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Research paper

A palaeoecological perspective for the conservation and restoration of wetland plant communities in the central French Alps, with particular emphasis on alder carr vegetation

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ABSTRACT

Wetland conservation and management are generally only based on present-day studies, without integrating historical considerations. However, wetlands contain palaeoecological archives that can provide accurate records of their own history. Our study aims at reconciling this paradox in the central French Alps, by reconstructing the past wetland diversity/richness and the controls of Holocene hydroseral dynamics, and by discussing on this historical basis their conservation, management and restoration. Previously published data, complemented by the palaeoecological study of a sedge mire, reveal three main stages in the regional hydroseral succession: initial aquatic plant communities (*Nymphaea alba*, *Nuphar* cf. *lutea*, *Menyanthes trifoliata*), carrs (*Alnus glutinosa/incana*, *Salix* spp., *Thelypteris palustris*), then sedge meadows (Cyperaceae, Poaceae, *Lythrum salicaria*...). This dynamic comprises (1) a classical evolution from open water bodies to treed wet communities, controlled by the relationships between sedimentation processes and climate, and (2) an unexpected return to herbaceous wet habitats mainly triggered by Subatlantic human-induced managements. Such recent changes induced in the studied region the decline of *Alnus* cf. *glutinosa*, the disappearance of *Thelypteris palustris*, and the extinction of the carr communities they constituted. The historically-based assessment of community naturalness and resilience appears critical for defining conservation priorities, refining management actions, and identifying baseline conditions for restoration initiatives. The main implications of our results are to reinforce conservation measures on the less impacted habitats and to increase the diversity/richness of isolated lowland mires, notably by restoring alder communities in some of them.

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1. Introduction

Wetlands house a significant part of the global biodiversity and are important ecosystems in regulating hydrological fluxes (Carter, 1986), filtering pollutants from water (Knight and Pasternack, 2000) or long-term carbon storage (Gorham, 1991). Despite their importance, they are often ignored in France and in many other countries by conservation programs and by public authorities, and exposed to different types of degradation, as draining for farming, and flooding

for fishing or swimming (Abramovitz, 1996; Moser et al., 1996). Wetlands are particularly sensitive to human impact in climatically dry zones, such as the Mediterranean Basin, where they are generally small and scarce, and today mostly disturbed or heavily damaged (García et al., 2010). Their current management essentially focuses on the protection of the threatened biodiversity based on present-day observations, without any historical considerations. Such conservation policies that ignore evolutionary and dynamical processes are however likely to disturb the adaptation and response of ecological systems to natural selection (Delcourt and Delcourt, 1998).

The historical significance of a particular community or population is somewhat indirectly considered through genetic concepts (evolutionary significant units; Moritz, 1994) or biogeographical criteria

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(endemism; Myers et al., 2000). Yet palaeoecological and historical records tend to be disregarded in conservation initiatives because they are perceived as too descriptive, imprecise and difficult to understand by non specialists (Willis et al., 2005), and because of the lack of palaeoecological data for particular ecological systems, notably in biodiversity hotspots (Willis and Birks, 2006). In this respect, one of the main difficulties in the use of pollen-derived palaeoecological data for conservation purpose is translating fossil pollen assemblages in terms of plant communities (Foster et al., 1990; Janssen, 1970). This difficulty is partly related to the uncertainty in defining pollen source areas and in assessing the variability of pollen production by different plant species. Complementary macrofossil analyses can be useful in order to obtain more local information (Birks and Birks, 2000), but their implementation is not solely very time-consuming and requires large palaeobotanical competences, but it also demands well-preserved sedimentary archives. Despite these limitations, there is growing evidence supporting the crucial value of historical data for conservation, management and restoration of ecosystems (e.g., Birks, 1996; Muller et al., 2009; Swetnam et al., 1999; Willard and Cronin, 2007; Willis and Birks, 2006). Moreover considerable advances have been made in the last decades in the quantification of the pollen–plant abundance relationship (e.g., Davis, 1963; Jacobson and Bradshaw, 1981; Prentice, 1985; Sugita, 1993, 1994; Tauber, 1965). Most of these works, however, deal with forests (Calcote, 1995; Mazier et al., 2008) and cultural landscapes (Broström et al., 2004; Bunting, 2003; Court-Picon et al., 2005; Gaillard et al., 1992). In contrast, very few studies focus on the pollen record of wetland plant communities (hereafter noted as ‘local pollen record’), with the aim of reconstructing their own past dynamics (Bunting et al., 1998; Janssen, 1967; Muller et al., 2003, 2008). Such a ‘local’ approach is likely to remove problems related to the identification of the relevant pollen source area.

The central French Alps, located at the boundary between the Southern and the Northern Alps (Ozenda, 1985), offer an opportunity for discussing the management and conservation of wetlands in regard to historical data. First, this region is characterised by a high wetland diversity induced by a large range of altitudes, substrates and climates (Ozenda, 1985). Second, these wetlands are partly included in a list of priority zones for conservation (ZNIEFF, i.e. *Zones Naturelles d'Intérêt Ecologique Faunistique et Floristique*) or protected by diverse administrative status (prefectural biotope protection, national and regional parks, natural reserves, RAMSAR sites, directive habitats, public ownerships...), generally because of the presence of endangered species and rare microhabitats (Chas et al., 2006; DIREN PACA, 2004). Nevertheless, despite these protection statuses, most of them present traces of ancient and modern anthropogenic disturbances (drainage ditches, dams, wheel tracks, grazing...). And third, a number of these wetlands have been thoroughly investigated for more than thirty years. Previous studies provide invaluable insights into morphogenesis of landscapes (e.g., Jorda et al., 2002; Miramont et al., 1998), regional vegetation dynamics (e.g., Court-Picon, 2007; de Beaulieu, 1977; Miramont et al., 2000; Muller et al., 2007; Nakagawa, 1998), disturbance regimes (e.g., Genries et al., 2009; Nakagawa et al., 2000), and regional climate changes (Digerfeldt et al., 1997).

The present paper aims at drawing the regional pattern of ecological changes in wetlands of the central French Alps during the Holocene, in order to provide a historical background for their conservation and restoration. Based on the reinterpretation of published palaeoecological data (see the compilation by Muller et al., 2007) and new pollen data from a sedge mire, we reconstructed the developmental history of wetlands in two valleys of the central French Alps and addressed the following questions: Are the past and modern biodiversities comparable in wetlands? How and how much did the climate and anthropogenic activities affect wetlands and wetland plant communities? What strategies can be drawn for conservation, management and restoration of wetlands from palaeoecological data?

2. Materials and methods

2.1. Biogeographical setting and studied sites

The studied zone encompasses the high valleys of Durance and Drac, at the boundary between the southern and northern French Alps (Fig. 1). This area, so-called central French Alps, comprises few wetlands, because of its climate, known as the driest of the French Alps ($P = 714 \text{ mm yr}^{-1}$, $T = 7.56 \text{ °C}$; Ozenda, 1985). This climatic stress on wetlands is likely to make them particularly sensitive to any environmental changes. The sites used in the present study include all wetland types occurring in the region: peatlands, lakes and peaty ponds (Table 1). The wetlands located at the highest altitudes are fens, dominated by small sedge communities (*Carex bicolor*, *C. davalliana*, *C. echinulata*, *C. fimbriata*, *C. frigida*, *C. microglochis*, *C. nigra*, *C. panicea*, *Eriophorum* spp., *Trichophorum* spp.) often mixed with *Parnassia palustris*, *Primula farinosa*, *Salix myrsinifolia*, *Saxifraga aizoides*, *Selaginella selaginoides*, *Swertia perennis* and *Tofieldia calyculata*. Wet meadows and tussock communities are found at lower altitudes, and are generally dominated by tall helophytes (*Carex* spp., *Juncus* spp., *Molinia caerulea*, *Phragmites australis*, *Typha* spp.), and comprise a number of broad-leaved forbs such as *Gentiana pneumonanthe*, *Lathyrus palustris*, *Lysimachia vulgaris*, *Lythrum salicaria*, *Mentha longifolia* and *Pedicularis palustris*. Their rich plant communities house some of the most endangered species of plants (e.g., *Carex buxbaumii*, *C. diandra*, *C. hordeistichos*, *C. lasiocarpa*, *C. limosa*, *Hierochloa odorata*, *Sparganium minimum*, *Salix pentandra*, *Schoenus ferrugineus*) and insects (e.g., *Maculinea teleius*, *Parnassius phoebus*, *Stetophyma grossum*) of the region (Chas, 1994; Chas et al., 2006; DIREN PACA, 2004). Lakes and

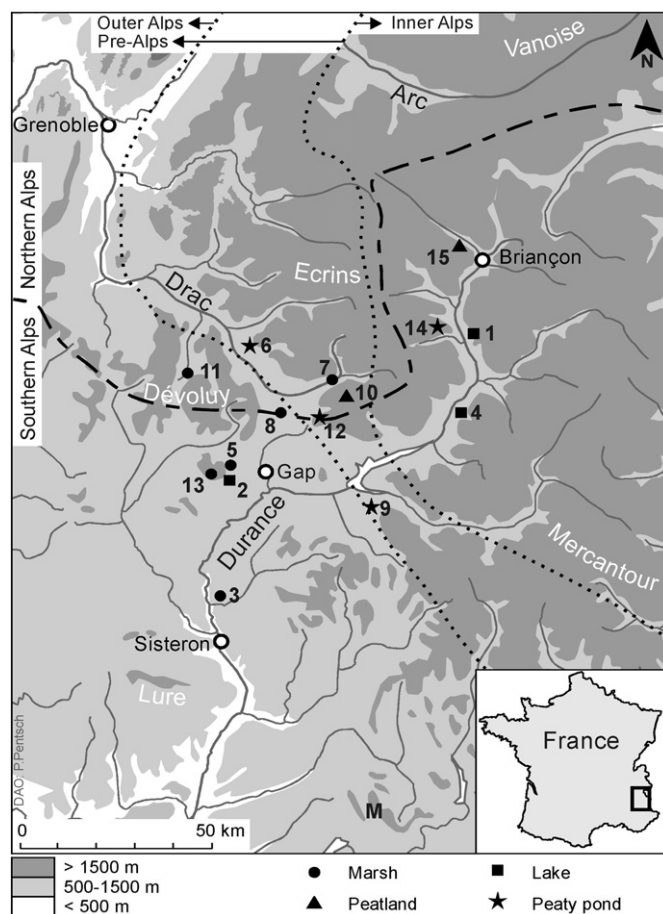


Fig. 1. Location of La Gourre (3) and other selected sites. Numbers refer to Table 1. The site named M corresponds to the travertine sequence of Moursesse, on the Serre-de-Montdenier range.

