

# The late glacial–Holocene transition as inferred from ostracod and pollen records in the Lago Piccolo di Avigliana (Northern Italy)

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## ABSTRACT

Ostracod and pollen records of Lago Piccolo di Avigliana were used for the reconstruction of aquatic and terrestrial palaeoenvironments between 17 and 10 kyr cal BP.

A combination of multivariate ordination techniques (PCA and RDA) made it possible to describe ostracod and pollen biostratigraphies and to evaluate whether changes in the aquatic ecosystem were associated with those in the terrestrial environments. Samples and taxa in the ordination plots were grouped into three clusters: a first cluster representing herbaceous and shrub pollen taxa (*Juniperus*, Chenopodiaceae, Gramineae, *Artemisia*, and Rubiaceae) associated with ostracods typical of oligotrophic and well oxygenated aquatic environments (*Cytherissa lacustris*), a second cluster containing pollen taxa representing boreal forests (*Betula*, *Pinus sylvestris*, and *Pinus cembra*) associated with ostracod taxa from shallow oligo-mesotrophic aquatic environments (*Candona candida*, *Darwinula stevensoni*), and a third cluster including pollen of thermophilous trees and shrubs (*Corylus*, *Quercus ilex*, *Fraxinus*, *Quercus robur*-type, and *Ulmus*) connected to ostracods representing warm mesotrophic aquatic conditions with aquatic vegetation (*Cypria ophthalmica*, *Metacypria cordata*). Hypothesis testing with constrained Monte Carlo permutations rejected the null hypothesis that no relationship exists between ostracod and pollen datasets at 2% level of significance. As a whole, changes in temperature and precipitation–evaporation balance that influenced terrestrial vegetation were represented by changes in trophic level and water level in the aquatic environment.

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## 1. Introduction

The autoecology of animal and plant species has proven to be a useful tool to estimate trends and changes in past environmental conditions. In the case of non-marine ostracods (Crustacea), an increasing number of studies provide quantitative estimates of the tolerance and optima to environmental factors (e.g. temperature, salinity, and ion concentrations) (Nüchterlein, 1969; Hiller, 1972; Curry, 1999; Mezquita et al., 1999). These estimates are the basis for palaeoecological reconstructions of water salinity (Anadón et al., 1986), trophic state of lakes (Scharf, 1998; Meisch, 2000), meromixis (Löffler, 1997), and lake–water level changes (Colman et al., 1994; Mourguiart and Carbonel, 1994).

Environmental data are in general abundant, complex, redundant, and rich in internal relationships. Their subjective interpretation may overlook intrinsic aspects that are not readily evident (Jongman et al., 1987). Nevertheless, the development of multivariate-analysis techniques makes it possible to handle a large amount of quantitative data in order to explore the underlying patterns that drive environmental

factors and changes in species composition (ter Braak and Prentice, 1988). Modern ordination techniques construct theoretical variables (explanatory variables), which maximize the variance of the species data assuming either linear or unimodal responses.

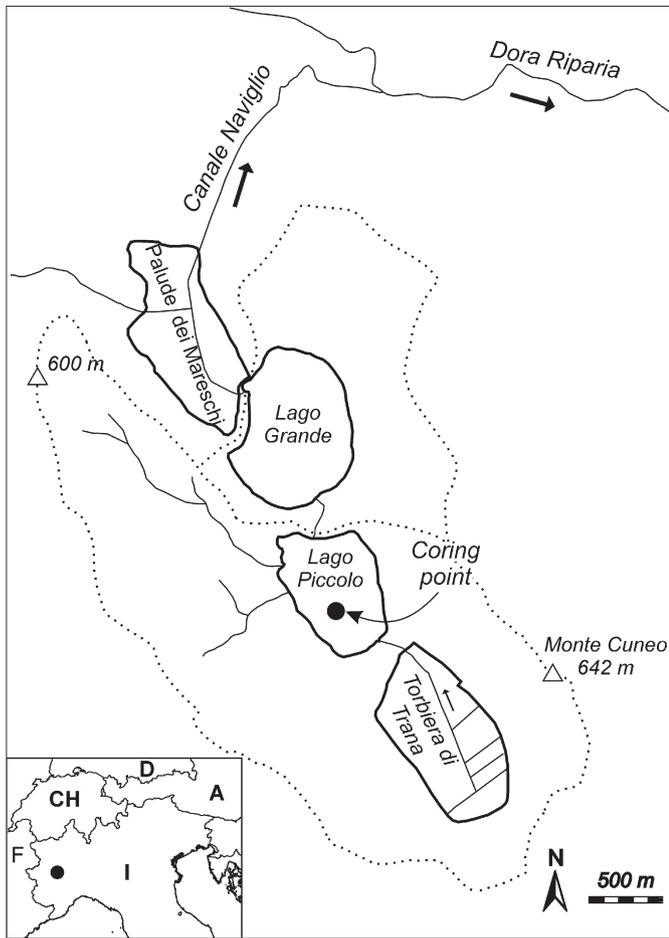
In indirect gradient analysis the theoretical variables are computed considering only the abundance of the species (response variables). Comparisons with the observed environmental variables for the interpretation of the theoretical variables are made separately. On the other hand, in the case of direct gradient analysis the theoretical variables are a combination of both response and environmental variables.

The main output of ordination techniques is a two dimensional diagram representing sites (or depths). The axes of the diagram represent the theoretical variables that better explain the dispersion of species scores. Points that are close in the diagram stand for sites (depths) with similar species composition.

The present study aims to establish whether changes in the aquatic environment estimated on the basis of ostracod biostratigraphy matched changes in the terrestrial environment as inferred from pollen assemblages. The late glacial–Holocene transition is particularly appropriate for this purpose for it represents the highest amplitude of climatic and environmental change since the end of

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**Fig. 1.** Location of Lago Piccolo di Avigliana. Continuous line: surface hydrology; dotted line: limits of hydrological catchment.

the last glacial maximum (Lowe, 2001; Lotter, 2004) making it possible to evaluate changes of considerable amplitude in the terrestrial and in the aquatic ecosystems.

## 2. Study site

Lago Piccolo di Avigliana (45°03'N, 07°23'E) lies in the southern foothills of the Alps in northwestern Italy in a north–south oriented lateral valley of the Val di Susa (Fig. 1). The ca. 0.6 km<sup>2</sup> lake, located at

350 m a.s.l., is surrounded in its catchment (8.1 km<sup>2</sup>) by hilltops lower than ~1000 m a.s.l., which provide a sheltered position from southern winds. Lake mean and maximum depths are 7.7 and 12 m respectively. The mean lake-water volume is  $4.5 \times 10^6$  m<sup>3</sup> and its residence time is 0.9 yr (Gaggino and Cappelletti, 1984).

The lake is dammed by a last glacial maximum (LGM)-moraine system deposited by a lateral tongue of the Val di Susa valley glacier (Petrucci et al., 1970). During the Younger Dryas glaciers were confined to small cirques located exclusively outside the hydrological catchment of the lake (Carraro et al., 2002).

Mean annual temperature at Avigliana is 13.0 °C, and mean temperatures of the coldest and warmest months are 2.2 °C (January) and 23.9 °C (July), respectively (Biancotti et al., 1998). Mean annual precipitation is 880 mm, with rainfall distributed mainly in autumn and in spring (Biancotti et al., 1998), following the activity of the Genoa Low.

## 3. Materials and methods

The lake sediments were cored with a modified piston corer (Merk and Streif, 1970) from a floating platform at the center of the lake (12 m water depth) in autumn 2001. Meter-long drives were transferred into plastic half-tubes, wrapped in plastic foil, transported to the laboratory, stored at 4 °C in a dark room, and then sub-sampled.

The chronology is given by 10 radiocarbon dates on terrestrial plant macrofossils and by the Laacher See Tephra (LST), which was extracted and geochemically fingerprinted by Blockley et al. (2005). The age–depth model was calculated with a non-parametric locally weighted least squares regression (LOWESS; span=0.3; order=1) (Finsinger et al., 2006). For the LST an age of 12,900 cal yrs BP was adopted, following Baales et al. (2002). This age scarcely differs from the 12,836 GRIP years age obtained by Schwander et al. (2000) for the Gerzensee and Leysin records. Sediment changes in the analysed core are described in Finsinger (2004).

