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A temporary gravel pit as a biodiversity hotspot for aquatic plants in the Alps

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Abstract

Lake Bois d'Avaz is a shallow former gravel pit situated in the Arve valley (Haute-Savoie, France) which experiences fluctuating environmental conditions and shelters an exceptional aquatic plant community. We are interested to elucidate why this community is so rich and how the main factors affecting this lake explain the plant species distribution. During a survey period of four years (2009-2012), we recorded the aquatic vegetation and measured several local abiotic factors related to hydrology, climate and physico-chemistry of the water. The lake exhibits a high species richness with a high conservation value. 75 plant species, among them 12 charophytes species, were inventoried. We highlight that the coexistence of the large number of species is likely to be explained by the synergy of several key abiotic factors: an intermediate level of productivity and of drought disturbance, a long growth season and a partial connection to groundwater. The study of the functioning of Lake Bois d'Avaz represents an interesting basis for conservation and restoration targets. We provide evidence that temporary small waterbodies can be created artificially in floodplains and become naturally biodiversity hotspots for aquatic plants.

Keywords: *macrophytes, charophytes, species richness, threat status, productivity, temperature, temporary waterbody, ground water*

Résumé

Une gravière temporaire, un haut lieu de biodiversité pour les plantes aquatiques dans les Alpes. – *Le lac du Bois d'Avaz est une ancienne gravière peu profonde située dans la vallée de l'Arve (Haute-Savoie, France), qui est soumise à des conditions environnementales fluctuantes et qui héberge une communauté de plantes aquatiques exceptionnelle. Nous nous intéressons à élucider pourquoi cette communauté est tellement riche et comment les facteurs principaux affectant ce lac expliquent la distribution des espèces végétales. Au cours d'un suivi de quatre années (2009-2012), nous avons relevé la végétation aquatique et mesuré une série de paramètres locaux abiotiques relatifs à l'hydrologie, au climat et à la physico-chimie des eaux. Le lac montre une flore à la richesse spécifique très élevée et à forte valeur de conservation. 75 espèces végétales, dont 12 espèces de Charophytes, ont été répertoriées. Nous mettons en évidence que la coexistence d'un maximum d'espèces peut être probablement expliquée par la synergie de plusieurs facteurs abiotiques clés : un niveau intermédiaire de productivité et de perturbation liée aux assèchements, une longue saison de croissance et une connexion partielle aux eaux souterraines. L'étude du fonctionnement du lac du Bois d'Avaz représente une base intéressante pour des objectifs de conservation et de restauration. Nous apportons la preuve que des plans d'eau temporaires peuvent être créés artificiellement dans les plaines alluviales et devenir naturellement des hotspots de biodiversité pour les plantes aquatiques.*

Mots-clés: *macrophytes, charophytes, richesse spécifique, statut de menace, productivité, température, plan d'eau temporaire, eaux souterraines*

Introduction

Current legal framework and conservation plans concentrate almost entirely on large and deep lakes which contribute to explain that studies on standing waters often overlooked small waterbodies (included under terms of "shallow lakes", "ponds" or "wetlands") (Boix et al. 2012). However, an increasing number of studies established that ponds (i) cover a total area greater than large lakes on a global scale (Downing et al. 2006) (ii) play a crucial role in global geochemical cycles (Downing et al. 2008), (iii) shelter a very high biodiversity (Nicolet 2001; Oertli et al. 2002; Biggs et al. 2004). At the local scale, depending

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on the bathymetry of the waterbody, the fluctuations of water level may result in bottom air exposure which should strongly impact the aquatic vegetation through the elimination of species sensitive to desiccation and the initiation of a new succession (Coops et al. 2003; Van Geest et al. 2005). In these types of habitat, the macrophyte communities are generally abundant and arranged along a gradient of flooding conditions, influenced by inter and intra annual water depth fluctuations (Casanova and Brock 2000; Van Geest et al. 2007; Leira and Cantonati 2008). Shallow lakes with fluctuating water levels, thus constitute important refuges for a large number of pioneer macrophyte species. Macrophytes are major components of freshwater ecosystems in that they play key functions, contribute to maintain the related biodiversity, and supply services to human society. Indeed, they are primary producers that provide habitat, food and refuges for periphyton, invertebrates, fish, amphibians and birds. They also participate to ensuring the clear water state of shallow waterbodies through their effect on biogeochemical cycles (e.g. organic carbon production, phosphorus immobilization), and on the sediment deposition process (Bornette and Pujalon 2011).

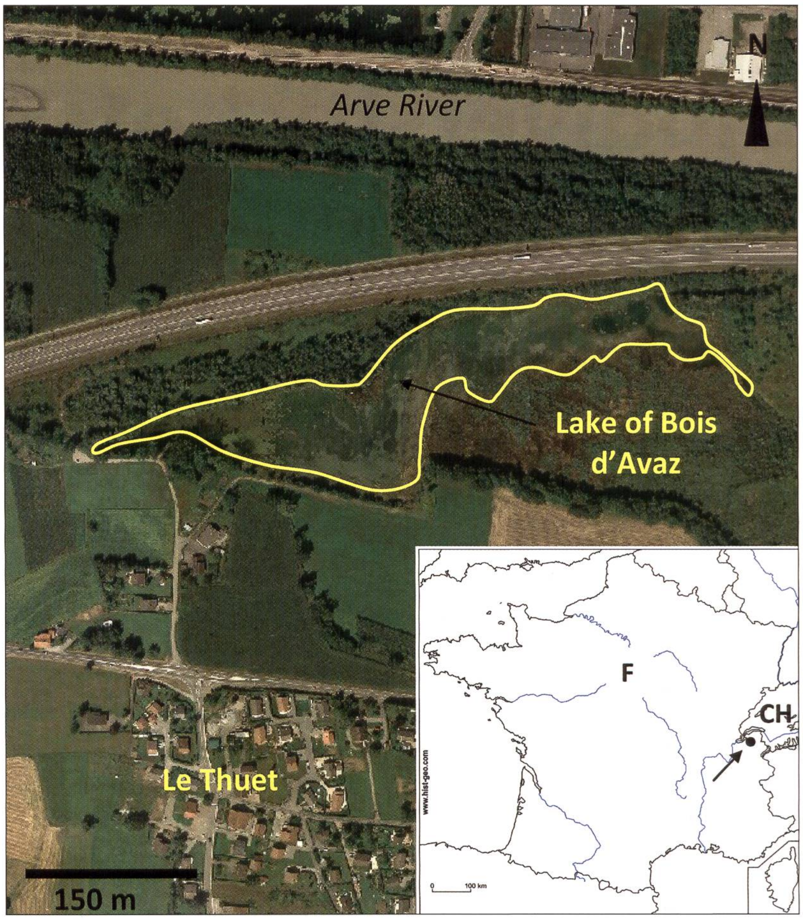

Fig. 1. Situation of Lake Bois d'Avaz near the French –Swiss border. (Aerial picture: www.geoportail.fr).

