat-*

*anus* are found only in more forested areas. The local climate is cold and wet (annual means ca. 3°C and 1,600 mm/year), but periodic droughts may occur because water is quickly drained through the permeable limestone bedrock. Traditional land-uses are summer grazing and forestry (Gillet and Gallandat 1996). In the past decades the area has become popular for recreational activities such as hiking, cross-country skiing and picnicking.

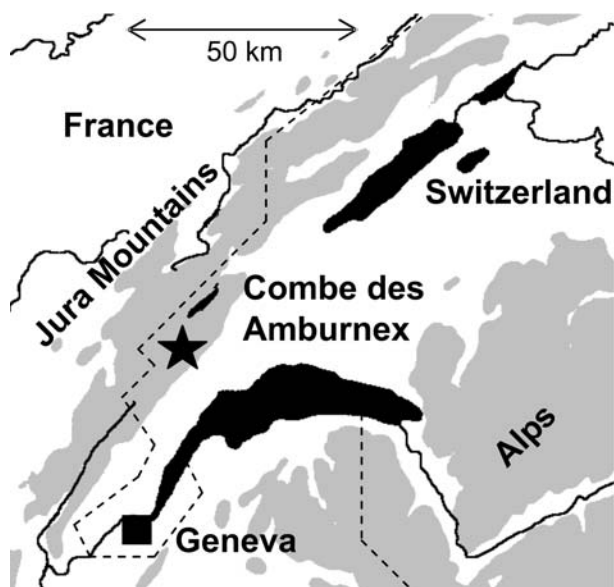
The area around the site investigated has been under protection since 1973 as part of the 70 km<sup>2</sup> Parc Jurassien Vaudois. Written sources reveal that pastures were already well established in the Amburnex valley in A.D. 1301, and charcoal production in this part of the Jura Mountains is indicated from the 16th century (Rochat 1995). The exploitation of the forest seems to have been very intense during the 18th and 19th centuries until different cantonal laws allowed an organised forestry from A.D. 1902.

The mire Les Amburnex (Lat 46°32'23"N, Long 6°13'54"E, 1,370 m a.s.l.) is situated on the side of Combe des Amburnex, a small valley 1,300 m a.s.l. The mire has a peanut-shaped area of approximately 0.2 ha. The markedly raised surface suggests a history as a raised bog, although strong decomposition along the edges may have exaggerated the raised appearance. Large parts of the mire are today overgrown by *Picea* and a badger colony is present in the southwestern driest part. The peat profile (Table 1) was extracted from the northeastern treeless part. Several test cores in the northeastern part showed a similar lithology, while the southwestern part was considered unsuitable for palaeoecological investigations. The mire was used for water extraction since the beginning of the last century by the nearby summer farm and is today fenced and protected from cattle. The vegetation of the mire and the valley is described by Vittoz (1997, 1998), and the vegetation history by Wegmüller (1966) and Sjögren (2006).

#### Methods

##### Laboratory methods and analysis

The peat profile studied was retrieved with a spade as a 0.5 m long monolith. The total peat depth at the sampling point is ca. 3 m, underlain by calcareous clay. Samples (2 cm<sup>3</sup>) for testate amoebae analysis were prepared according to standard procedures (Charman et al. 2000; Hendon and Charman 1997; Tolonen 1986; Warner 1990a). Approximately 150 testate amoebae shells were counted per sample except for the lower



**Fig. 1** Overall map. The broken line marks the border between France and Switzerland. Grey indicates areas above 1,000 m. Rivers and lakes are shown in black. The study area is marked by a star

**Table 1** Peat lithology

Depth (cm)	Characteristics
0–11.5	Light brown, loose, well preserved <i>Sphagnum</i>
11.5–14.5	Dark brown, decomposed <i>Sphagnum</i>
14.5–21	Dark brown, compact, decomposed peat
21–25	Black-brown, compact, decomposed peat

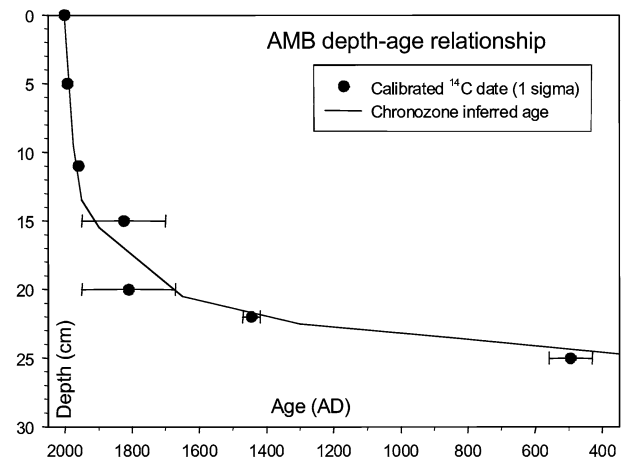
samples (at 17 and 18 cm), which had low concentrations. At 19 and 20 cm taxa were noted only as present. Identification follows Charman et al. (2000), Grospletsch (1958), Hoogenraad and de Groot (1940) and Ogden and Hedley (1980).

The residues from the testate amoebae sample preparation were used for plant-macrofossil analysis. The samples were sieved (300  $\mu\text{m}$  mesh) and examined under a stereoscopic microscope (20–100 $\times$ ). In addition one slide from each peat sample was prepared for detailed description of peat constituents and examined under a compound microscope (100–400 $\times$ ). A five-degree scale represents the peat constituents (e.g. *Sphagnum*, Campyliaceae or sedge rootlets) as follows: 1 = <5%, 2 = 5–25%, 3 = 25–50%, 4 = 50–75%, and 5 = 75–100%. Countable fossils such as sedge endocarps are presented as absolute values. Macroscopic charcoal was classified after maximum size in millimetre size classes. Available descriptions and keys were used for identification (Daniels and Eddy 1985; Grosse-Brauckmann 1975, 1986; Katz et al. 1965, 1977; Tobolski 2000; Warner 1990b).

