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ECOLOGICAL CLIMATOLOGY ALONG AN ELEVATIONAL TRANSECT IN THE OUTER BELT OF THE ITALIAN ALPS: MODERN POLLEN, VEGETATION AND CLIMATE

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ABSTRACT: Montane vegetation is traditionally known to be particularly sensitive to climate changes. The strong elevational climatic gradient that characterizes mountain areas results in a steep ecological slope, with several ecotones occurring in a small area. Modern pollen deposition is significantly predicted by both vegetation cover and pollen production; in turn, each predictor is significantly predicted by elevation and climate. Analyses of modern pollen deposition are essential to calibrate fossil pollen sequences accounting for site topography and depositional process, and thus for pollen-based palaeoenvironment and palaeoclimate reconstructions. This study analyzes the relationships among modern pollen assemblages, vegetation and climate along an elevational gradient in the outer belt of the European Alps. Results of Canonical Correspondence Analysis (CCA) demonstrated a general good agreement with previous studies, which identified elevation as the main gradient in the variation of modern pollen and vegetation assemblages in elevational transects. Modern pollen assemblages have been studied in pollen traps and moss samples from different vegetation communities along an elevational transect (stretching from 1240 to 2390 m asl), as well as the vegetation using the Braun-Blanquet system up to the 10 m radius scale, field vegetation surveys and aerial photographs for plant cover of the main species for larger surfaces. Moss samples are assumed to record an average of several years of pollen deposition and can be profitably used as analogues for fossil pollen assemblages; while pollen traps can be expressed as Pollen Accumulation Rates (PAR) and used as a modern reference to estimate past plant population densities. *Alnus viridis*, the main woody species forming dwarf forests in the oceanic-type timberline ecotone, shows a specific elevational PAR arrangement under modern climate conditions. Strong pollen producers (e.g. *Pinus sylvestris/mugo*, *Picea*, *Castanea*, *Corylus* and *Ostrya*) display enhanced uphill wind-transport to subalpine and alpine zones leading to wider pollen belts with less defined boundaries than vegetation. To overcome these limitations, potential indicator pollen taxa of alpine/subalpine belts (*Vaccinium*, *Rhododendron*, *Loiseleuria*) documented in this study and PAR of timberline species (e.g. *Alnus viridis*) could be useful. Thus, if it is possible to identify the major vegetation types and ecotones by means of their modern pollen deposition (e.g. timberline ecotone), other limits, poorly marked by changes in pollen dispersal (e.g. treeline) are not resolved by pollen proxies alone.

Keywords Alps, elevational transects, modern pollen assemblages, vegetation, climate.

1. INTRODUCTION

Ecological climatology is an interdisciplinary framework to understand the functioning of terrestrial ecosystems in the climate system (Bonan, 2016). Relationships between climate, ecosystems and forcing factors may be effectively understood by setting up training sets along ecogradients, and using proxies that allow to synthesize spatial variables such as vegetation (pollen proportions), terrestrial biomass (pollen accumulation rates), fire impact (number of fire events in the last 100 years), etc.

In turn, analyses of modern training sets are essential for a better understanding of fossil palaeoecological records in a particular region, and thus for pollen-based palaeoenvironment and palaeoclimate reconstructions. The variability associated to modern pollen deposition sampled in an extended Alpine calibration set responds mostly to July temperature (Furlanetto et al., 2019), a climate variable strictly related to elevation. Annual precipitation was instead found as the most significant climate variable for the Armentarga fossil record covering the last 10.3 ka cal BP (Furlanetto et al., 2018). Nowadays annual precipitation is not significantly related to elevation as July temperature but is instead strongly controlled by regional climate (Furlanetto et al., 2018).

Very few studies of modern pollen deposition have been attempted in mountain environments of southern European countries (Court-Picon et al., 2005, 2006; Cañellas-Boltà et al., 2009; Ortu et al., 2010). Moss samples are commonly used as surface samples for local modern pollen deposition. They are assumed to record an average of several years of pollen deposition (Räsänen et al., 2004; Pardoe et al., 2010; Lisitsyna &

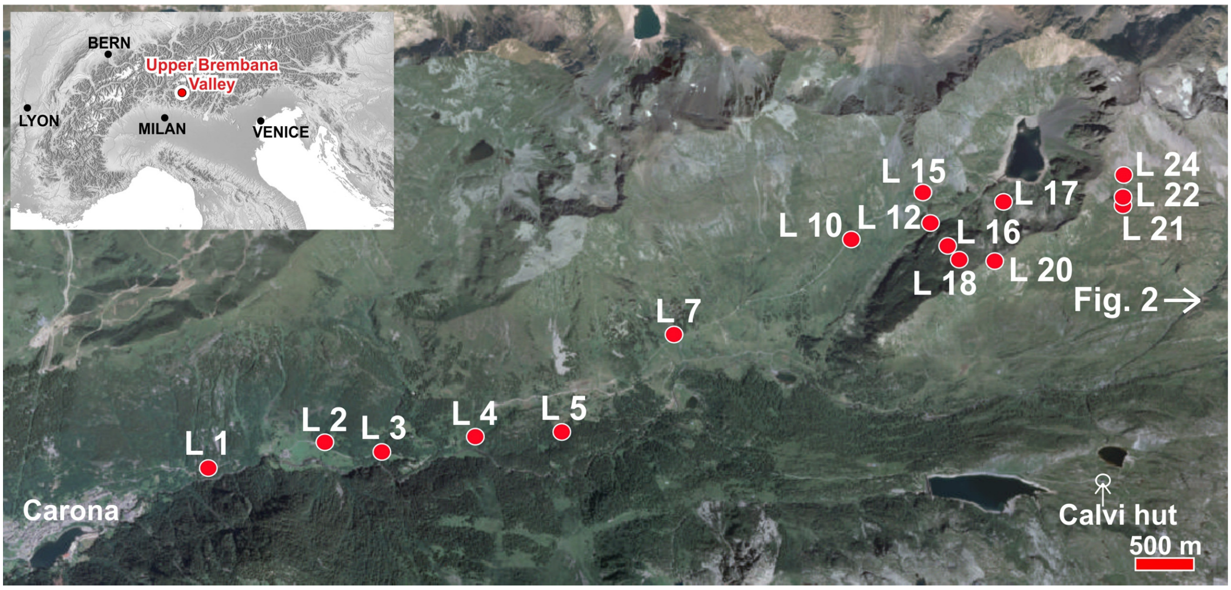

Fig. 1 - Sampling sites for modern pollen assemblages and vegetation data stretching along a typical mid-latitude ecoclimatic elevational gradient under oceanic cold temperate climate in the Upper Brembana Valley. For this study, only the upper elevational reach, spanning a lapse of 1200 m from 1200 to 2400 m asl, was considered.

Hicks, 2014) and can be profitably used as analogues for fossil pollen assemblages. Instead, pollen traps can be expressed both as percentages and Pollen Accumulation Rates (PAR). PAR measurements can be used as a modern reference to estimate past plant population densities buffering the study site (Hicks, 2001; Tinner & Theurillat, 2003; Badino et al., 2018; Furlanetto et al., 2018). Modern references allow also the so-called "site calibration" to be defined, accounting for site-specific features affecting either climate parameters and pollen deposition, such as local topography and sedimentary processes, and the local influence of runoff and, most conspicuously, snow runoff on PAR, barely considered in traditional palaeoecological studies.

