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Performance of the REVEALS model to reconstruct present mountain vegetation cover in the North-Western Alps: A model evaluation for past land cover reconstruction

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ABSTRACT

Mountain ecosystems have been significantly shaped by both climate and land use changes. In order to better understand the present status of mountain ecosystems, it is necessary to explore changes over a long-term period, i.e. centuries to millennia. While pollen analyses have provided a strong understanding of Holocene vegetation dynamics in the French Alps, quantitative and spatially detailed pollen-based estimates of vegetation change are still needed. Obtaining such estimates is challenging due to the complexity of mountain landscapes resulting from altitudinal gradients, topography, geology, exposure and anthropogenic activities. Pollen-based land cover models, such as the Landscape Reconstruction Algorithm (LRA), which corrects for inter-taxonomic differences in pollen production, dispersal and deposition mechanisms, have been developed for quantitative land cover reconstructions, mainly in lowlands. Applying these models in mountainous areas requires careful evaluation of input parameters (e.g. wind speed…) and consideration of the sampling design (i.e. number of sites…).

This study evaluates the performance of the REVEALS model in the North-Western Alps, i.e. the first module of the LRA scheme which aims to reconstruct vegetation at a regional scale. For this purpose, we are comparing raw pollen data (untransformed data), REVEALS estimates, and a contemporary vegetation map.

Our results demonstrate that REVEALS greatly improves estimations of the regional plant abundances (compared to untransformed pollen data), thus providing reliable reconstructions of regional vegetation for the study region. The study further underlines the need to understand the environmental context, in terms of altitudinal gradients of vegetation, atmospheric conditions and transfer processes (e.g. wind, insects, gravity, runoff), to set up model experiments. Furthermore, variability in site-specific topography and environmental conditions should be taken into account when applying REVEALS. The main limitations for the use of REVEALS in mountain regions concerned the integration of insect pollination and topography conditions. However, the results are very promising, especially when considering land cover types, which are very close to the vegetation map (closer than raw pollen data). The present study demonstrates the potential of REVEALS for long-term reconstructions of vegetation dynamics in mountain regions.

1. Introduction

Mountain regions are characterised by complex and heterogeneous landscapes resulting from topography, geology, climatic contexts and human activities (Beniston, 2006, 2016; Körner et al., 2011). The combined influences of climate change and land use over the last thousand years have accentuated these heterogeneous patterns (Houghton et al., 2001; Lamprecht et al., 2018; Steinbauer et al., 2018). Understanding the dynamics of human versus climate influences on vegetation over centuries to millennia is crucial for assessing tipping points and predicting future environmental trends, in particular in the current context of the ongoing climate warming and land cover changes

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(Beniston, 2006; Graumlich, 1994; Pauli and Halloy, 2019). More specifically, interactions between climate change and human activities in mountains affect and modify the altitudinal distribution of socio-ecosystems (Bahn and Körner, 2003; Körner et al., 2011; Lamprecht et al., 2018; Steinbauer et al., 2018).

To assess environmental changes from a long-term perspective, palaeoecological studies have already been carried out in the European Alps over the last fifty years. These palaeoecological studies have used biological proxies such as pollen, Non Pollen Palynomorphs (e.g. fungi spores), environmental DNA, and charcoal analyses to reconstruct past vegetation dynamics and/or to assess past agro-pastoral activities (Carcaillet and Blarquez, 2017; Garcés Pastor et al., 2022; Genries et al., 2009; Giguet-Covex et al., 2023; Hafner and Schwörer, 2018; Walsh and Giguet-Covex, 2020; Wick and Tinner, 1997). Several of these palynological studies have shown similar regional vegetation trends such as the expansion of spruce between 6000 and 4000 cal. BP in the western European Alps (Henne et al., 2011; Latałowa and van der Knaap, 2006; van der Knaap et al., 2005). This spruce expansion replaced the previous dominance of fir, though the underlying causes remain unclear (de Beaulieu et al., 1993; Pini et al., 2017; Schwörer et al., 2015). Local disparities are further observed, mainly resulting from human activities over the last five millennia. Agro-pastoral activities have developed unevenly across the Alps since the Neolithic period (Giguet-Covex et al., 2023; Walsh and Giguet-Covex, 2020), becoming more widespread and generalised during the Bronze Age, especially at high altitudes (Finsinger and Tinner, 2007; Giguet-Covex et al., 2023; Stahli et al., 2006; Thöle et al., 2016; Walsh et al., 2007). In the North-Western Alps, these activities intensified until the Roman Period. Several phases of anthropization can then be observed from the end of the Roman period to the modern times, leading to different phases of landscape opening. Human influences on the landscapes spread spatially and reached their highest intensity in the High Middle Ages (Giguet-Covex et al., 2023). While general regional trends can be observed, there are also regional and local differences, especially when a higher temporal resolution is considered.

Although pollen analyses provide valuable insights into past dynamics of mountain vegetation, the spatial resolution of these reconstruction remains unclear. Pollen grains can disperse over long distance across various altitudinal belts (Fall, 1992), resulting in a mix of regional and local pollen sources when untransformed pollen data are used. Quantitative pollen-based modelling has been a primary goal for palynologists since the 1960s aiming to translate pollen counts into estimates of plant cover at specific spatial scales (Andersen, 1970; Davis, 1963; Parsons and Prentice, 1981; Prentice and Parsons, 1983; Sugita, 1994).

Today, the Landscape Reconstruction Algorithm (LRA) is the soundest approach to achieving quantitative reconstruction of plant abundance as it corrects the non-linear pollen–vegetation relationship (Sugita, 2007a, 2007b). The LRA approach corresponds to a two-step process to account for inter-taxonomic variations in pollen production, dispersal, and deposition mechanisms. The LRA provide estimates of plant abundance at a regional scale (REVEALS-Regional Estimates of Vegetation Abundance; Sugita, 2007a) and at a local scale (LOVE-Local Vegetation Estimates; Sugita, 2007b).

The performance of REVEALS has primarily been assessed in North America (Sugita et al., 2010) and in northern European lowland regions, including Sweden (Hellman et al., 2008a, 2008b; Trondman et al., 2016), Denmark (Nielsen and Odgaard, 2010), Estonia (Poska et al., 2018) and Switzerland (Soepboer et al., 2010), using modern and historical data. More recently, the reliability of the LRA and REVEALS has been evaluated in western Norway (Hjelle et al., 2015) and in the French Pyrenees (Marquer et al., 2020a; Plancher et al., 2022). However, these studies are based on a limited number of sites and do not fully account for the heterogeneity of mountain landscapes, although Marquer et al. (2020a) suggested that REVEALS should be tested across a variety of sites situated in different contexts (e.g. varying valleys and altitudes).

The major challenge when applying REVEALS in mountain regions is to carefully consider the initial model assumptions, as there are many factors that cannot be corrected by REVEALS so far, e.g. sedimentary processes affecting pollen deposition, surface roughness of vegetation, patchiness of vegetation, topography, heights of pollen source and atmospheric and animal pollen dispersal (Sugita, 2007a).