For the ostracod analysis, 10–20 g of wet sediment was sieved through a 200 µm mesh. All ostracod remains were picked out and counted under a binocular microscope (magnification 20×–100×) (Van Morkhoven, 1962). Sample volume was determined by water displacement.

In order to estimate maximum environmental variability, ostracod analysis was carried out on selected samples with respect to major changes in lithology, loss-on-ignition, and pollen biostratigraphy (Finsinger, 2004).

No chemical treatment was used to separate the valves from the sediment (Belis et al., 1999). Taxonomic determinations were carried out according to Meisch (2000) and were documented by SEM photographs (not shown). The absolute abundance of valves (adults and juveniles) is expressed as valves per cubic centimetre of sediment.

Samples for pollen analysis (1 cm<sup>3</sup>) were prepared physically (decanting, sieving at 500 µm) and chemically (HCl, KOH, HF, HCl,

**Table 1**

List of ostracod and pollen taxa used in the multivariate analyses

Ostracod taxa	Code	Pollen taxa	Code
<i>Candona candida</i> (O.F. Müller, 1776)	C CAN	<i>Alnus glutinosa</i>	ALN GLT
Candoninae sp.	CAND	<i>Betula</i>	BETULA
juv. <i>Candoninae</i>	JUV CAN	<i>Corylus avellana</i>	CORYL AV
<i>Cyclocypris</i> sp.	CYC SP	<i>Fraxinus excelsior</i>	FRAX EXC.
<i>Cypria ophthalma</i> (Jurine, 1820)	CYP	<i>Juniperus</i>	JUNIPER.
juv. <i>Cypria</i>	JUV CYP	<i>Larix</i> spp.	LARIX
<i>Potamocypris</i> sp.	POT	<i>Pinus cembra</i>	PIN. CEMB.
<i>Herpetocypris</i> sp.	HER SP	<i>Pinus sylvestris</i> type	PIN DIPL.
<i>Cytherissa lacustris</i> (Sars, 1863)	CYT	<i>Quercus pubescens</i>	QUER. PUB.
juv. <i>Cytherissa lacustris</i>	JUV CYT	<i>Quercus ilex</i>	QUER. ILX.
<i>Metacypris cordata</i> Brady & Robertson, 1870	MTC	<i>Ulmus</i> spp.	ULMUS
Limnocytherinae sp.	LYM	<i>Artemisia</i>	ARTEMIS
<i>Darwinula stevensoni</i> (Brady & Robertson, 1870)	DAR	Chenopodiaceae type	CHENOP. T.
		Poaceae	GRAMINE.
		Rubiaceae	RUBIACE
		<i>Rumex acetosa/acetosella</i> type	RUM. ACET.
		<i>Pinus stomata</i>	PINUS ST.

**Table 2**  
Summary of ordination analyses on ostracod and pollen datasets

Ordination technique	Dataset	Gradient analysis	Response model	1st axis explained variance (%)	2nd axis explained variance (%)	Taxa	Samples	Environmental variables
CA	Ostracod	Indirect	Unimodal	46	15	13	21	
PCA	Ostracod	Indirect	Linear	58	23	13	21	
DCA	Terr. pollen	Indirect	Unimodal	45	15	17	21	
PCA	Terr. pollen	Indirect	Linear	56	33	17	21	
CCA	Ostr. and terr. pollen	Direct	Unimodal	40	9	13	21	5
RDA	Ostr. and terr. pollen	Direct	Linear	48	10	13	21	5
CCA	Ostr. and aq. pollen	Direct	Unimodal	41	3	13	21	4
RDA	Ostr. and aq. Pollen	Direct	Linear	32	6	13	21	4

Acetolysis, KOH) and were embedded in glycerine following Lotter (1988). Identification of pollen grains was conducted at 400× with the aid of identification keys (Moore and Webb, 1978; Punt et al., 1976–1996) and photographic collections (Reille, 1992). Conifer stomata were identified following Trautmann (1953). At least 400 pollen grains of terrestrial plants were counted. Percentages were calculated upon the terrestrial pollen sum including tree, shrub, herb, and fern pollen. Pollen concentration was calculated by means of added *Lycopodium* spores (Batch number 938934) following Stockmarr (1971).

### 3.1. Ordination techniques

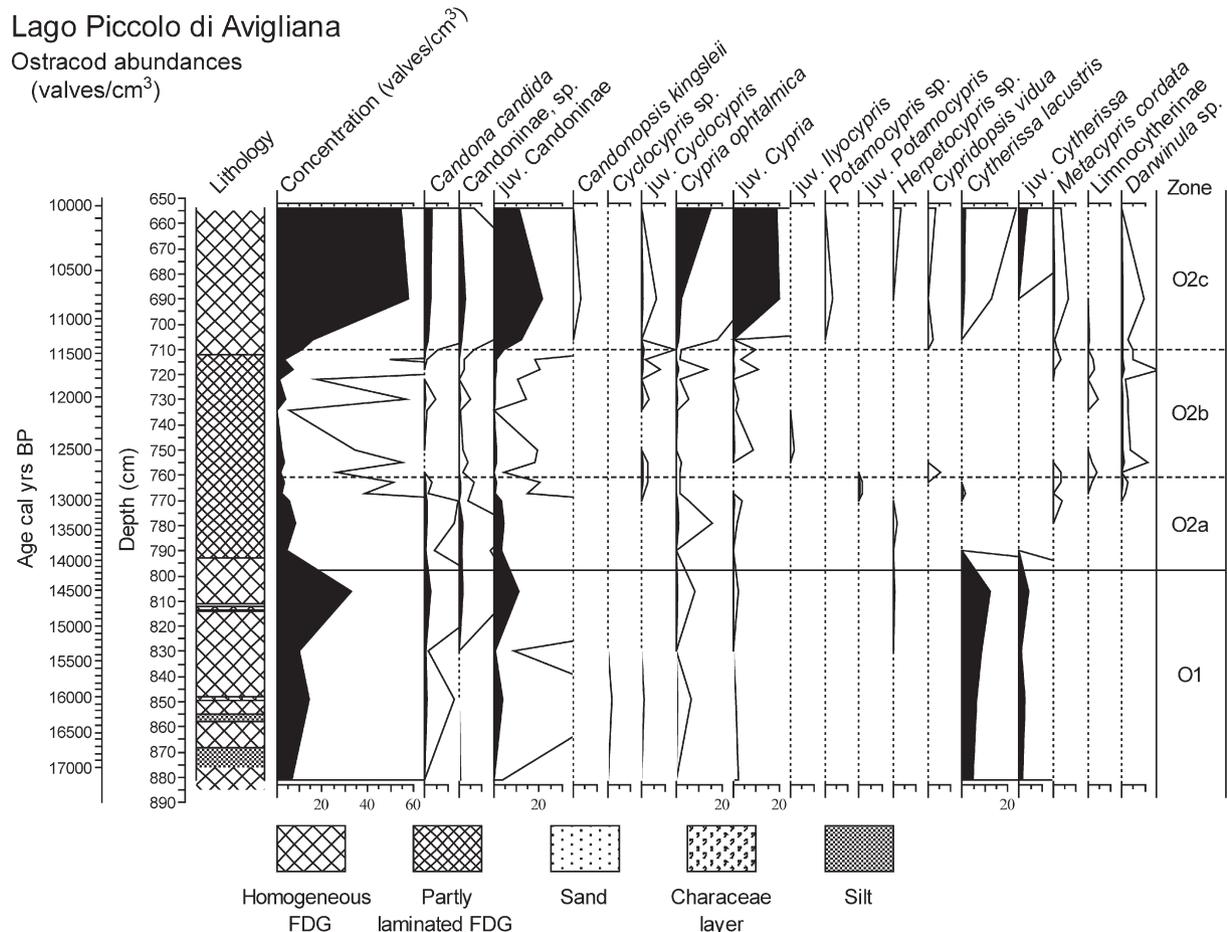
In order to compare the two records, only samples between 881 and 654 cm core depth containing both ostracod and pollen data were included in the numerical analyses ( $n=21$ ). Ordination analyses and

Monte Carlo tests were performed with the program CANOCO version 4.52 (ter Braak and Šmilauer, 2003).