The aim of this study is to investigate modern pollen assemblages-vegetation-climate relationships along an elevational gradient. This paper presents a new elevational transect developed in the Upper Brembana Valley (Orobie Alps), recording a typical mid-latitude ecoclimatic elevational gradient under oceanic cold temperate climate (Furlanetto et al., 2018). Here modern pollen assemblages, vegetation and climate have been collected at 16 sampling sites placed along an elevational gradient stretching from 1240 m asl to 2390 m asl. The transect has been designed (1) to estimate the relationships linking modern assemblages, vegetation, elevation and climate; (2) to understand how is the modern vegetation reflected in modern pollen assemblages from pollen traps and moss samples; (3) to calculate specific elevational PAR arrangement under modern climate conditions; (4) to provide a robust modern reference for reliable palaeoenvironmental and quantitative interpretations of past vertical shifts and changes in vegetation composition, as recognized in the pollen records from high-elevation sites.

2. STUDY AREA

The Upper Brembana Valley elevational transect extends along the uppermost section of a typical prealpine valley open to moist southern winds orographically forced uphill, between 1100 m and the headwalls at 2500-2700 m asl (Fig. 1). This region is marked by a *Dfc* climate accordingly to Köppen-Geiger classification (Peel et al., 2007), i.e. nival, persistently wet throughout the year; locally, the annual temperature is 1.3 °C and July lapse rate ranges from 0.56 °C/100 m in the mountain belt to 0.77 °C/100 m above the open forest limit (Furlanetto et al., 2019). Annual precipitation is not significantly related to elevation (Tab. 1). The site actually represents a snowfall extreme in the entire Alps, snow accumulation being concentrated in late winter and spring, and net snow accumulation summing up to 7 m at 1950 m asl (1964-1973 period, Belloni & Pelfini, 1990). The glacier Equilibrium Line Elevation under current climate conditions exceeds the mountain peaks; it was about 2600 m in 1994 AD (Caccianiga et al., 1994). The vegetation of the area provides a representative example of elevational ecological gradient in an oceanic climatic regime common in the Eastern and Northern Alps, heavily affected by pastoralism in the last 4 ka, which however, did not alter the fundamental traits of the timberline structure (Furlanetto et al., 2018, Fig. 2).

3. METHODS: DEVELOPMENT OF AN ELEVATIONAL TRANSECT AND SAMPLING STRATEGY

A transect composed by 16 sampling sites was developed (Fig. 1). The precise location and descriptive information of the sampling sites are listed in Tab. 1. At the center of each site, a pollen trap was located on the ground fixed to iron bars, in order to avoid snow runoff at the soil level. Three moss samples were collected within

Site acronym	Landscape and vegetation main features (from site center to 100 m radius)	Latitude (site centre)	Longitude (site centre)	Elevation m asl	Tjuly (°C)	Tjan (°C)	Pann (mm)
L 24	Open air shed ("bàrech") with droppings and discontinuous ruderal vegetation, in the distance petrophytic herb vegetation.	46° 2' 33.189" N	9° 52' 43.901" E	2393	11.5	-4.6	1865
L 22	Wet, low-tall grassland (*Nardus*) bordering a sedge peat bog and parcels of snow-bed and scree vegetation (*Salix herbacea, Chrysanthemum alpinum*).	46° 2' 26.642" N	9° 52' 44.263" E	2345	11.1	-4.9	1865
L 21	Tussock grassland (*Festuca* and *Nardus*).	46° 2' 25.534" N	9° 52' 44.319" E	2341	10.3	-5.5	1858
L 20	Juniper-Ericaceae dwarf heath (*Vaccinium* and *Rhododendron*) beyond the treeline, not grazed.	46° 2' 14.601" N	9° 52' 4.840" E	2283	9.5	-6.0	1843
L 18	Continuous *Rhododendron*-heath with larch tree individuals (4 m high, 30/40 years old).	46° 2' 15.344" N	9° 51' 51.616" E	2180	10.0	-5.7	1838
L 17	Ericaceae heaths in mosaic with low tall grassland and scattered larch trees.	46° 2' 26.690" N	9° 52' 6.433" E	2169	10.0	-5.7	1838
L 16	Mountain alder scrub with continuous understory of Ericaceae heath, and residual pasture clearings.	46° 2' 18.490" N	9° 51' 48.631" E	2106	11.2	-5.0	1852
L 15	Tussock grassland (*Festuca*) with mountain alder groves and scattered larch individuals.	46° 2' 28.870" N	9° 51' 40.735" E	2105	11.5	-4.6	1864
L 12	Tussock grassland (*Festuca*) in mosaic with juniper and Ericaceae dwarf scrub and a parcel of pasture.	46° 2' 22.194" N	9° 51' 43.051" E	2009	12.1	-4.3	1865
L 10	Mountain alder scrub with thickets of the endemic tall herb *Sanguisorba dodecandra*.	46° 2' 18.621" N	9° 51' 18.009" E	1941	12.5	-4.1	1866
L 7	Grassland rich in basophilous herbs and petrophytic vegetation along an avalanche corridor.	46° 1' 57.943" N	9° 50' 21.535" E	1776	13.3	-3.5	1842
L 5	Pasture at the border of a mixed coniferous forest (*Larix* and *Picea*).	46° 1' 37.134" N	9° 49' 45.206" E	1672	13.9	-3.1	1834
L 4	Tussock grasslands (*Festuca*), legume bushes (*Genista radiata*) in mosaic with mountain alder scrubs and tall herbs; thickets of the endemic tall herb *Sanguisorba dodecandra*.	46° 1' 36.211" N	9° 49' 17.909" E	1552	14.6	-2.7	1828
L 3	River corridor and waterfalls with mountain alder scrub and tall herbs (including *Sanguisorba dodecandra*). In the surroundings, coniferous woodlands (*Picea-Larix*), *Larburnum* understory and mowed leans (*Pimpinella* and *Rumex*).	46° 1' 33.239" N	9° 48' 48.401" E	1422	15.4	-2.2	1820
L 2	Mowed leans surrounded by thickets of broad-leaved trees (*Acer, Fraxinus*).	46° 1' 35.235" N	9° 48' 30.007" E	1360	15.7	-2.0	1821
L 1	Hazelnut scrubland and mixed coniferous (*Picea-Larix*), broad-leaved forests (*Sorbus aucuparia*, *Sorbus aria*), petrophytic habitats.	46° 1' 29.681" N	9° 47' 53.160" E	1244	16.4	-1.7	1783

Tab. 1 - Site metadata for the Upper Brembana Valley elevational transect.

a circular area of 1.8 m radius (Fig. 3, zone A) and mixed together (Cañellas-Boltà et al., 2009), while concentric circles of 1.8 and 10 m-radius were considered for vegetation surveys following the Braun-Blanquet method (Fig. 3, zone A and B). Furthermore, main arboreal species were listed and a cover estimation was carried out within a 100 m radius circle with the help of orthoimages (Fig. 3, zone C).