The present study aims at testing the influence of different variables on the REVEALS outputs; in particular specific input parameters (e.g. wind speed, entomophilous taxa, and maximum spatial extent of regional vegetation) and site characteristics (i.e. number of sites and location of sites in the different vegetation belts). Many of these factors are important for the application of REVEALS in mountain regions (e.g. Fall, 1992; Leunda et al., 2017; Markgraf, 1980; Marquer et al., 2020a), as they are likely to affect the palaeoecological reconstructions based on the REVEALS model.

The present study evaluates the performances of the REVEALS model by using pollen counts from top sediment cores collected in lakes and bogs, along with modern vegetation maps and botanical surveys in a region of ca. 50 km radius situated in the North-Western Alps (Fig. 1). Our objectives are: i) to identify the strengths and weaknesses of applying the REVEALS model to pollen data from mountainous areas; ii) to test the effect of site selection (altitudes of the sites, types of sedimentary basin and number of sites) and parameter setting (wind speed) on REVEALS-model estimates of regional plant abundance; iii) to compare REVEALS-based estimates to untransformed pollen data; and iv) to provide recommendations for applying REVEALS to reconstructing past plant cover in mountain regions.

The locations of lakes and bogs sampled to test the performance of REVEALS are shown, in combination with the present vegetation map. Pollen samples collected in lakes are represented by dots and samples collected in bogs by triangles. The correspondence between pollen sites and labels shown in the figure is given in Table 1. The vegetation map has been created by combining information from CNRS vegetation map, CBNA habitat map, the CORINE Land Cover, and inventories (IFN) and botanical surveys (more general than an inventory and on a smaller scale) (CBNA, ASTER). For more details, see method section.

2. Materials and methods

2.1. Study area

The study area is located in the North-Western Alps, encompassing an area of 50 km radius that includes Lake Léman in the north part, Lake Annecy in the southwest, and the Mont-Blanc Massif in the southeast. This area is mostly located in France but also extends into Switzerland and Italy. In the foreland area where the large peri-alpine lakes Annecy and Léman are located, the relief is not very pronounced and the landscape is characterised by urban areas, cereal crops and hay meadows. Then, moving south-east, the subalpine massifs of Chablais, Haut-Giffre, Bauges and Bornes-Aravis are present in France and the Valaisanne Alps in Switzerland. The Aiguilles Rouges and Pormenaz subalpine massifs in France are in a more internal position, leading to upper altitudes.

These subalpine massifs, are mostly covered by mixed or coniferous forests and, in the upper parts by grasslands, heathlands and bare rocks. The collinean zone (<800 m) consists of deciduous forests dominated by *Quercus, Corylus, Carpinus, Acer, Fraxinus* and *Fagus*. In the montane belt (<1600 m), deciduous forests are gradually replaced by mixed *Fagus* and *Abies* forest dominated by *Fagus, Acer, Betula, Corylus, Picea* and, to a lesser extent, *Abies*. The herbaceous plant taxa are dominated by Rubiaceae. The lower subalpine belt (<1800 m) is characterised by coniferous forest, mainly dominated by *Picea* and Ericaceae in the herbaceous stratum. Up to the tree line, in upper subalpine to lower alpine belts, grassland and heathland dominate the landscape, with some meadows. The grasslands and meadows are mainly composed of Poaceae, Cyperaceae, Asteraceae and Apiaceae, and the heathlands are mainly made up of Ericaceae (*Vaccinium myrtillus, Rhododendron ferrugineum*) and *Juniperus*. *Picea, Betula* and *Salix* also occur in some parts of

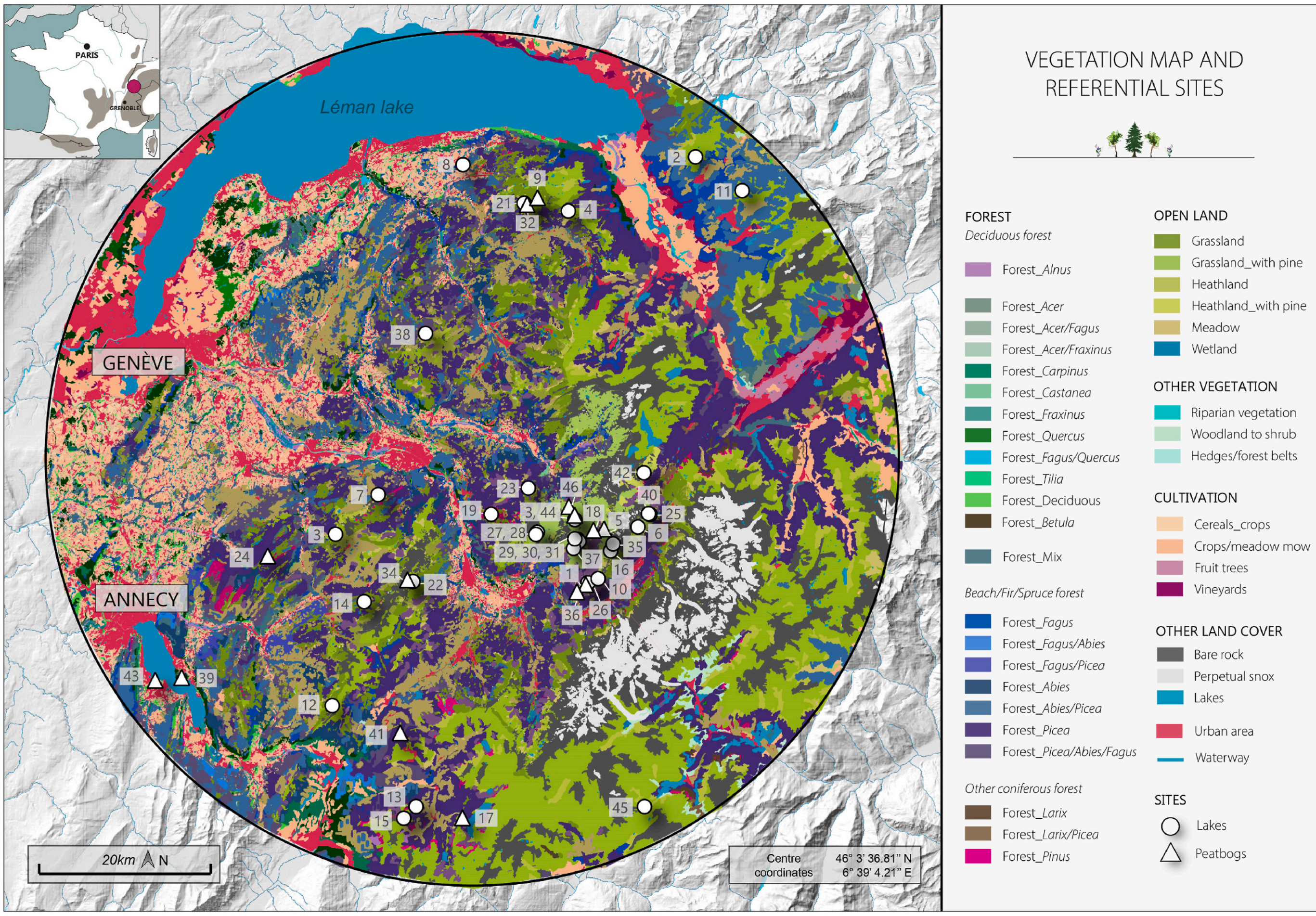

Fig. 1. Study region in the French Alps.

these vegetation belts. In the upper alpine and nival belts (>2300 m) bare rocks and leptosols dominate, with some herbaceous taxa such as Saxifragaceae, Asteraceae Asteroïdeae, Ranunculaceae, *Androsace*, *Sempervivum* and small shrubs such as *Salix herbacea* and *Salix retusa*.