### 3.2. Indirect gradient analysis

The ostracod dataset included 13 selected taxa. Rare species with low frequency (present in less than two samples) were excluded (Table 1). For the analysis of the pollen record, a reduced dataset with 17 selected taxa was used. These 17 pollen taxa were chosen because their abundances show the highest variability within the studied time window, and were, therefore, expected to provide more information about environmental changes.

The length of the gradient was estimated by means of a preliminary DCA. These datasets were then analysed separately by Correspondence Analysis (CA) and a Principal Component Analysis (PCA). In both cases PCA



**Fig. 2.** Ostracod stratigraphy for Lago Piccolo di Avigliana. Black shaded areas: number of Ostracod valves/cm<sup>3</sup>; continuous line: exaggeration ×15; horizontal lines: Ostracod assemblage zone limits. FDG = fine detritus gyttia.

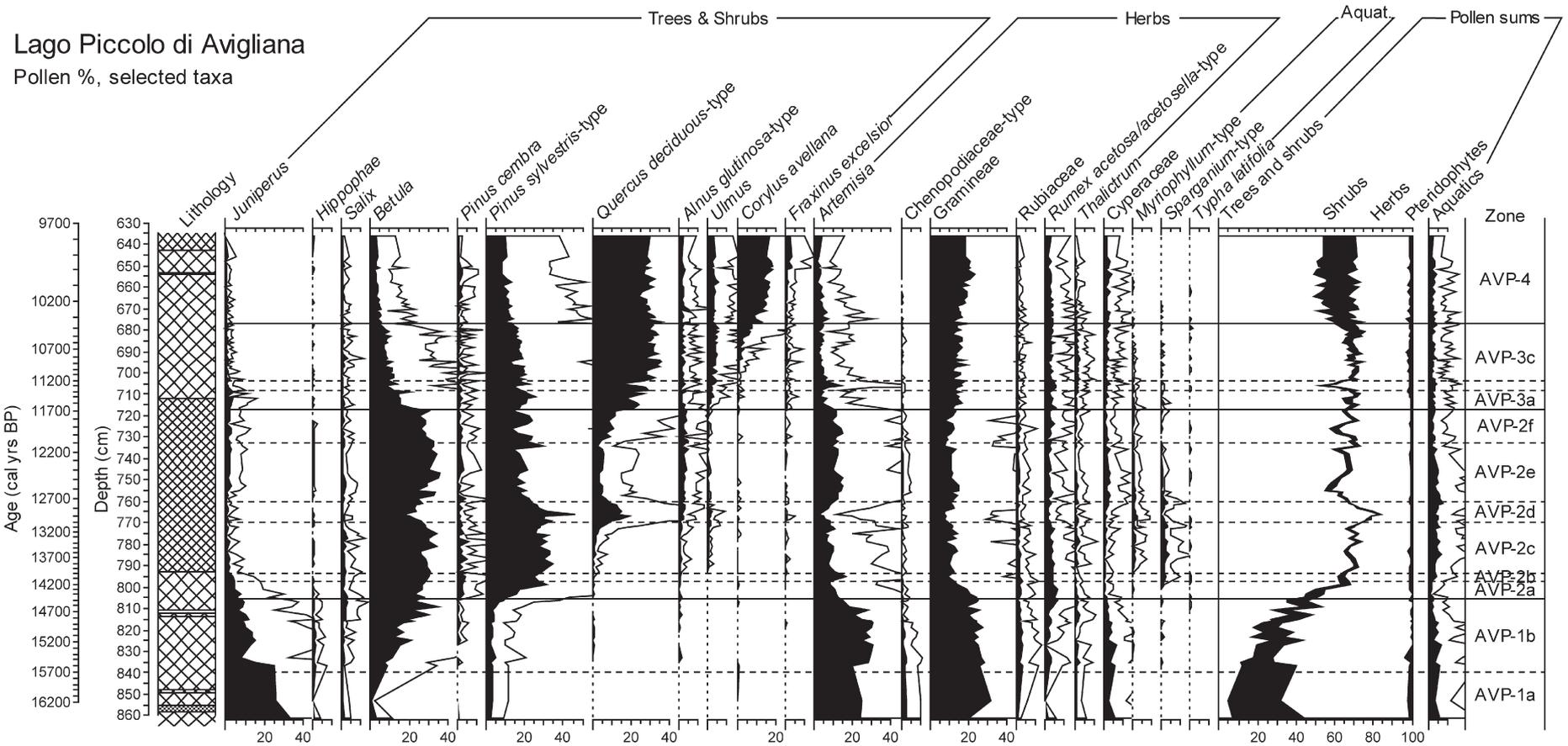


Fig. 3. Late-glacial pollen stratigraphy for Lago Piccolo di Avigliana (selected pollen taxa only, taxa ordered according to groups). Black shaded areas: pollen %; continuous line: exaggeration  $\times 15$ ; horizontal lines: pollen assemblage zone limits. For lithology legend see Fig. 2.

(linear response model) performed better, in terms of explained variance, than CA and DCA (unimodal response model) (Table 2). Sample and species scores were reported in covariance biplots (Corsten and Gabriel, 1976).

### 3.3. Direct gradient analysis

In order to distinguish variations in the aquatic environment from external factors, terrestrial and aquatic pollen were treated separately. Canonical analyses were carried out with ostracods as response variables and pollen as environmental variables, an approach similar to the one used by Anderson et al. (1996) to estimate the influence of agricultural activity on diatom assemblages.

In direct gradient analyses, the exclusion of redundant environmental variables is strongly advisable in order to allow as tight as possible restrictions on response variables (Jongman et al., 1987). Hence, in order to identify relationships among pollen taxa and then to exclude redundant variables, the reduced pollen dataset was pre-processed with a two-step procedure. First a Hierarchical Cluster Analysis (HCA) was computed with a cutoff level based on the correlation coefficient distance ( $r=0.4$ ), to identify clusters of pollen taxa. Then the number of pollen taxa was reduced with a forward selection procedure, and significance of each pollen taxon was tested by Monte Carlo permutation tests (Manly, 1992). In this way a reduced number of pollen taxa was obtained, each one representing, in a statistical sense, the cluster to which it belonged. One representative of each cluster chosen by forward selection was included in the canonical analysis.

As was the case for the indirect gradient analysis (Table 2), the linear response model (redundancy analysis; RDA), performed better than the unimodal model (Canonical correspondence analysis; CCA).

### 3.4. Zonation

In order to apply quantitative criteria, zonation of the ostracod and pollen diagrams was also carried out by optimal sum of squares partition (Birks and Gordon, 1985). The significance of zones was thereafter assessed against a model of random partitioning of the stratigraphical sequence using the simple broken-stick model, following Bennett (1996). In addition to these boundaries, zones were also visually defined by the operator on the basis of major changes in species composition and abundance. In the ostracod and pollen diagrams, statistically significant zones are shown as continuous lines, while other boundaries are shown as dashed lines. Local pollen assemblage zones should not be considered as chronozones (Mangerud et al., 1992) but as biozones, following Ammann et al. (2000).