3.1. Canonical Correspondence Analysis (CCA)

Ordination techniques are considered appropriate for assessing and displaying the relationship between pollen percentages recorded in modern pollen assemblages, vegetation data, elevation and climatic parameters. These statistical analyses have been frequently used to detect structures or patterns within pollen and vegetation data. They provide an efficient low-dimensional representation of complex multivariate data and serve to indicate their major gradients and the relative contribution of each *taxon* to each of these gradients. All the plants present an ecological optimum and tolerance to most environmental gradients, justifying the use of a biological unimodal response model (ter Braak, 1987, ter Braak and Prentice, 1988). In this work, Canonical Correspondence Analysis (CCA), the constrained form of Correspondence Analysis (CA) (ter Braak 1986) was used as direct gradient analysis to highlight the relationships between pollen, vegetation, elevation and climate. Several CCA ordinations have been performed using elevation, July temperature, Janu-

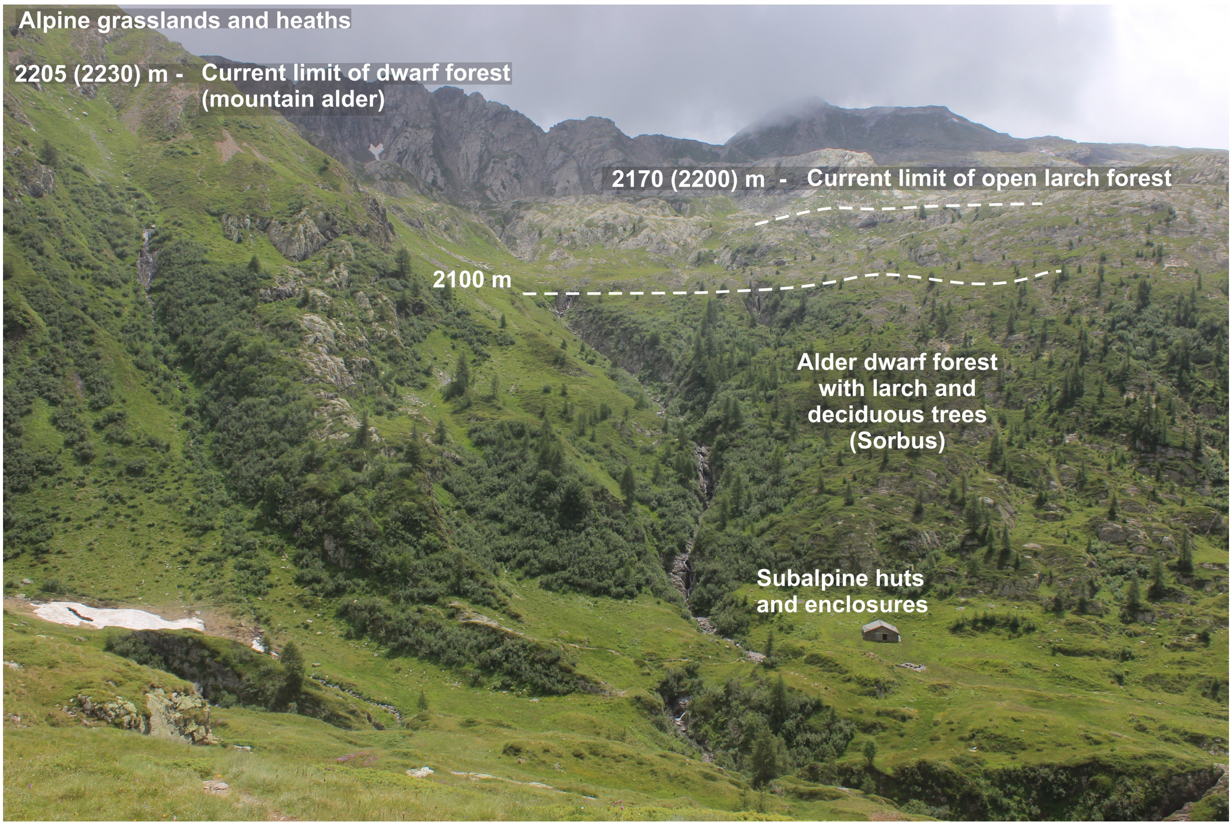

Fig. 2 - Picture showing the structure of the oceanic-type timberline ecotone at the headwall of the Brembana Valley in the outer Italian Alps. Elevation values refer to current limits in the studied area (in brackets the maximum elevations recorded in the Orobie Alps). The natural extent of forest vegetation is the result of long-term effects of pastoralism, wildfire, and climate changes. According to paleobotanical data, the current timberline structure still reflects the dominance of pristine dwarf forests which become established in the second half of the Holocene (Furlanetto et al., 2018).

ary temperature and annual precipitation as the sole constraining variable to assess their importance on the variance of pollen and vegetation (1.8 m and 10 m radius) assemblages (Tab. 2). Prior to the CCA analysis, pollen percentages were square-root transformed, for variance stabilization (Prentice, 1980) and taxa with percentages below 2%, were removed. The significance of all CCA were tested with ANOVA (p <0.05, after 999 unrestricted permutations).

3.2. Estimation of climate normals along the elevational transect

Site-specific instrumental temperature and precipitation series, covering the 1951-2015 period, were reconstructed for each sampling site by means of the anomaly method (New et al., 2000; Mitchell & Jones, 2005) as described in Brunetti et al. (2012), to obtain a climate reconstruction as much representative of the specific locations as possible, thanks to the huge amount of meteorological observations available for Italy and surrounding areas. The closest meteorological station (Foppolo, 1520 m asl) is situated ca 4 km far from site L 1 and ca 9.5 km far from site L 24. The interpolation procedure consists in the independent reconstruction of the climatological normals over a given reference period (i.e. climatologies) and the departures from them (i.e. the anomalies): the former, characterized by remarkable spatial gradients, were reconstructed by evaluating the local dependence of the meteorological variable on elevation (Brunetti et al., 2014; Crespi et al., 2018), and a high spatial density network of stations (even if with a limited temporal coverage) was used; anomalies are linked to climate variability and are characterized by a higher spatial coherence, therefore, a more simple interpolation technique and a low spatial density of stations are enough, but long temporal coverage and accurate homogenization (i.e. the procedure that removes the non-climatic signals introduced by stations and instruments relocation, changes in measurement practices and so on) are mandatory. Finally, climatologies and anomalies were superimposed to get temperature and precipitation monthly series in absolute values for each sampling site. Information about the techniques and their accuracy are provided in Brunetti et al. (2012, 2014) and Crespi et al. (2018). From these monthly series, mean temperature of the warmest month (July), coldest month (January) and the total annual precipitation over the 1981-2010 period were calculated for the sampled sites (Tab. 1).