Floodplains are disconnected from the main channel or even completely destroyed (Ward and Stanford 1995; Bunn and Arthington 2002). This results in an absence of fluvial dynamism driving the rejunevation of floodplain waterbodies. In this situation of fossil floodplain, artificial waterbodies created by material excavations, can be seen as surrogates for natural ones and represent interesting conservation targets. However, little is known about the composition and the succession of macrophyte communities in artificial waterbodies that are subjected to occasional droughts.

We recently surveyed a former gravel pit situated in the French Alps that was colonized naturally by an exceptionally rich aquatic plant community with an important conservation value. Our aim is to provide a better understanding of the functioning of this waterbody and new assumptions about its impact on the macrophyte community. Over four years (2009-2012), we surveyed the aquatic vegetation and measured several local abiotic factors in relation to the hydrology, climate and physico-chemistry of water to acquire a longitudinal survey of the dynamics of the lake. We present here a first description of the aquatic vegetation and of the abiotic conditions that may explain the composition of the vegetation. The examination of one of these artificial temporary waterbodies shows that they can harbour a high species richness and conservation value, depending on the morphology and the dynamic of the ecosystem.

Materials and Methods

Study site

Lake Bois d'Avaz is situated in the French pre-Alps (Haute-Savoie département) in the intermediate basin of the Arve River (06°26'35.0" E / 46°04'17.6" N) at an altitude of 452 m (Fig. 1). It has a surface area of approximately 47 000 m² and a perimeter of 1600 m.

The study site is a former gravel pit that was partially filled by silt originating from an exploited gravel pit. The lake receives water from a diversity of sources: rain, a hillslope aquifer and a small temporary tribu-

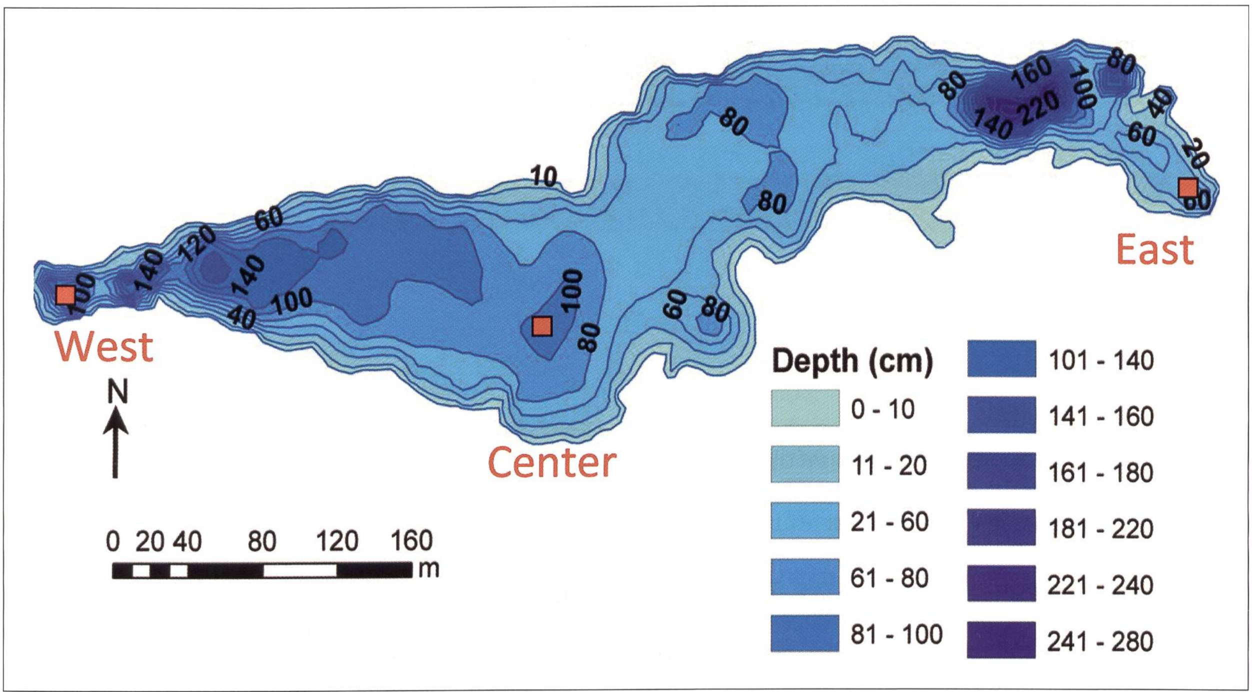

Fig. 2. Bathymetric map of the lake Bois d'Avaz during high water level. Red squares indicate the data loggers.

tary. The water coming from the hillslope aquifer is not feeding the lake uniformly, but influences differently the east and the west part of Lake Bois d'Avaz. Despite its location in the Arve floodplain, the lake has no surface water connection with the Arve River. The immediate surroundings of the lake are relatively natural; almost all shores of the lake are surrounded by a strip of riparian trees.

Bathymetry

Bathymetry (cm) was recorded in May 2010 at 257 points equally spaced along 20-meter spaced transects covering the whole lake using the method described by Oertli et al. (2005). This date corresponds to the highest water level observed during the 4 years of our survey (2009-2012). Summary statistics about the depth of the lake were calculated. Coordinates of points were recorded by a GPS (GPSmap 76CSx, Garmin, Cayman Island) according to the Swiss Grid system. The bathymetric map was constructed using the coordinates and the depth recorded for each of these 257 points. Depth between the points was spatially interpolated using the radial basis function ("RBF") in ArcGIS 9.3 and the "geostatistical analyst" tool (ESRI, Redlands, USA). This method forces the model to treat all input values. RBF gives thus a good picture of the variability of the surface, capturing global trends and picking up local variations. It is appropriate for the construction of topographic and bathymetric maps.