Table 1
Selected sites. The sites noted Peatland/Lake correspond to recently disturbed peatlands, today transformed in artificial lakes. ZNIEFF: Zones Naturelles d'Intérêt Ecologique Faunistique et Floristique.

No	Site	Code	Core	Nature	Altitude (m)	Longitude	Latitude	Surface (ha)	Protection status	Reference(s)
1	Roche-de-Rame	RDR	D20	Lake	950	06°35'E	44°44'N	2	Natura 2000	de Beaulieu, 1977
2	Pelleautier	Pel	D1/5	Peatland/Lake	975	06°11'E	44°31'N	12		de Beaulieu, 1977; de Beaulieu and Reille, 1983
3	Gourre (La)	Gou	Gou-1	Peatland	992	06°00'E	44°23'N	2.5		This study
4	Siguret	Sig	D17	Lake	1066	06°33'E	44°37'N	3	ZNIEFF, Natura 2000	de Beaulieu, 1977; de Beaulieu and Reille, 1983
5	Corréo	Cor	–	Peatland	1090	05°59'E	44°33'N	1	ZNIEFF, Natura 2000	Nakagawa, 1998
6	Laux-du-Villardon	LDV	–	Peaty pond	1108	06°03'E	44°44'N	1		Pothin, 2000
7	Lauza	Lau	Lau-3	Peatland	1140	06°13'E	44°39'N	1.5		Wegmüller, 1977; Court-Picon, 2007
8	Sagne-de-Canne	SDC	–	Peatland	1270	06°06'E	44°37'N	3	ZNIEFF	Court-Picon, 2007
9	St-Léger	SL	D9	Peaty pond	1308	06°20'E	44°25'N	0.5	ZNIEFF, Natura 2000	de Beaulieu, 1977; Digerfeldt et al., 1997
10	Libouse	Lib	–	Peatland/Lake	1455	06°13'E	44°38'N	0.6		Court-Picon, 2007
11	Forest-en-Dévoluy	FED	D8	Peatland	1460	05°54'E	44°45'N	0.5	ZNIEFF, Natura 2000	de Beaulieu, 1977; Wegmüller, 1977
12	Faudon	Fau	–	Peaty pond	1577	06°13'E	44°36'N	0.25		Court-Picon, 2007
13	Raux	Rau	–	Peatland	1770	05°56'E	44°30'N	1.7	ZNIEFF, Natura 2000	Nakagawa, 1998
14	Col-des-Lauzes	CDL	D22	Peaty pond	1784	06°32'E	45°46'N	0.2		de Beaulieu, 1977
15	Pré-Rond	PR	–	Peatland	1800	06°35'E	44°55'N	0.06		Muller et al., 2000

peaty ponds are much rarer, and mostly located at high elevations, up to 2000 m a.s.l. The few ones located at lower altitudes are generally strongly damaged, such as Pelleautier and Roche-de-Rame (numbers 9 and 12, Fig. 1), presently transformed in pleasure ponds. The most preserved of these habitats is St-Léger (number 15, Fig. 1), where a marginal belt of *Phragmites australis* protects floating carpets of *Carex diandra*, *C. lasiocarpa*, *C. limosa*, *Menyanthes trifoliata*, *Pedicularis palustris*, *Schoenus*

ferrugineus, and *Utricularia vulgaris* (DIREN PACA, 2004). St-Léger houses one of the two populations of *Nymphaea alba* of the region (the other one is Siguret; number 14, Fig. 1).

Sediment cores analysed in this study were taken in La Gourre peatland (number 5, Fig. 1), located on the left side of the Durance River, 20 km north of Sisteron. This peatland lies within a morainic depression (Fig. 2), on the western flank of the *La Montagne* massif,

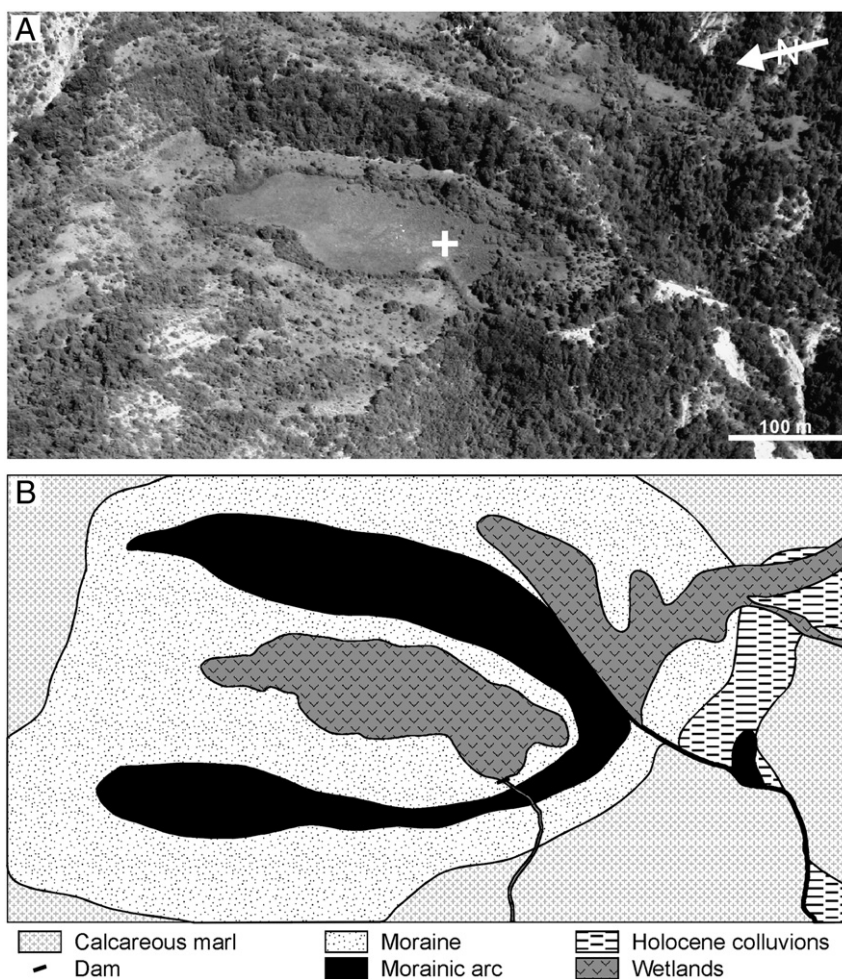


Fig. 2. A. Aerial photograph of La Gourre showing the moraines delimiting the depression and the *Salix* thickets developed on the western extremity (on the right of the picture). The three white dots visible at the left of the cross are cattle, which are left grazing for most of the year on the peatland. B. Geomorphological map indicating the extent and location of moraines and wetlands (from C. Boutterin, unpublished data). Crosses indicate the coring location (Gou-1).

far away from roads and hamlets except for a small farm in ruin located 1 km east of the site. The outlet is blocked by a little undated dam that attests past human hydrological modification. The peatland is covered by high tussocks of *Carex paniculata*, *Phragmites australis* and *Molinia caerulea*, associated with *Lysimachia vulgaris*, *Lythrum salicaria*, *Mentha longifolia*, *Juncus inflexus*, *Galium palustre*, and *Dactylorhiza majalis*. The margins are covered by thickets of *Salix capraea*, colonising the western extremity of the depression (Fig. 2). Cattle, located most of the year on the site (visible as white dots just left of the cross on Fig. 2a), are probably responsible for the contrasted microtopography, by eroding the between-tussocks hollows. The vegetation of the surrounding slopes consists of degraded deciduous oak forests dominated by *Quercus pubescens*, *Pinus sylvestris* and *Genista cinerea*, of calcicolous forests of *Fagus sylvatica*, and of discontinuous riparian woodlands of *Alnus incana*.

Plant nomenclature follows Tela Botanica (<http://www.tela-botanica.org/>).

2.2. Field and laboratory work

In order to identify the hydroseral stages of La Gourre development, we combined a description of the sediment stratigraphy (Von Post's method; Aaby and Berglund, 1986) and a palynological analysis (including pollen, algae, fungi, stomata and other non-pollen palynomorphs). Macrofossil analyses were performed on several levels (notably on the wood layer), but the results were very poor and uniquely used here for providing material for AMS dating. 10 cores, taken with a 100×5 cm modified Russian sampler from different parts of the peatland, allowed us to locate the zone of maximal sediment depth and to check the homogeneity of the sediment stratigraphy over the entire depression. In particular, a 10–25 cm-thick wood layer was found in all cores within the upper meter of sediments. The longest core (Gou-1, 7 m) was taken and subsampled for palynological analysis and radiocarbon dating. Palynological analyses were completed after chemical treatments (Berglund and Ralska-Jasiewiczowa, 1986), performed on 1-cm³ samples taken at regular depths every 8 cm along the upper 400 cm of core Gou-1. Pollen percentages were based on sums excluding the spores of Pteridophytes. Pollen sums exceeded 500 grains, except for the 10 poorest levels, in which pollen sums range from 159 to 494 grains. The pollen diagram was constructed with the GPalWin computer program (Goeury, 1997). Pollen nomenclature follows Birks and Birks (1980) and Faegri and Iversen (1989).

2.3. Recognition and interpretation of the local pollen record

In the pollen diagrams, the local (i.e., from local hydrophytic communities) and regional (i.e., from meso-xerophilous communities) pollen inputs were discriminated through the approach defined by Janssen (1973), Jacobson and Bradshaw (1981) and Prentice (1985), and based on the ecological requirements of the concerned taxa. Past wetland plant communities were reconstructed using pollen indicators (Janssen, 1967, 1970), complemented by local habitat conditions inferred from sediment types and non-pollen palynomorphs (Muller et al., 2003, 2008). We only considered here the main stages of the hydroseral succession, easily identifiable from pollen assemblages and sedimentology (Muller et al., 2003; Tallis, 1983; Walker, 1970): lakes (open water bodies), peaty ponds (small water bodies partly overrun by marginal herbaceous belts), peatlands (herbaceous wet meadows dominated by herbs or sedges), and carrs (treed wet habitats, corresponding to dry swamps). Such hydroseral successions from limnic to terrestrial communities characterise the 'terrestrialization' process, as the result of the progressive infilling of an initial depression.