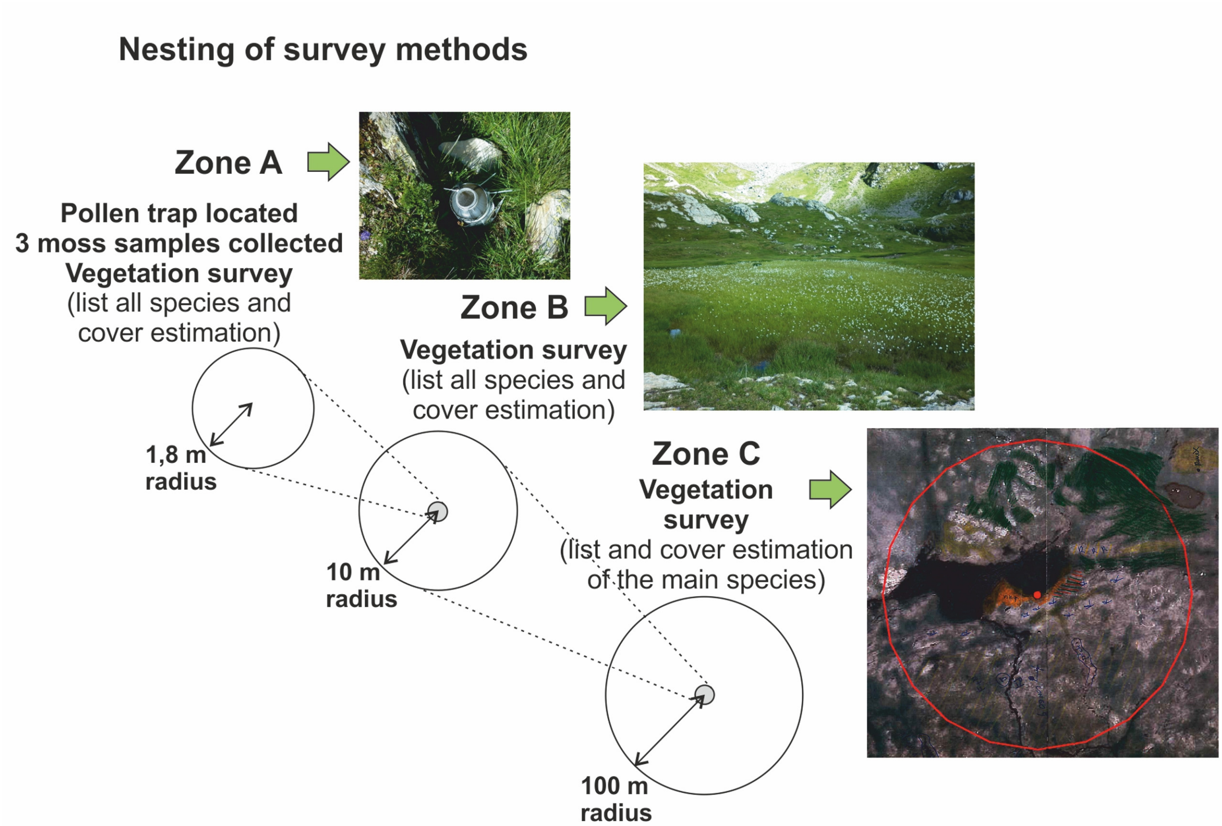

Fig. 3 - Site sampling method scheme used for vegetation survey.

	elevation	Tjuly	Tjan	Pann
Pollen traps				
variance explained	17.06	16.61	16.91	12.66
p	0.001 ***	0.001 ***	0.001 ***	0.009 **
Moss samples				
variance explained	14.58	14.41	14.49	10.87
p	0.005 **	0.008 **	0.01 **	0.108
Vegetation 1.8 m Radius				
variance explained	12.64	12.34	12.35	12.02
p	0.001 ***	0.003 **	0.001 ***	0.001 ***
Vegetation 10 m Radius				
variance explained	15.61	15.39	15.43	13.99
p	0.001 ***	0.001 ***	0.001 ***	0.001 ***

Significance codes: *** 0.001; **0.01

Tab. 2 - Proportions of variance explained by each explanatory variable as the sole constrained and permutational-repeated measures analysis (ANOVA) obtained for modern pollen assemblages (pollen traps and moss samples) and vegetation data (surveys at 1.8 m and 10 m radius circles).

3.3. Vegetation data: surveying strategy (Braun-Blanquet system)

At each sampling site, vegetation surveys were carried out using the Braun-Blanquet abundance/dominance scale (Braun-Blanquet, 1979) within circular areas of 1.8 m radius (ca 10 m^2) and 10 m radius (ca 314 m^2). In this system, a semi-quantitative abundance-dominance index is used to estimate the plant cover for each species, according to the following scale: 5 (80-100%), 4 (60-80%), 3 (40-60%), 2 (20-40%), 1 (1-20%), + (scarce), r (rare). Finally, within the circular areas of 100 m radius was estimated the cover of the main species. This methodology was focused on producing good estimates of the abundance of the major taxa (the producers of the pollen types which are the major components of current and past pollen deposition in the study area) rather than recording every species present. Compared to plant species identification, pollen usually presents lower taxonomic resolution, in most cases only reaching genus or family level. To facilitate comparative data analyses plant species recorded in the vegetation surveys were grouped into higher taxonomic levels to match their corresponding pollen types and presented as percentages.

3.4. Pollen analysis - modern pollen assemblages

At the center of each site, a pollen trap was located (Fig. 3, zone A). The trap has a circular opening on top (4.5 cm in diameter), through which the airborne pollen can freely enter. Glycerine and thymol were placed in the trap to inhibit the growth of mould and the opening was covered by a 2 mm mesh fixed to the trap with duct tape. Pollen monitoring data represents the period 2016-2017. In each site, three moss polsters were also collected within a circular area of 1.8 m radius (ca 10 m^2) and mixed into one sample. Mosses were sampled down to, but not including, the mineral soil. Samples were processed following standard methods at the Laboratory of Palynology and Palaeoecology of CNR-IDPA in Milan, after adding *Lycopodium* tablets for pollen and pollen-slide microcharcoal concentration estimations (Stockmarr, 1971). A minimum count of 600 pollen grains was obtained at each sampling site, aquatics, spores and non-pollen palynomorphs were excluded from the pollen sum. Identification was carried out at x400, x630 and x1000 magnifications under a Leica DM -LB light microscope. Pollen identification followed Moore et al. (1991), Punt & Blackmore (1976-2009), Reille (1992-1998), Beug (2004) and the CNR pollen reference collection. Microbiological particles were named after van Geel et al. (1981), van Geel (1978) and van Geel & Aptroot (2006) and expressed as percentages out of the pollen sum. Pollen-slide microcharcoal particles were counted under a light microscope at 400x. Black, completely opaque and angular fragments (Clark, 1988) were identified as charcoal and grouped in two size classes (10-50 μm and 50-250 μm length).

3.5. Pollen Accumulation Rates (PAR)

Pollen monitoring using annual pollen traps helps to quantify and calibrate pollen deposition with present-day vegetation and meteorological conditions, as well as providing insights into local pollen dispersal and sedimentation mechanisms (Hicks, 2001). Pollen Accumulation Rates (PAR) measurements can also be used as a modern reference to estimate past plant population densities buffering the study site (Hicks, 2001; Tinner & Theurillat, 2003; Badino et al., 2018). Modern PAR values were calculated for *Alnus viridis*, one of the main timberline ecotone shrub species in the outer oceanic districts of Central Alps.

4. RESULTS

4.1. Canonical Correspondence Analysis (CCA)

This study aims at emphasizing pollen/vegetation/climate relationships at a local scale. Indeed, although extra-local and regional non-arboreal pollen is present in the modern pollen spectra, herbaceous pollen assemblages appear to reflect predominantly local vegetation rather than wider landscape units, as also demonstrated by Caseldine & Pardoe (1994), Hjelle (1999) and Pardoe (2001). The variances explained by elevation and each climate parameter (Tjuly, Tjan and Pann), calculated with CCA ordinations with unique constrained, are presented in Tab. 2. The Canonical Correspondence Analysis (CCA) of the vegetation data and pollen assemblages suggests that the variation in vegetation and pollen is strongly correlated to the elevational gradient (Tab. 2). In both vegetation data and pollen assemblages elevation explains more variance than the climate parameters, although alike percentages of variance are explained by Tjuly and Tjan. For the pollen traps the variance explained by elevation is 17.0%, 16.6% by Tjuly, 16.9% by Tjan and 12.7% by Pann. For the moss samples the variance explained by elevation is 14.6%, 14.4% by Tjuly, 14.5% by Tjan and 10.9% by Pann. Pann is not significant in the moss samples assemblage ($p > 0.05$, after 999 unrestricted permutations). For the vegetation 1.8 m the variance explained by elevation is 12.6%, 12.3% by Tjuly, 12.4% by Tjan and 12.0% by Pann. Finally for the vegetation 10 m the variance explained by elevation is 15.6%, 15.4% by Tjuly, 15.4% by Tjan and 14.0% by Pann.