Pollen slides were prepared by the acetolysis method (Berglund and Ralska-Jasiewiczowa 1986; Faegri and Iversen 1989). Identification used the literature (Punt and Clarke 1984; Moore et al. 1991; Reille 1992, 1995, 1998; Punt et al. 1995; van Geel et al. 2003) and the reference collection at the Institute of Plant Sciences in Bern. The pollen values are expressed as percentages of all upland taxa; wetland and local pollen are excluded from the pollen sum. At least 500 upland pollen grains were counted per sample (mean 660). For dry-bulk density measurements peat samples were dried at 40°C in open containers for 1 week before weighing (Aaby 1986). Ash content (LOI residue) was measured on the same samples (drying at 105°C overnight, heating at 550°C for 4 h; Heiri et al. 2001).

### Depth–age relationship

The depth–age model follows an established chronostratigraphy (Sjögren 2006) in which radiocarbon dates from three peat profiles were combined, including six radiocarbon dates from the present peat sequence



**Fig. 2** Depth–age relationship for the Les Amburnex mire based on linear interpolation between chronostratigraphic levels. Calibrated radiocarbon age-intervals are shown for comparison

(Fig. 2). Correlation between the peat cores was achieved by using the extra-regional pollen assemblages. The chronostratigraphy was checked against regional biostratigraphical markers (van der Knaap et al. 2000) and gave a maximum deviation of 50 years. Considering the high accuracy of post-bomb  $^{14}\text{C}$  calibration (Goslar et al. 2005; Sjögren et al. 2006) the precision of the depth–age relationship for the past 50 years is higher, approximately  $\pm 5$  years. To achieve a continuous depth–age relationship linear interpolation is used between chronostratigraphic levels. The deviation from the actual age may thus be somewhat higher between than on the stratigraphic levels, especially when the peat accumulation is not constant.

### Numerical methods

Numerical analyses were conducted on three data sets: the testate amoebae assemblage, the wetland pollen assemblage, and the upland pollen assemblage. No numerical analyses were conducted on macrofossils, charcoal or peat characteristics as the qualitative heterogeneity was too large.

Assemblage zones were determined statistically according to the recommendations by Bennett (1996), by optimal sum-of-squares partitioning (Birks and Gordon 1985; Birks 1986) and their significance was tested with the broken-stick method (MacArthur 1957). The uppermost zone boundary for the upland pollen assemblages at 2.5 cm depth is not considered in interpretation, as no local ecological significance could be found; this zone boundary might be an effect of the yearly fluctuations in pollen accumulation rates (van der Knaap and van Leeuwen 2003).

The most important changes within the assemblages of testate amoebae (42 species/types), wetland pollen (18 species/types, including spores) and upland pollen (133 species/types) were determined using detrended correspondence analysis (DCA, ter Braak and Prentice 1988). For the wetland pollen and upland pollen assemblages an additional analysis of the top 18 cm was conducted for comparison with the testate amoebae data set that covered that depth. The analysis was performed with CANOCO 4.5 (ter Braak and Šmilauer 1998). Detrending was made by segment, the data were square-root transformed and rare taxa were downweighted.

The direction of change between samples (positive/negative) was used to determine the significance of correlation between the DCA scores of the data sets (Pearson's chi-square test with Yates' continuity correction; Sokal and Rohlf 1995). The same approach was used to test for correlation with the NAP value (non-arboreal pollen), as the scores for the upland DCA axis 1 in particular are visually similar to the NAP curve. The low number of samples and low variation in scores from the first DCA axis (primarily for testate amoebae and wetland pollen) above 12 cm depth (A.D. 1960) made statistical correlation problematic. The other statistical correlations are also based on a rather low number of samples (17–25), and details of the results should be viewed with some caution. The analysis was conducted with S-PLUS (Crawley 2002).

In pollen analysis it is preferable (if possible) to use only the pollen assemblage that derives from the area of investigation. For interpretations concerning the surrounding mountain landscape the highland pollen assemblage (i.e. pollen from upland taxa abundant >1,000 m a.s.l. in the modern vegetation) would be more accurate than the upland pollen assemblage (i.e. pollen from all non-wetland taxa, including those from the Swiss Plateau). In order to test if there are major differences in the dynamics of the two data sets the same numerical methods (zonation and DCA) were applied for the highland pollen assemblage. The results were very similar between the data sets and it can be assumed that the results for the upland pollen assemblage also are valid for the high parts of the Jura Mountains. As the two data sets are statistically similar (88% similar direction of change between 1st DCA axes,  $P = 0.001$ ), only the upland pollen assemblage was used for further interpretation. Also this is common practice and requires fewer assumptions (Wright and Harvey 1963).

#### Interpretation of proxies

Several proxies were used to study different environmental variables on different spatial scales; the most

important of these were testate amoebae, macrofossils, pollen and charcoal particles. Testate amoebae indicate local changes in the mire itself (primarily humidity) on the scale of a few cm (Mitchell et al. 2000). Macrofossils primarily reflect the local vegetation (Birks and Birks 2003). The degree of decomposition varies greatly in the profile and few identifiable plant remains exist below the depth of 15 cm. Pollen and spores from wetland plants reflect the vegetation on the mire itself and in the immediately surrounding (wet) minerogenic soil. They can also be referred to as the local component, i.e. pollen and spores that originate from within 0 to 20 m of the edge of the mire (Jacobson and Bradshaw 1981, Prentice 1985).

The upland pollen assemblage records the landscape development. There are two major source areas for this pollen: the Jura Mountains (>1,000 m a.s.l.) and the Swiss Plateau (<800 m). The source area can partly be determined on the basis of species composition, but the difference in general development is small and there is therefore no need for such separation in the current context. Where highland pollen (i.e. from taxa abundant >1,000 m a.s.l. in the modern situation) has been separated it is primarily to confirm the local relevance of the upland pollen assemblages. The relevant source area of pollen (RSAP, sensu Sugita 1994) in the area is estimated as being from 700 to 800 m a.s.l. (Florence Mazier, personal communication). Note that *Picea*, *Abies*, *Fagus* and *Acer* are the only tree taxa that are present in any numbers in the area above 1,000 m today. *Alnus*, *Corylus* and *Betula* might have grown locally in earlier times, but the large fluctuations in their abundance on the Swiss Plateau (Ammann 1988) make direct assessments from pollen values problematic. Charcoal particles and dust allow a reconstruction of past fire intensity at local (macro particles) to regional (dust particles) scales (Tinner et al. 1998).