The Grées Alps in Italy, part of the internal Alps, are dominated by grasslands and bare rocks. In Switzerland, the upper Rhone Valley is characterised by extensive vineyards and orchards.

2.1.1. *Sites selection and coring*

One of the assumptions of the REVEALS model is that the pollen records are from large lakes. There are no large lakes (>50 ha) in the study area for the application of REVEALS. Trondman et al. (2016) have shown that a combination of small lakes and/or bogs can be used for the model runs. Note that the number of study sites is important for the use of REVEALS, in particular in mountain regions (Marquer et al., 2020a; Plancher et al., 2022). Therefore, for the model runs we have selected a large number of sites situated in various environmental and topographical contexts and vegetation belts. Unfortunately, the Chablais Massif, located in the Northern part of the study area, has few lakes and bogs, which means that there are fewer suitable sites in this part of the region. A total of 45 sites were cored: 16 bogs and 29 lakes. Surface sediment sequences were collected using an Uwitec gravity corer for lakes and a Russian corer for peat bogs. Twenty-eight sites were cored in 2021 (coring information is available on the "Cybercarotheque"[1] website under the MODALP project), and the other nineteen sites were cored prior to the present study, between 1992 and 2021. Seven of these sites have already been analysed for pollen analysis: GLI (Julien et al., Under Review), LAO, LAOB (Giguet-Covex et al., Under Review), BEN (Bajard et al., 2018), VER (Bajard, 2017), GERS (Bajard et al., 2020) and ANT. The data for Lake Aï (van der Knaap et al., 2000) and Lake Bretaye (Thöle et al., 2016) are from the Neotoma database, and the data for the Saint-Jorioz peat bog was provided by the authors (Magny et al., 2022).

These sites are distributed along an altitudinal gradient from 450 m to 2505 m of altitude (Fig. 1) and have a radius area of 0,05 ha–190 ha (Table 1). The radius area of the sites corresponds to the radius of a defined circle containing the two extremities of the basin. Most of the sites have a radius less than 10 ha. It is important to note that the largest sites correspond to peat bogs.

2.1.2. *Core chronology: A multi-method approach*

In similar studies, modern samples are collected at the very top of the core, i.e. the last few centimeters of sediment (Hellman et al., 2008b; Herzschuh et al., 2010; Theuerkauf et al., 2013; Zhao and Herzschuh, 2009). In the European Alps, sedimentation rates can vary significantly from one site to another. Under these conditions, it is essential to collect samples with a similar date. In order to obtain robust data on current vegetation (i.e. maps and botanical surveys) various sources of data have been used covering the last 50 years. The data from pollen top cores also focus on the last five decades, which also corresponds to a period relatively stable in terms of vegetation cover. Indeed, the reforestation dynamic partly due to the agricultural decline mostly occurred between the 50's and 70's (e.g. Elleaume et al., 2022). Note that the core dating does not allow to work with a more precise temporal resolution.

To select modern samples, we used a protocol based on a non-

[1] https://cybercarotheque.fr/index.php?mission=&date1=&date2=&projet=MODALP&carotte=&repository=&recherche=Rechercher.

Table 1
Study sites information.