4.2. Modern pollen assemblages and their relationship to vegetation

The pollen spectra of 18 pollen traps and 16 moss samples are presented in synthetic percentage diagrams, which include selected pollen types and total microcharcoal concentrations (Figs. 4-5). Plant species recorded in the 10 m vegetation surveys, grouped into higher taxonomic levels to match their corresponding pollen types are presented in a synthetic percentage diagram (Fig. 6).

In the site L 1 located at 1244 m asl (Fig. 6) the main vegetation species are *Corylus avellana*, *Picea abies* and *Larix decidua* among trees and shrubs; *Festuca* sp. and *Laserpitium halleri* and *Laserpitium krapfii* among herbs. In the pollen traps the dominant taxa are *Picea*, *Corylus* and Poaceae (Fig. 4, TL1-TL2) while *Corylus*, *Ostrya* type, *Fraxinus excelsior* type, *Pinus sylvestris/mugo,* and *Larix* represent the main taxa in the moss samples (Fig. 5, ML1-ML2). Pollen taxa from broad-leaved tree (e.g. *Castanea*, and *Ostrya* type) occur in high proportions (Figs. 4a-5a). *Alnus viridis* reach-

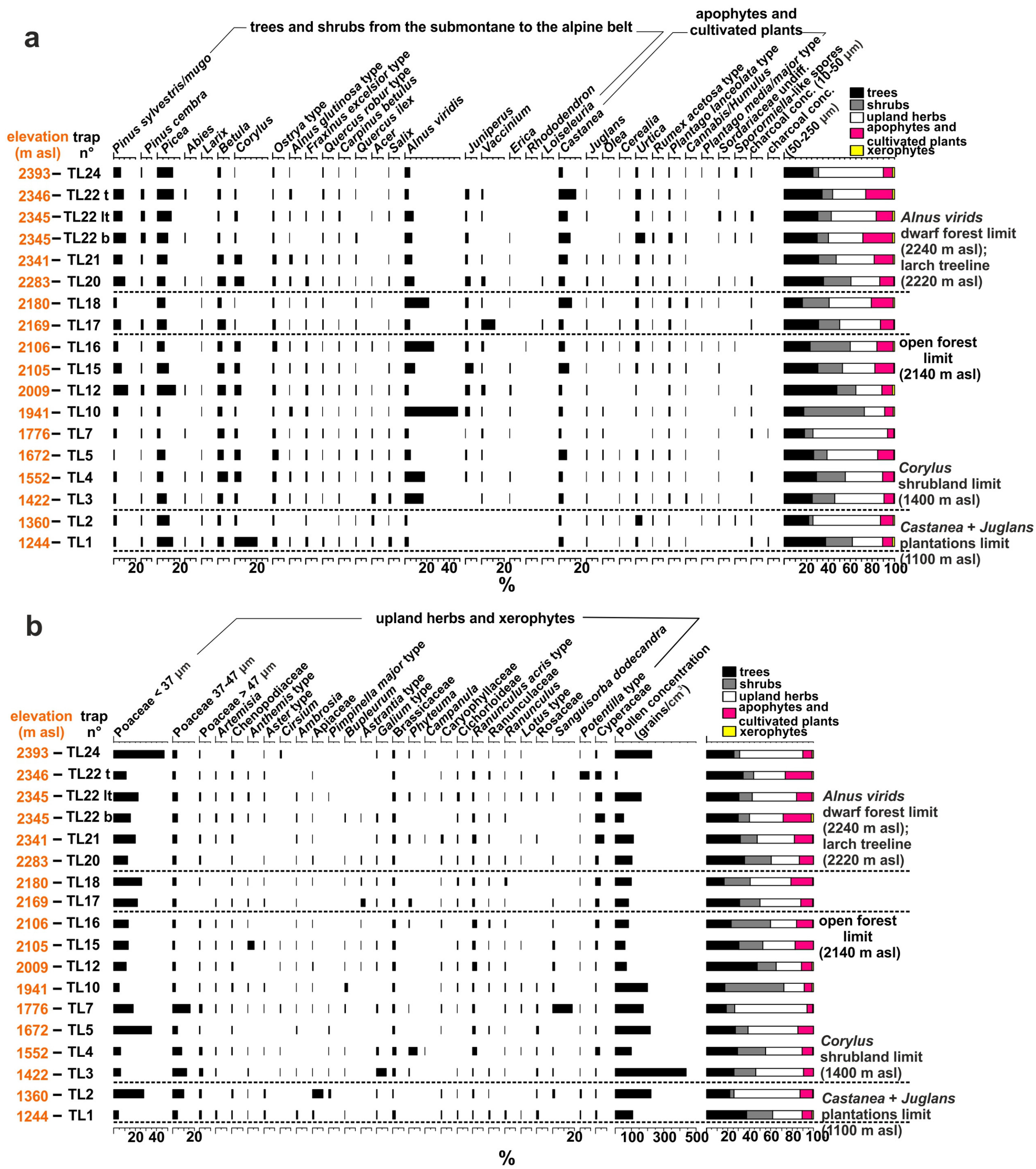

Fig. 4 - Percent diagram obtained from pollen traps from the Upper Brembana Valley elevational transect showing selected pollen taxa and main vegetation zones.

es high cover percentages (10-30%) in sites L 3 and L 4 located next to streams and also in the site L 10 (30%) located in an avalanche corridor/stream (Fig. 6), this abundance in *Alnus viridis* is also presented in modern pollen assemblages (Figs. 4a-5a). Sites L 3 and L 4 show also high cover percentages of *Festuca scabriculmis* (50-70%), *Galium lucidum* (30%), *Pimpinella major* (10%) and the endemic tall herb *Sanguisorba dodecandra* (10%), while the site L 10 shows the 50% of *Agrostis* sp., 30% of *Festuca scabriculmis* and 30% cover of *Sanguisorba dodecandra*. The sites L 2 and L 5 are respectively located in mowed leans surrounded by thickets of broad-leaved trees and in a pasture at the border of a mixed coniferous forest. In the 10 m vegetation survey (L 2) *Pimpinella major* has the 30% of cover, followed by 10% of *Alchemilla vulgaris*, *Geranium sylvaticum*, *Hera-*