Water regime and water temperature

Three permanent data loggers (HOBO®; onsetcomp.com) recording water pressure and temperature every 4 hours were installed at three points (Fig.2). When collecting in situ observations and data, some problems might be encountered. The "west" data logger disappeared, so that water level data were available from March 2009 to February 2011. During 2011, the water level fluctuations were derived from occasional measurements of the depth at a fixed point (tab.1). Water pressure was corrected with atmospheric pressure recorded by a logger and transformed into water depth. As we assume that the periods of drought and their duration are more important for the vegetation than the water level variations, the periods of high levels and of drought were calculated using the quartiles of the lake depth. Duration of high water levels was defined as a period during which more than 75% of the lake area was inundated. Duration of drought of more than 50% of the lake area was calculated by counting days of water level below the median depth of the lake. Low water level period was defined as a drought period of more than 75% of the area.
Water temperature was measured by the 3 data loggers and sampling date concluded on the date of the logger vanishing (Table 1). "West", "Center" and "East" loggers were localized at 1.63 m, 1.15 m and 1.65 m deep respectively. According to occasional temperature measurements made along depth profiles in the western and eastern parts (see Results sec-

Table 1. Available water level and temperature data at Lake Bois d'Avaz

	Water level		Temperature	
	Logger	Occasional	Logger	Occasional
West	**707 days** (16/03/2009 to 21/02/2011)	**11 days** (21/02/2011 to 03/10/2011	**707 days** (16/03/2009 to 21/02/2011)	–
Center	–	–	**1289 days** (16/03/2009 to 25/09/2012)	–
East	**–** – –	**–** – –	**104 days** (15/04/2010 to 28/07/2010)	**7 days** (16/03/2009 to 03/12/2009) **9 days** (16/08/2010 to 04/05/2011)

tion, Fig. 5 C), no stratification process occurred, allowing the comparison of records from the three loggers.

Daily, monthly and seasonal temperature statistics were calculated using the measurements from the "center" logger because they covered the longest period of time.

Using the water temperature recorded by the central logger, we calculated degree-days ("°D") above 10°C ("lower developmental threshold") from 16th march to 15th December of each year and averaged them. We applied the single triangle method described by Zalom et al. (1983) (Snyder et al. 1999; Spencer and Ksander 2006). This method uses the day's low and high temperatures to produce an equilateral triangle over a 24-hour period. Degree-day is then estimated by calculating the area within the triangle and above the lower developmental threshold. This formula is easy to apply and gives good estimates of heat units, similar to those produced with more complicated procedures (sine and cutoff methods) (Roltsch et al. 1999). Groundwaters coming from hillslope aquifers or seepage water filtered from the main rivers in floodplains can interact with surface water (Bornette et al., 1998; Sophocleous, 2002; Jansson et al., 2007). The existence of different types of water supply can be deduced by looking at the thermal signature. The slope of linear regression between air and water temperature gives indirect information about the presence of groundwater input (Caissie 2006; Lachal, personal communication). The slope value decreases as the influence of groundwater increases. In extreme cases of sites receiving the majority of their water from aquifers, water temperature is almost independent of air temperature and the slope of the regression is null. We compared the thermal signature of the three datasets to explore the West to East thermal gradient. Values from emerged thermometers and from "ice-periods" (below 6°C) were excluded from our analyses on the thermal signature. We tested the "logger" effect on the linear regression between air and water temperature using an analysis of covariance (ANCOVA). A significant interaction term indicates a significant difference in this regression relationship between loggers.

Chemistry

Water samples were collected on two occasions in 2009 (October and December), on three occasions in 2010 (February, May and August) and on six occasions in 2011 (February, April, May, June, July, October). They were brought to the laboratory in a refrigerated box and analyzed the day after sampling. Total phosphorus ($\mu g\ l^{-1}$) was measured after a persulphate digestion according to the ascorbic method (Clesceri et al. 1999). Nitrates, sulphates, chlorides, calcium and magnesium ($mg\ l^{-1}$) were measured by ionic chromatography (Dionex ICS-3000). Dissolve oxygen ("DO", %), turbidity (NTU) and conductivity ($\mu S\ cm^{-1}$) were measured in the field (HACH HQd Field Case probe; HACH 2100Qis portable turbidimeter; WTW 3210 conductivity probe). At five occasions between February 2011 and May 2012, we made field measurements of DO, conductivity (missing values for February 2011 because of probe failure) and temperature along a depth gradient in eastern deepest part of the lake, in order to highlight stratification process. Chlorophyll a concentration was used as a proxy for phytoplankton biomass. Water samples were filtered through GF/F glass filters. After extraction over 24 h in a 100% ethanol solution, chlorophyll a was measured with a UV / VIS spectrophotometer (Shimadzu Spectronic 1201, Milton Roy) at 665, 710 and 770 nm before and after acidification. The chlorophyll a concentration ($\mu g\ l^{-1}$) was then calculated using the formula of Lorenzen (1967). We then estimated the phytoplancton biomass using the following function:

Phytoplankton biomass ($\mu g\ l^{-1}$) = [*Chl a*] * 67

Vegetation data

We confirmed and completed the existing vegetation data from "ASTERS" (Conservatory of natural spaces of Haute-Savoie) thanks to seven detailed prospections of the lake and its shoreline between June 2009 and July 2012. As far as possible, vascular plants were determined using the Swiss key of Aechimann and Burdet (1994) and charophytes were determined using the German key of Krause (1997).

Aquatic plants are important components of waterbodies and within them; the Charophytes is a very special group. We are particularly interested in understanding the ecology of these macroalgae. The European directive Natura 2000 identifies them as natural habitats with a community interest (Lambert 2002; Lambert and Guerlesquin 2002). At the European scale, this macroalgae family is strongly threatened as proved by the degree of threat of the majority of species in the Red Lists developed in numerous European territories (Stewart and Church 1992; Hamann and Garniel 2002; Blazencic et al. 2006a; Sieminska et al. 2006; Langangen 2007; Gärdenfors 2010; Auderset Joye and Schwarzer 2012). The territories of the Haute-Savoie French département and of Switzerland belong to the same biogeographic unity, the Northern Alps, and thus present similar plant populations. Stagnant waterbodies in the floodplains of both regions are submitted to the same human pressures, as the mountainous relief has favored the intensive development of agriculture and urbanisation in lowland areas. The status of charophyte species inventoried in Switzerland (Auderset Joye and Schwarzer 2012) is probably applicable to those of the Haute-Savoie. Consequently, as there is still no French Red List of Charophytes, we decided to attribute the threat status from the Swiss Red List of charophytes to the species of Lake Bois d'Avaz.
To assess the local threat status of vascular plants, we used (i) the Red List of Geneva (Lambelet-Haueter et al. 2006) (ii) the Red List of Switzerland (Moser et al. 2002) and (iii) the Red list of Haute-Savoie (Jordan 1986).
The protection of vascular hydrophytes of lake Bois d'Avaz was determined according to the ministerial decree related to protected species in the Rhône-Alpes region (Art.1; J.O 29/01/1991; NOR: ENVN9061670A).

Table 2. Bathymety of Lake Bois d'Avaz during high water level period (May 2010, n=257). All values are in meter.

Mean depth (min-max)	0.74 (0.02-3.00)
Median depth (1st Qu-3rd Qu.)	0.68 (0.49-1.00)

Table 3. Hydrological regime of Lake Bois d'Avaz (16th march 2009 -3rd October 2011).
HL = high water level when more than 75% of the lake was flooded (>-0.49m). L_{50}= water level when more than 50% of the surface area was dried (<-0.68 m), L_{75}= water level when more than 75 % of the surface area was dried (< -1m).