#### Results and interpretation

The main results are presented in three diagrams (Figs. 3, 4, 5) and described together with short interpretations in Table 2. The results and interpretations are summarised in Table 3.

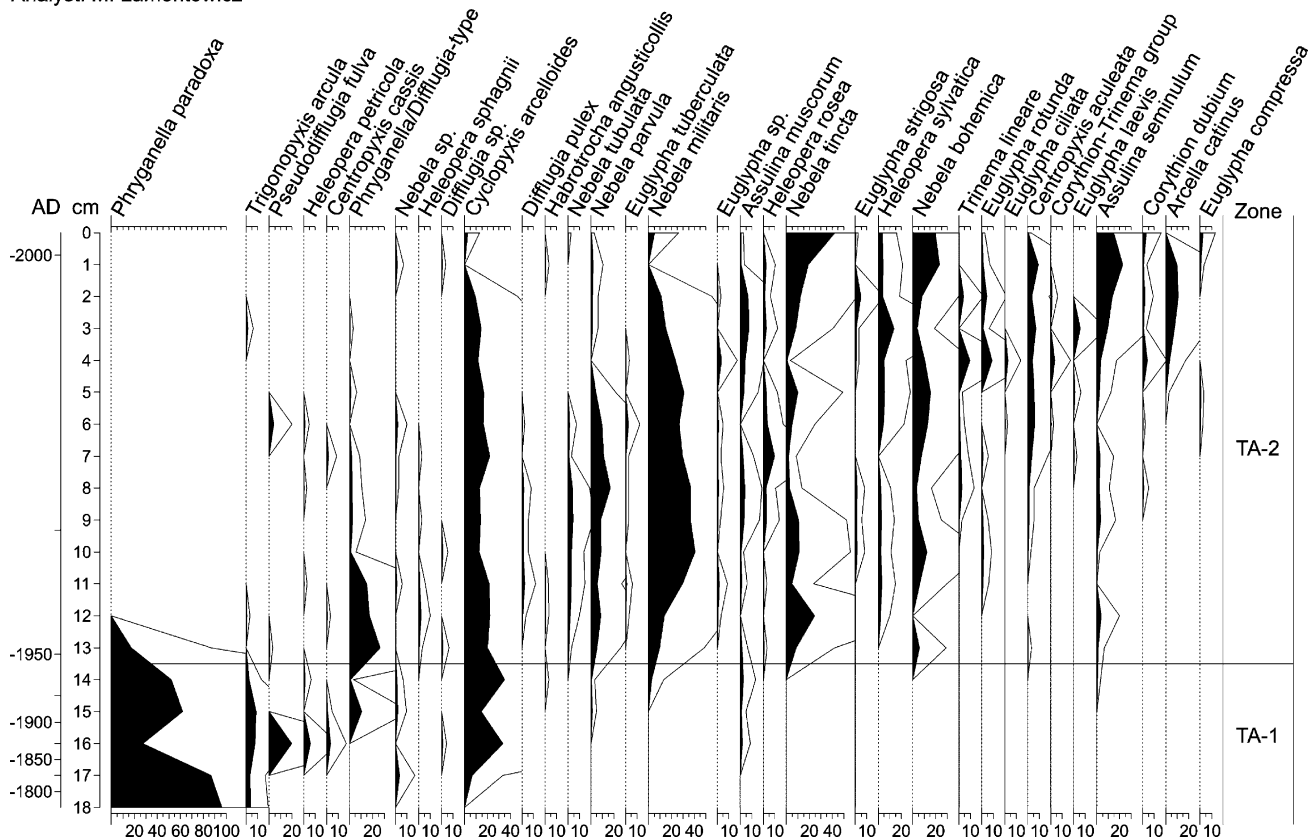
#### Vegetation history of the Les Amburnex mire

Before A.D. 1700 the mire was relative dry, dominated by *Vaccinium* and ferns. It is possible that deciduous trees such as *Alnus*, *Corylus* and *Betula* were growing on the wet soils close to the mire, but the pollen

## Les Amburnex (AMB), Testate amoebae

Selected testate amoebae percentage values sorted by weighted average

Analyst: M. Lamentowicz



**Fig. 3** Percentage diagram of selected testate amoebae and rotifera (*Habrotrocha angusticollis*). Lines show  $\times 5$  exaggeration of the percentage values