Site number	Label	Type of site[a]	Site name	GPS Coordinates (Decimal degrees DD)		Massif	Year of coring	Altitude (m)	Vegetation belt*	Site area (ha)	Site radius (ha)	Reference
1	AHOU	Lake	Aiguillette des Houches	45,924822	6,8115	Aiguilles Rouges	2021	2211	Subalpine	0,37	0,96	this paper
2	AI	Lake	Aï	46,363928	7,00506	Valaisannes	1992	1893	Subalpine	0,91	1,72	van der Knaap et al. (2000)
3	ANT	Lake	Anterne	45,991301	6,79691	Haut-Giffre	2007	2059	Subalpine	11,14	37,91	this paper
4	ARV	Lake	Arvouin	46,314103	6,80962	Chablais	2015	1668	Subalpine	2,96	5,08	this paper
5	BAL	Small bog	Balme	45,980199	6,83972	Aiguilles Rouges	2018	1894	Subalpine	0,09	0,25	this paper
6	BAR	Lake	Blanc	45,981484	6,89094	Aiguilles Rouges	2008	2356	Alpine	1,98	4,49	this paper
7	BEN	Lake	Benit	46,027572	6,50467	Bornes-Aravis	2014	1451	Montane	4,11	7,50	Bajard et al. (2018)
8	BEU	Lake	Beunaz	46,367685	6,65492	Chablais	2021	955	Montane	1,58	3,49	this paper
9	BIS	Small bog	Bise	46,329318	6,7644	Chablais	2021	1498	Montane	6,31	20,24	this paper
10	BRE	Lake	Brevent	45,929068	6,82733	Aiguilles Rouges	2012	2130	Subalpine	2,46	5,00	this paper
11	BRET	Lake	Bretaye	46,326147	7,07195	Valaisannes	2012	1774	Subalpine	4,43	8,62	Thöle et al. (2016)
12	CHAR	Lake	Charvin	45,808877	6,4227	Bornes-Aravis	2021	2011	Subalpine	1,06	1,87	this paper
13	CLOU	Small bog	Clou	45,701239	6,54045	Beaufortain	2021	1713	Subalpine	0,22	0,48	this paper
14	CONF	Lake	Confins	45,915959	6,47586	Bornes-Aravis	2021	1358	Montane	4,21	6,98	this paper
15	CORB	Lake	Corbeau	45,6884	6,52317	Beaufortain	2021	1905	Subalpine	0,03	0,05	this paper
16	CORU	Lake	Cornu	45,957994	6,84793	Aiguilles Rouges	2019	2276	Alpine	6,42	15,14	this paper
17	CPRE	Small bog	Col du pre	45,686529	6,60868	Beaufortain	2021	1720	Subalpine	1,18	2,59	this paper
18	ECU	Small bog	Ecuelles	45,97864	6,82422	Aiguilles Rouges	2010	1889	Subalpine	2,28	8,34	this paper
19	FLA	Lake	Flaine	46,001496	6,67284	Haut-Giffre	2021	1416	Montane	4,97	13,34	this paper
21	FONT	Lake	Fontaine	46,323419	6,74337	Chablais	2021	1338	Montane	0,61	3,65	this paper
22	FOUR	Lake	Fours	45,935014	6,54997	Bornes-Aravis	2021	2032	Subalpine	0,13	0,23	this paper
23	GERS	Lake	Gers	46,026794	6,72927	Haut-Giffre	2016	1530	Montane	5,36	10,59	Giguet-Covex et al. (unpublished)
24	GLI	Large bog	Glieres	45,967687	6,33671	Bornes-Aravis	2021	1415	Montane	20,86	190,14	Julien et al
25	GOLL	Small bog	Golliet	45,993444	6,91121	Aiguilles Rouges	2021	2065	Subalpine	0,08	0,41	this paper
26	HOU	Small bog	Houches	45,923191	6,80904	Aiguilles Rouges	2021	2119	Subalpine	0,36	0,91	this paper
27	LAO	Lake	Laouchets	45,978698	6,74014	Haut-Giffre	2018	2133	Subalpine	0,29	0,69	this paper
28	LAOB	Lake	Laouchets bis	45,977342	6,73846	Haut-Giffre	2018	2137	Subalpine	0,63	1,30	Giguet-Covex et al. (In press)
29	LAOU1	Lake	Laouchet1	45,970558	6,79783	Haut-Giffre	2021	1945	Subalpine	0,30	0,94	this paper
30	LAOU2	Lake	Laouchet2	45,969851	6,80076	Haut-Giffre	2021	1959	Subalpine	0,08	0,16	this paper
31	LAOU3	Lake	Laouchet3	45,968773	6,8015	Haut-Giffre	2021	1969	Subalpine	0,16	0,23	this paper
32	LECH	Small bog	Lechere	46,322222	6,74742	Chablais	2021	1344	Montane	7,14	24,50	this paper
33	LES	Lake	Lessy	45,98733	6,43814	Bornes-Aravis	2021	1735	Subalpine	5,88	18,73	this paper
34	MAU	Small bog	Chalets de Maury	45,935645	6,54379	Bornes-Aravis	2021	2010	Subalpine	0,84	1,73	this paper
35	NOR	Lake	Noir	45,963982	6,85241	Aiguilles Rouges	2012	2498	Alpine	1,82	6,62	this paper
36	PEU	Small bog	Peutets	45,915349	6,79229	Aiguilles Rouges	2021	1635	Subalpine	0,46	3,10	this paper
37	PMZ	Lake	Pormenaz	45,962408	6,79397	Haut-Giffre	2006	1945	Subalpine	4,36	7,00	this paper
38	PTZ	Lake	Petetoz	46,193585	6,5876	Chablais	2021	1433	Montane	0,44	0,72	this paper
39	RDC	Small bog	Roc de chere	45,844242	6,1990	Bornes-Aravis	2021	595	Collinean	0,90	3,58	this paper
40	RMZ	Lake	Remuaz	45,994187	6,9077	Aiguilles Rouges	2021	2150	Subalpine	0,26	0,36	this paper
41	SAI	Large bog	Saisies	45,777558	6,52155	Beaufortain	2021	1568	Montane	34,50	118,26	this paper
42	SAS	Small bog	Gouille du Sassey	46,036999	6,90379	Aiguilles Rouges	2021	1955	Subalpine	0,34	0,81	this paper

(continued on next page)

Table 1 (*continued*)

Site number	Label	Type of site[a]	Site name	GPS Coordinates (Decimal degrees DD)		Massif	Year of coring	Altitude (m)	Vegetation belt*	Site area (ha)	Site radius (ha)	Reference
43	SJZ	Large bog	Saint-Jorioz	45,842808	6,16194	Bauges	2018	450	Collinean	22,80	99,06	Magny et al. (2022)
44	TANT	Small bog	T.Anterne	45,995239	6,79747	Haut-Giffre	2021	2079	Subalpine	3,54	8,26	this paper
45	VER	Lake	Verney	45,688118	6,8817	Grées	2012	2088	Subalpine	20,62	34,42	Bajard (2017)

This table presents the study sites with their main characteristics.
[a] Site characteristic whose influence is being analysed.

destructive method to date the upper part of cores using modern lead pollution peaks detected by X-ray fluorescence measurements (Avaatech Core Scanner) (https://doi.org/10.13140/RG.2.2.26109.95202). Based on lead measurements in natural archives, several studies have shown significant and well-dated episodes of atmospheric lead pollution since the beginning of the 20th century (Arnaud et al., 2004; Bindler, 2011; Boutron et al., 1991; Moor et al., 1996; Rosman et al., 2000; Shotyk et al., 1996). Older pollution are also clearly identified by numerous studies, particularly in the French Alps, Switzerland and Greenland, during the Medieval and Roman periods due to the development of important lead mining activities at those times (Giguet-Covex et al., 2011; Hong et al., 1994; Shotyk et al., 1996, 1998). These lead contamination phases will be used within this study to add some chronological markers for the top core deposits. All cores were first described to characterize the lithology and especially to identify instantaneous deposits which can often occur in mountain lakes due to flood events, avalanches, earthquakes, etc. The cores were then analysed by X-ray fluorescence using an XRF Core Scanner (Avaatech) to get high resolution and continuous measurements of lead as well as other the elements to assess the geochemical composition of the sediment. The Pb signal, Pb/Rb ratio (to eliminate particular inputs from the geological substratum) and Pb/Br ratio (to eliminate affinities of lead to organic matter) were then compared with three selected “reference curves”, Anterne (Arnaud et al., 2004), Mont-Rosa (Gabrieli and Barbante, 2014) and Mont-Blanc (Rosman et al., 2000), to identify three landmarks in the history of lead pollution: (1) the marked increase in atmospheric lead pollution due to coal burning at the onset of the second industrial revolution around 1900 CE; (2) the rise around 1950 CE, mostly due to increased use of leaded gasoline; and (3) the peak in 1973 CE, i.e. just before the oil crisis, which is the most easily identifiable landmark (Fig. 3). Based on these chronological markers, the sedimentation rates were calculated to assess the reliability of the chronologies, considering the sediment composition and associated formation processes. For instance, minerogenic sediments are expected to yield higher sedimentation rates than organic sediments, after compaction (i.e. excluding the water content). This protocol was applied to most sites (24 out of 31) (Fig. 3, Appendix A - Figure A2 a and b, Table A2). However, seven sites (FONT, CPRE, BAL, CORB, CONF, CLOU, LECH) did not show enough structured lead signals to be compared with the “reference curves”. However, for six of the sites some trends may correlate with the 20th century lead pollution increase. Only one site (LECH) clearly shows no trend; in this case a surface sample was collected following the previous methods.