Mean (max;min)	-0.68 (0; 1.33)
1st Qu.; 3rd Qu.	-0.97; -0.38
Duration of HL	295 days
Duration of L_{50}	481 days
Duration of L_{75}	209 days

Results

Bathymetry and water regime

The site can be considered as a shallow lake characterized by a depth below 1 metre for 75% of its surface area (Table 2). The deepest parts of the lake are the western (up to 1.4m) and the eastern (up to 3m) edges (Fig.2).
The amplitude of water level fluctuations reached 1.33 m (Table 3). Between the 16th march 2009 and the 3rd october 2011 (932 days), we recorded 481 days (50% of the time) during which 50% of the surface area of the lake had been dried. Approximately 75% of the lake area was dried 25% of the time (209 days). More than 75% of the lake area was inundated 32% of the time (295 days).
In 2007 and 2008, almost all the surface area of the lake was inundated the whole year (Fig. 3 A, B). In 2009 and 2010, a water level decrease occurred in summer, leading to low automnal levels (Fig. 3 C, D). Low regional precipitations during the 2010-2011 winter prevented the complete filling of the groundwater coming from the hillslope aquifer. Thus low level period continued until October 2011 (Fig. 3 E). In spring 2012, the water level was high again, and an automnal drawdown occurred (Fig. 3 F). As a consequence, the shallow parts were submitted to wet/dry cycles and only the deepest parts remained inundated during the whole monitoring. A decrease of the water level of 0.6 metres led to the division of the lake into two parts during which the connection through surface water was absent.

Water temperature

During the 1289 days of recording we measured a minimum daily water temperature of 1.0°C and a maximum daily temperature of 27.8°C. A daily temperature average of 14.5°C with an amplitude of 4.4°C was recorded in the central part of the site (Table 4).
A difference of 20°C was observed between the mean temperature of the coldest and the warmest month (December 2011 and July 2010). Heat energy accumulation reached 2056 degree days on average when the curve reached a maximum (October-December 2009, 2010 and 2011). A difference of around 400°D separated the coldest year (2010) from the warmest one (2009). The relations between air temperature and water temperature recorded by each logger were explored. The lake could not be characterized by a unique thermal regime and showed variation in space (Fig. 4). The analysis of covariance indicated no significant difference in the linear regression between western and central log-

Fig. 3. Pictures showing Lake Bois d'Avaz during several successive autumns. A: October 2007, B: October 2008, C: September 2009, D: October 2010, E: September 2011. F. September 2012.

gers (p-value=0.392), and a significant difference between those two loggers and the eastern one (p-value<2.10^{-16}). The water temperature was more closely linked to air temperature at the western and central points (slope around 0.7) than at the eastern one (slope around 0.4). The intercept of the regression line indicates the values of water temperature when the air temperature reached 0°C. So, in the western and central parts, the water temperature fell to approximately 7°C (values during ice-period not included) whereas in the eastern part the minimum temperature was 11°C.

Chemistry

Lake Bois d'Avaz had oligo to mesotrophic waters according to the OCDE classification (OCDE 1982) with a moderate concentration of phytoplankton, as indicated by the mean concentrations of total phos-

Table 4. Thermal regime of Lake Bois d'Avaz.
Daily and monthly statistics were calculated using data from the logger "center". Data from thermometer and logger were compiled to calculate the thermal signature of the eastern part.

Parameter	Period	Values
Daily temperature (°C)	16/03/2009-25/09/2012	
Mean (min-max)		14.5 (1.0-27.8)
Amplitude: mean (min-max)		4.4 (0.1-26.7)
Monthly temperature (°C)	16/03/2009-25/09/2012	
Mean of the coldest month	December 2011	4.3
Mean of the hottest month	July 2010	24.1
Amplitude: mean (min- max)		6.9 (1.1-12.5)
Vegetation season growth degree day	16/03-15/12	
Mean (min-max)		2056 (1807-2246)
Thermal signature slope / intercept	16/03/2009-21/02/2011	
West		0.677 / 6.77
Center		0.675 / 7.57
East		0.375 / 11.2

phorus, nitrates and phytoplankton biomass (Table 5). However, we observed large variations of productivity in the lake as demonstrated by the maximum concentrations of those parameters. The turbidity never exceeded 15 NTU which indicated clear to slightly turbid waters.

The lake was strongly mineralized (conductivity > 500 µS cm^{-1}), mainly because of high calcium concentrations averaging 95 mg Ca l^{-1}. No stratification was recorded by conductivity measurements along depth profiles (Fig. 5 A). Sulfates and chlorates were two other major components (around 30 mg l^{-1} and 19 mg l^{-1} respectively). Oxygenation fluctuated in time, from anoxic (9.2%) to hyper-saturated (221%). In the eastern part, oxygenation in the water column did not vary during February 2011 and decreased with increasing depth during the following Spring and Summer (Fig. 5 B).