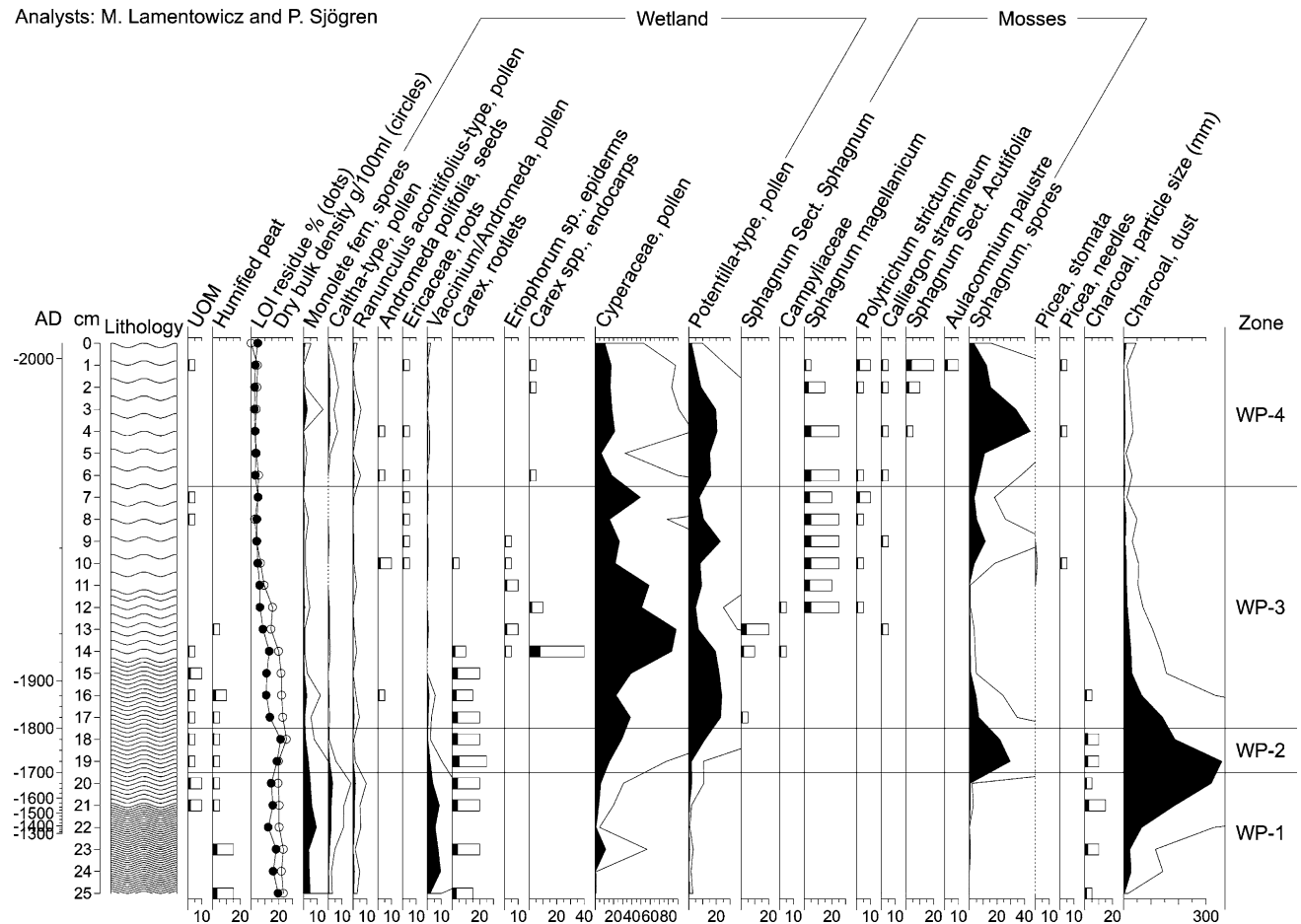
evidence is inconclusive. Pollen of *Caltha*-type and *Ranunculus aconitifolius*-type suggests nearby open areas on moist soils. Grazing seems to have been continuous in the area from at least the middle of the first millennium A.D. (indicated by *Hypericum* and *Plantago lanceolata*) and the surrounding forest was probably relatively open and/or included small glens. An increase in openness is indicated during the High Middle Ages (A.D. 1000–1300), mostly in phase with the general landscape development of the time (Williams 2000; Gauthier 2004; Sjögren 2006), but the low temporal resolution in this part of the pollen diagram makes it impossible to detect any details. From the 15th century onwards there is an increase in openness and grazing pressure (indicated by Poaceae, *Plantago media*, Compositae Subfam. Cichorioideae and Cruciferae) and it is likely that large open pastures were present. Cattle also seem to become more common (indicated by *Podospora*, a cattle-dung fungus; Jacqueline van Leeuwen personal communication). *Fagus*, *Alnus*, *Corylus* and *Betula* decline at the same time,

suggesting that the species were locally present before they were cut down or their preferred habitats turned into pastureland (*Fagus* is still present in the area). High values of charcoal particles and dust are present A.D. 1500–1900 with a strong peak ca. A.D. 1700. These are probably related to charcoal and glass production and would imply deforestation of large areas. A small glass industry was established a few kilometres east of the site in A.D. 1698 and was active until A.D. 1708 (Piguet 1998), i.e. about the same time as the most profound changes in the mire and surrounding landscape occurred. Some of the charcoal might also come from burning of brushwood in connection with clearance. The time period of highest openness and grazing pressure occurred A.D. 1750–1925 (indicated by Poaceae, *Trifolium pratense*, *Lotus*, *Botrychium*, Rubiaceae, *Plantago media*, Compositae Subfam. Cichorioideae and *Plantago montana*). The local mire vegetation also changed in the 18th century. Around A.D. 1700 *Caltha*-type, *Ranunculus aconitifolius*-type, ferns and *Vaccinium* decreased, while Cyperaceae,



## Les Amburnex (AMB), Wetland pollen and Macrofossils

Analysts: M. Lamentowicz and P. Sjögren



**Fig. 4** Diagram of macrofossils, peat characteristics and pollen percentages of local plants. Percentage values of pollen and charcoal-dust particles are based on the sum of upland pollen and spores. Macrofossils are in absolute counts or on a scale from 1 to 5 (i.e. peat constituents, moss parts and roots; 1 = <5%, 2 = 5–25%, 3 = 25–50%, 4 = 50–75%, and 5 = 75–100%).

Maximum size of charcoal particles is given in millimeter. Lines and unfilled boxes show  $\times 5$  exaggeration. The lithology shows strongly decomposed (close line spacing), decomposed, slightly decomposed and undecomposed (broad line spacing) peat. UOM = unidentified organic material

*Potentilla* and *Sphagnum* spores increased, resulting in a vegetation similar to today. Around A.D. 1800 *Sphagnum* spores decreased again and did not reach high values again until the late 20th century. Macroremains of *Sphagnum* indicate on the other hand that *Sphagnum* was locally present all the time, and the spore value may be affected by some environmental variable controlling spore production/dispersal rather than the presence/absence of the moss.