3. Results

3.1. Stratigraphy and pollen record

The stratigraphy of Gou-1 is composed of lake sediments (clay, marl and gyttja) from the bottom to 105 cm depth, and of herbaceous peat from 105 cm depth to the surface (Fig. 3). The basis of the peat deposit is characterised by a wood fragments layer containing numerous *Alnus/Betula* perforation plates (Barthelmes et al., 2006; Prager et al., 2006). The upper 10 cm of this layer is palynologically sterile, except for a few *Alnus glutinosa/incana* pollen grains and monolet spores. We interpret this layer as highly decomposed litter of a treed formation dominated by *Alnus glutinosa/incana* (alder carr). The pollen diagram of Gou-1 (Fig. 4) presents a high richness of plant taxa, which increases from the bottom to the top of the sequence. The lower part, corresponding to lake sediments, is moreover characterised by algae assemblages comprising *Botryococcus*, *Pediastrum boryanum* and *Tetraedron minimum*. The stratigraphical change from lake sediments to peat (Fig. 3), marked by a strong increase in pollen concentrations, corresponds to the disappearance of *Pediastrum* and *Tetraedron*. The zonation of the diagram (Fig. 4), which only concerns the local dynamics of the site, is based on sedimentology, microfossils and local pollen input.

The stratigraphy of La Gourre is, in its main features, representative of the stratigraphies of the other sites (Fig. 5), which generally present a sequence from the bottom upwards to the surface, of clay, marl, gyttja, and sometimes peat. Most of the sites have small dimensions, and with the exception of Pelleautier, Roche-de-Rame and Siguret, cores were taken from the central part of the basins.

3.2. Chronology

Seven radiocarbon AMS measurements (Table 2) were completed on plant macroremains extracted from the Gou-1 core after soft

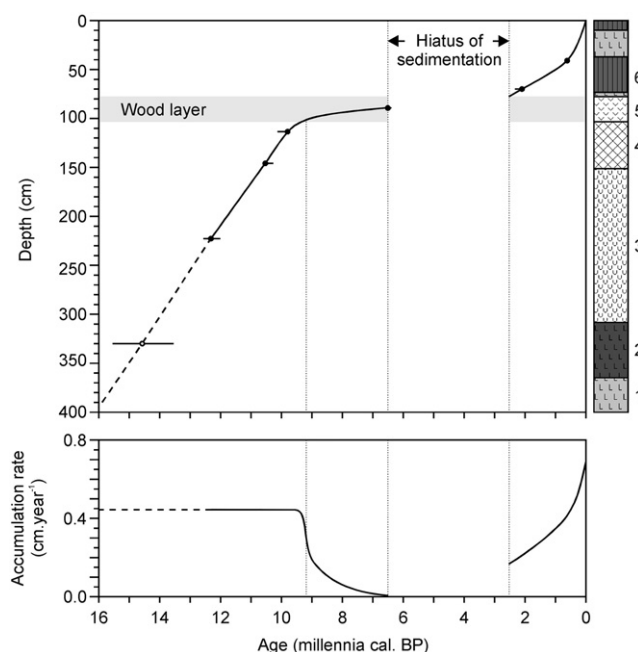


Fig. 3. Age-depth model, sediment accumulation rates and stratigraphy of the profile Gou-1, La Gourre. The putative extrapolation below 225 cm is based on a palynostratigraphic correlation with St-Léger (SL) and on the attribution of a pleniglacial age (21,445–22,532 cal. BP; Jorda et al., 2000) to the depth of 650 cm (see text for details). Sedimentary changes seem to have not affected the chronology. Numbers noted at the right of the stratigraphic log indicate the nature of sediment: 1. Inorganic clay; 2. Organic clay; 3. Marl; 4. Gytja; 5. Wood fragments layer (grey zone); 6. Herbaceous peat.

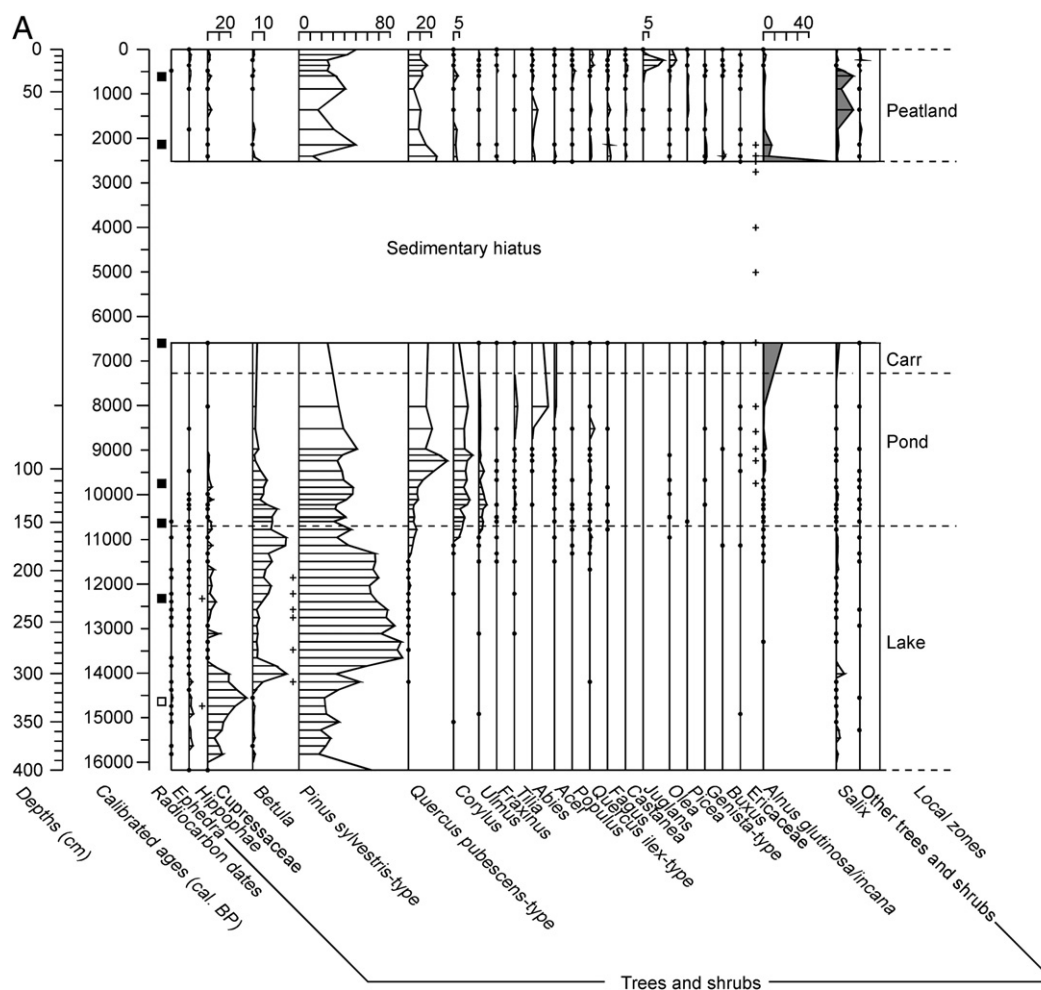


Fig. 4. Simplified pollen diagram of the profile Gou-1, La Gourde (analysis: S.D. Muller and P. Schevin, 2007): A. Arboreal pollen; B. Non-arboreal pollen and main aquatic non-pollen palynomorphs. Percentage scales are constant and dots represent percentages less than 1%. Pollen concentrations are given in grains cm^{-3} . The chronological control is indicated right of the time scale: radiocarbon ages (black squares) and palynostratigraphic correlations (white squares). Crosses indicate non-pollen palynomorphs related to pollen taxa: *Juniperus stomata*, *Pinus stomata*, *Alnus/Betula* scalariform punctuations and *Carex radicles*, respectively. Algae and *Ceratophyllum* microfossil abundance, estimated during pollen counting, is given in three classes (low, medium, high).

sediment sieving. Calibrated ages (cal. BP, i.e. calendar years before present) were computed with the Calib 5.0 program (Stuiver and Reimer, 1993), using the calibration dataset IntCal04.14c (Reimer et al., 2004). Palynological and sedimentological considerations lead to reject the age of 9120 ± 50 BP, obtained at 451–452 cm depth within clays, characteristic of the glacial deposits of the region. The total absence of carbon and of terrestrial macroremains within these clays precluded the estimation of a reliable radiocarbon age for them. Nevertheless, the presence within these clays of a striated rock at 650 cm depth allows correlating this depth with a close pleniglacial moraine, dated at 21,445–22,532 cal.BP (Jorda et al., 2000). We propose an age-depth model (Fig. 3) based on the interpolation of the simplest curve connecting calibrated dates within the 2-sigma confidence intervals. The model shows a strong decrease in the sediment accumulation rate from 9600 to 6500 cal.BP, followed by a sterile 10 cm-high zone, interpreted as a sedimentary hiatus from 6500 to 2500 cal.BP. This progressive halt of the sediment accumulation is located within the wood fragments layer, and can be attributed to an increase in decomposition rate, becoming at least equal to the production rate. The age-depth models of the other sites were calculated with this same method. They are based on 81 radiocarbon ages (see Muller et al. (2007) for details), completed by palynostratigraphic regional correlations, which give a reliable chronological control on the two undated sequences (Raux and Roche-de-Rame).

3.3. Local (hydrophytic) vegetation dynamics

Similar changes between the largest sites of the studied region allow to characterise the regional pollen record, successively dominated by *Artemisia*, Cupressaceae (*Juniperus*), *Betula*, *Pinus sylvestris*-type, *Corylus*, *Quercus pubescens*-type, *Ulmus*, *Abies*, *Fagus* and by anthropogenic indicators (de Beaulieu, 1977; Muller et al., 2007). On the contrary, important discrepancies between sites indicate local signals, without regional significance (Figs. 5 and 6). This is notably the case for *Alnus glutinosa/incana*, *Salix* and herbaceous hydrophytes (*Cyperaceae*, *Equisetum*, *Lysimachia*, *Lythrum salicaria*, *Menyanthes trifoliata*, *Nymphaea alba*, *Nuphar*, *Polygonum amphibium*-type, *Potamogeton*, *Thelypteris palustris*...). Modern pollen spectra (Court-Picon, 2007; de Beaulieu, 1977) confirm that *Alnus glutinosa/incana* and *Salix* contribute little to the regional pollen flux. The development of local populations is identified when percentages exceed 3% of the total pollen sum (or 5% when *Cyperaceae* and other hydrophytes are excluded from the pollen sum). Uncertainties on the pollen origin remain for some taxa, such as the Poaceae, characterised by an important regional pollen input, as well as a possible local origin from local hydrophytic communities (e.g., *Phragmites australis* or *Molinia caerulea*). Ecological evidences have been used in order to refine the taxonomical identification of some taxa. These speculative identifications are then given in brackets after the taxon name.