For each core, two samples covering approximately the same 10 to 20-year time resolution. The time periods (ages and durations) corresponding to these samples are described in the appendices (Appendix A, Table A2.). The first sample was mostly collected in the period post 1973 CE and the second between 1970 CE and 1950 CE. For only five sites, in which the sedimentation rates were too low, a single sample was taken, covering the period from 1950 CE to the present. Only the first sample, corresponding to the period after 1973 CE, was used to apply the REVEALS model (Fig. 2). Except 3 ″outliers” (at 2, 4 and 30 years), these samples represent between 5 and 27 years (median 17 years), from 1973 to 2021 (Appendix A, Table A2.). They are considered representative of the period 2021–1973, which also corresponds to the current vegetation data used to produce the current vegetation mapping.

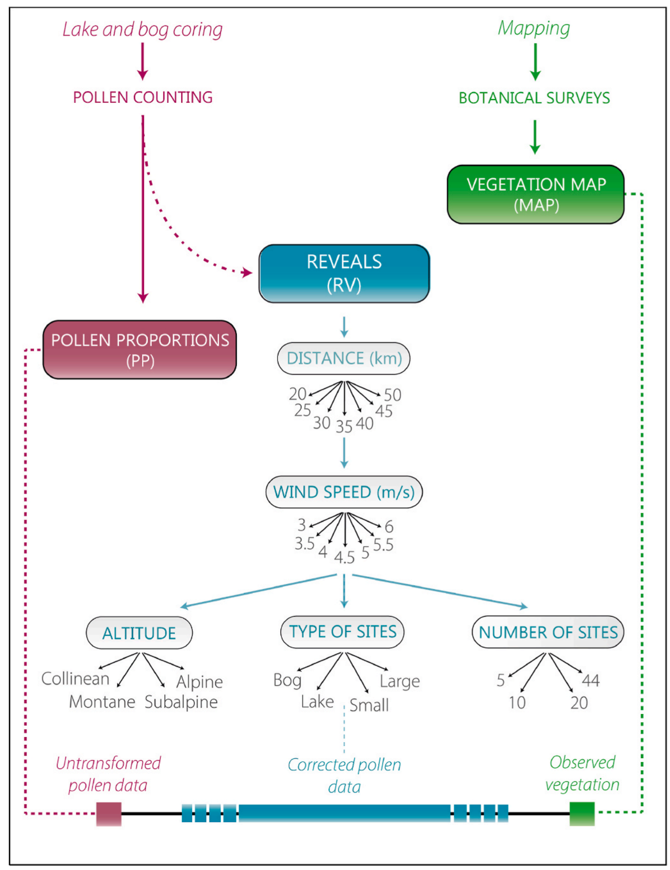

Fig. 2. Flow chart of the methodological approach.

The second sample was used as an independent validation of the chronologies. In this region of the Alps, agricultural decline, mountain land restoration laws and global warming, led to a phase of reforestation which was particularly significant from the 50’s to the 70’s and lasted until today. This phenomenon is visible in all the sequences of the region (Bajard et al., 2015, 2017, 2018; David, 2010a, 2010b; Elleaume et al., 2022; Messager et al., 2022; Thöle et al., 2016). The sequences are expected to show similar or increased proportions of arboreal pollen in the upper sample.

This figure presents some of the Pb/Rb ratio results obtained from X-ray fluorescence analysis (Avaatech Core Scanner) for 12 coring sites out of 31. The two different markers of the history of lead pollution are identified for each of them (A): In yellow, the increase in atmospheric lead pollution from the second industrial revolution around 1900 CE; in green, the second rise around 1950 CE; and in pink, the peak at 1973 CE.

Six sites (FONT, CPRE, BAL, CORB, CONF, and CLOU) show an increasing trend at the top of the core (panel B), which may be

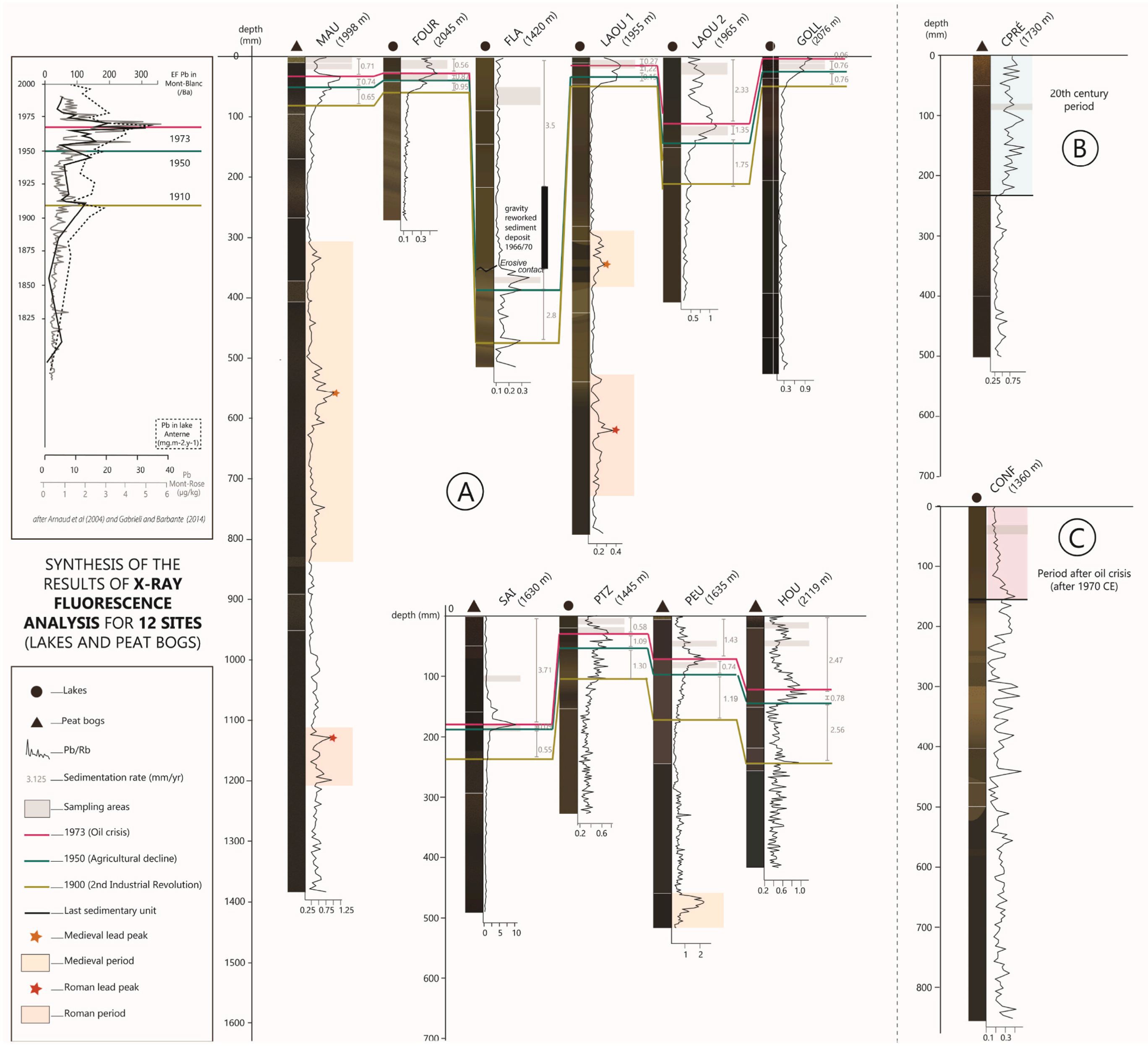

Fig. 3. Synthesis of the Pb/Rb results from X-Ray fluorescence analysis.

associated with the increase in the 20th-century. Category (C) shows a decreasing trend of the Pb/Rb ratio, which could correspond to the decrease after the oil crisis.