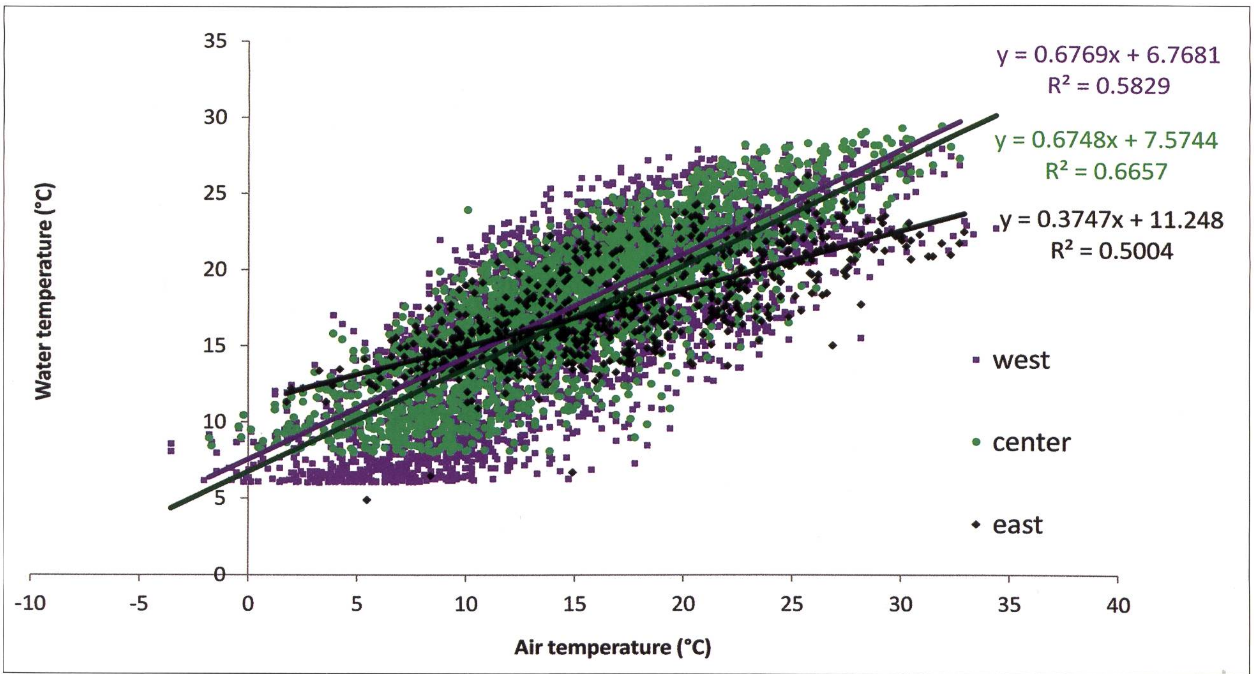

Fig. 4. Thermal signatures given by occasional measurements and 3 loggers installed at the western (violet), central (green) and eastern (black) sides of Lake Bois d'Avaz. Values recorded from 16/03/2009 to 21/02/2011 were included. Values from emerged thermometers and from ice-periods (< 6°C) were excluded.

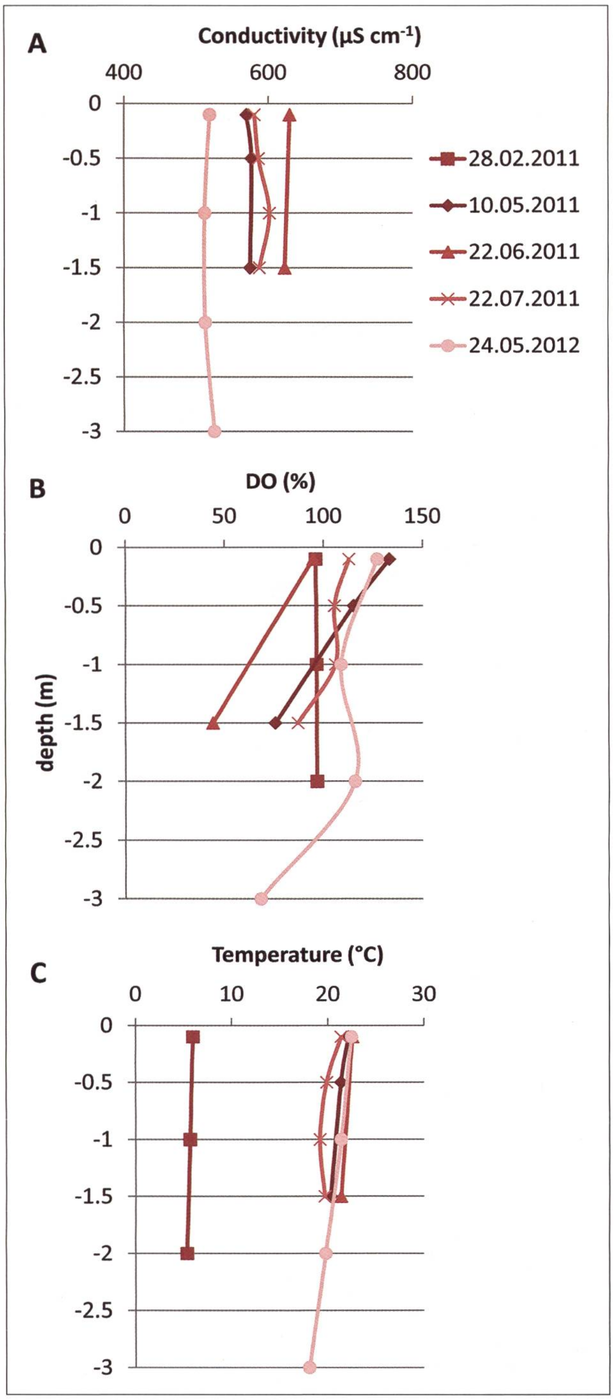

Fig. 5. Conductivity (A), Dissolved oxygen (B) and temperature (C) profiles in the Eastern part of the Lake Bois d'Avaz from February 2011 to May 2012. Maximum depth of records was different between dates because of water level fluctuations.

Composition and conservation value of the plant community

The total number of plants species recorded in Lake Bois d'Avaz was 75 (Fig. 6, Table 6), consisting of 12 species of Charophytes and 63 vascular plants. Among them, 23 are submerged species, 3 species have floating leaves, 10 are helophyte species growing on flooded soil and 39 other wetland species were present.

The presence of 61 vascular species recorded by the Conservatory of natural space of Haute-Savoie (personal communication) was confirmed. *Potamogeton gramineus* and *Ranunculus trichophyllus* was newly recorded by our study. According to the Red List of Haute-Savoie (Jordan 1986), *Potamogeton crispus*, *Potamogeton gramineus* and *N. marina* are considered as rare. *Potamogeton nodosus* and *Typha domingensis* are endangered. *Eleocharis acicularis* is "vulnerable". Only two species are protected by the French ministerial decree related to protected species list in Rhône-Alpes region (Art.1; J.O 29/01/1991; NOR: ENVN9061670A): *Najas marina* and *Utricularia minor*.

Considering the conservation value in the Geneva region (Lambelet-Haueter et al. 2006) or in Switzerland (Moser et al. 2002; Auderset Joye and Schwarzer 2012), more than 50 % (38 species out of 75 recorded) are threatened: 4 species are extinct, 9 species are critically endangered, 9 are endangered, 12 are vulnerable and 3 are near threatened. The twelve charophytes species represent one third of species inventoried in France and half of species recorded in Switzerland. According to the Swiss Red List (Auderset Joye and Schwarzer 2012), 10 out of 12 species are threatened: one is extinct, 2 species are critically endangered, 3 are endangered, 3 are vulnerable, and one is near threatened.