## 4. Results

### 4.1. Ostracod and pollen biostratigraphies

The first ostracod biozone (O1; >14,200 cal yr BP) was dominated by *Cytherissa lacustris* and *Candona candida* (Fig. 2). A gradual afforestation is inferred from the increase of *Betula* pollen starting

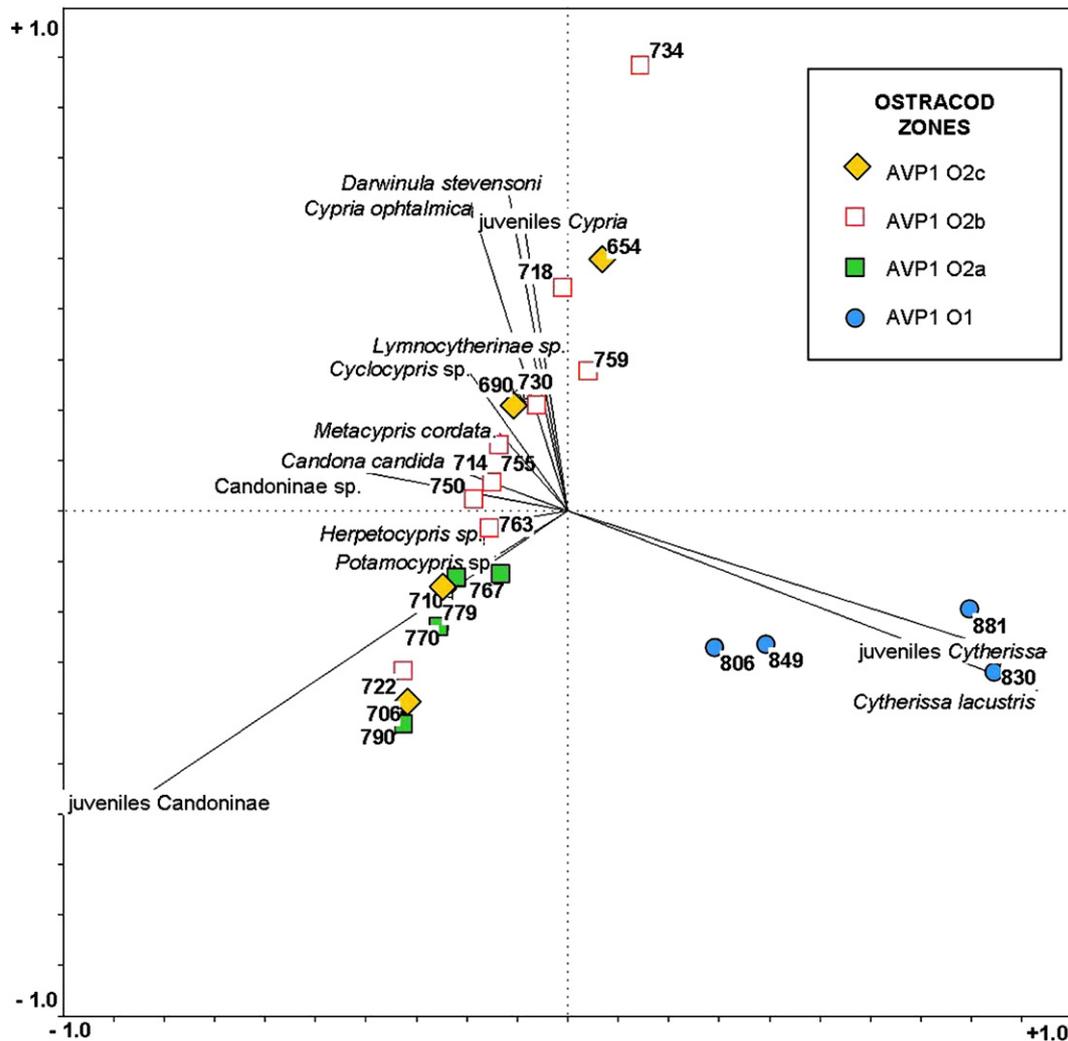


Fig. 4. Ordination diagram of the PCA with the late glacial and early Holocene ostracod dataset ( $n$ . taxa=13;  $n$ . =21;  $\lambda_1$  58%,  $\lambda_2$  23%). Samples are labelled according to their core depth (cm).

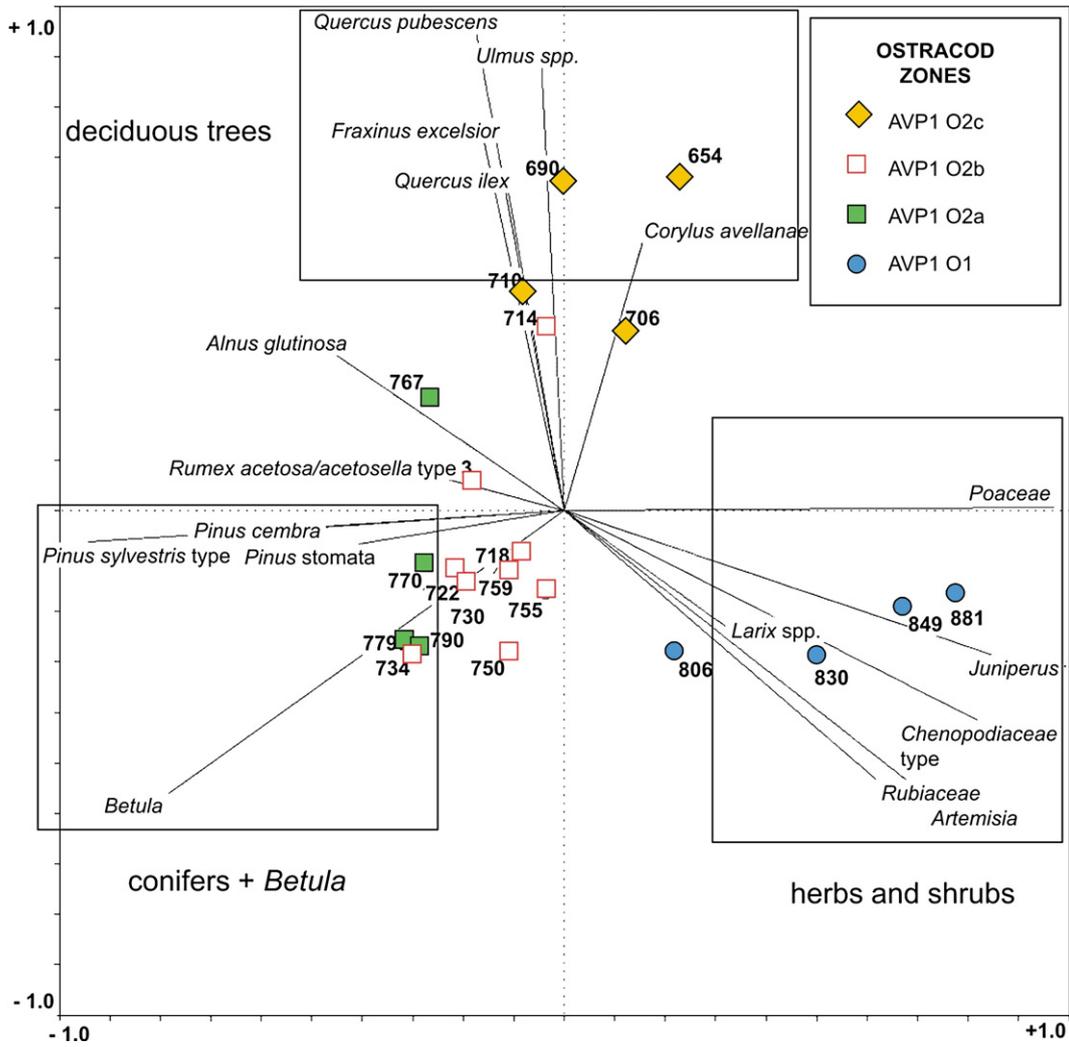


Fig. 5. Ordination diagram of the PCA with the reduced late glacial and early Holocene pollen dataset ( $n. taxa = 17, n = 21; \lambda_1 56\%, \lambda_2 33\%$ ). Samples are labelled according to their core depth (cm). Sets of similar species are bounded by continuous lines.