All the sedimentation rates calculated between each period identified with the lead signal are also indicated in grey. Grey rectangles indicate the samples taken in each core.

2.2. Observed vegetation data – (MAP)

A current vegetation map has been created for the study region to compare REVEALS estimates to the observed vegetation (https://doi.org/10.48579/PRO/8YH0AN) (Fig. 2). As highlighted in numerous studies, comparing pollen outcomes with observed vegetation is not straightforward (Hjelle et al., 2015; Nielsen and Odgaard, 2004; Poska et al., 2018). Precise vegetation data is crucial for evaluating the efficiency of REVEALS (Hjelle et al., 2015).

In the French Alps, there are several sources of spatial land cover data sets providing various levels of information, such as the CLC (Corine Land Cover) (European Union's, Copernicus Land Monitoring Service, 2022) or the "BD IGN Forest" (IGN – Inventaire forestier national français, 2018) database. Although these maps provide homogeneous information on a large scale (Europe or France), they do not have sufficient resolution for the categorisation of vegetation types (broad categories such as coniferous forest or deciduous forest, with no indication of the dominant species). The uncertainties in such maps further increase when one looks at a local scale. Therefore, for the local scale we used habitat maps that have been produced for specific areas of our study region by the National Nature Reserves (RNN) and the Alpine National Botanical Conservatory (CBNA). As mentioned above, part of the area located in Italy and Switzerland required additional spatial data to complete the CLC information. Although these spatial datasets offer varying degrees of details, none provide homogeneous and precise data at the required scale for comparison with pollen data.

The vegetation map created for the present study (https://doi.org/10.48579/PRO/8YH0AN) considers 55 land cover types related to vegetation and pollen production (46 more than the CLC), and 7 land

Table 2
Set of RPP values.

Pollen type	Code name	Land cover type	RPP	SE	FSP	Source
Abies	Abies	Coniferous forest	6875	1442	0,12	Githumbi et al. (2022)
Acer	Acer	Deciduous forest	0,800	0,23	0,056	Githumbi et al. (2022)
Alnus	Alnus	Deciduous forest	13,562	0,293	0,02	Githumbi et al. (2022)
Apiaceae	Apiac	Open land	0,260	0,01	0,04	Githumbi et al. (2022)
Artemisia	Artemis	Open land	3937	0,146	0,03	Githumbi et al. (2022)
Asteraceae Asteroïdeae	Ast ast	Open land	0,100	0,01	0,03	Githumbi et al. (2022)
Asteraceae Cichorioïdeae	Ast cich	Open land	0,160	0,02	0,05	Githumbi et al. (2022)
Betula	Betula	Deciduous forest	5106	0,303	0,02	Githumbi et al. (2022)
Carpinus	Carpi	Deciduous forest	4520	0,425	0,04	Githumbi et al. (2022)
Castanea	Castan	Deciduous forest	3258	0,059	0,01	Mazier et al., unpublished
Cerealia	Cereal	Open land	1850	0,38	0,060	Githumbi et al. (2022)
Chenopodiaceae	Cheno	Open land	4280	0,27	0,02	Githumbi et al. (2022)
Corylus	Coryl	Deciduous forest	1710	0,1	0,03	Githumbi et al. (2022)
Cyperaceae	Cyperac	Open land	0,962	0,05	0,04	Githumbi et al. (2022)
Ericaceae	Ericac	Open land	0,070	0,04	0,04	Mazier et al. (2012)
Fagus	Fagus	Coniferous forest	5863	0,176	0,057	Githumbi et al. (2022)
Fraxinus	Fraxi	Deciduous forest	1044	0,048	0,02	Githumbi et al. (2022)
Juniperus	Junip	Coniferous forest	2070	0,04	0,02	Githumbi et al. (2022)
Picea	Picea	Coniferous forest	5437	0,097	0,056	Githumbi et al. (2022)
Pinus	Pinus	Coniferous forest	6058	0,237	0,03	Githumbi et al. (2022)
Plantago lanceolata	Pl lanc	Open land	2330	0,201	0,03	Githumbi et al. (2022)
Plantago media	Pl med	Open land	1270	0,18	0,02	Githumbi et al. (2022)
Plantaginaceae	Planta	Open land	1270	0,18	0,02	Githumbi et al. (2022)
Poaceae	Poac	Open land	1	0	0,04	Githumbi et al., 2022
Quercus	Quer	Deciduous forest	4537	0,086	0,04	Githumbi et al. (2022)
Ranunculaceae	Ranun	Open land	2038	0,335	0,02	Mazier et al., unpublished
Rubiaceae	Rubiac	Open land	3710	0,34	0,02	Githumbi et al. (2022)
Rumex	Rumex	Open land	3020	0,278	0,02	Githumbi et al. (2022)
Salix	Salix	Deciduous forest	1182	0,077	0,02	Githumbi et al. (2022)
Tilia	Tilia	Deciduous forest	1210	0,116	0,03	Githumbi et al. (2022)
Ulmus	Ulmus	Deciduous forest	1270	0,05	0,03	Githumbi et al. (2022)
Urtica	Urtica	Open land	10,520	0,31	0,01	Githumbi et al. (2022)

RPP (Relative Pollen Productivity) values used for the REVEALS runs with their associated standard errors (SE) and the Fall Speed (FSP) for each pollen type. These values mainly come from Githumbi et al. (2022) and Mazier et al., (unpublished). The RPP and FSP values for *Rumex*-type are taken from *Rumex acetosa t* (Githumbi et al., 2022). and those for *Plantaginaceae* from *Plantago media. Plantaginaceae* is a pollen type that corresponds mainly to unidentified grains of *Plantago*-type. In our area, the *Plantago* species are mainly *Plantago lanceolata, Plantago media* and *Plantago alpina*. The *Plantago media* values were taken for the *Plantaginaceae*, as they are intermediate between those of *Plantago lanceolata* and *Plantago alpina*.
The code name of each pollen type, which will be used for the analyses of the study, is presented as well as the classification of each pollen type in the land cover types. The shaded cells correspond to pollen types that were excluded for the model runs.

cover types that assume to do not produce pollen (such as bare rock, lakes, urban areas, etc.) For creating the map different maps have been combined such as the Corine Land Cover, the CNRS vegetation maps and the CBNA habitat map. Complementary information from the National Forest Inventory (IFN) and botanical surveys archived and partly produced by the CBNA and Aster-CEN73 (Conservatory of Natural areas) was also used. All areas associated with these vegetation categories were calculated using QGIS software (QGIS.org, 2023). In addition, a botanical composition was associated with each vegetation map category, with an abundance value for each of the 32 pollen types we used in this study. Plant compositions were derived from approximately 5000 phytosociological surveys carried out in the area; Braun-Blanquet abundances were transformed for each taxon according to the vegetation stratum (arboreous, sub-arboreous, shrubby, sub-shrubby, herbaceous), where available. Each botanical survey was associated to a vegetation map category and an average proportion for each taxon was calculated for each vegetation category. A R script (Binet, Unpublished) was applied to transform the abundances of each taxon for each category into an abundance of each taxon for the whole area (https://doi.org/10.48579/PRO/8YH0AN).