Discussion

The vegetation of lake Bois d'Avaz has an exceptional diversity, richness and conservation value. Almost all families and all growth forms of aquatic and wetland vegetation are represented by several species (Characeae, Potamogetonaceae, Haloragaceae, Cyperaceae, etc…). Among sites prospected in Switzerland, lake Bois d'Avaz is the unique station known to harbour such a high richness of aquatic plants, in particular charophytes (Fig. 7). The lake exhibits a richness much higher (45 aquatic plant species) than the richest one out of the 80 (32 species) studied in Switzerland with the same method (Oertli et al. 2002). The charophyte community of lake Bois d'Avaz is also the richest one among the 1400 sites prospected during the fieldwork for the Red List of Charophytes (Auderset Joye and Schwarzer 2012). The authors did not find charophyte community with similar richness even in largest Swiss lakes. The exceptional nature of the richness of the aquatic vegetation of lake Bois d'Avaz is also confirmed by several observational studies addressing biodiversity of ponds in some European regions. For example, Biggs et al. (2005) recorded a maximum macrophytes richness of 15 species through 15 years-

Table 5. Physical and chemical characteristics of the water of Lake Bois d'Avaz based on 11 dates. n = total number of analysis.

	units	mean	min	max	sd	n
Total Phosphorus	µg l^{-1}	20.95	2.00	167.00	29.97	43
NO_3^-	mg l^{-1}	1.25	0.00	7.34	1.81	35
NH_4^+	mg l^{-1}	0.16	0.00	0.45	0.15	24
SO_4^{2-}	mg l^{-1}	29.82	9.19	69.50	11.38	33
Cl^+	mg l^{-1}	18.52	9.20	26.80	6.03	24
Ca^{2+}	mg l^{-1}	94.01	22.73	152.73	29.44	33
Mg^{2+}	mg l^{-1}	6.89	3.36	10.14	1.51	33
Conductivity	µS cm^{-1}	529	204	758	138	58
Turbidity	NTU	5.5	1.1	15.2	3.2	58
Dissolve oxygen	%	85.2	9.2	221.0	36.3	51
Phytoplancton biomass	µg l^{-1}	131	0	771	174	24

survey of 200 ponds in Britain. Della Bella et al. (2005) investigated the diversity of aquatic plants in 20 permanent and temporary ponds in central Italy (charophytes were only determined to family level) and identified that richness of sites ranged between 1 and 26 species. More recently, a comparative research about biodiversity of aquatic habitats was made in five locations in Europe (Davies et al. 2008). Among the 101 studied ponds, the average macrophytes richness was below 16 species and the richest one sheltered 41 species. Arthaud et al. (2012) studied 60 shallow lakes (<1 ha to more than 100 ha) in the Dombes region of south-east France which are emptied out every 5-7 year for 1 year. The authors inventoried between 0 and 29 species with an average of 11.5 species. Potential centres of diversity of European Charophytes were identified in the Balkan peninsula (Blazencic et al. 2006b). The coexistence of more than 10 charophytes species per site was observed only in lakes which are 8000 to 12000 times larger than our study site (Skadar and Ohrid lakes shelter respectively 24 and 15 charophytes species).

Consequently, lake Bois d'Avaz seems to be the only known waterbody in Europe giving refuge to such à high number of aquatic plants species, in particular of charophytes. Its richness is exceptional especially since it belongs to the smallest ones (<1 ha).

If the species richness of the site is outstanding, its patrimonial value is also very noteworthy. Lake Bois d'Avaz is the only known locality in Haute-Savoie for *Nitella batrachosperma*. The nearest French site for this species is a floodplain lake along the Doubs River

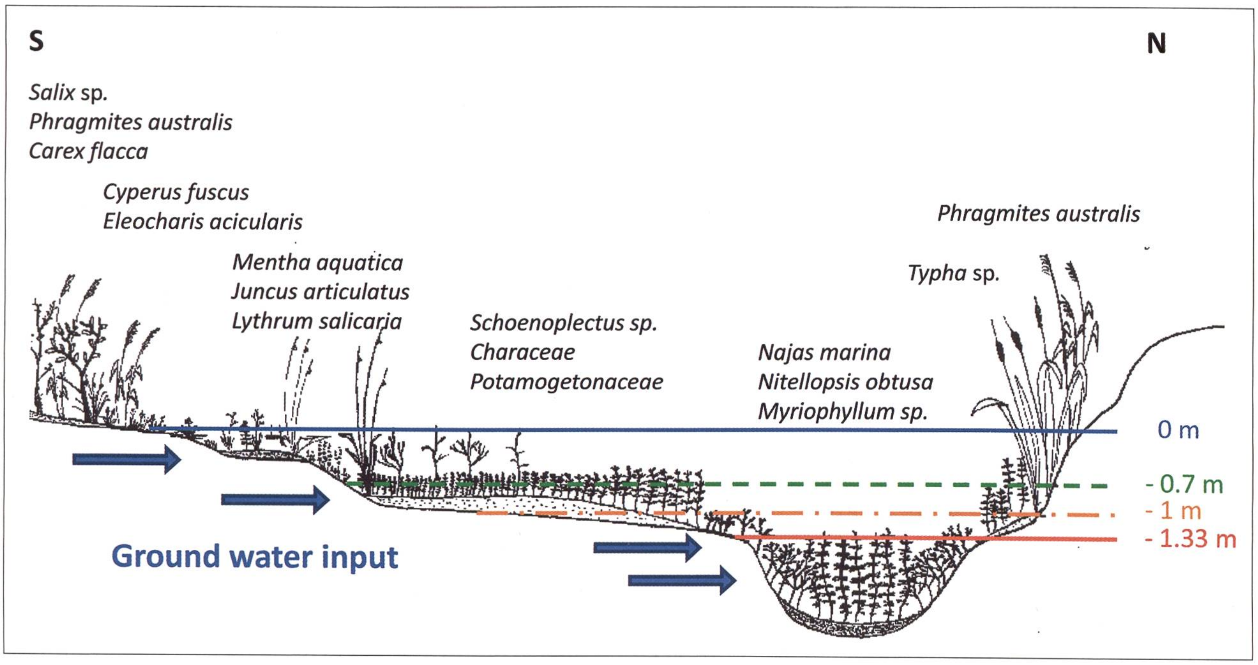

Fig. 6. Macrophytes species spatial distribution along the gradient of flooding in Lake Bois d'Avaz (North-South cross section). Blue and red horizontal lines indicate the maximum (0 m) and the minimum water level respectively (1.33 m). The green and orange dashed lines indicate water levels leading to the dessication of 50% (0.7 m) and 75% of the lake area respectively (1 m).

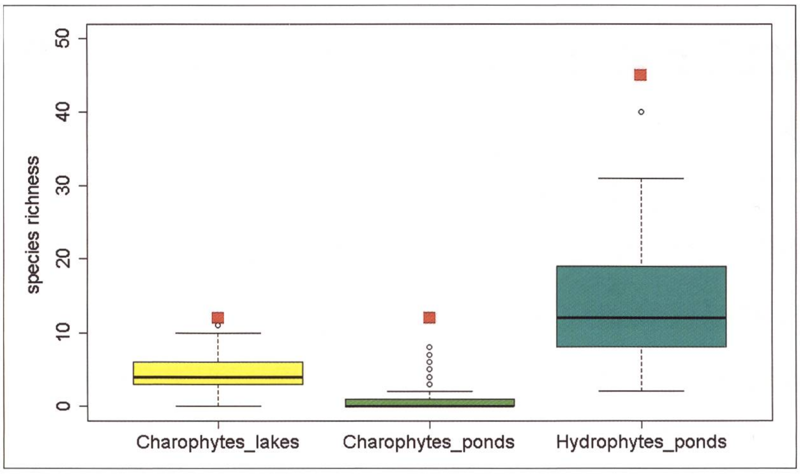

Fig. 7. Aquatic plant species richness of Lake Bois d'Avaz vs Swiss waterbodies. Charophytes richness of large lakes and ponds situated below an altitude of 500m are represented in yellow and green respectively (data from the Swiss Red List of Charophytes; Auderset Joye and Schwarzer 2012). Hydrophytes richness (including charophytes determined at species level) of small lakes and ponds situated in lowland areas is illustrated in blue (data from the study of Oertli et al. 2002). Corresponding richness recorded in Lake Bois d'Avaz are represented by red squares.