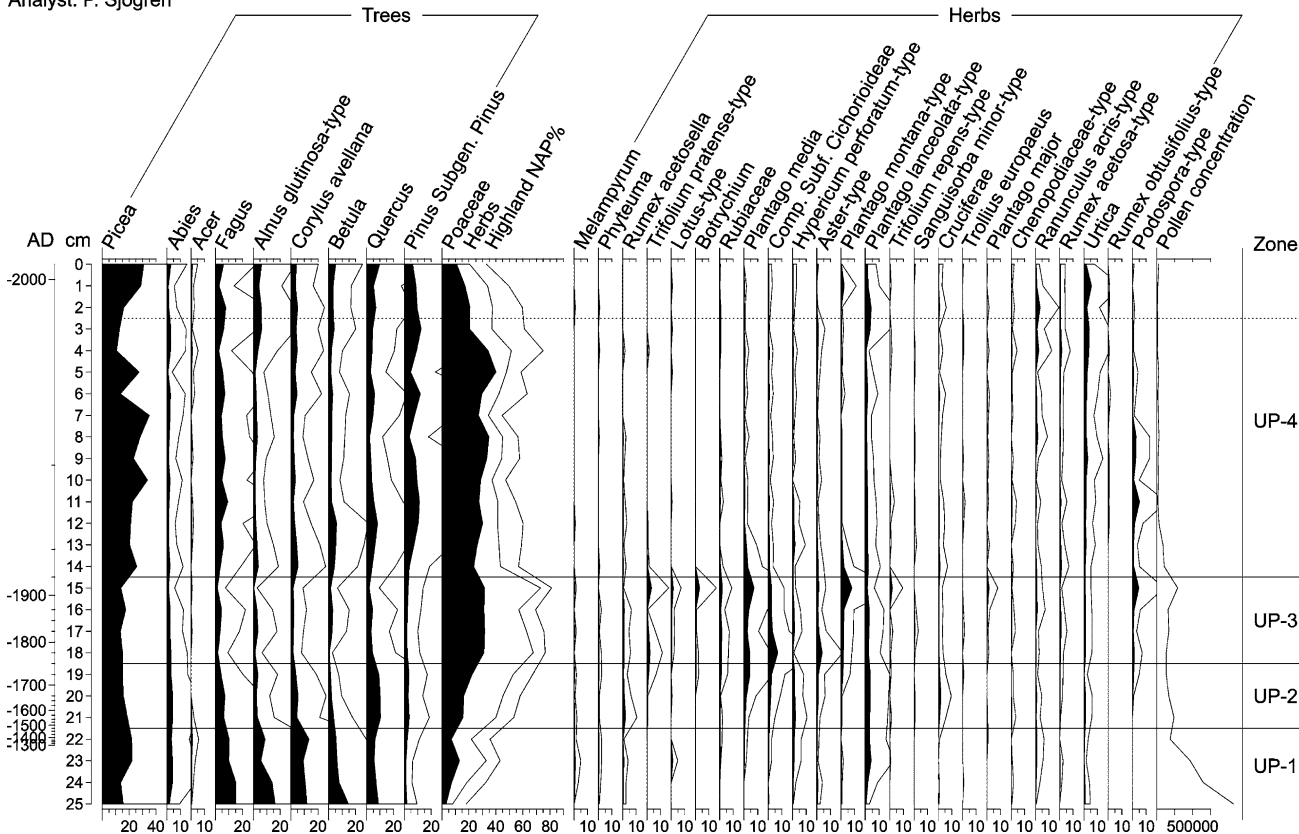
In A.D. 1950 the previously high but varying water-table indicated by *Phryganella paradoxa* (wet; Schönborn 1962) and *Trigonopyxis arcuata* (dry; Charman et al. 2000; Mitchell et al. 1999, 2000), became lower. *Sphagnum magellanicum* is the most common moss from this time onwards. This is a lawn species with an

optimum depth to the water-table of 19 cm (Janssens 1989; Dierßen and Dierßen 2001). From the late 1980s the mire experienced a further decrease in the water-table together with acidification and hummock development (indicated by *Sphagnum* Sect. *Acutifolia*, *Aulacomnium palustre*, *Assulina seminulum* and *Arcella catinus*).

The mire is today partially covered by *Picea* trees. *Picea* needles and stomata have been found in the peat dated to the later half of the 20th century, but a felled tree was dated to the late 19th century so this is probably a more accurate date for the establishment of *Picea* on the mire. Today small trees are removed to stop continuing *Picea* expansion on the mire (Vittoz 1997).

### Les Amburnex (AMB), Upland pollen

Analyst: P. Sjögren



**Fig. 5** Percentage diagram of upland pollen types. Highland NAP% is based on the sum of highland pollen and spores (taxa abundant >1,000 m a.s.l. in the modern vegetation). Percentage values are based on the sum of upland pollen and spores. Lines

show  $\times 5$  exaggeration. Among trees, only *Picea*, *Abies*, *Acer* and *Fagus* occur locally (<ca. 5 km) today. Herb taxa are sorted on weighted average. The dotted line is a significant zone boundary, but is not considered relevant in the current context

#### Main gradient of change

The first DCA axes for the different data sets can be considered to represent the main gradient of change. By reducing the complex data sets into single variables it is possible to compare the data sets directly with each other (Fig. 6). The first DCA axis of the testate amoebae assemblage explains 39.5% of the total variance, of the wetland pollen assemblage 56.7% (32.6% for the top 18 cm) and of the upland pollen assemblage 20.1% (26.7% for the top 18 cm). There is a striking similarity between the first DCA axis of upland pollen and the curve for the same data set (84% of the samples show same direction of change,  $P = 0.003$ ). NAP is a relatively good measurement of grazing/openness (Aaby 1994) and the good correlation suggests that the main change in the upland pollen assemblage is related to grazing/openness. Comparison of the first DCA axes between the upland and wetland pollen assemblages shows a clear negative relationship until A.D. 1985