2.3. Pollen analysis (PP)

The 1 cm^3 samples were processed according to standard procedures (see Faegri and Iversen, 1989). The procedures involved decarbonation using HCl and KOH baths, treatment with HF to digest silica particles, and acetolysis. Samples were mounted in glycerol and counted using a Leica DM 1000 LED microscope at 400× magnification to the lowest taxonomic level using pollen identification keys (Beug, 2004; Reille, 1992, 1995, 1998) and the EDYTEM pollen reference collections. A minimum of 1000 pollen grains per pollen sample were counted for most samples, except for SAI, FONT, GLI, LAO, LAOB, BEN, VER, GERS, ANT, BRET, AÏ and SJZ, for which the pollen counts were obtained from other studies or because there was not enough pollen in each sample.

A total of 98 terrestrial pollen types were identified, and 29 of them were used for data analysis (Table 2) due to the integration of several pollen taxa into pollen types (e.g. *Thalictrum* into Ranunculaceae).

The Pollen Proportions (Pollen percentages, hereafter PP) were calculated based on the pollen sum of the 29 selected pollen types.

2.3.1. REVEALS (RV)

The REVEALS version *LRA. reveals.v6.2.5. exe* (Sugita, 2007a) was used for the model runs. REVEALS was applied with neutral and stable atmospheric conditions with fixed values for vertical and horizontal diffusion coefficients and turbulence parameters (Jackson and Lyford, 1999; Sugita, 2007a; Sutton, 1953; Tauber, 1965), with the exception of wind speed, for which we have tested different scenarios. The GPM (Gaussian Plume Model) dispersion model was used to assess the pollen dispersal. Theuerkauf et al. (2016, 2013) suggested that a LSM (Lagrangian Stochastic Model) dispersal modelling scheme (Kuparinen et al., 2007) might better estimate long-distance pollen transport than a GPM model. However, due to limited availability of RPP (Relative Pollen Productivity) values in our area based on LSM modelling, the LSM model was not utilized to assess pollen dispersal mechanisms in our study. Further discussion on the advantages and disadvantages of using LSM or GPM as a dispersal modelling scheme can be found in Marquer et al.

(2020b).

The radius of each lake and bog corresponds to that of a circle enclosing the two further extremities of the basin. These values were calculated using the "Minimum enclosing circles" function in QGIS.

Thirty-two pollen types were selected for the present study, see Table 2. For Ericaceae the corresponding Relative Pollen Productivity (RPP) values with their related standard errors and the fall speed of pollen (FSP) are from Githumbi et al. (2022) and Mazier et al. (2012). Note that Cyperaceae, Asteraceae Cichorioïdeae and Asteraceae Asteröideae were removed for the model application due to unreliable results based on the first REVEALS runs (Appendix B, Figure B1) and so only 29 taxa were used; REVEALS estimates including these pollen types differed too much from the observed vegetation. Cyperaceae are growing directly on the basin site (lake or bog), which is likely to affect the REVEALS outcomes in estimating the regional plant cover, i.e. over-estimation of the local vegetation component. Regarding Asteraceae Cichorioïdeae and Asteröideae, these pollen types are dispersed by insects. REVEALS assumes that all pollen grains should come to the sedimentary basin by wind transportation (Sugita, 2007a), and such deviation of model departures is likely to increase the biases when one compares REVEALS estimates to observed vegetation maps. Trondman et al. (2015) and Githumbi et al. (2022) already excluded entomophilous taxa such as Asteraceae, *Potentilla, Leucanthemum, Ranunculus acris t.*, Rubiaceae and Ericaceae. In contrast, Serge et al. (2023) shows that excluding or considering entomophilous taxa do not change significantly the REVEALS estimates at the European scale. In mountain regions, some entomophilous plant families such as Ericaceae are an important component of the regional and local vegetation. Therefore, as in Marquer et al. (2020b) and Plancher et al. (2022) a selection of entomophilous taxa has been used for the runs (see Table 2).

2.3.2. Evaluation of input parameters

2.3.2.1. Spatial extent of the regional vegetation. The Zmax value corresponds to the maximum distance within which most of the pollen of the regional vegetation originates (Sugita, 2007a). Most studies have set the Zmax at 50 km (Githumbi et al., 2022; Marquer et al., 2014, 2017, 2020a; Serge et al., 2023; Trondman et al., 2015), as the majority of pollen grains originate within this radius (Hellman et al., 2008b). However, in the Pyrenees mountain region, the Zmax was set at 25 km, in order to exclude cultivated areas in the most remote lowlands (Plancher et al., 2022). We have here tested a range of Zmax values from 20 km to 50 km with 5 km intervals to assess how the Zmax influences the REVEALS reconstructions (Fig. 2, Appendix B, Figure B2, Table B1).

2.3.2.2. Wind speed. The REVEALS model was generally applied assuming neutral atmospheric conditions and a wind speed of 3 m s^{-1} (Sugita, 2007a). In the present study, we tested the effect of the wind speed; wind speed is an important variable in mountain regions (Markgraf, 1980). The previous studies that have tested the effect of wind speed on the REVEALS outcomes (Nielsen and Sugita, 2005; Soepboer et al., 2010; Zhang et al., 2021) have shown that this variable influences the REVEALS estimates for pollen types characterised by long-distance transportation (Nielsen and Sugita, 2005), in particular heavy and large pollen such as *Abies* and *Fagus* (Soepboer et al., 2010; Zhang et al., 2021). *Abies* is one of the most important pollen types in the study region, especially for past land cover reconstructions (e.g. de Beaulieu et al., 1993; Pini et al., 2017; Rey et al., 2013; Schwörer et al., 2015). Here we have tested different wind speeds every 0.5 m s^{-1}, ranging from 3 to 6 m s^{-1} (Fig. 2), based on the previous study by Zhang et al. (2021). These values are based on the actual wind speed in the study region (Appendix A, Figure A5). The average of the annual maximum values of wind speed is 6.22 m s^{-1}, while the minimum value is 0.79 m s^{-1}. Average calculations are based on the values for each month of pollen production (January to September). The mean value of wind speed between the maximum and minimum values is 3.51 m s^{-1}. However, there do not seem to be important variations from one month to the next, except for the first three months of the year in the highest mountain ranges (Mont-Blanc, Aiguilles Rouges, Haut-Giffre) (Appendix A, Figure A5). The wind speed with the most accurate results was selected for final analyses.