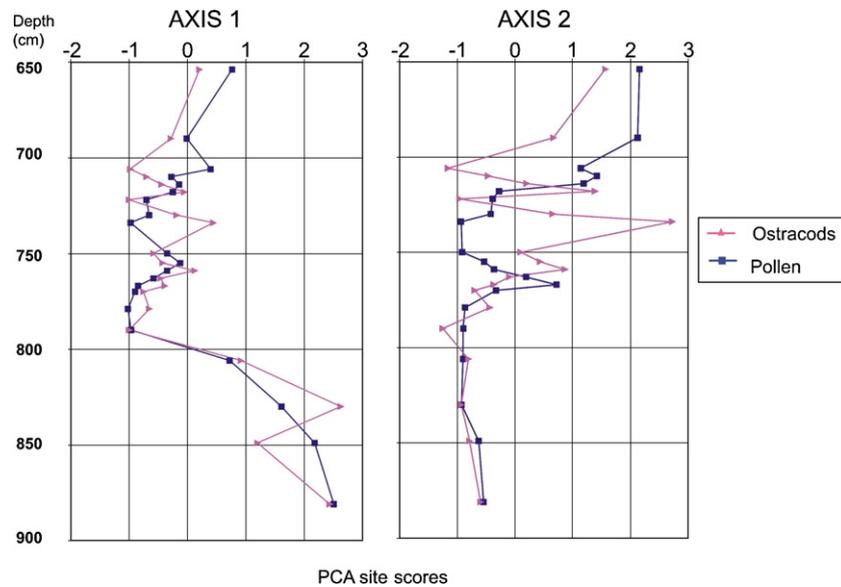


Fig. 6. Site scores on the first and second PCA axes on both ostracod and pollen datasets ( $n = 21$ ) reported in stratigraphical order.

prior to 14,200 cal yr BP, while a more rapid increase of *Pinus* pollen (onset zone AVP-2a) probably indicates a more rapid population expansion (Fig. 3). At ~14,500 cal yr BP a peak in the total abundance of ostracods occurred without changes in species composition and in sediment lithology.

At the beginning of subzone O2a (14,200–12,750 yr BP) the total concentration of valves decreased, numbers of *C. lacustris* were strongly reduced, and *C. candida* and *Cypria ophthalmica* dominated the ostracod assemblage. The continuous presence of low percentages of *Quercus* pollen suggests the presence of the tree at low population densities in the catchment (subzones AVP-2a to AVP-2c). Subsequently, an expansion of thermophilous trees (*Quercus* and *Ulmus*) occurred (subzone AVP-2d), while *Pinus* remained stable at high levels.

A further strong decrease of both total valve concentration and ostracod species abundance occurred between 12,750 and 11,450 cal yr BP (subzone O2b – Younger Dryas). *Darwinula stvensoni* and *Metcypris cordata* occurred especially at the beginning and at the end of this subzone. During the Younger Dryas, pollen of arboreal taxa decreased while shrub and herbaceous taxa (i.e. *Juniperus*, *Artemisia* and *Chenopodiaceae*) increased (subzone AVP-2e and AVP-2f).

At the onset of the Holocene (subzone O2c; 11,450–10,100 cal yr BP) total valve abundance increased. After an abrupt increase *C. candida* was progressively exceeded by *C. ophthalmica*. At the top of the sequence, *C. lacustris* presented an increasing trend, whereas *D. stvensoni* decreased. *Quercus* and *Ulmus* were the first thermophilous trees to re-expand at the onset of the Holocene (subzone AVP-3a), and they were followed by *Corylus* (subzone AVP-3c).

In general, preservation of ostracod valves is good with no sign of valve decalcification. Therefore it can be excluded that changes in the total abundance of ostracods (Fig. 2) were influenced by poor valve preservation.

In order to evaluate whether the pool of ostracods in the sediments (thanatocoenosis *sensu* Boomer et al., 2003) represents an autochthonous living biocoenosis or is the result of post-mortem transport, an analysis of the structure of the population was carried out on *C. candida*, the most abundant species throughout the sequence. The ratio adult to juvenile valves (stages A-1 to A-3) is in general relatively constant (mean  $0.3 \pm 0.1$ ) and close to 0.3, the expected value for autochthonous thanatocoenosis (Boomer et al., 2003; Fig. 2). However, in the middle of zone O2b, where the total valve abundance was low, post-mortem transport of the valves cannot be excluded.

#### 4.2. Numerical analyses

The biplot in Fig. 4 represents the first and second axis of the PCA on the ostracod dataset (13 selected taxa). The length of the gradient, as estimated from DCA, is 3.1. The first two principal components explain 58% and 23% of the total variance, respectively.

The first axis is mainly related to the abundance of *C. lacustris*. The second axis, instead, represents a transition of samples containing *C. ophthalmica*, *D. stvensoni*, *Limnocythere* sp., *Cyclopyris* sp., and *M. cordata* to samples with *C. candida* and *Herpetocypris* sp. (*Potamocypris* sp. is a minor component). In the PCA biplot, plots of samples belonging to zone O1 are closely related to each other and are well segregated from those of other zones, while samples of subzones O2a cluster in a small area of the biplot but overlap with samples of other subzones. Plots of samples in subzones O2b and O2c present a strong dispersion with respect to the second axis and marginally overlap samples of other subzones.

Main changes in the pollen assemblages are summarized in the PCA biplot (Fig. 5). The length of the gradient estimated from DCA is 2.0, and the first and second axes explain 56% and 33% of the species data variance, respectively.

Herbs are well segregated from arboreal taxa along the first axis, whereas thermophilous tree taxa are segregated from the other taxa

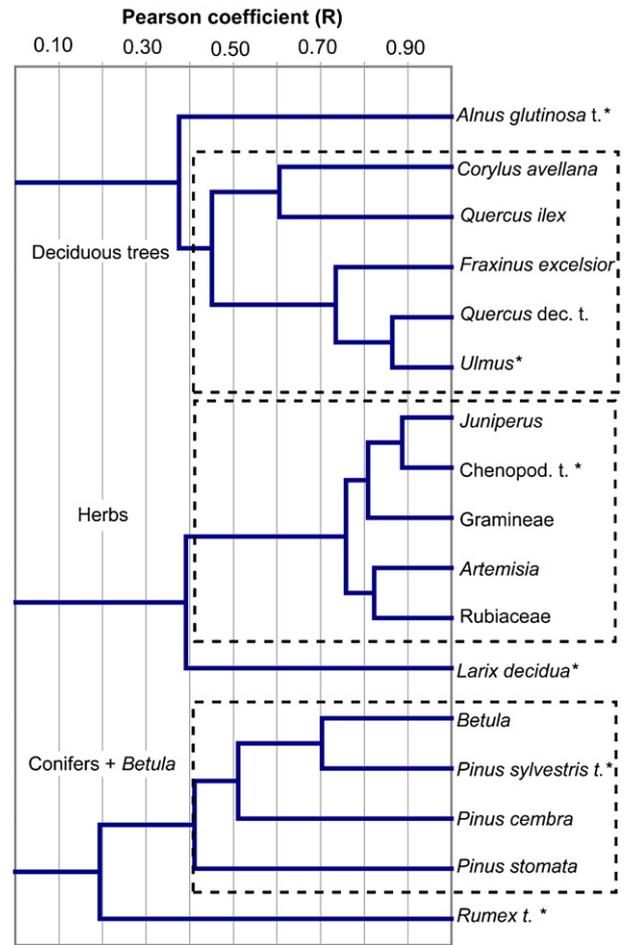


Fig. 7. Hierarchical Cluster Analysis (HCA) on terrestrial pollen taxa ( $n. \text{ taxa} = 17, n = 21$ ; Pearson coefficient distances, average linkage). Sets of similar species are bounded by dotted lines. Representative taxa of each cluster chosen by forward selection (with Monte Carlo permutation tests) are marked with an asterisk.