(88% of the samples show opposite direction of change,  $P = 0.008$ ) and a positive relationship with the testate amoebae until A.D. 1985. This suggests that the most important variable for all the data sets until A.D. 1985 is grazing/openness. The upper parts of the first DCA axes of the testate amoebae and of the wetland pollen assemblages seem related, while the relation with the upland pollen assemblage is less clear. But the major change in the testate amoebae assemblage around A.D. 1950 has neither a parallel in the short wetland pollen data set nor in the long, and though it seems that both the testate amoebae and the wetland pollen assemblages are affected by grazing/openness it is clear that the relationship is not linear and that the different proxies respond in different ways. A direct comparison with different upland pollen taxa (Figs. 5, 6) shows that the most important change in the testate amoebae assemblage is related to a reduction in heavy grazing indicators such as *Plantago media* and *Plantago montana*-type. The most important change in the

**Table 2** Description and interpretation of statistically significant assemblage zones

Proxy/zone	Description	Interpretation
Testate amoebae		
TA-1 A.D. < 1750–1950	<i>Phryganella paradoxa</i> is dominant. <i>Trigonopyxis arcuata</i> and <i>Cyclopyxis arcelloides</i> have high values. Single shells of these taxa were also recorded at 20–19 cm depth (ca. A.D. 1650–1750), with almost total dominance of <i>Phryganella paradoxa</i> . It is, therefore, likely that a similar composition of testate amoebae also occurred some time prior to A.D. 1750	High but variable water-table
TA-2 A.D. 1950–2000	<i>Phryganella paradoxa</i> and <i>Trigonopyxis arcuata</i> almost disappear. <i>Nebela parvula</i> , <i>N. militaris</i> , <i>N. tincta</i> and <i>N. bohemica</i> increase. <i>Phryganella/Diffugia</i> -type is common at the transition to TA-1. Major changes in the testate amoebae assemblage in the 1990s include decreasing <i>Cyclopyxis arcelloides</i> , <i>Nebela parvula</i> and <i>N. militaris</i> and increasing <i>Assulina seminulum</i> and <i>Arcella catinus</i>	Lowering of water-table, accentuated in the 1990s. Acidification
Wetland pollen and macrofossils		
WP-1 A.D. 1000–1700	Relatively high values for monolet fern spores, <i>Caltha</i> -type, <i>Ranunculus aconitifolius</i> -type and <i>Vaccinium/Andromeda</i> -type. Charcoal particles increase in abundance	Dry mire surface. Nearby open wetlands. Local fires
WP-2 A.D. 1700–1800	Pollen and spore values of monolet ferns, <i>Caltha</i> -type, <i>Ranunculus aconitifolius</i> -type and <i>Vaccinium/Andromeda</i> -type decrease, while those of Cyperaceae and <i>Potentilla</i> -type increase. <i>Sphagnum</i> spores peak. Charcoal-dust particles reach maximum values around the transition to WP-1	Wet mire surface. Possibly raised bog development. Local fires and maximum in regional use of fire
WP-3 A.D. 1800–1985	High pollen values of Cyperaceae and <i>Potentilla</i> -type. <i>Carex</i> rootlets are common until A.D. 1950, at which time there is a peak in Cyperaceae pollen and <i>Carex</i> spp. endocarps. <i>Sphagnum</i> macrofossils become common after A.D. 1950, while <i>Sphagnum</i> spores first become frequent in the 1970s. Charcoal-dust particles decrease to almost zero in the 20th century	Sedge mire. Development of a <i>Sphagnum</i> carpet from A.D. 1950
WP-4 A.D. 1985–2000	<i>Sphagnum</i> Sect. <i>Acutifolia</i> and <i>Aulacomnium palustre</i> macrofossils appear and <i>Sphagnum</i> spores increase. <i>Caltha</i> -type and <i>Ranunculus aconitifolius</i> -type pollen shows a minor increase	Lowering of water-table. Hummock formation
Upland pollen		
UP-1 A.D. 1000–1450	Relatively high pollen values of <i>Picea</i> , <i>Abies</i> , <i>Fagus</i> , <i>Alnus</i> , <i>Corylus</i> , <i>Betula</i> and <i>Quercus</i> . <i>Hypericum perforatum</i> -type and <i>Plantago lanceolata</i> -type pollen increase during the period. Pollen concentration decreases	Open/grazed mixed forest
UP-2 A.D. 1450–1750	Pollen of <i>Fagus</i> , <i>Alnus</i> , <i>Corylus</i> and <i>Betula</i> decreases, that of Poaceae and many herbs increases. Indicators for heavy grazing, i.e. <i>Plantago media</i> , <i>P. montana</i> and <i>Podospora</i> -type, appear or increase towards the top of the zone	Half-open landscape, mixed forest. Increase in grazing pressure
UP-3 A.D. 1750–1925	Low pollen values for deciduous trees. Decrease in <i>Abies</i> pollen. High pollen values for Poaceae and maxima for <i>Trifolium pratense</i> , <i>Lotus</i> , <i>Botrychium</i> , Rubiaceae, <i>Plantago media</i> , Compositae Subfam. Cichorioideae, <i>Aster</i> -type and <i>Plantago montana</i>	Very open landscape, conifer forest
UP-4 A.D. 1925–2000	Pollen of <i>Picea</i> , <i>Pinus</i> and most deciduous trees increases, while that of many herbs decreases. Poaceae show rather stable pollen values and <i>Urtica</i> and <i>Rumex obtusifolius</i> -type increase	Open landscape, conifer forest. Regeneration of forests. Manuring



**Table 3** Summary of results. Local water-table is inferred from testate amoebae, moss types and degree of decomposition

A.D.	Water-table	Peat growth rate	Mire vegetation	Openness	Fire	Climate	Period
1985–2000	Decreasing	Very high	Cyperaceae, <i>Potentilla</i> , <i>Sphagnum</i>	Open	Very low	Warming	8
1950–1985	Decreasing	Very high	Cyperaceae, <i>Potentilla</i>	Open	Low	Warm	7
1925–1950	High (varying)	High	Cyperaceae, <i>Potentilla</i>	Open	Moderate	Warming	6
1800–1925	High (varying)	Moderate	Cyperaceae, <i>Potentilla</i>	Very open	Moderate	Cool	5
1750–1800	High (varying)	Moderate	Cyperaceae, <i>Potentilla</i> , <i>Sphagnum</i>	Very open	High	Warming	4
1700–1750	High? (varying)	Moderate	Cyperaceae, <i>Potentilla</i> , <i>Sphagnum</i>	Open	Very high	Cold	3
1450–1700	Low?	Low	Ferns, <i>Vaccinium</i> , Cyperaceae	Half open	High	Cooling	2
1000–1450	Very low?	Very low	Ferns, <i>Vaccinium</i> , Cyperaceae	Closed	Moderate	Warm	1