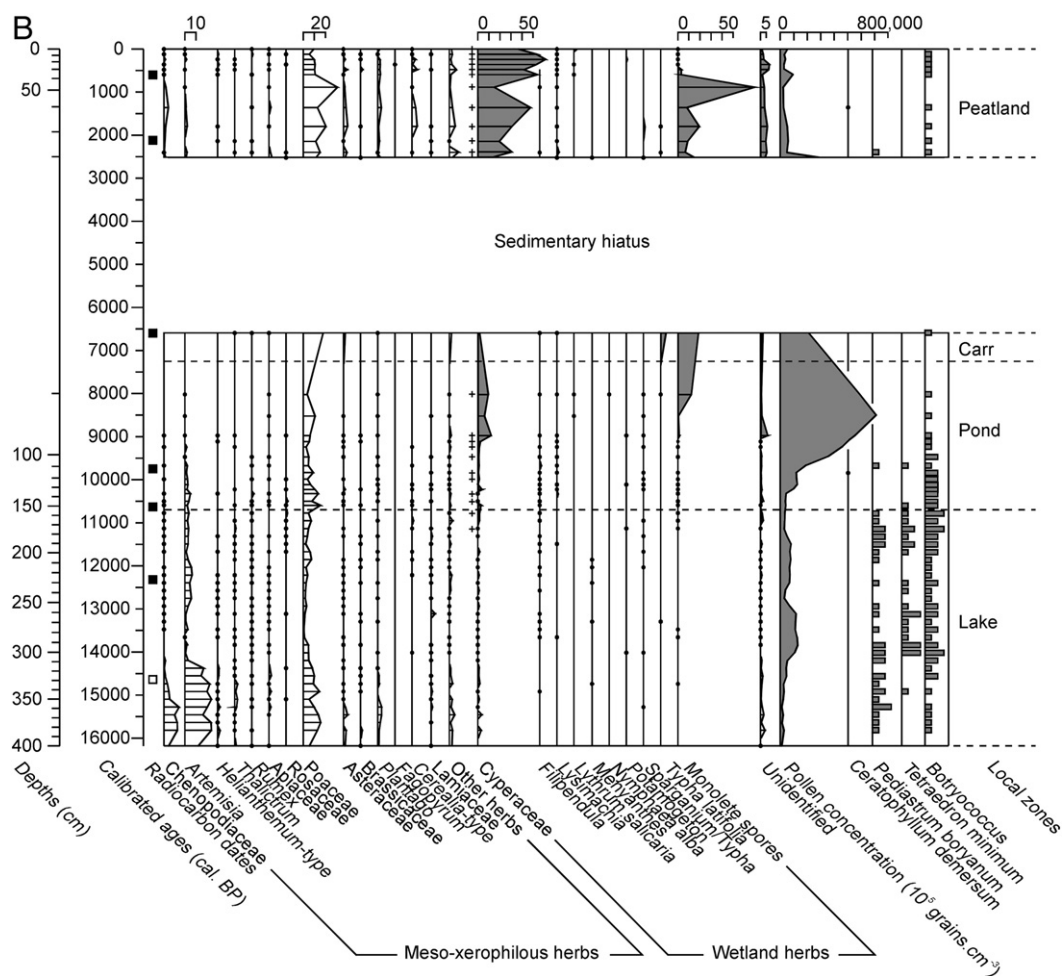


Fig. 4 (continued).

At La Gourre. In the lower part of Gou-1, along with the presence of microscopic algae (*Botryococcus*, *Pediastrum boryanum*, *Tetradion minimum*), the sediment type (clay, marl and gyttja) indicates that the site was an open water body from its initiation in the glacial period to ca. 9200 cal.BP (Figs. 3 and 4). Since at least 16,000 cal.BP, the lake was bordered by a riparian vegetation composed of *Salix* and *Cyperaceae*. Then, the appearance around 10,750 cal.BP of *Lysimachia*, *Lythrum salicaria*, ferns and *Alnus glutinosa/incana* reveals the development of peaty margins around the lake. Erdtman et al. (1963) defined two criteria to distinguish the pollen of the two *Alnus* species: the shape of the pore (slightly ellipsoidal in *A. glutinosa*; circular in *A. incana*) and the angle between endexine and ectexine inside aspides (about 30° in *A. glutinosa*; about 40–45° in *A. incana*). Based on these criteria, most of the pollen grains found at La Gourre, within the wood layer comprised between 104 and 78 cm below the surface, can be attributed to *A. glutinosa*. Unfortunately, no seed was preserved in the sediment, so it was not possible to verify these controversial pollen-based identifications (Beug, 2004). The peaty margins development, simultaneous with the Late-glacial–Holocene transition, could indicate either water enrichment due to the spread of deciduous hazel-oak forests on surrounding slopes or a water-level drawdown. The increase in *Cyperaceae* pollen percentages around 9300 cal. BP proves the reduction of the central water body, overrun by the marginal formation of *Alnus glutinosa/incana* and *Cyperaceae*, maybe associated with *Salix*. The occurrence of *Nymphaea* pollen at 90 cm depth indicates the persistence of

open waters close to the coring site until at least 8000 cal.BP. The completion of the centripetal infilling process was marked by the extension of the alder carr, probably developed on an understorey of ferns (Fig. 4). Finally, the resumption of the sedimentation around 2500 cal. BP, marked by a thin clay layer, was simultaneous with the local spread of *Cyperaceae* (attested by the abundance of *Carex radicles*), *Poaceae*, *Lysimachia*, *Lythrum salicaria* and *Salix*, and corresponded to the constitution of the present-day peatland.

At the regional scale. The dynamics of the 15 sites used in this study (Table 1) are summarized and compared in Fig. 6. They show similar patterns to those described for La Gourre, mostly consisting in hydroseral successions from open water bodies to plant communities characterised either by *Alnus glutinosa/incana* and ferns or by *Cyperaceae* (Fig. 5). While *Alnus glutinosa/incana* and ferns were not systematically recorded together, they generally largely overlapped. The variability of their pollen records between sites, as well as the strong fluctuations of their pollen curves, are typical features of habitats characterised by heterogeneous micro-topography and hydrology, which prevents the quantitative reconstruction of the past local plant cover. However, because *Alnus glutinosa/incana* and ferns are almost absent from the regional pollen rain (de Beaulieu, 1977; Court-Picon et al., 2005; Court-Picon, 2007; S.D.Muller, unpublished data) and because *Alnus glutinosa/incana* pollen is strongly associated with wood fragments at La Gourre (Fig. 4), their records are interpreted as translating their local growth within plant communities assignable to alder belts or carrs (Chambers and Price, 1985).

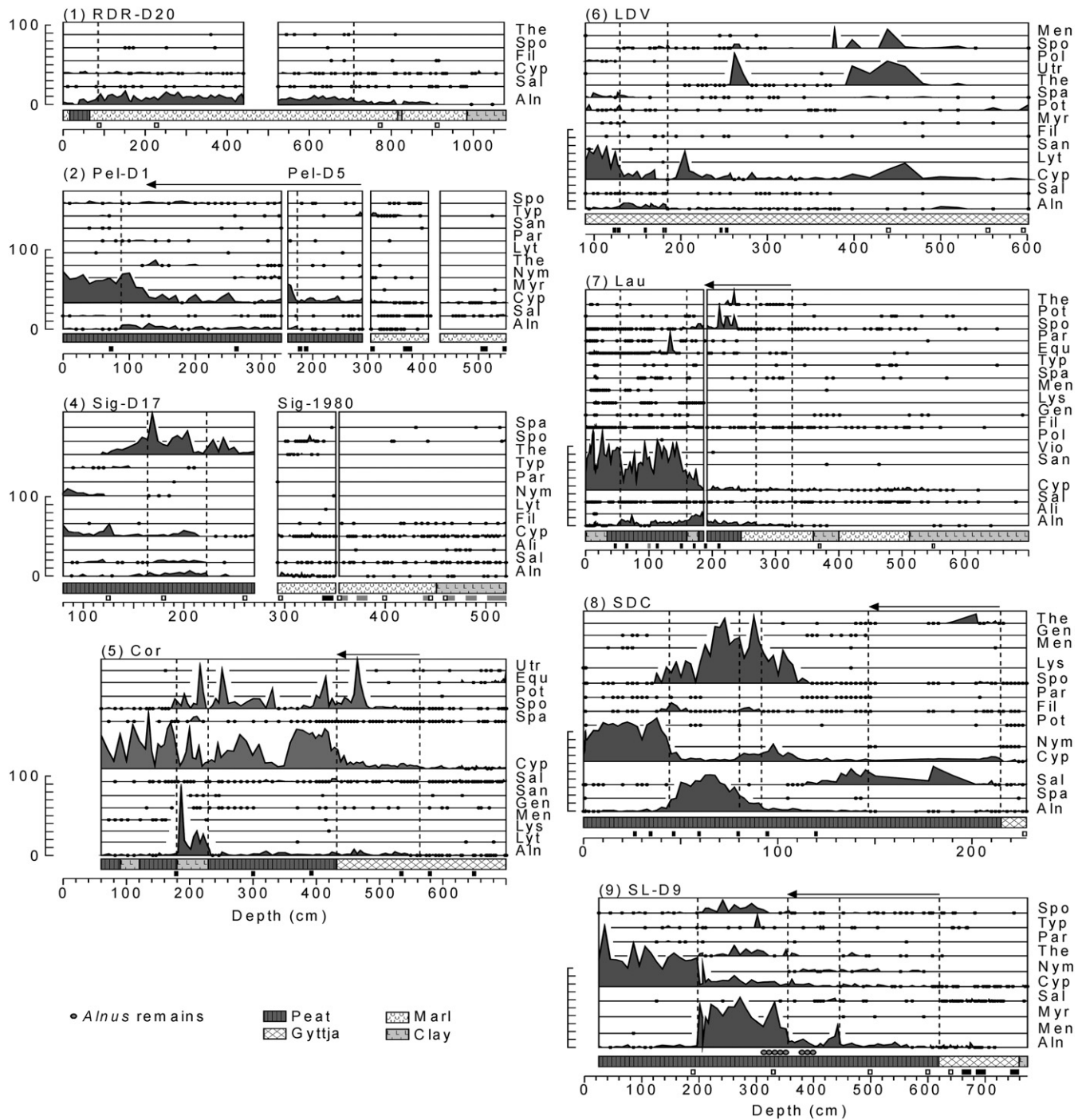


Fig. 5. Regional pollen diagrams of hydrophytic plant communities (references in Table 1). Percentage scales are constant. Dots represent percentages less than 1%. Arrows indicate approximate periods of centripetal infilling of depressions. The chronological control is indicated above depth scales: accepted radiocarbon ages (black bars), rejected ones (grey bars) and palynostratigraphic correlations (white bars). Taxon names are abbreviated as follows: Aln, *Alnus glutinosa-incana*; Cyp, Cyperaceae; Equ, *Equisetum*; Gen, *Gentiana pneumonanthe*-type; Lys, *Lysimachia*; Lys, *Lythrum salicaria*; Men, *Menyanthes trifoliata*; Myr, *Myriophyllum spicatum*-type; Par, *Parnassia palustris*; Pol, *Polygonum amphibium*-type; Pot, *Potamogeton*; Sal, *Salix*; San, *Sanguisorba officinalis*; Spa, *Sparganium-Typha*; Spo, monoletic spores; The, *Thelypteris palustris*; Typ, *Typha latifolia*-type; Utr, *Utricularia*.