(Bornette and Arens 2002). In Switzerland, the species is considered as extinct (Auderset Joye et Schwarzer 2012; situation in 2010). *Chara polyacantha* and *Nitella tenuissima* are critically endangered according to the Swiss Red list (Auderset Joye et Schwarzer 2012). In the past, *C. polyacantha* was recorded in a small number of sites in France; its current distribution is unknown. *N. tenuissima* was recently described in some French localities (Lambert-Servien et al. 2006; Bailly and Schaefer 2010). It is considered as a rare species in Central and South Europe (Urbaniak et al. 2008). Out of the twelve charophytes species observed, 3 other charophyte species are "endangered" in the Swiss red list: *Chara strigosa, Tolypella glomerata* and *Chara intermedia*. *C. strigosa* is a relict species from glacial periods that is currently only found in alpine lakes and some waterbodies in Northern and Eastern Europe (Poland). *T. glomerata* is characteristic of temporary waterbodies of the Atlantic and Mediterranean coasts and is rare in eastern France (Corillion 1957). Among vascular plants, *T. domingensis* was discovered in Haute-Savoie recently in three sites (one of them was recently destroyed). Lake Bois d'Avaz marks the northern limit of the distribution of this southern and rare species for which it constitutes a site of major interest (only present in the eastern part of the lake). *Eleocharis acicularis* is "vulnerable" and is known in only three stations in Haute-Savoie.

Despite its anthropogenic origin and its relatively small size, lake Bois d'Avaz became naturally a biodiversity hotspot for aquatic plants. Moreover, more than 50% of the species are threatened according to the Red Lists of Geneva and Switzerland. Until now, no equivalent ecosystem is known in Europe.

We suppose that the water regime and the water quality of this waterbody could be an explanation for the coexistence of a maximum number of species. Indeed, two major ecological hypotheses addressing biodiversity patterns can be used, one dealing with disturbance-diversity relationship, the other dealing with energy-diversity relationship. First, according to the intermediate disturbance hypothesis ("IDH") (e.g. Grime 1977; Connell 1979), maximum species richness should occur in habitats submitted to an intermediate level of disturbance. The second hypothesis relates that an intermediate level of productivity provides the highest species richness (Rosenzweig 1995; Dodson et al. 2000; Mittelbach et al. 2001). Our results showed that those two intermediate levels in environmental gradient are met in lake Bois d'Avaz that is thus expected to harbour a maximum number of species.

Ecological disturbances such as flooding or drought events are known to have a strong impact on aquatic organisms. The wet/dry cycles are key disturbance events that govern diversity patterns of shallow waterbodies (Rorslett 1991; Coops et al. 2003). The hydrological gradient, from permanently dry to permanently wet, drives the bathymetric zonation of species. The hump-shaped pattern of species richness response to flood or drought disturbances was demonstrated by several regional studies on regulated lakes in Minnesota (Wilcox and Meeker 1991), on Australian wetlands (Casanova and Brock 1999; Barrett et al. 2010), on New Zealand lakes (Riis and Hawes 2002), on lakes connected to a Brazilian river (Sousa et al. 2011), on floodplain lakes in the Netherlands (Van Geest et al. 2005) and on cut-off channels of French rivers (Bornette et al. 2001). More recently, Arthaud and al (2012) considered the macrophyte richness of shallow lakes in the south-east of France in relation with the succession stage (short term vs. long term colonization after the last disturbance), the lake productivity and the connectivity to similar nearby habitats. In lakes with intermediate productivity, they found that richness responded positively and immediately after a disturbance event and then, decreased with succession. The hump-shaped relationship between macrophyte richness and the productivity-disturbance gradient

Table 6. List of plant species, their threat and protection status, recorded in the Lake Bois d'Avaz.
***GE**: plants with threat status according to the Geneva Red List (Lambelet-Haueter et al. 2006); **CH**: plants with threat status according to the Swiss Red Lists (Moser et al. 2002; Auderset Joye and Schwarzer, 2012); **74**: plants with threat status according to Haute-Savoie Red List (Jordan 1986); **RP**: plants protected in Rhône-Alpes region by French ministerial decree (Art.1; J.O 29/01/1991; NOR:ENVN9061670A). **RE**: Extinct in the Region; **CR**: Critically Threatened; **EN**: Endangered; **VU**: Vulnerable; **NT**: Near Threatened; **LC**: Least Concerned; **NE**: Not Evaluated; **R**: Rare.*
*Data source: Asters (Conservatory of natural spaces of Haute-Savoie) and *Rey-Boissezon & Auderset Joye (2007-2012; LEBA-UNIGE).*

	GE	CH	74	RP
Aquatic plants with submerged organs				
***Characeae**				
Chara aspera Deth. ex Willd.		VU		
Chara contraria A. Braun		LC		
Chara globularis Thuillier		LC		
Chara hispida L.		VU		
Chara intermedia A. Braun		EN		
Chara polyacantha A. Braun		CR		
Chara strigosa A. Braun		EN		
Chara vulgaris L.		VU		
Nitella batrachoperma (Richenbach) A. Br.		RE		
Nitella tenuissima (Desv.) Kütz.		CR		
Nitellopsis obtusa J. Groves		NT		
Tolypella glomerata (Desv. in Lois.) Leohnardi		EN		
Vascular plants				
Myriophyllum spicatum L.	LC	NT		
Myriophyllum verticillatum L.	RE	NT		
Najas marina L.	-	VU	R	1
Potamogeton berchtoldii Fieber	LC	NT		
Potamogeton crispus L.	EN	LC	R	
Potamogeton pectinatus aggr.	LC	LC		
Potamogeton pusillus aggr.	LC	VU		
**Ranunculus trichophyllus* Chaix	CR	NT		
Utricularia australis R. Br.	LC	NT		
Utricularia minor L.	RE	VU		1
Zannichellia palustris L.	NT	VU		
Aquatic plants with floating leaves on the water surface				
**Potamogeton gramineus* L.	RE	EN	R	
Potamogeton nodosus Poir.	LC	VU	EN	
Potamogeton natans L.	EN	LC		
Aquatic plants growing on flooded soils				
Alisma lanceolatum With.	VU	VU		
Alisma plantago-aquatica L.	VU	LC		
Carex elata All.	VU	LC		
Cladium mariscus (L.) Pohl	CR	NT		
Eleocharis acicularis (L.) Roem. & Schult.	CR	VU	VU	
Nasturtium officinale R. Br.	VU	LC		
Schoenoplectus lacustris (L.) Palla	EN	LC		
Typha angustifolia L.	NE	NT		
Typha domingensis (Pers.) Steud.			EN	
Veronica anagallis-aquatica L.	VU	LC		