Peat growth rate is based on the depth-age model. Mire vegetation is derived from the dominant wetland pollen types. Openness is inferred from the upland NAP. Fire activity is inferred from the abundance of charcoal-dust particles. Climate is according to Begert et al. (2005), Casty et al. (2005) and Moberg et al. (2005). Periods are combinations of statistically significant assemblage zones

(long) wetland pollen assemblage seems primarily related to an increase in the NAP curve. It is thus possible that the testate amoebae assemblage here primarily reacts to grazing pressure (local disturbance) while the wetland pollen assemblage primarily reacts to openness (deforestation).

**Discussion**

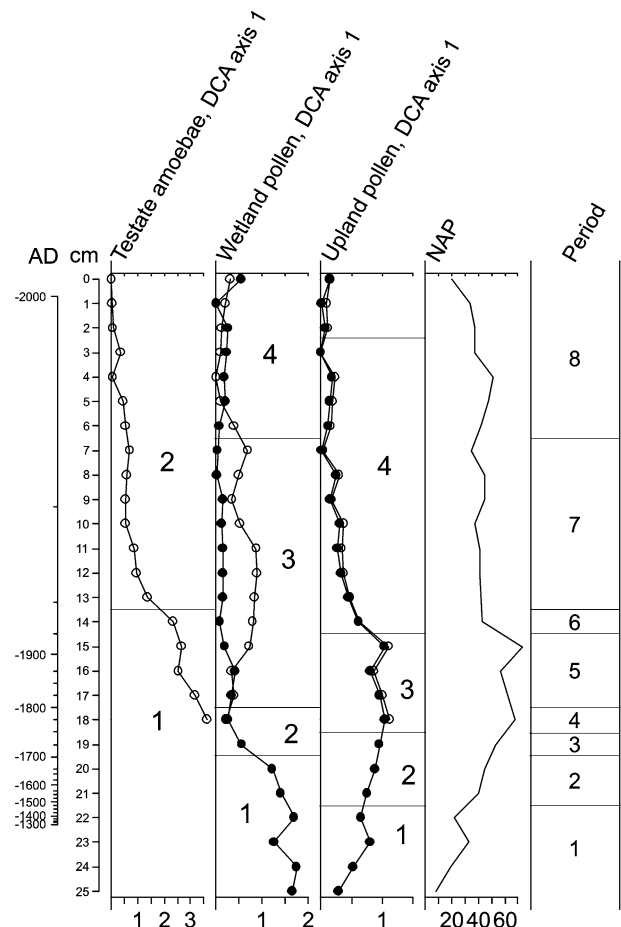
The two most important shifts in the local mire conditions occurred around A.D. 1700 and A.D. 1950. Two other major shifts occurred around A.D. 1800 and A.D. 1985. Comparison between the DCA analysis and the upland pollen diagram suggests that the most important changes in the data sets before A.D. 1985 are related to openness/grazing. However this is only one parameter and the potential causes for the main changes in the mire conditions will be discussed more in detail below.

**Human and climatic impact on mires**

Deforestation of the landscape surrounding a mire may cause a rise in the water-table because of reduced evapotranspiration. This connection between deforestation and water-table has been demonstrated by Moore and Willmot (1976). However in a karst landscape, such as our study region, the mire hydrology is not necessarily connected with the surrounding ground water. In the nearby Val de Joux, Mitchell et al. (2001) showed that in fact drying of the bog surface was caused by increased exposure to wind because of deforestation. Nevertheless for our study site the results suggest that the water-table of the mire and of the surroundings are connected. Forestation of the mire surface itself will in any case reduce the water-table. A full-grown *Picea*, for example, transpires up to 100 l water on a sunny day (Zweifel and Häslar 2001).

Plantation of *Picea* has deliberately been done in many places to convert wetlands into more productive areas.

Grazing will keep the landscape open, but it will also affect mires directly through trampling, which might



**Fig. 6** Comparison of first DCA axes between proxies. Circles refer to data sets of 0–18 cm depth and dots refer to data sets of 0–25 cm depth. The longest series is referred to in the text unless otherwise stated. Numbers adjacent to the curves correspond to the assemblage zones. The NAP curve and the period boundaries have been added for comparison

cause increased erosion, surface run-off and peat compaction. This will increase the decomposition and compaction of the top peat layers. It may also change the water movement in the mire and bring more mineral-rich water to the surface.

Climate also has a strong effect on mires. Lower evapotranspiration caused by wetter and/or cooler climate raises the water-table, thus reducing the decomposition rate of the peat (e.g. Aaby and Tauber 1974; Nilssen and Vorren 1991; Mauquoy et al. 2002). The species composition will also be affected (e.g. Barber et al. 2003). Primarily relatively undisturbed mires of the raised bog type have been studied, but there is no reason to expect the Amburnex mire would react differently in this respect.