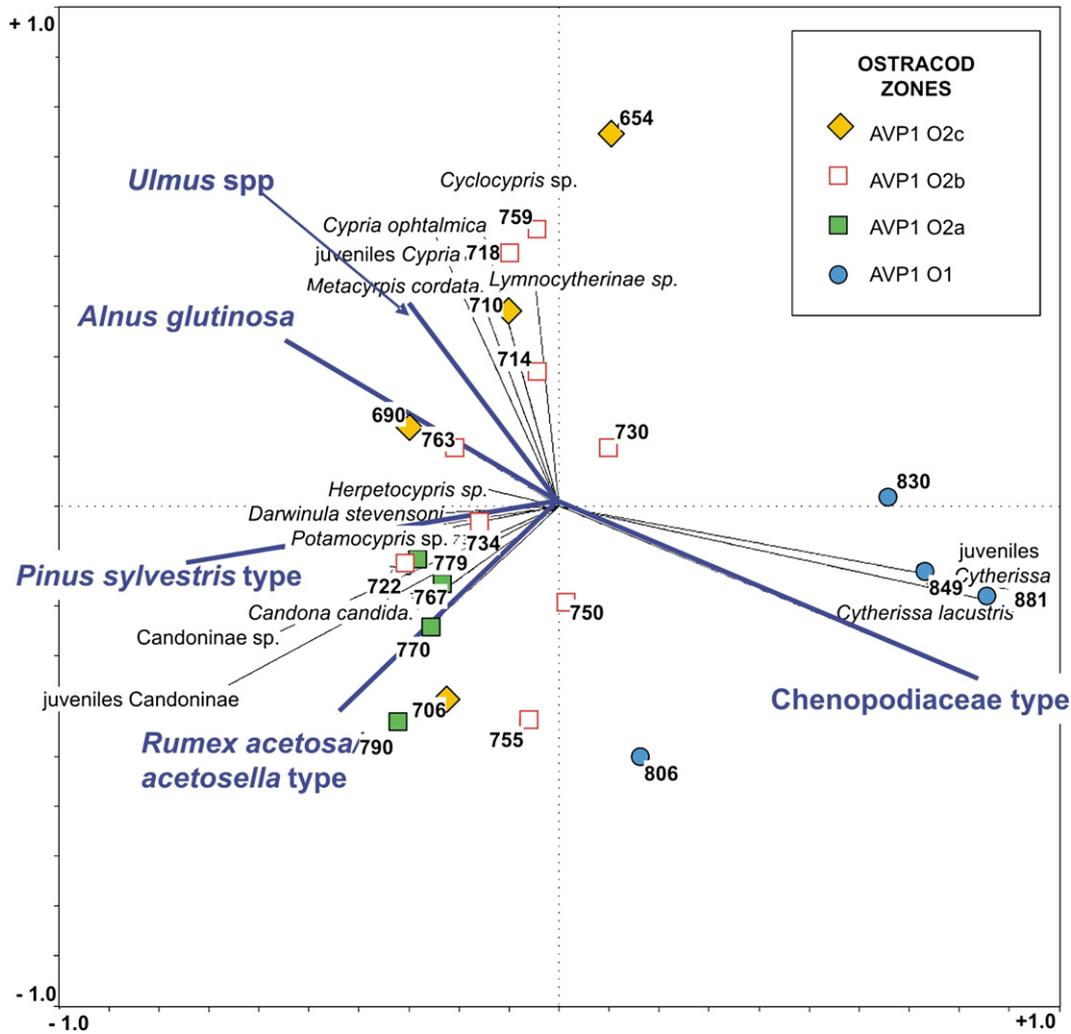
along the second axis. The projections of the loadings of *Pinus* and *Betula* on this axis fall close to those of the herbaceous taxa (e.g. *Artemisia*, *Rubiaceae*).

In order to compare the main changes in the ostracod and pollen assemblages from a stratigraphical point of view, sample scores were plotted against core depth (Fig. 6). Scores in ostracod and pollen assemblages along the first axis are more comparable than changes of sample scores along the second PCA axes, in particular between 734 and 706 cm core depth.

In order to reduce the number of pollen taxa for the direct gradient analyses, the output of the Hierarchical Cluster Analysis (HCA) was cut at the 0.4 level (Fig. 7). Pollen taxa were grouped in six clusters, three of which were formed by a single taxon (*Alnus glutinosa*, *Larix* and *Rumex actosa/acetosella* type). The three main clusters grouped thermophilous tree and shrub taxa (*Corylus*, *Quercus ilex*, *Fraxinus*, *Quercus robur*-type, and *Ulmus*), herb taxa (*Juniperus*, *Chenopodiaceae*, *Gramineae*, *Artemisia*, and *Rubiaceae*), and boreal tree taxa (*Betula*, *Pinus sylvestris*, and *Pinus cembra*), respectively.

The forward selection procedure (with Monte Carlo permutation test) on the same pollen dataset singled out 5 taxa ( $p \leq 0.12$ ) each one of which represented one of the clusters resulting from the HCA, except for the unitary cluster with *Larix* (Fig. 7). In this way, a set was obtained of the few species that explain the variance of the whole pollen dataset.

In order to analyse the relationship between ostracod and pollen assemblages, a redundancy analysis (RDA) was computed with a



**Fig. 8.** Triplot diagram of the Redundancy analysis (RDA) with the late glacial and early Holocene dataset. Ostracod (response variables  $n$  taxa=13; small font) and terrestrial pollen (explanatory variables  $n$  taxa=17; large bold font),  $n=21$ ;  $\lambda_1$  48%,  $\lambda_2$  10%. Samples are labelled according to their core depth (cm).

dataset of 13 ostracod taxa (response variables) and 5 pollen taxa (environmental variables) selected in the previous step (Fig. 8). The first and second canonical axes account for 48% and 10% of the variance, respectively. The ratio  $\lambda_1 + \lambda_2 / \text{total variance}$ , a measure of the goodness of fit equivalent to  $R^2$  (Jongman et al., 1987), was 0.9. As shown in Fig. 8, the shrub and herbaceous pollen types (i.e. *Juniperus*, *Chenopodiaceae*, *Gramineae*; *Artemisia*, and *Rubiaceae*), are correlated with *C. lacustris*. On the other hand, *C. ophtalmica*, *M. cordata* and *Limnocytherinae* sp. are correlated with pollen of thermophilous trees and shrubs (*Corylus*, *Quercus ilex*, *Fraxinus*, *Quercus robur*-type, and *Ulmus*). *C. candida*, *Potamocypris* (juveniles), and *D. stevensoni* are associated with the boreal-forest pollen types (*Pinus sylvestris*, *P. cembra*, and *Betula*), and also with *Rumex acetosa/acetosella* type.

Both *Rumex acetosa/acetosella* type and *Alnus glutinosa* pollen, which were weakly correlated to other species, presented low abundances in the pollen assemblages throughout the sequence.

Canonical analyses including ostracods and pollen of aquatic plants (4 taxa) did not produce satisfactory results since the first two RDA axes explained less than 50% of the total variance (Table 2).

Ordination techniques are exploratory analyses that provide useful tools for data interpretation. However, they are not designed to accept or reject hypotheses. Therefore the null hypothesis that no relationship exists between ostracod and pollen taxa was tested with a non-parametric Monte Carlo permutation test in order to evaluate the significance of the canonical axes. Monte Carlo permutations with specific restrictions for time-series analysis were used for both a test

concerning only the first RDA axis and a second test including all eigenvalues. Both tests rejected the null hypothesis that no relationship exists between species and the environmental variables at 2% level of significance.

## 5. Discussion

The sampling strategy adopted in the present study was adjusted to assess the changes in ostracod assemblages in relation to periods of rapid changes in pollen composition. Accordingly interpretation of results actually aims at establishing whether changes in terrestrial vegetation were marked by periods of inferred changes in hydrology and/or in trophic level.

### 5.1. Palaeoenvironmental interpretation of ostracod and pollen biostratigraphies

The ostracod assemblages in the first ostracod biozone (O1; >14,200 cal BP) were dominated by *C. lacustris*, indicating oligotrophic conditions with oxygenated waters (Geiger, 1990a; Danielopol et al., 1993). At the same time, a gradual afforestation with *Betula* was followed by an expansion of *Pinus*.

*C. lacustris* is considered a typical representative of the sublittoral to deep zone of large lakes, reaching its maximum abundances between 12 and 40 m water depths (Geiger, 1990b; Geiger, 1993). However, it has been found in shallow waters of some lakes in northern Europe and the

British Isles (Delling, 1981; Fryer, 1993 in Meisch, 2000), indicating that the species is probably tolerant of a wide range of temperatures (Danielopol et al., 1993). In the sequence under study *C. lacustris* is present in a rich thanatocoenosis that is well structured in terms of the adult/juveniles ratio. This probably indicates that the living population was in optimal condition for the species development, not under a situation of stress. Therefore *C. lacustris* is considered in the present record as an indicator of sublittoral aquatic environments.