These changes, which occurred at all studied sites, indicate the progressive infilling of all regional topographic depressions. Among the 15 studied sites, 12 recorded the past local development of alder populations: seven experienced the development of peaty margins with alder populations, and five experienced the past local development of alder carrs (Fig. 6). Only three sites (Col-des-Lauzes, Forest-en-Devouly and Raux; numbers 1, 4 and 11, Fig. 1) did not record the presence of alder during their postglacial history. The alder populations dynamic in the central French Alps (Fig. 7) was revealed by combining the 15 *Alnus glutinosa-incana* records (Fig. 7). It shows a progressive

increase from 9000 to 3200 cal.BP, followed by a rapid decrease from 3200 to 900 cal.BP, with the disappearance of alder carrs between 2500 and 2000 cal.BP. It should be noted that six sites experienced one or several sedimentation stops during their history (Fig. 6). While some of these events may be attributed to local disturbances or coring problems (de Beaulieu, 1977), the spread of alder is most probably due to complete dryings, at least at La Gourre, Lauza and Siguret, where sediment hiatuses began between 6700 and 6000 cal.BP (Fig. 6), simultaneously with a low water level recorded at St-Léger (Digerfeldt et al., 1997). Finally, it appears that between 3600 and

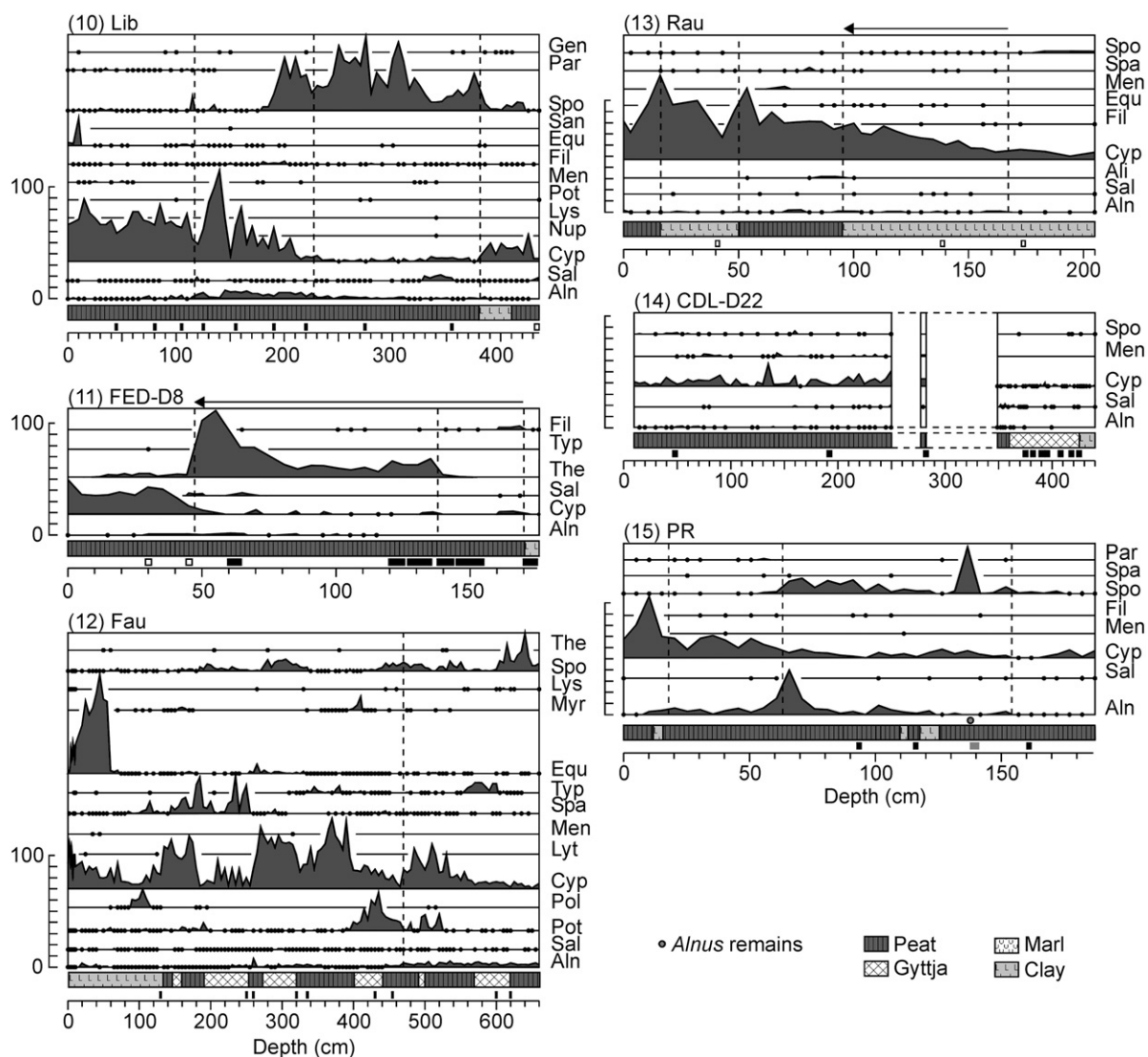


Fig. 5 (continued).

1600 cal.BP most of the studied sites experienced dramatic changes characterised by the opening of local vegetations: carrs shifted to peatlands, while lakes and ponds lost their wooded margins. These changes, associated to the regional decline of alder communities, favoured sedge mires, which still cover today most of the wetlands in the studied area.

4. Discussion

4.1. Past diversity of wetland plant communities

The available palaeoecological data (Table 1) reveal three main stages of the regional hydrosereal dynamics, corresponding roughly to the three main types of communities developed today within the wetlands of the central Alps: aquatic plant communities, carrs and sedge meadows.

4.1.1. Initial aquatic plant communities

While some lakes and peaty ponds still exist today in the region, open water bodies were undoubtedly more abundant and larger during Lateglacial and early-Holocene periods, and harboured diversified aquatic plant communities (Table 3). *Nymphaea alba*, *Nuphar* sp. and

Menyanthes trifoliata are three taxa of particular conservation significance in SW Europe, and are easily identifiable by their pollen grains and seeds. These insect-pollinated taxa are characterised by weak pollen production and dispersion, complemented by an intense vegetative multiplication. Their pollen record, even very low and discontinuous, undoubtedly reveals their local presence. *Nymphaea alba* occurs today within the studied area in only two sites (Siguret and St-Léger), where its native or introduced status has long been questioned. Pollen records clearly attest its native status, and its past presence around the city of Gap (Fig. 1, Table 3). While the two French species of *Nuphar* (*N. lutea* and *N. pumila*) are absent today from the studied area, we suspect that the pollen recorded at Libouse lake (Table 3; Court-Picon, 2007) and in the Briançon and Grenoble regions (Nakagawa, 1998) corresponds to *N. lutea*, which is the only species largely penetrating into the Mediterranean zone and occurring in adjacent regions (Garraud, 2003). Finally, *Menyanthes trifoliata* occurs today in about 20 sites in the study region, including the St-Léger lake and some fens and riparian wet meadows in the Briançon and Gap regions, distributed from 1110 to 2470 m a.s.l. (Chas, 1994; Muller et al., 2000). The comparison between palaeoecological and botanical data reveals its disappearance from 10 out of the 11 sites

Table 2

AMS and conventional radiocarbon dates of the selected sites. See references in Table 1.