#### Cause and effect of changes in the Les Amburnex mire

The shift in local vegetation around A.D. 1700 (a decrease in *Caltha*-type, *Ranunculus aconitifolius*-type, ferns and *Vaccinium*, and an increase in Cyperaceae, *Potentilla* and *Sphagnum*) occurred simultaneously with a marked peak in charcoal-dust particles (A.D. 1650–1750) and an increasingly open landscape (maximum grazing/openness A.D. 1750–1925). It seems therefore likely that the recorded changes in the mire vegetation are the effect of a rise in the water-table following major deforestation and opening of the landscape. The surrounding slopes and the small size of the mire probably make it sensitive to a general increase in the ground water-table. Interestingly the climatic cooling of the Little Ice Age ca. A.D. 1300–1850 and the increasing water levels in mid-European lakes from ca. A.D. 1400 (Magny 2004) coincide with a decreased decomposition rate in the mire. Also the change in mire vegetation in A.D. 1700 coincides with the Maunder Minimum in solar activity (A.D. 1645–1715; Eddy 1977), a very harsh period in the Alps during the A.D. 1690s (Casty et al. 2005). Furthermore it coincides with glacier advances in the Alps A.D. 1600–1900 (maxima ca. A.D. 1650 and A.D. 1850; Waner et al. 2000). The end of the 17th century was in fact the coldest period in Europe during the last 500 years (Luterbacher et al. 2004). Peat bogs with no or little human impact show a major change in species composition (i.e. *Sphagnum*) both at the beginning of the Little Ice Age (Barber et al. 2003) and during the coldest phase A.D. 1650–1850 (Barber et al. 2000). The major change in mire vegetation in A.D. 1700 at the Amburnex mire can thus be explained both by deforestation and by climatic cooling. During the High Middle Ages (A.D. 1000–1300) the mire vegetation

seems to have reacted in a similar way (e.g. increase in Cyperaceae). This was also a phase of deforestation and agricultural expansion (Williams 2000; Gauthier 2004; Sjögren 2006), but it occurred during the favourable Medieval Warm Period. If this period is used as an analogue for the changes in A.D. 1700 then deforestation is the more probable cause, as there was no equivalent to the climatic deterioration of the Little Ice Age. Unfortunately, the High Middle Ages are not well represented in the pollen record because of low temporal resolution, and any analogies are therefore weak. Still, considering the very strong human impact in the area this is likely to have been the strongest forcing factor. Climatic change would then work in phase with human impact, and the two probably enhance the effects of each other.

The decrease in *Sphagnum* spores in A.D. 1800 could imply climatic forcing as it coincides with the end of the coldest and wettest phase of the Little Ice Age and there is no apparent reduction in openness. An alternative explanation is that trampling increased and created tussock vegetation dominated by Cyperaceae and *Potentilla*, where *Sphagnum* growth was hampered simply by repeated disturbance. The varying water-table can be explained by varying wet (hollows) and dry (tussocks) areas, but summer drought is an alternative explanation, which also would explain the disappearance of *Sphagnum*.

The second most important shift in the mire conditions occurred in A.D. 1950 (major changes in the testate amoebae assemblage indicating a lower water-table and acidification, peat decomposition decrease and *Sphagnum* re-appearance). This shift occurred simultaneously with a strong peak in Cyperaceae pollen. Grazing pressure and openness decreased in A.D. 1925, and the reduced grazing would allow higher pollen production as Cyperaceae were not damaged prior to flowering (Segeström and Emanuelsson 2002). The Cyperaceae peak could thus be interpreted as a sign of reduced grazing on the mire, either as an effect of a general decrease or because the mire became fenced (as today) and thereby protected from grazing. With reduced trampling *Sphagnum* could form peat in the areas between the tussocks, resulting in the recorded succession of wet lawn to relatively dry hummock. The modern surface is flat and consists of a mosaic of Cyperaceae, *Potentilla* and *Sphagnum* patches (the peat profile is extracted from a *Sphagnum* patch) that can be the stage following tussock vegetation. A similar succession of peat regeneration is described by Grosvernier et al. (1995), who also stress the importance of the microstructure for peat regeneration. Another indication of this development is *Nebela*

*tubulata*, which had its main distribution during A.D. 1950–1985. This taxon has been recorded on regenerating *Sphagnum* mires elsewhere in the Swiss Jura Mountains and indicates a less disturbed mire surface (EAD Mitchell, personal communication). There is a strong warming trend starting in the late 19th century that peaks around A.D. 1950 (Begert et al. 2005). This could have enhanced some of the changes in the mire conditions, e.g. the lowering of the water-table, which have been shown in other mires (Hendon and Charman 2004). Still there is no clear ecological reason why a warming trend would suddenly initiate *Sphagnum* growth. Rapid changes in climate could change the pollen productivity, but for Cyperaceae this does not seem to be the case as the relative pollen productivity of this taxon is negatively correlated to temperature (Sjögren et al. 2006). Therefore, the changes in mire conditions in A.D. 1950 were most probably caused by reduced trampling.

Around A.D. 1985 there is a change to even drier and more acidic conditions in the mire (*Sphagnum Sect. Acutifolia* and *Aulacomnium palustre* appear, *Assulina seminulum* and *Arcella catinus* increase). There are no detectable changes in the land-use of the surrounding landscape, and the shift in species composition must be attributed to either natural succession or climatic change. After rather stable values since A.D. 1950 temperatures rose sharply around A.D. 1985 (Begert et al. 2005) and reached values unprecedented in the last 500 years (Casty et al. 2005). Considering that a clear relationship between mire taxa (especially *Sphagnum* species) and climate has been shown (Barber et al. 1994), it is quite possible that the recorded shift in species composition around A.D. 1985 is related to these rising temperatures.

## Conclusions

The most important factor for the local development of the Les Amburnex mire during the last millennium was human impact, primarily deforestation and grazing (trampling). Climatic change played a secondary role and first became the most important factor when human impact was relatively stable (i.e. late 20th century). Still, climatic change probably played a role in most major changes (especially A.D. 1700), and should be taken into consideration even for mires strongly affected by human activities.

Many high-altitude mires in the Jura Mountains and the Alps show a similar peat stratigraphy as the Les Amburnex mire (Sjögren et al. 2005) and it can be assumed that they react in a similar way. Grazing

pressure in the high parts of the Alps has decreased dramatically during the 20th century, and together with rising temperatures it can be expected that the forest limit will move considerably upward in the near future (Hofgaard 1997; van der Knaap and van Leeuwen 2003). Grazing pressure (trampling), openness and climate are here shown to be very important factors for mire development, and dramatic changes in the mires can thus be expected. Initial peat regeneration may be an effect of reduced trampling and collapsed drainage systems, but subsequent reforestation (which takes a longer time) and the warmer climate may finally turn the mires into forests.

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