	GE	CH	74	RP
Wetland plants				
Agrostis stolonifera L.	LC	LC		
Bidens tripartita L. s.str.	VU	NT		
Calamagrostis epigejos (L.) Roth	LC	LC		
Carex acutiformis Ehrh.	LC	LC		
Carex alba Scop.	VU	LC		
Carex flacca Schreb.	LC	LC		
Carex hirta L.	LC	LC		
Carex viridula Michx.	CR	LC		
Centaurium pulchellum (Sw.) Druce	CR	VU		
Cyperus fuscus L.	EN	VU		
Equisetum palustre L.	EN	LC		
Iris pseudacorus L.	LC	LC		
Juncus alpinoarticulatus Chaix	-	LC		
Juncus articulatus L.	LC	LC		
Juncus bufonius L.	LC	LC		
Juncus conglomeratus L.	LC	LC		
Juncus inflexus L.	LC	LC		
Juncus subnodulosus Schrank	CR	LC		
Lycopus europaeus L. s.str.	LC	LC		
Lysimachia nummularia L.	LC	LC		
Lysimachia vulgaris L.	LC	LC		
Lythrum salicaria L.	LC	LC		
Mentha aquatica L.	NT	LC		
Panicum capillare L.	LC	LC		
Phragmites australis (Cav.) Steud.	LC	LC		
Polygonum persicaria L.	LC	LC		
Populus tremula L.	LC	LC		
Pulicaria dysenterica (L.) Bernh.	LC	LC		
Rorippa palustris (L.) Besser	VU	LC		
Salix alba L.	LC	LC		
Salix caprea L.	LC	LC		
Salix daphnoides Vill.	RE	LC		
Salix elaeagnos Scop.	LC	LC		
Salix myrsinifolia Salisb.	CR	LC		
Salix triandra L.	EN	LC		
Schoenoplectus tabernaemontani (C. C. Gmel.) Palla	LC	VU		
Scirpus sylvaticus L.	LC	LC		
Solanum dulcamara L.	LC	LC		
Trifolium fragiferum L.	LC	VU		

may explain the outstanding species richness of our study site. Indeed, the depth gradient of lake Bois d'Avaz and the "semi-permanent" water regime (seasonal drawdown and partial drought not occurring every year) create a panel of inundation conditions of diverse frequency and duration which could explain the spatial succession of vegetation observed in the lake (Table 6, Fig. 6). Temporal succession along the year may also contribute to the high macrophyte diversity of our study site. The growth season lasts around 7 months, from March to the end of October, allowing the expressions of a maximum of phenology patterns: spring (e.g. *Tolypella glomerata*), summer (e.g *Chara contraria*, *Potamogeton pectinatus*) and autumn species (eg. *Nitella batrachosperma*).

The ***quality of the water*** probably also influences the species richness and distribution in the site. At a regional scale, the relationship between productivity and aquatic plant species richness often produced a hump-shaped curve (e.g. Rosenzweig 1995). The intermediate level of productivity (oligo-mesotrophic) measured in lake Bois d'Avaz could contribute to the high species richness we observed.

The connection to ***groundwater*** is known to favour the installation of charophytes (Corillion 1975; Bornette and Arens 2002). The high conductivity, and particularly the calcium concentration measured during our study, indicated that lake Bois d'Avaz received groundwater influx. This resurgence of groundwater noticed on the South shores of the lake influenced the western and eastern parts differently. The thermal signature recorded in the eastern part (Table 4) suggested that the surface water in this area received more groundwater than the western part. As groundwater fluxes also govern the nutrients and the mineralization of surface water, we may assume that the dissimilar physico-chemical conditions between the western and the eastern parts of the lake contributed to increase the diversity of local abiotic conditions (Sophocleous 2002). We found some species predominantly in the eastern part, where the groundwater was prominent. This may indicate the influence of groundwater input on the distribution of these species, which belong to the more threatened ones in Switzerland and Haute-Savoie: *Myriophyllum verticillatum, Potamogeton nodosus, Typha domingensis, Utricularia minor* and three charophytes *Chara aspera, Nitella batrachosperma and Nitella tenuissima*.

Lake Bois d'Avaz is a biodiversity hotspot for aquatic plants, in particular for charophytes, apparently of European importance. Several coexistence mechanisms occurred in the lake Bois d'Avaz. Intermediate conditions of productivity crossed to intermediate conditions of disturbance allow the growth of a maximum number of species. Spatial and temporal successions of species are also probably favoured by the connection to groundwater and the long-growth season.
Lake Bois d'Avaz represents an interesting conservation and restoration target. It is an example of man-made pond that was successfully and naturally colonized by a very rich aquatic plant community with an important conservation value. In most floodplains, natural fluvial dynamic driving rejunevation of waterbodies is not possible anymore. In this context, lake Bois d'Avaz constitutes an evidence that artificial floodplain waterbodies can become surrogates for natural ones. This waterbody was created by gravel extraction in the Arve floodplain. An important characteristic that distinguish this former gravel pit from many others may be the presence of large shallow areas with fine sediment and the shore complexity. Indeed it was partially filled by silt originating from another exploited gravel pit. This heterogeneity of abiotic conditions, which favoured high species diversity, is generally not possible in "classic" gravel pits shaped like swimming pool, having steep slopes, high mean depth and homogeneous coarse substrate. The occasional and partial autumnal drought is also a distinctive feature of the lake Bois d'Avaz. This dynamic is possible thanks to the connection to a fluctuating hillslope aquifer. Another major characteristic of the lake Bois d'Avaz is the absence of surface connection with the main river, preventing the lake to be rapidly filled by fluvial sedimentary deposits. This would increase the speed of terrestrialization process and thus decrease the waterbody lifespan.
The water quality and the semi-permanent nature of the lake Bois d'Avaz need to be preserved to insure the conservation of its outstanding macrophyte community. That implies that land-use policy manages the surroundings and the watershed to prevent long-term hydrological perturbations (level of aquifer table) and qualitative degradation (pollution by herbicides and fertilizers used in agricultural activities). As a European biodiversity hotspot for aquatic plants and for charophytes, Lake Bois d'Avaz would deserve a special protection status.

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