Site number	Core	Depth (cm)	Laboratory code	Dated material	¹⁴ C age (BP)	2σ interval (cal. BP)
2	Pel-D1	70–76	Ly-581	Marl	660 ± 210	0–1060
		260–265	Ly-797	Peat	4640 ± 190	4840–5740
	Pel-D5	175–180	Ly-1211	Peat	6430 ± 190	6900–7660
		185–190	Ly-1212	Peat	7620 ± 230	7980–9010
		305–310	Ly-1213	Peat	9090 ± 280	9540–11,080
		465–478	Ly-1214	Marl	11,000 ± 460	11,410–13,820
		505–515	Ly-1215	Marl	11,750 ± 500	12,790–15,120
		540–550	Ly-1216	Marl	13,210 ± 410	14,280–16,750
3	Gou-1	41–42	Poz-11237	Unidentified charcoal	630 ± 30	550–660
		70–71	Lyon-4284	Organic matter	2180 ± 30	2120–2310
		88–89	Poz-14103	<i>Alnus/Betula</i> charcoal	5720 ± 40	6410–6630
		114–115	Poz-10799	<i>Cladium mariscus</i> seed	8850 ± 50	9740–10,170
		147–148	Poz-10800	Unidentified bud	9290 ± 60	10,270–10,650
		224–225	Poz-10811	<i>Juniperus</i> leaves	10370 ± 60	12,000–12,590
		451–452	Poz-11212	Unidentified fibres	9120 ± 50	Rejected
		4	Sig-D17	335–345	Ly-2125	Marl
320–332	Lv-711			Peat	2560 ± 75	2360–2780
Sig-D18	431–440		Lv-712	Marl	13,190 ± 260	14,930–16,440
	215–225		Lv-709	Peat	2920 ± 70	2870–3320
Sig-D19	275–285		Lv-710	Peat	3360 ± 75	3440–3830
5	Cor	177.5	GrA-6601	<i>Betula</i> wood	2580 ± 80	2370–2850
		301–302.5	GrA-7789	Unidentified leaves	5450 ± 80	6000–6400
		390	GrA-6612	Unidentified leaf	5810 ± 80	6410–6790
		530.5–534.5	GrA-6602	<i>Abies</i> needles	7110 ± 80	7750–8150
		579–582	GrA-6595	<i>Abies</i> needle	7550 ± 80	8180–8520
		649–652	GrA-6607	<i>Betula</i> scales	9670 ± 90	10,750–11,230
		713.5–720.5	GrA-6597	<i>Betula</i> fruits	9220 ± 480	Rejected
		6	LDV	122–125	Gif-11554	Gyttja
127–130	Gif-11555			Gyttja	2115 ± 70	1930–2310
158–160	Gif-11556			Gyttja	3740 ± 60	3910–4290
179–181	Gif-11557			Gyttja	3930 ± 50	4180–4520
181–184	Gif-11558			Gyttja	4175 ± 45	4570–4840
245–248	Gif-11559			Gyttja	5520 ± 60	6210–6440
252–255	Gif-11560			Gyttja	5430 ± 80	6000–6400
7	Lau			46–47	AA-50229	Peat
		64–65	AA-50228	Peat	1132 ± 51	940–1180
		99–100	AA-50227	Peat	200 ± 34	Reject
		112–113	AA-50226	Peat	1694 ± 37	1530–1700
		152–153	AA-50225	Peat	2021 ± 62	1830–2140
		172–173	AA-50224	Peat	3018 ± 38	3080–3340
		189–190	AA-50223	Peat	6027 ± 56	6730–7150
		209–210	AA-50222	<i>Salix</i> wood	7513 ± 55	8200–8410
8	SDC	26–27	AA 50236	Peat	1083 ± 32	930–1060
		34–35	AA 50235	Peat	1888 ± 35	1720–1920
		46–47	AA 50234	Peat	2179 ± 35	2070–2320
		59–60	AA 50233	Peat	3378 ± 37	3480–3700
		79–80	AA 50232	Peat	3996 ± 38	4320–4770
		94–95	AA 50231	Peat	6736 ± 45	7510–7670
		119–120	AA 50230	Peat	7858 ± 58	8520–8980
		660–675	Ly-1138	Gyttja	8400 ± 220	8720–10,120
9	SL-D9	685–700	Ly-1139	Gyttja	9330 ± 430	9490–11,960
		745–758	Ly-963	Gyttja	12,520 ± 360	13,700–15,690
		260.0	Ua-4127	<i>Carex</i> fruits	970 ± 65	730–1050
	SL-B135m	342.5	Ua-4126	<i>Carex</i> fruits	1195 ± 70	970–1270
		402.5	Ua-4125	<i>Carex</i> fruits	1665 ± 60	1410–1700
		462.5	Ua-4124	<i>Betula</i> fruits and scales	2490 ± 65	2360–2730
		612.5	Ua-4123	<i>Betula</i> fruits and scales	3405 ± 65	3480–3830
		625.0	Ua-4140	<i>Betula</i> fruits and scales	3650 ± 80	3720–4230
		652.5	Ua-4139	<i>Betula</i> fruits and scales	4860 ± 85	Rejected
		715.0	Ua-4138	<i>Abies</i> seeds and needles	4580 ± 80	4970–5580
		745.0	Ua-4137	<i>Abies</i> seeds and needles	5220 ± 105	5740–6270
		767.5	Ua-4122	<i>Abies</i> seeds and needles	6920 ± 65	7620–7930
		777.5	Ua-4136	<i>Abies</i> seeds and needles	7255 ± 90	8000–8170
		800.0	Ua-4135	<i>Betula</i> fruits	8975 ± 105	9920–10,240
		10	Lib	44–45	AA-50221	Peat
79–80	AA-50220			Peat	1168 ± 46	970–1230
104–105	AA-50219			Peat	1657 ± 42	1420–1690
124–125	AA-50218			Peat	2164 ± 54	2000–2020
154–155	AA-50217			Peat	2534 ± 44	2470–2750
189–190	AA-50216			<i>Abies</i> wood	3189 ± 35	3360–3470
219–220	AA-50215			Peat	4421 ± 37	4870–5280
274–275	Poz-4748			Peat	6250 ± 35	7020–7260
354–355	AA-50214			Peat	7888 ± 57	8560–8980

(continued on next page)

Table 2 (continued)

Site number	Core	Depth (cm)	Laboratory code	Dated material	¹⁴ C age (BP)	2σ interval (cal. BP)
11	FED-D8	60–65	Ly-783	Peat	5100 ± 150	5580–6270
		120–125	Ly-1143	Peat	7570 ± 190	7980–8970
		125–135	Ly-782	Peat	8310 ± 180	8720–9630
		138–143	Ly-1142	Peat	8440 ± 320	8610–10,210
		145–155	Ly-781	Peat	9220 ± 220	9770–11,100
		170–175	Ly-780	Grey marl	10,850 ± 300	11,830–13,360
12	Fau	129–130	AA-50213	<i>Larix</i> wood	411 ± 31	330–520
		249–250	AA-50212	<i>Salix</i> wood	1053 ± 31	920–1050
		259–260	AA-50211	<i>Salix</i> wood	1121 ± 32	960–1170
		319–320	AA-50210	<i>Salix</i> wood	1574 ± 32	1390–1530
		334–335	AA-50209	<i>Salix</i> wood	1603 ± 33	1410–1550
		429–430	AA-50208	<i>Abies</i> wood	2266 ± 34	2160–2350
		454–455	AA-50207	<i>Abies</i> wood	2350 ± 34	2320–2480
		599–600	AA-50206	<i>Abies</i> wood	2875 ± 39	2870–3140
14	CDL-D22	619–620	AA-50205	<i>Abies</i> wood	3004 ± 47	3040–3350
		45–50	Ly-1234	Peat	2980 ± 130	2810–3450
		190–195	Ly-1279	Peat	5680 ± 170	6020–6900
		280–285	Ly-1280	Peat	7510 ± 150	8010–8590
		373–378	Ly-1281	Gyttja	9860 ± 200	10,710–12,040
		380–385	Ly-1282	Gyttja	10,870 ± 330	11,770–13,420
		387–392	Ly-1332	Gyttja	11,160 ± 320	12390–13740
		392–398	Ly-1283	Gyttja	11,800 ± 540	12725–15290
		404–410	Ly-1334	Clayey gyttja	11,730 ± 200	13,220–13,990
		415–420	Ly-1209	Clayey gyttja	13,060 ± 270	14,970–16,020
15	PR	423–427	Ly-1210	Clayey gyttja	13,750 ± 450	15,140–17,810
		92	Lyon-648	<i>Pinus</i> wood	3965 ± 50	4250–4570
		115	Poz-10818	<i>Abies</i> wood	4660 ± 40	5310–5570
		136–140	Poz-10819	<i>Alnus</i> wood	7900 ± 50	Rejected
160	Lyon-649	<i>Acer</i> wood	7660 ± 65	8360–8590		

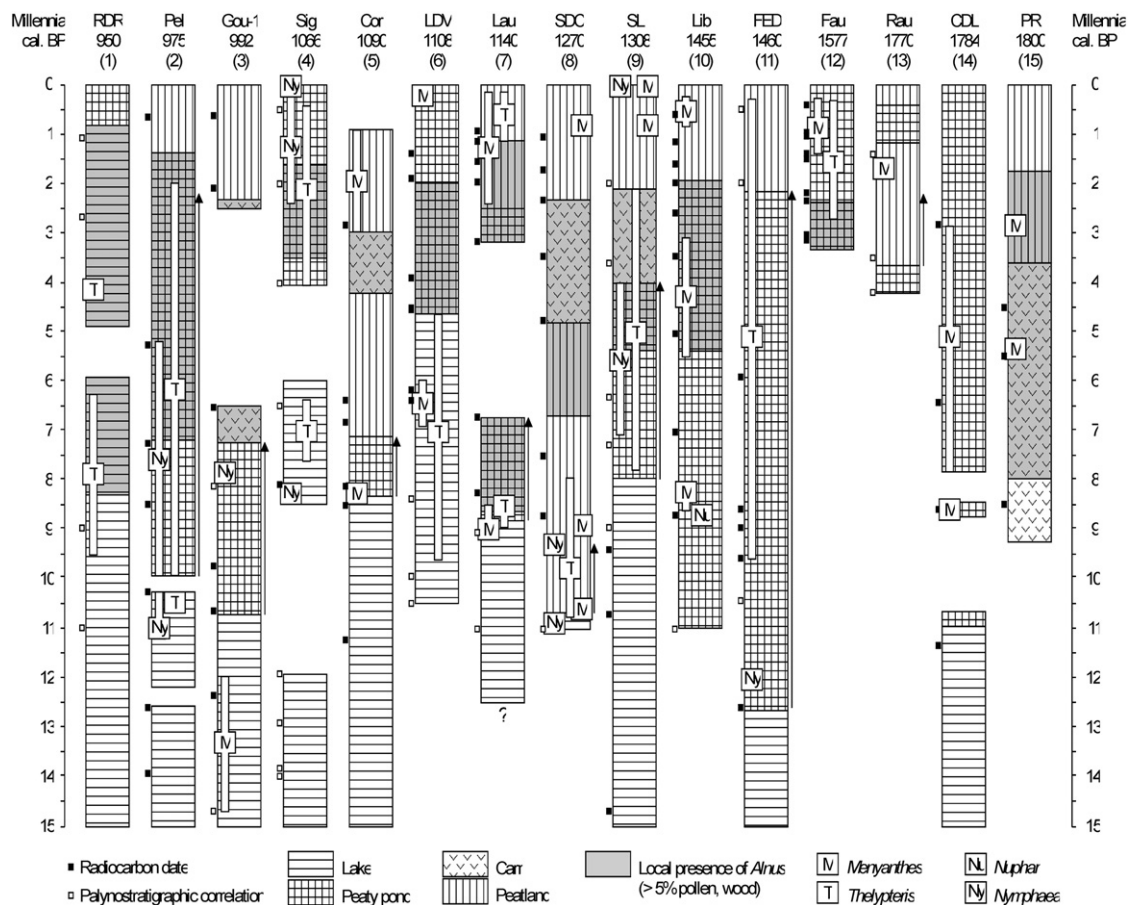


Fig. 6. Wetland plant dynamics in the high valleys of Durance and Drac. The site numbers indicated into brackets refer to Fig. 1 and Table 2. The sites are ranged by increasing altitude (given in m, below the site numbers). Sedimentary hiatuses are indicated by vertical dotted lines. The occurrences of the rarer hydrophytes (*Menyanthes*, *Nuphar*, *Nymphaea*) are noted. Arrows indicate approximate periods of centripetal infilling of depressions (see Fig. 5).