At the beginning of the second biozone (subzone O2a; 14,200–12,750 cal yr BP) the total concentration of valves decreased, *C. lacustris* was strongly reduced, and *C. candida* and *C. ophthalmica* dominated the ostracod assemblage. *C. ophthalmica* survives in waters with high concentration of organic matter (Meisch, 2000), while the retreat of *C. lacustris* in a modern alpine lake has been associated with low oxygen concentrations superposed on high organic or low porosity of the sediments (Danielopol and Casale, 1990). Therefore it is likely that the rise of *C. ophthalmica* and the contemporary retreat of *C. lacustris* were caused by the lowering of oxygen concentrations associated with increasing organic loads. Thermophilous trees expanded at the beginning of this zone, and *Artemisia* as well as Gramineae decreased, suggesting warmer conditions in contrast to the previous zone.

Total valve concentration and ostracod species abundance strongly decreased between 12,750 and 11,450 cal yr BP (subzone O2b – Younger Dryas), indicating that the factor or the combination of factors (e.g. low temperatures, low oxygen concentration, or reduced availability of food) that curbed the abundance of ostracods reached its maximum influence. The occurrence of *D. stevensoni* suggests shallow water levels, and the presence of *M. cordata* in the transition phases at the beginning and the end of this biozone indicate shallow environments with aquatic vegetation. In the terrestrial environment, either colder or drier climatic conditions are indicated by the collapse of thermophilous arboreal taxa (e.g. *Quercus*) and the contemporary increase in shrub and herbaceous taxa (i.e. *Juniperus*, *Artemisia*, and *Chenopodiaceae*).

At the onset of the Holocene (Subzone O2c; 11,450–10,100 cal yr BP), total valve abundance increased, indicating a gradual change in the aquatic environment that led to more favourable conditions for ostracods. After an abrupt increase, *C. candida* was progressively overcome by *C. ophthalmica*. The dominance of the latter species and the high abundance of valves indicate a gradual increase in the lake's trophic state, while the presence of *C. lacustris* and the contemporary decrease of littoral species (*D. stevensoni*) at the top of the sequence testify to a lake-water level increase. The re-expansion of thermophilous trees indicates a climatic amelioration.

The estimated correspondence between ostracod zones and pollen biozones in the chrono- and biostratigraphic framework of Lago Piccolo di Avigliana proposed by Finsinger (2004) is reported in Table 3.

## 5.2. Inferences from multivariate analyses

The output of the PCA of the ostracod dataset is presented in Fig. 4. A well defined cluster, including samples in the ostracod biozone O1, is associated with *C. lacustris* and likely represents oxygenated waters with relatively low trophic level. On the left side of the diagram, a continuum of scores is scattered along the second axis. In the lower branch of the axis are placed sites dominated by *C. candida* (including

*C. ophthalmica* and *Herpetocypris* sp.), an assemblage that indicates warmer conditions with respect to the previous cluster and shallower waters with a higher trophic level. This group includes principally scores of subzone O2a and part of those of subzone O2c. The positive ramus of the second axis includes mainly scores of subzones O2b and part of those in subzone O2c and are associated with *D. stevensoni*, *C. ophthalmica*, *M. cordata*, Limnocytherinae sp. and *Cycloocypris* sp. This area of the diagram is heterogeneous for it includes samples with different total ostracod abundance and different ostracod assemblages. The dispersion of the samples in this subzone with respect to the second ordination axis suggests a time window with associated environmental variables in continuous evolution.

In the biplot diagram of the PCA on terrestrial pollen taxa there are three distinct clusters.

The first cluster, includes samples in subzone O1, with a pollen assemblage dominated by herbaceous vegetation indicating a cold terrestrial environment. The second cluster includes samples of subzones O2a and O2b and represents an environment dominated by boreal forests, indicating a climatic amelioration with respect to the zone O1. Although samples of subzones O2b present more negative scores in the first axis than samples of subzone O2a, no discontinuity exists to justify their separation into two groups.

In the third cluster, where mainly samples of subzones O2c are included, thermophilous trees and shrubs clearly denote a climatic warming.

In both ostracod and pollen PCAs the first axis is by far the one that explains the major portion of the total variance. On the basis of the evidence provided by the pollen biostratigraphy, the first axis represents a strong environmental gradient likely associated with climatic warming between biozones O1 and O2.

According to the ostracod analysis the first axis may be interpreted as warming, because of the presence of thermophilous species in the negative branch of the axis. However, considering that the ostracod assemblages indicate a transition from sublittoral and oxygenated waters to littoral conditions with higher contents in organic matter, the latent theoretical variable represented in this axis likely reflects also changes in the lake-water level and changes in the lake trophic level. Despite minor differences, the trend of the first axis scores plotted in stratigraphical sequence in the ostracod analysis is comparable with the one observed in pollen record.

On the other hand, ostracod sample scores on the second axis, which represent a small portion of the total variance, diverge from those of pollen especially in subzones O2b and O2c. The different arrangement of samples in the PCA biplots may either be due to the different responses of ostracod and vegetation assemblages to an external climatic forcing during a climatic change (namely the Younger Dryas) or to the fact that environmental factors affecting the terrestrial and the aquatic communities were different.

The shoreline in a small catchment basin like that of Lago Piccolo di Avigliana can be considered as an asymmetric boundary (*sensu* Margalef, 1986) where organic matter, nutrients, and clastic material, among others, move primarily from the terrestrial environment to the lake (Odum, 1983). This assumption provides the rational basis for a direct gradient ordination analysis with ostracod abundances as aquatic environmental response variables and pollen abundances as terrestrial environmental variables.

Major relationships between ostracod and pollen assemblages and environments associated with them according to canonical analysis (RDA) are summarized in Table 4.

In direct gradient analysis, constraining the ordination axes to reflect environmental information contained in pollen biostratigraphy results in a better discrimination of ostracod subzones O2a and O2c, but it does not affect the scattering and overlapping of samples in subzone O2b with the previous ones. This result confirms that the environmental interpretation of the second axis in the ostracod PCA is not the same as the one in pollen PCA and RDA.

**Table 3**

Estimated correspondence between ostracod and pollen biozones in the chrono- and biostratigraphic framework of Lago Piccolo di Avigliana (modified from Finsinger, 2004)

Ostracod zones	Core depth (cm)	Age (yr cal BP)	Pollen biozones
AVP1 O2c	<710	<11500	Preboreal (Holocene)
AVP1 O2b	755–710	12500–11500	Younger Dryas
AVP1 O2a	800–755	14200–12500	Allerød
AVP1 O1	>800	>14200	Bølling

**Table 4**  
Relationships between ostracod and pollen taxa and between different kinds of environments according to the RDA analysis

Env. var.	Terrestrial environment (according to pollen)	Associated ostracod taxa	Ostracod zone	Aquatic environment (according to ostracods)
Chenop t	Herbs and shrubs, forest opening	<i>Cytherissa lacustris</i>	1	Oligotrophic, high oxygen concentration, cold, relatively deep
<i>Pinus</i> dipl. ( <i>Rum. acet.</i> )	Boreal forest	<i>Candona candida</i> , <i>Darwinula stevensoni</i> , <i>Herpetocypris</i> sp., <i>Potamocypris</i> sp.	2a, 2b	Oligo-mesotrophic shallow
<i>Ulmus</i> ( <i>Aln. glt.</i> )	Deciduous forest	<i>Cyprina ophthalmica</i> , <i>Cyclocypris</i> sp., <i>Metacypris cordata</i> , <i>Limnocytherinae</i> sp., <i>Darwinula stevensoni</i>	2c, 2b	Shallow, mesotrophic, aquatic veget., warm

Differences between ostracod and pollen records, as inferred from the sample scores of the ordination analyses (Fig. 6), during the Younger Dryas may be related to a different reaction of these communities to that climate change. For ostracods, a condition of stress during the phase of low lake-water level possibly constrained populations to low abundances, while changes in terrestrial vegetation involved the retreat of some species (*Quercus*, *Pinus*) and the increase of cold-adapted species (*Betula*, *Artemisia*).