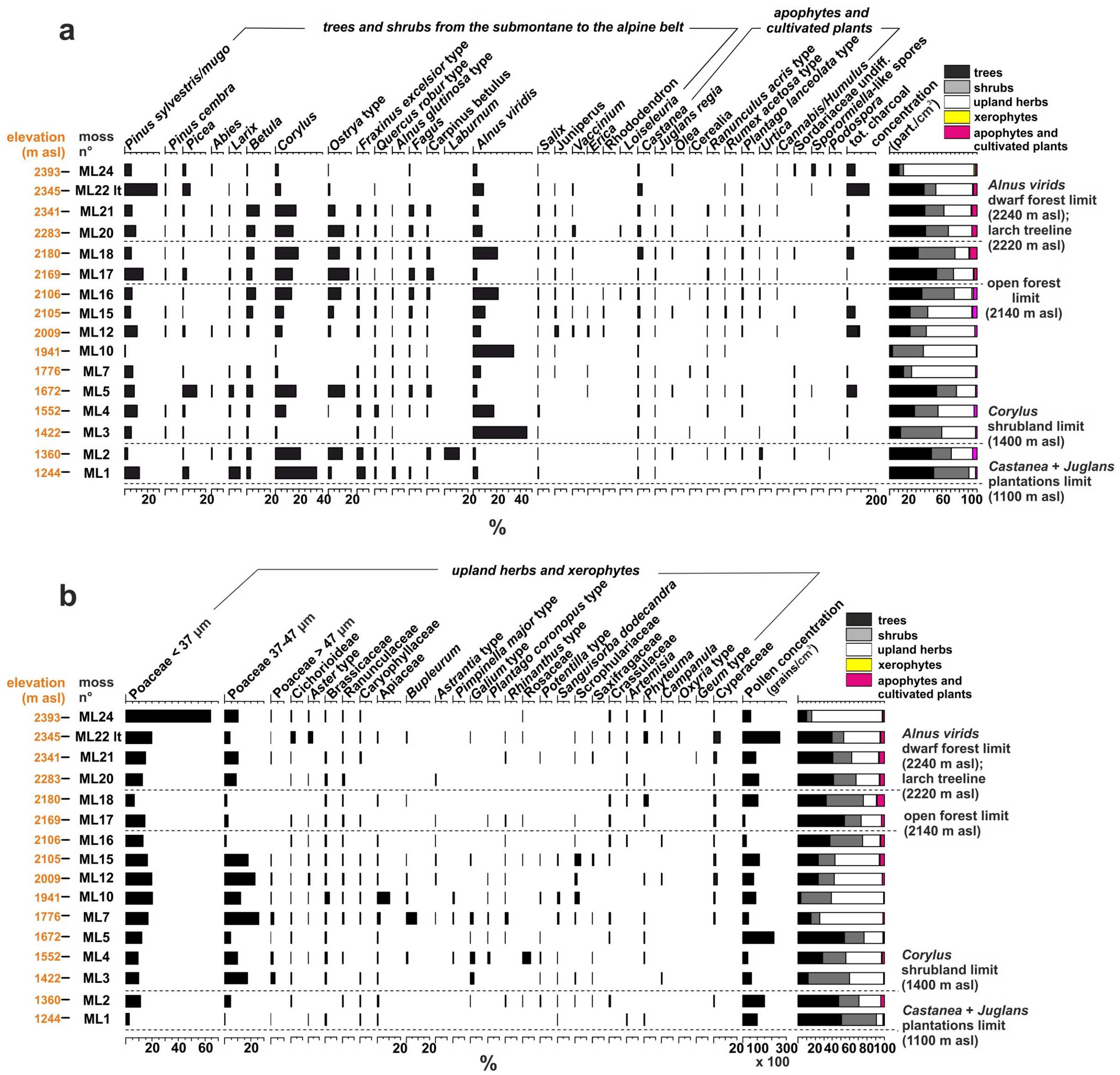

Fig. 5 - Percent diagram obtained from moss samples from the Upper Brembana Valley elevational transect showing selected pollen taxa and main vegetation zones.

cleum sphonodylium, Rumex scutatus, *Trifolium pretense* and *Polygonum bistorta;* in the site L 5 *Laburnum alpinum* has 50% of cover, *Picea abies* 20%, *Larix decidua* 10%, among herbs *Festuca pratensis* has 20% of cover. The site L 7, a grassland along an avalanche corridor presents 10% of *Picea abies* and *Larix decidua* (Fig 6a); among herbs 30% of *Calamagrostis* sp., *Rhinanthus* sp. and *Sanguisorba dodecandra*. This latter herb is well represented in the pollen trap (trap TL7, Fig. 4b) reaching 18%. The sites L 12-L 18 are located in the upper subalpine belt with Ericaceae moorlands (*Erica carnea, Vaccinium gaultherioides*, *Vaccinium myrtillus, Rhododendron ferrugineum* and *Loiseleuria procumbens*) and *Alnus viridis* thickets with *Larix decidua* individuals; larch treeline is located at 2220 m. *Juniperus nana* shows high cover percentages in the sites L 12 and L 15, that are little reflected in the pollen percentages. In the sites (L 12-L 18) the pollen trap and moss sample assemblages are dominated by *Alnus viridis*, *Pinus sylvestris/mugo,* and Poaceae, the Ericaceae moorland is well represented by *Vaccinium* while *Erica*, *Rhododendron* and *Loiseleuria* show sporadic occurrences (Figs. 4a-5a). Above 2100 m asl the wind-driven uphill transport of pollen from the lower belts shows increased percentages of *Pinus sylvestis/mugo*, *Betula*, *Corylus*, *Ostrya* type, *Fagus,* and *Carpinus betulus* in