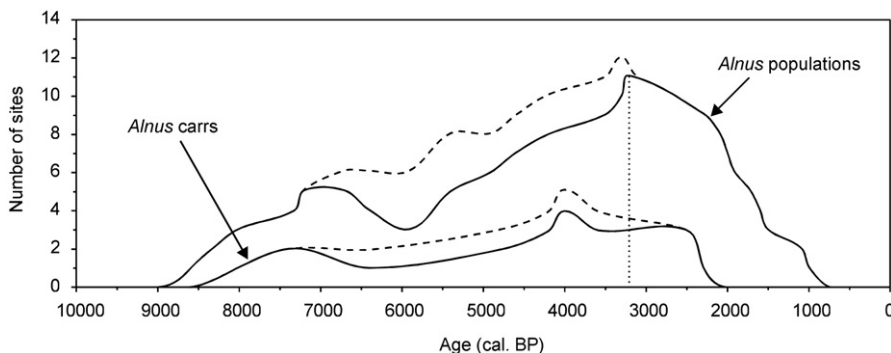


Fig. 7. Postglacial dynamics of *Alnus* populations and *Alnus* carrs in the central French Alps. The total number of sites used in this survey is 15. The dashed lines represent the sites presenting sedimentation hiatuses preceded and followed by *Alnus* carrs.

where palaeoecological records attest its past occurrence (Figs. 5 and 6) and suggests that its modern distribution does not reflect its past regional abundance.

The presented data thus highlight the decline, and sometimes the regional extinction of some aquatic taxa. This trend, starting in the first half of the Holocene, can be linked to the general decline of wetlands (Abramovitz, 1996), mainly as a result of the autogenic infilling process. The modern populations of *Nymphaea alba* and *Menyanthes trifoliata* of the high valleys of Durance and Drac therefore appear as relicts of the Lateglacial and early-Holocene aquatic communities of the region.

4.1.2. Carr communities

Most of the studied sites experienced from the Lateglacial to 6600 cal. BP fast hydrosere successions from hydrophytic communities to peat-forming communities, through the centripetal development of their margins (Fig. 6). Among these peat-forming

communities composed by Cyperaceae, ferns, *Alnus glutinosa/incana* and *Salix* (Fig. 5), a few appear to be assignable to alder carrs (Fig. 6). Alder communities been recorded during the Holocene throughout the whole Europe, from southern Spain (Carrion et al., 2003) and southern Italy (Watts et al., 1996) to Fennoscandia (Tallantire, 1974). Their postglacial dynamics have been strongly dependent on local conditions: some alder carrs were successional stages that have been later replaced by mature forests (Tallis, 1983; Walker, 1970), but others were stable and long-persisting communities (Barthelmes et al., 2006; Marek, 1965), sometimes through cyclic successions with sedge fens (Pokorný et al., 2000). While present in the central and southern French Alps at the mid-Holocene, the alder carr community is today absent from these regions. Most of the pollen grains found at La Gourre, within the wood layer comprised at 104–78 cm depth, were attributed to *A. glutinosa*. This was surprising, because this species is today much rarer than *A. incana* in the studied region (Chas, 1994; Garraud, 2003). The past regional development of *A. glutinosa* is however attested by the presence of leaf imprints within the early-Holocene travertine sequence of Mouresse, located ca. 80 km southeast of La Gourre (Roiron et al., 2006; Fig. 1). Moreover, *Alnus glutinosa/incana* pollen is often associated in pollen diagrams with fern spores: this also supports the identification as *A. glutinosa*, which is the only alder species of the French flora reported to commonly form swamps or carrs in association with ferns like *Osmunda regalis* and *Thelypteris palustris* (Rameau et al., 1989–2008; Sbrulino et al., 2011), probably because of its better tolerance to flooding (Tallantire, 1974). The fern spores were identified in eight sites as *Thelypteris palustris* (Fig. 5), based on perine surface with small echinae. Today, *T. palustris* occurs in most of the western and northern regions of France, and is everywhere considered rare and declining because of human-induced destruction of its habitat (Prelli, 2001). Our results suggest that the decline of that fern species began during the last millennia, by the extinction of its mountain populations.

Regional pollen and macrofossil records of *Salix* and *Betula* (Court-Picon, 2007; de Beaulieu, 1977; Digerfeldt et al., 1997; Muller et al., 2000; Nakagawa, 1998) suggest their past development in or around wetlands. The sporadic pollen records of *Salix* reveal its past widespread development in the central French Alps, but only two sites showed large populations: Sagne-de-Canne, where dense willow thickets occurred over 2 millennia, and Libouse, where they were associated with alder (Fig. 5; Court-Picon, 2007). The uniform pollen morphology of *Salix* and the number of willow species of close ecologies and distributions definitely prevent identifying its fossil records at the species level. Nevertheless, the past willow thickets were probably composed of the same species as today (*Salix capraea*, *S. cinerea*, *S. myrsinifolia*, *S. nigricans*, *S. pentandra*, *S. purpurea* and *S. repens*). The modern populations, while common in the study area, are rarely dominant, and some of these species are rare (Chas et al., 2006): the palaeoecological records suggest that the past willow formations

Table 3

Pollen (p), spores (s), non-pollen palynomorphs (np) and macrofossil (M) occurrences of hydrophytes and helophytes in Lateglacial and early-Holocene records from the high valleys of Durance and Drac, central French Alps. The site numbers indicated in brackets refer to Fig. 1 and Table 2.

Site code	Pel	Gou	Sig	Cor	LDV	Lau	SDC	SL	Lib	CDL
Site number	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(14)
Altitude (m)	975	992	1066	1090	1108	1140	1270	1308	1455	1784
<i>Alisma</i> -type			p							
<i>Callitriche</i> sp.										
<i>Ceratophyllum demersum</i>		np						P		
<i>Chara</i> sp.								M		
<i>Equisetum</i> sp.				s		s			s	
<i>Menyanthes trifoliata</i>		p		p		p	p		p	p
<i>Myriophyllum</i> spp. ^a	p				p			M		
<i>Nuphar</i> sp.									p	
<i>Nymphaea alba</i>	p	p	p				p	p		
<i>Polygonum amphibium</i>		p								p
<i>Potamogeton</i> spp. ^b		p		p	p	p	p	M		p
<i>Sparganium-Typha</i>		p	p	p	p	p	p			
<i>Typha latifolia</i>	p	p				p		P		
<i>Utricularia</i> sp.				p	p					

^a *Myriophyllum* remains were identified as *M. spicatum* (Faudon) and *M. verticillatum* (St-Léger).

^b *Potamogeton* macrofossils were identified as *P. natans*, *P. perfoliatus*, *P. praelongus* and *P. pusillus* (St-Léger).

of the central French Alps were similar to the modern ones in terms of abundance, geographic extent and ecological role. The genus *Betula* is represented today in the Alps by two pioneer species: *Betula pendula*, which penetrates largely in the Mediterranean massifs, and *B. pubescens*, rarer and confined to a few peatlands in the inner Alps. As elsewhere in the French Alps, *Betula* is abundant in the palynological records of the studied region during the Lateglacial and the first half of the Holocene (David and Barbero, 1995; de Beaulieu, 1977). While we cannot exclude the possibility of a past higher abundance of *B. pubescens*, the large-scale uniform dynamics of birch populations suggests a climate-driven spread of regional pioneer formations and their subsequent competition-induced decline (David and Barbero, 1995). This suggests that *Betula* was essentially represented by *B. pendula* and that it played only a negligible role, if any, in the hydroseral dynamics of the central French Alps.

The extinct carrs, mainly composed of *Alnus (glutinosa)*, *Salix* spp. and *Thelypteris palustris*, appear as original communities without regional modern analogues. The past occurrence of *Alnus (glutinosa)* and *Thelypteris palustris*, today respectively rare and absent from the studied region, notably confers them a high biogeographical, ecological and historical value. The modern willow populations can be considered as the last remnants of these communities. The extinct alder communities are characterised in most of the sites by very low sediment accumulation rates, even culminating in complete halt in sedimentation at La Gourre, Siguret and Lauza (Figs. 4, 5 and 6). That feature constitutes an important difference with alder swamps of European and North African lowlands, which are known as productive peat-forming ecosystems (Barthelmes et al., 2006). This could be related to the dry Mediterranean climate of the region, which similarly prevents the development of *Fagus sylvatica* in the inner French Alps and allows the persistence of steppe species such as *Juniperus thurifera* and *Astragalus alopecurus* (Barbero and Quézel, 1986; Ozenda, 1985). Such climate conditions were certainly not so favourable to *Alnus (glutinosa)* and *Thelypteris palustris*, which probably found there boundary conditions for their development. Surviving in these boundary climatic conditions may explain the unequal development of the two species in different sites, the very low peat accumulation of their community, and possibly also the gaps between their respective past developments within the same wetlands (Fig. 5), possibly explained by different hydrological requirements.

4.1.3. Sedge mires

Finally, most of the studied sites are today dominated by sedge mires or surrounded by herbaceous floating carpets (Fig. 1). These communities are now recognised as priority habitats for conservation. The data presented here clearly show that these habitats originated from modification of previous communities, including peaty ponds and alder carrs, since ca. 3000 years ago (Fig. 5). Such a recent origin at the Holocene timescale implies that their forming species were previously included in other communities or developed in mosaic with willow thickets and alder carrs, into complex habitats. As suggested by three relatively undisturbed wetlands located in small valleys of the region (Bourget, Manteyer and Névache), these communities could have occupied the alluvial plains, before their extensive drainage and cultivation by human populations. They also probably formed extensive floating carpets around most of open water bodies, today almost completely destroyed by four centuries of institutionalised “wetland sanitization” (Cizel, 2006).

4.2. Past dynamics of wetland plant communities

Our results present complex but rather homogeneous wetland histories over the studied region (Fig. 6). The first developmental stages fit well with the classic hydroseral model: during the first half of the Holocene, lakes tend to evolve into carrs or peatlands probably depending on hydrology or nutrient status, often with a transitional development

of peaty margins. This trend undoubtedly reveals the process of infilling through sediment accumulation, mostly controlled by the autogenic production of organic matter by planktonic algae and macrophytes. The allogenic mineral matter supplied by the erosion of watershed slopes only played a significant role during the first stages of lake infilling, marked by clay deposition. Since 8000 cal. BP, most of the sites began to be overrun by marginal peat-forming formations, and some of them shifted to alder carrs. Between 6600 and 2500 cal. BP, several sites experienced low lake levels (St-Léger lake, Digerfeldt et al., 1997) or complete drying out (La Gourre, Siguret, Lauza; Fig. 6), contemporaneously to low lake levels in western Mediterranean regions (Magny et al., 2002) and in North Africa (Damnati, 2000), to the development of *Pinus cembra* forests in the whole upper Subalpine range of the western Alps (Muller et al., 2006), and to a strong decrease in sedimentation rates in southern Alps torrents (Miramont et al., 2008). These concurrent events suggest a common climate forcing possibly due to seasonal changes, with drier winters and/or warmer summers. This scenario appears similar to the one described for a North American marsh (Singer et al., 1996), where the progressive infilling of the basin by autogenic sediment accumulation did not act as a direct mechanism of change, but created favourable conditions for climate-driven vegetation changes.