An alternative hypothesis to explain the differences between ostracod and pollen records takes changes in the water oxygen concentration into account. In the sequence under study sediments are composed of homogeneous fine detritus gyttia (FDG) with a relatively constant content of carbonates. Only sediments at 792–712 cm core depth (ca. 13,800–11,500 cal yr BP) present partial laminations that may indicate a situation of limited circulation at the bottom of the water column possibly associated with a low oxygen concentration at the water–sediment interface. Oxygen limitation represents a factor of stress for ostracod populations that may lead to the disappearance of the most sensitive species at an initial stage and to the reduction in the total number of ostracods in case of more pronounced anoxia. Such processes that are limited to the water body would affect only aquatic populations contributing to uncoupling the response of terrestrial and aquatic communities to climatic forcing. The latter hypothesis is consistent with the low concentrations of *D. stevensoni* in the middle of the Younger Dryas (12,500–11,700 cal yr BP) where re-deposition from shallower zones of the lake cannot be excluded.

On the other hand, the hypothesis of a low lake-water level during Y.D., based upon the presence of littoral ostracods, is consistent with the arid climatic conditions in the southern margin of the Alps reported in recent studies for this time window (Baroni et al., 2006, Frisia et al., 2005).

With the exception of the Younger Dryas, biozones defined on the basis of ostracod assemblages are well discriminated in the RDA diagram (Fig. 8) and are well correlated with specific terrestrial environmental conditions. On the other hand, the response of the ostracod community to climatic change during the Younger Dryas becomes evident in their total abundance rather than in changes in the species composition and is therefore poorly reflected in the ordination diagrams. In this regard the negative excursion of total absolute ostracod concentration matches quite well the shift of the thermophilous taxa *Quercus* deciduous type during the Younger Dryas (Figs. 2 and 3).

Very likely ordination techniques are little sensitive to changes in total ostracod abundance due to the kind of input data. The use of relative abundances makes multivariate analyses more sensitive to quantitative relationships among species. However, this kind of data does not reflect major changes in the total abundance of specimens in the community, which may provide environmental information about stress or favourable conditions.

### 5.3. Comparison with other palaeoenvironmental studies

In the maar lakes of the Eifel region (Germany) the most common species in the “early Lateglacial” (pre-Allerød) were *C. lacustris* and

*Limnocytherina sanctipatricii* (Scharf, 1993). During the Allerød a generalized increase in the number of species occurred, partly related to the development of submerged macrophytes, which provided food and protection for ostracods. In these lakes, no ostracods were present in post post-glacial sediments probably because of the decalcification of shells caused by eutrophication.

Ostracod and pollen biostratigraphies were both studied in a short late-glacial sequence extending from ca. 15,000 yr cal BP to the Laacher See Tephra (12,800 yr BP) in a palaeolake of the Eifel district (Scharf et al., 2005). In this site (Miesenheim) arboreal pollen was dominated by *Betula* and *Pinus*, which, however, expanded later than in the pollen record at Lago Piccolo di Avigliana (AVP). On the other hand, *Artemisia* pollen remained more or less stable throughout the sequence, while in AVP this taxon showed in the same time window a decreasing trend.

In Miesenheim the ostracod assemblages were more diverse and were composed exclusively of ostracods from shallow waters. The environmental reconstruction of the lake evolution indicates higher lake-water levels in the time window matching biozone O1 of AVP (Bølling) and a lowering of the lake-water level in correspondence with the first half of subzone O2a of the AVP record (Allerød). Because of the advent of adverse conditions in Miesenheim, ostracods disappeared from the record at the end of the Allerød. Hence the beginning of the ostracod depletion in Miesenheim coincides with the period of lower ostracod total abundance in AVP biozone O2b (Younger Dryas). The evolution of ostracod assemblages and the related environmental reconstruction in terms of changes in lake-water level in the lakes of the Eifel region are in general terms consistent with those observed in AVP.

A study of a sequence from Lake Neuchâtel (Switzerland) collected at –40 m depth reports a major shift in the dominant species between late glacial and Holocene (Schwalb et al., 1994; Schwalb et al., 1998). During the Bølling the assemblage dominated by *L. sanctipatricii* and *Leucocythere mirabilis* and including also *C. lacustris* indicates a deep, cold, oligotrophic lake. In the Allerød, *C. lacustris* was replaced by *C. neglecta*, a species more tolerant to lower oxygen concentrations and to the increase in water temperature. In these biozones the environmental reconstructions are consistent with those of the present study. On the other hand, in contrast with AVP, ostracod abundances in the Younger Dryas, in particular *L. sanctipatricii*, *L. mirabilis* and *C. lacustris* reached a maximum.

During the Preboreal these three species collapsed and were replaced by *C. neglecta*, a species that prefers cold environments but is present in a wide range of habitats.

In addition to the lake size and the coring depth, differences between the late-glacial sequence of AVP and the one in Lake Neuchâtel may be related to the input of glacial meltwater in the latter lake. The discharge of the Aar River into Lake Neuchâtel contributed to the mixing and the oxygenation of hypolimnetic waters. The authors concluded that the Younger Dryas was characterized by warm and dry summers, which would have had a negative influence on the precipitation–evaporation balance.

A comparison that includes ostracod and pollen data dating back to 12,000 yr B.P. is available for Lake Mondsee (Austria) in a core retrieved from the littoral of the lake (Handl, 1989). According to this study the full-glacial assemblage dominated by *C. lacustris* was

replaced after the Bølling/Allerød transition by a fauna dominated by *C. candida*, *Cyclocypris ovum* and *L. sanctipatricii*. This community remained at very low densities during the Younger Dryas and had a peak abundance at the beginning of the Preboreal. Except for the low abundances of macrophytes, the resemblance with the sequence of AVP is remarkable.

## 6. Conclusions

According to numerical analyses and ordination diagrams major changes in the species composition occurred in both ostracod and vegetation assemblages between the late glacial and the early Holocene (~16,000–10,000 cal. yr BP). These changes are reflected in the first ordination axes and are certainly related to climatic warming, which in the aquatic ecosystem is expressed as changes in hydrology (lake–water level) and in the trophic level, especially oxygen concentrations.

The evolution from Allerød to Preboreal in the terrestrial environment may be summarized as a transition from boreal forests to thermophilous forests interrupted by the Younger Dryas. At the same time in the aquatic environment there was a slight increase in the trophic level associated with the development of aquatic vegetation. During the Younger Dryas, a time window with high rate of change, ostracod communities were unstable and were likely influenced by stress. The response of the ostracod community to climatic forcing in this stadial is confined to changes in their total abundance rather than changes in the species composition. The negative excursion in the ostracod total abundance, however, is poorly reflected by the ordination techniques for the input data are relative abundances. With the exception of the Younger Dryas, biozones defined on the basis of ostracod assemblages are well discriminated in the RDA diagram and are well correlated with specific terrestrial environmental conditions.

Late-glacial ostracod assemblages in Lago Piccolo di Avigliana (Italian Prealps) are altogether comparable with those in sites in the north of the Alps and in Central Europe, if the influence of local factors (latitude, hydrology, lake morphometry, etc.) are duly taken into consideration. The latter suggests a common pattern at a wide geographical scale in the response of aquatic ecosystems to the climatic changes during the late glacial–Holocene transition. From a biogeographic point of view the wide distribution over Europe of *C. lacustris* in the assemblages corresponding to the Bølling biozones is striking.

Multivariate analyses highlight relationships between species and samples, reinforcing the environmental reconstruction obtained with a discretional biostratigraphical approach. The contribution of numerical techniques was particularly useful in choosing between evenly ranked alternative hypotheses. Eliminating noisy and redundant information contributed to the identification of associations between ostracod and pollen taxa and their environments. Hypothesis testing with Monte Carlo permutations with specific constraints for time-series analysis rejected the null hypothesis that no relationship exists between ostracod and pollen assemblages.

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