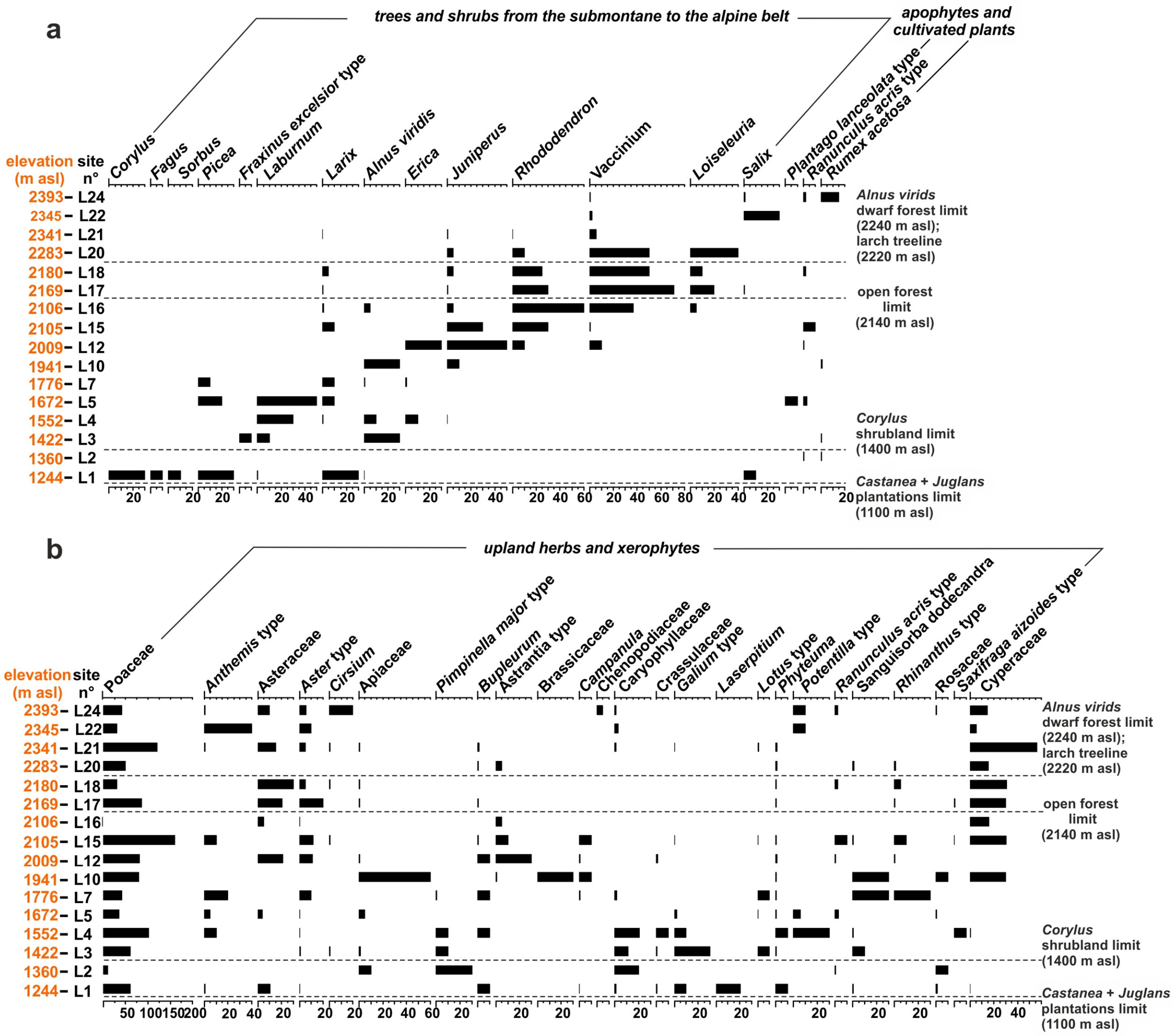

Fig. 6 - Percent diagram of plant cover of selected plant species from the Upper Brembana Valley elevational transect recorded in the 10 m vegetation surveys. Species were grouped into higher taxonomic levels to match their corresponding pollen types. In order to allow comparison with pollen assemblages the same taxa presented in the pollen diagrams were selected.

the moss samples and increased percentages of *Picea*, *Betula*, *Corylus* and *Castanea* in the pollen traps. In sites (L 21-L 24) the 10 m vegetation is dominated by *Festuca scabriculmis*, *Festuca quadriflora*, *Carex sempervirens* (L 21); *Salix herbacea*, *Chrysanthemum alpinum* and *Potentilla aurea* (L22); *Cirsium spinosissimum*, *Poa alpina*, *Rumex alpestris* and *Potentilla aurea* (L 24). The site L 24 (2390 m asl) is located in an extensive pasture, reflected in modern pollen assemblages by high percentages of Poaceae and of dung spores (Sordariaceae undiff., *Sporormiella*-like spores, and Podospora).

4.3. Pollen Accumulation Rate (PAR)

Alnus viridis, the main woody species forming extensive dwarf forests in the Upper Brembana Valley timberline ecotone (Fig. 2), shows a specific elevational PAR arrangement under modern climate conditions (Tab. 3). The highest PAR values in the local elevational transect are observed in sites L3 and L10 (1420 and 1940 m asl, respectively) in river corridors and waterfalls with mountain alder scrub. Here PAR values range between 2400 and 3100 pollen grains cm^{-2} yr^{-1} (Tab. 3, traps TL3 and TL10). On the other hand, pollen traps at subalpine elevation (Tab. 3, traps TL16, TL18; respectively 2100 and 2180 m asl), located at the border of mountain alder scrub with continuous understory of Ericaceae, display PAR values of about 700 pollen grains cm^{-2} yr^{-1}.

5. DISCUSSION: POLLEN-VEGETATION-ELEVATION AND CLIMATE RELATIONSHIPS

Our data are in agreement with previous studies which identified elevation as the main gradient controlling modern pollen assemblages and vegetation distribution across mountain regions (Bonnefille et al., 1993; Vincens et al., 1997; Weng et al., 2004; Court-Picon 2005, 2006; Rull, 2006; Cañellas-Boltà et al., 2009). The Canonical Correspondence Analysis (CCA) showed that elevation explains the major percentage of variance in both vegetation data and pollen assemblages (Tab. 2); although alike percentages of variance are explained by the temperature climate parameters (Tjuly and Tjan). All the temperature parameters vary accordingly with elevation due to a stable lapse rate. July lapse rate ranges from 0.56 °C/100 m in the mountain belt to 0.77 °C/100 m above the open forest limit (Furlanetto et al., 2019). A lower percentage of variance is explained by annual precipitation (Tab. 2), that is not significantly related to elevation as temperature but is instead strongly controlled by regional climate (Fig. 2B in Furlanetto et al., 2018).

In spite of the uphill pollen transport, pollen-elevation and climate relationships are strong since pollen is directly correlated to elevation and climate. Pollen and vegetation data are independent.

5.1. Uphill pollen transport

The uphill transport of pollen by wind to subalpine and alpine zones was first recorded in the European Alps (Markgraf, 1980; David, 1997; Frei, 1997; Brugiapaglia et al., 1998; Ortu, 2002). Markgraf (1980) showed that, in a steep valley-slope system of Alpine type, the proportion of pollen dispersal from local uphill winds in daytime decreases with increasing elevation in favor of regional (medium-distance) dispersal. This high-elevation dispersal component relies significantly on pollen washout by rain, which cleans the atmosphere of suspended pollen (Markgraf, 1980). Pollen belts tend to be wider and with less defined boundaries than vegetation; this is likely due to the homogenizing effect of wind dispersal, especially from lower to upper elevational levels. Thus, if it is possible to identify the major vegetation types by means of their modern pollen deposition, it becomes more difficult to identify specific thresholds (e.g. treeline).

The over-representation of *Pinus* in the pollen assemblages is well documented by numerous authors (e.g. Broström et al. 1998; Brugiapaglia et al. 1998; Ortu et al. 2005, 2006; Court- Picon et al., 2005, 2006, Cañellas-Boltà et al., 2009). The strong pollen signal of *Pinus sylvestris/mugo* is recorded in the moss samples above the treeline (Fig. 5a, ML17-24), while *Pinus mugo* is not recorded in the vegetation data (Fig. 6). In the study area, isolated stands of mountain dwarf pine (*Pinus mugo*) form part of the timberline structure at 1800-2000 m asl at dry edaphic sites.

A dark coniferous forest (*Picea abies, Abies alba, Larix decidua*) occurs only on shaded slopes, therefore *Picea abies* appears in the 10 m vegetation surveys only in sites L 1, L 5 and L 7 (Fig. 6a). In the pollen traps

pollen trap	Elevation (m asl)	Alnus viridis PAR (pollen grains cm^{-2} yr^{-1})
TL24	2393	353
TL22 lt	2345	409
TL22 t	2345	101
TL21	2341	227
TL20	2283	277
TL18	2180	722
TL17	2169	120
TL16	2106	724
TL15	2105	173
TL12	2009	70
TL10	1941	3191
TL7	1776	173
TL5	1672	363
TL4	1552	302
TL3	1422	2441
TL2	1360	132
TL1	1244	116

Tab. 3 - Modern *Alnus viridis* Pollen Accumulation Rate values based on pollen monitoring data in the Upper Brembana Valley, representing the period 2016-2017. The location of the sites is shown in Fig. 1.

and moss samples *Picea* shows a marked uphill transport to subalpine and alpine zones in the pollen traps (Fig. 4a).

Deciduous trees of the mountain belt (e.g. *Corylus, Betula, Ostrya, Castanea*) also show uphill wind transport. *Castanea* uphill transport is marked in pollen traps (Figs. 4a) while *Corylus* and *Ostrya* show high percentages in the moss samples ML16-21 between 2106 and 2341 m asl (Fig. 5a). The influence of upslope wind dispersal of medium- to long-distance transported pollen types (e.g. *Castanea* and *Ostrya* type) have to be taken into account and interpreted with caution in the fossil records.