The progressive spread of alder populations in the central French Alps (Fig. 7), resulting from the interaction between sedimentation processes and climate forcing, then appears as the main feature of the past dynamics of regional wetlands. However, a widespread and rapid decline of these populations occurred by 3200 cal. BP (Fig. 7), representing an unexpected return towards more humid states, such as herbaceous mires and open water bodies. This change occurred at the same time as both a regional increase in precipitation documented at St-Léger lake (Digerfeldt et al., 1997) and a rapid intensification of regional human activities during the Iron Age and the Gallo-Roman period (Court-Picon, 2007; Coûteaux, 1983; de Beaulieu, 1977; de Beaulieu and Goëury, 2004; Nakagawa et al., 2000). Agricultural practices are notably revealed at La Gourre for the last 2500 years by the occurrence of *Cerealia*-type, *Plantago*, *Olea*, *Juglans* and *Castanea*. Several wetlands (e.g., La Gourre, Pelleautier, Roche-de-Rame, Siguret...) present a dam on their outlet, which proves their artificial flooding for livestock and/or irrigation. Such human-induced flooding of wetlands has been noted during the Subatlantic period in most of the mires of the eastern Massif Central (Cubizolle et al., 2003). Moreover, a general decline of *Alnus glutinosa* has been documented for the last four millennia over the whole Europe, mainly as a result of increasing human pressure. In England, *A. glutinosa* declined by 4000 cal. BP along with mesophilous forests as a consequence of clearance activity (Brown, 1988; Waller, 1994; Waller and Schofield, 2007). It disappeared around 4500 cal. BP from the western islands of Scotland (Tallis, 1975; Fossitt, 1996). In northern Germany, a high-resolution study evidences the alternation between sedge-dominated fen vegetation, *A. glutinosa* carr and *Salix* shrubland between 2500 and 1700 cal. BP, probably in response to human activity and to increased runoff resulting from large-scale deforestation (Barthelmes et al., 2010). In the eastern Baltic region (southern Finland and Estonia), numerous sites recorded temporary declines of *A. glutinosa* between 1700 and 700 cal. BP, likely due to Iron Age human activities and in particular, rye cultivation (Saarse et al., 2010; Sarmaja-Korjonen, 2003). Finally, *A. glutinosa* disappeared by about 1000 cal. BP from the Sierra de Guadarrama (central Spain), because of severe deforestation in the region (Franco Múgica et al., 1998), and from the Sierra de Gádor (southern Spain) along with *Taxus*, *Corylus*, *Myrtus* and *Betula celtiberica*, certainly as a result of human activities such as lead production (Carrión et al., 2003).

Past human-induced extinctions of plant species have been mainly reported from insular contexts, where isolation and small population sizes make them more sensible to environmental changes (MacArthur and Wilson, 1967). Such extinctions have for instance been reported from Easter Island (Diamond, 2007), Canary Islands

(de Nascimento et al., 2009) and the western islands of Scotland (Fossitt, 1996). Our data, as well as those from Spain (Carrión et al., 2003; Franco Múgica et al., 1998), exemplify human-driven extinctions in a continental context, where the concerned populations were located at the rear edge of their main distribution area (Hampe and Petit, 2005), in boundary conditions for their development.

4.3. Implications for conservation and management

The peatlands (mainly lowland sedge meadows) of the central French Alps are shown to be of recent origin (less than 3000 years ago; Fig. 6) and simultaneous with a strong increase in human activities. Some of these habitats are now protected due to the rare species and microhabitats they harbour (Chas et al., 2006). Since the historical data show that such herbaceous communities have probably never been as extended as today for two millennia but confined within isolated wetlands, their protection could appear paradoxical. In this context, the present study provides a long-term perspective for discussing the consistency of their present-day management with general conservation goals, and for proposing some avenues for the future.

The present-day management of wetlands in the central French Alps protects most of the taxa recognised in our work as having high historical values, essentially because their present-day rarity is triggered by the decline of their habitats. Palaeoecological data however show that these taxa (and the communities they constitute) have neither the same historical significance nor the same sensitivity to climate change and human disturbance. Some represent the heritage of the most ancient hydrophytic plant communities of the region (e.g., *Menyanthes trifoliata*, *Nymphaea alba*), while others constitute secondary formations favoured by climate change and autogenic processes (e.g., *Alnus glutinosa*, *Thelypteris palustris*) or human disturbances (e.g., *Salix* spp., Cyperaceae). While most of these taxa are declining, their respective responses to human activities are very different: (1) some persist within 'natural' communities in the less impacted habitats (peaty lakes, mountain peatlands), (2) some others persist within human-shaped communities in disturbed sites (sedge mires, willow thickets, riparian forests), and (3) a few have disappeared from the regional flora. We believe that such an assessment of the community naturalness and resilience provided by palaeoecological data is very valuable for conservation, to better define conservation priorities and to refine management actions (e.g., traditional agricultural practices, controlled grazing), and to assess baseline conditions for restoration initiatives (Feurdean and Willis, 2008; Willis and Birks, 2006).

Our results clearly show that the past diversity and species richness of wetlands, even during periods of strong human pressure such as the Neolithic (Morin, 2003), were higher than in the present-day. This could appear contradictory with some previous works (e.g. Tinner et al. 1999) showing that forest diversity strongly decreased in the past whereas total biodiversity increased, mainly as a consequence of the creation of open land for agricultural purposes. However, this statement is highly dependent on the observation scale: it can be correct at the local scale, when a monotonous forest ecosystem is replaced by a mosaic of richer open lands, but it appears on the contrary incorrect if we consider a larger territory, where natural disturbances maintained on the long term the heterogeneity and diversity of landscapes, including all stages and species of the ecological succession. Moreover, because the present study focuses on the regional wetland plant diversity, we consider that past extinctions of species and/or communities represent biodiversity impoverishments.

These reconstructed potential (or baseline) biodiversity and richness can be used in order to design conservation policies at the regional level. In terms of management, this would imply: (1) to

reinforce conservation measures on the less impacted (i.e. the most preserved) habitats such as peaty ponds and alluvial sedge meadows, notably by also protecting border areas of wetlands (e.g. Sottocornola et al., 2009), and (2) to increase the regional diversity and richness of isolated mires, for instance by operating some restoration to favour the recovery of alder communities in some of them. The insight provided by the palaeoecological data into the species responses to human disturbances could be used in order to assess their vulnerability and thus to design appropriate management actions. The surviving hydrophytic species prove to have sufficiently large ecological amplitudes for supporting more or less moderate disturbances. Consequently, the regional rarity of *Nymphaea alba* and *Menyanthes trifoliata* is probably not due to their own sensitivity to disturbance, but rather to the destruction of their habitats. The status of sedge-mire communities appears more complex. While we lack palaeoecological data from the bottom of valleys, it is probable that they suffered from the destruction of most of alluvial plain meadows for agriculture, and that they spread (maybe with simplified or modified compositions) within isolated wetlands thanks to their artificial recent flooding. In contrast, the regionally extinct species certainly presented higher vulnerabilities, due to the rarity of favourable habitats (*Nuphar*) or to boundary climatic conditions for their development (*Alnus glutinosa*, *Thelypteris palustris*). Such extinctions definitely cannot be regarded as only natural hazards related to climate-driven changes of distribution areas, but as human-induced disturbances in particularly sensible geographic areas.

These considerations raise questions about active or passive management of biodiversity (Carey, 2006). In the case of the central French Alps, some degraded lowland mires could be restored by regenerating their natural hydrological dynamics with the aim to favour their colonisation by disappeared species (e.g., *Alnus glutinosa*), and by completing this by specific reintroductions of certain rare species in suitable habitats (e.g., *Thelypteris palustris* or *Nuphar lutea*) as it is currently made for animals (Sarrazin and Barbault, 1996). This could notably allow regenerating extinct plant communities such as alder carrs. Such reintroductions could trigger local (in the concerned wetlands) biodiversity decreases by competitive exclusion, but they certainly would increase the regional wetland plant diversity by creating new habitats, new communities and by increasing the number of species involved in the regional wetlands. Nevertheless, they would only modify the species diversity, but not the genetic one. In order to preserve the genetic structure of species, reintroductions should be made carefully, and only from individuals taken from the geographically closest populations. This would allow reinforcing certain peripheral populations, known to strongly contribute to the genetic diversity of species (Hampe and Petit, 2005).

5. Conclusion

The palaeoecological data presented in this paper exemplify complex wetland dynamics resulting from the interplay between autogenic processes, climate change and human disturbances. They provide a long-term perspective for analysing the historical significance of wetland plant communities, and the related conservation policies, which are today essentially based on structural parameters (rarity, endemism, biodiversity, threats, disturbances...). Such a short-term approach is especially designed to identify and document declining endangered species and to provide a global assessment of biodiversity change (Vié et al., 2008; Willis et al., 2007). Although some of the used parameters integrate the notion of evolution and short-term population trends (Myers et al., 2000), it does not take into account long-term dynamics, which are generally ignored by scientists and managers working in the field of conservation (Willis et al., 2005). In this context, our results contribute to highlight the interest of defining 'historical values' for plant species and communities. The well-known partial picture of past environments provided by

palaeoecological data (Janssen, 1970; Svensson, 1986) clearly constitutes the main limit of the approach. However, conservation policies are never based on complete assessments of ecosystems, but only on incomplete data concerning well-known groups or indicator taxa (Gibbons et al., 2006; Streever et al., 1996; Zampela and Bunnell, 1998). Consequently, despite some species are rarely found or absent in palaeoecological archives, such data should be taken into account together with other descriptors. They should notably contribute to clarify critical conservation issues, such as assessment of naturalness, fragility, resilience and potential value (Birks, 1996).

The issues focusing on wetland functioning are centred on the maintenance of biodiversity, at the scale of individual wetlands and, most importantly, at the landscape level (Whigham, 1999; Willis and Whittaker, 2002). Palaeoecological studies, which provide a picture of the potential regional biodiversity, constitute a sound baseline for preserving or restoring wetland plant communities. Although the restoration of disappeared habitats or the re-introduction of locally extinct species raise a number of ethical questions, they obviously would allow increasing biodiversity and balancing the worldwide homogenisation of biological communities resulting from human disturbances. This issue however implies accurate preliminary studies in order to define the stakes, dangers and chances of success of such actions, and in particular the multiplication of 'applied' palaeoecological studies (Birks, 1996). These works should allow meeting some of the main needs for wetland conservation: (1) dating the origins of sites and communities, (2) determining their naturalness and resilience, and (3) assessing regional past wetland biodiversities. This new approach is now urgent for evaluating the general decline of wetlands, and for adapting management policies to long-term conservation goals.

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