5.2. Potential indicator taxa of subalpine/alpine belts

Extensive mountain alder shrublands develop in the subalpine elevational belt under oceanic, cool temperate climates, that hinder cembran pine fitness. Edaphic geodiversity allows mountain alder to compete with dwarf pine (*Pinus mugo*), the latter also tolerating oceanic climates, but escaping edaphic wetness. *Alnus viridis* vegetation needs a continuous water supply during the growing season, enhanced by high annual snowfall rate and good soil water balance (Richard, 1968, 1969; Mauri and Caudullo, 2016). In Alpine oceanic

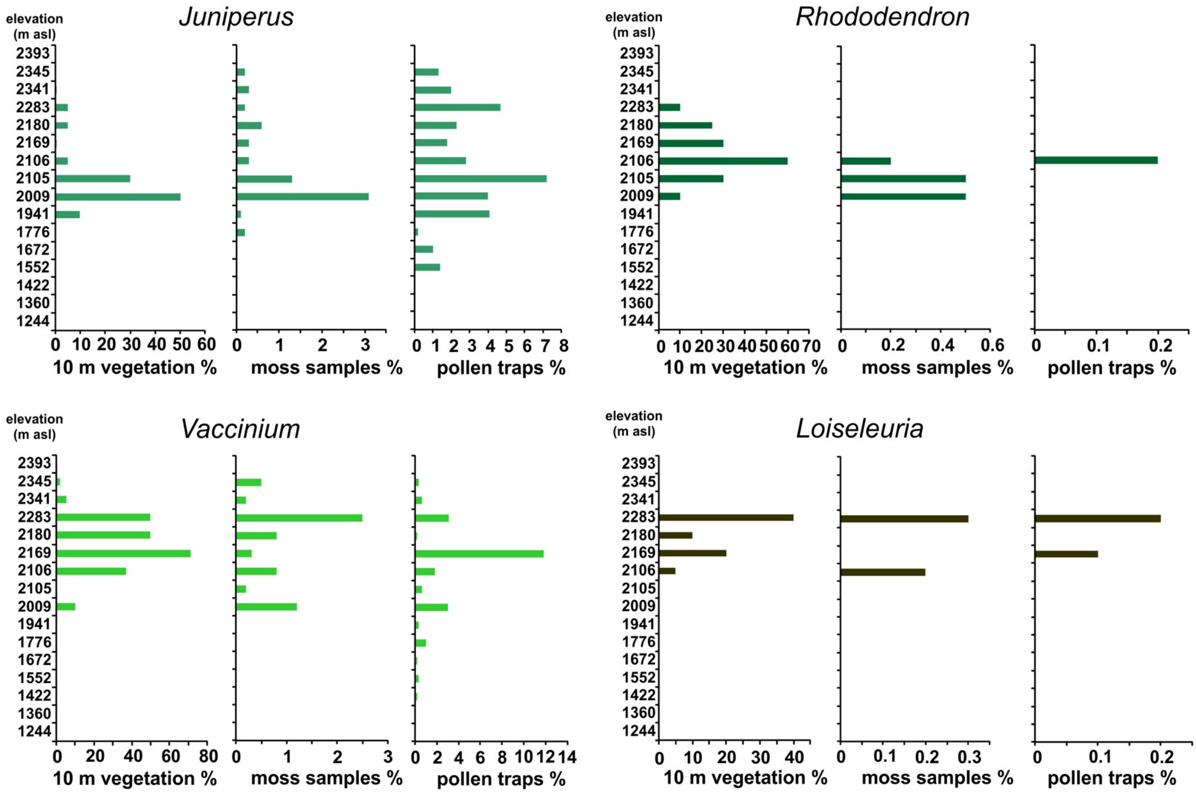

Fig. 7 - Histograms showing the elevational distribution of plant cover % (10 m vegetation surveys) and of pollen % (moss samples and pollen traps) for potential indicator taxa of subalpine/alpine belts.

climates, its ecological range expands downstream especially along avalanche corridors but also on northern slopes, due to a general increase in soil moisture, and thus species optima are shifted towards lower elevations (e.g. Fig. 2); for this reason, it shows lower elevation optima compared to continental inner valleys (Furlanetto et al., 2019). *Alnus viridis* PAR measurements from pollen traps at subalpine elevation (2100-2180 m asl), located at the border of mountain alder dwarf forest can be used as a modern reference to estimate past plant population densities (Furlanetto et al., 2018). Caution is due because the pattern of decreasing pollen production with elevation (Furlanetto et al., 2018) also affects PAR values. Pollen Productivity Estimates (PPEs) were not calculated from modern pollen samples because regional (10^4-10^5 km^2—REVEALS model) and local (<1 km^2 up to 5 km^2—LOVE model) vegetation reconstruction methods were not applied to the fossil record (Furlanetto et al., 2018) as the application of LOVE model (fossil pollen from small study sites) was not possible. The LOVE model estimates the vegetation composition within the source area subtracting the background pollen from the pollen signal. As pollen records from large sites closed to the study area for regional vegetation composition were lacking this model was not applied to the fossil record.

Ericaceae is considered an excellent indicator of the montane/subalpine belts (Cañellas-Boltà et al., 2009). In our study, the identification of pollen types within this family allows to highlight different elevational patterns of pollen and relative parent taxa. *Vaccinium*, *Rhododendron* and *Loiseleuria* show a consistent pollen -vegetation elevational pattern restricted to the timberline belt between 2000 and 2300 m asl (Fig. 7). Whereas *Erica* pollen type shows a wider distribution especially in pollen traps from 1422 to 2345 m asl (Fig. 4a) even though it is recovered in the 10 m vegetation surveys between 1550 and 2000 m asl (Fig. 6). Also *Juniperus* shows an elevational pattern in both vegetation and pollen traps with major abundance at the lower limit of the open forest, ca. 2000 m (Fig. 7).

6. CONCLUSIONS

Relationships between climate, ecosystems and forcing factors may be effectively understood by setting up training sets along ecogradients, and using proxies that allow to synthesize spatial variables such as vegetation (pollen proportions) and terrestrial biomass (pollen accumulation rates). The development of an elevational transect in the Upper Brembana Valley (Central Italian Alps) represents a first step for analyzing ecological gradients with multivariate analysis of modern pollen assemblages as synthetic proxies addressing relationships between modern vegetation, elevation and climate.

The results of CCA analysis demonstrated a general good agreement with previous studies, which identified elevation as the main gradient in the variation of modern pollen and vegetation assemblages in mountain areas); although alike percentages of variance are explained by the temperature climate parameters (Tjuly and Tjan).

Alnus viridis, the main woody species forming the dwarf forests in the timberline ecotone, shows a specific elevational PAR arrangement under modern climate conditions. The highest PAR values are observed in sites from river corridors and waterfalls with mountain alder scrub.

The uphill transport of pollen by wind to subalpine and alpine zones implies wider pollen belts with less defined boundaries than vegetation. This is mainly due to the increase in extra-local transport of strong pollen producers (e.g. *Pinus sylvestris/mugo*, *Picea*, *Castanea*, *Corylus* and *Ostrya*) and lead to some homogenization of pollen assemblages. To overcome these limitations, potential indicator pollen taxa of alpine/subalpine belts (*Vaccinium*, *Rhododendron*, *Loiseleuria*) documented in this study and PAR of timberline species (e.g. *Alnus viridis*) could be useful. Thus, if it is possible to identify the major vegetation types and ecotones by means of their modern pollen deposition (e.g. timberline ecotone), other limits, poorly marked by changes in pollen dispersal (e.g. treeline) are not resolved by pollen proxies alone.

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