2.3.2.3. Vegetation belts. As mentioned above, the 44 sites are distributed along four altitudinal belts from 450 m in the collinean belt to 2505 m in the alpine belt (Appendix A, Figure A1). They have been grouped according to their vegetation belt. The sites below 800 m correspond to the collinean belt (3 sites), the sites between 800 and 1600 m to the montane belt (11 sites), the sites between 1600 and 2250 m to the subalpine belt (28 sites) and the sites above 2250 m to the alpine belt (2 sites); see Table 1.

REVEALS was then applied to each of these four altitudinal ranges (Fig. 2). Note that in the alpine belt there are only lakes and in the collinean belt there are only bogs. In the subalpine belt there are 19 lakes and 9 bogs and in the montane belt, 7 lakes and 4 bogs.

2.3.2.4. Site characteristics. To test the effect of the basin type, sites were categorised based on their nature (lakes or bogs) and size (small or large). The threshold between a small and a large site is defined at 50ha (Sugita et al. (2010) and Trondman et al. (2015). Note that the categorisation of sites as large or small depends on how the radius area has been calculated, e.g. circle including all extremities of the basin.

Five REVEALS scenarios have been tested: All Lakes (AL), Small Bogs (SB), Large Bogs (LB), All Small Lakes and Bogs (SLB), All Bogs (AB) (Fig. 2). In addition, the effect of exposure has been tested with three scenarios (north, north/south and south site exposure).

2.3.2.5. Number of sites. To evaluate the impact of the number of sites, and in particular determine the minimum number of sites required for the REVEALS application, we randomly selected (using the random selection function in QGIS software) 10 sets of 5 sites, 10 sets of 10 sites, and 10 sets of 20 sites. REVEALS was subsequently applied to each of these 30 sets, and the results were compared to those obtained when REVEALS was applied to the full set of 44 sites (Fig. 2).

2.3.2.6. Land cover. The 29 pollen taxa were grouped into three main land cover categories (Table 2): coniferous forest, deciduous forest and open land. Sugita's programme (unpublished) based on the delta method and Monte Carlo simulation was used to calculate the standard errors for each land cover category.

2.3.3. Statistical analyses

2.3.3.1. Dissimilarity between MAP, RV and PP for all the parameters tested. A dissimilarity index was calculated using the squared chord distance method (Prentice, 1980) with the "squared_chord" function of the "Philenthropy" package (Drost, 2018) in R studio (Posit team, 2022). This index provides the calculation the dissimilarity between the different sets of data, i.e. RV, PP and MAP.

2.3.3.2. Dirichlet regression model: test of the significance of similarities in vegetation assemblages for different Zmax. The Dirichlet regression model ("DirichletReg" package developed in Rstudio) was used to test the significance of the variation in pollen taxa abundance in relation to different Zmax. This model provides an evaluation of the influence of an explanatory variable (i.e. spatial extent) on the response variables (i.e. each taxon), independently of the REVEALS, PP and MAP results. The taxon with the lowest variability (lowest standard error) was selected (*Urtica* for REVEALS, *Plantago media* for MAP, *Acer* for PP) as a response variable for comparison with the other response variables.

2.3.3.3. Non-metric multiDimensional scaling (NMDS) analyses. Non-Metric Multidimensional scaling analyses, specifically designed to analyse ecological communities, were performed using the "metaMDS" function of the "Vegan" package in R studio to analyse the potential effect on REVEALS reconstructions of wind speed, altitude, basin type and number of sites. These analyses consider the ecological communities as a whole and highlight the proximity or otherwise of the samples in terms of vegetation composition. The NMDS ellipses were generated using the "ordiellipse" function in the "Vegan" package in R studio and represent the standard deviation of the samples for each group of sites (number of sites used: 5, 10 and 20). The NMDS analysis is an indirect (unconstrained) gradient analysis ordination method that involves only response variables. It is considered the most robust ordination analysis for studying this type of variable (Minchin, 1987).

2.3.3.4. Linear regression: evaluation of REVEALS performance. Linear regression analyses were performed to assess the performance of the REVEALS model in estimating plant covers compared to pollen proportions. The "ggmisc" package (Aphalo, 2024) in R Studio was used. The graphs were plotted using the 'stat_poly_line' function. Furthermore, the equation of the linear regression line and R^2 value were calculated using the 'stat_poly_eq' function.

3. Results

3.1. Pollen analysis of modern samples

All detailed results for the modern period (two modern samples, i.e. 1970 CE to present and 1950–1970 CE) are given in Appendix A (Figure A4). Results for the main taxa categories (coniferous, deciduous, shrubs and herbs) are given in Fig. 4. The results show that pollen assemblages are generally dominated by *Picea, Pinus, Alnus* and Poaceae (>10%). The proportion of *Fagus* is relatively low, except for seven sites (BEU, CHAR, CLOU, CONF, CORB, PTZ, LES) where its proportions range between 10 and 20%. Cyperaceae is also abundant, particularly for bogs. *Abies* proportions are quite low (<10%), except for two sites (>10% at BAL and >15% at SJZ). Pollen grains from Ericaceae are found in low proportions, below 5%, and are absent at several sites (AI, ARV, BIS, FLA, LAO, LECH, LES, MAU, SAI, and SJZ).

The pollen types categories (Fig. 4) indicate that most sites, except BIS, ECU, FLA, and LAOU3, have a higher abundance of Arboreal Pollen (AP) than NAP (Non-Arboreal Pollen) for the period post 1970 CE. Fifteen of the forty-four sites have modern pollen assemblages (1970 CE to present) dominated by deciduous taxa. This mainly corresponds to the high proportions of *Alnus*, and at a lesser extent to *Fagus* and/or *Corylus*. The shrub category has low proportion of Ericaceae.

The results are heterogeneous and highlight an inter-site variability in the study region, partly influenced by site exposure and vegetation belt (Fig. 4). As an example, sites with the highest proportions of herbaceous taxa are mostly subalpine sites with southern exposure.

Although most sites show a high ratio of AP/NAP, this ratio is lower for the time period 1970–1950 CE) compared to the period post 1970 CE, except for five sites, BRE, LECH, PMZ, LAOU3 and PTZ, where the ratio is higher in the period 1970–1950 CE, in particular for LAOU3. In more than 80% of cases, our hypothesis for the validation of the chronology, which consists of a higher percentage of forest categories indicating the reforestation phase around the middle of the 20th century, is fulfilled. For the four sites, where the results are quite similar, we cannot rule out that an uncertainty in the dating could occur. To maximize the likelihood of obtaining the most recent samples for the model evaluation, the first sample corresponding to the period after 1970 CE was used for each of these sites (BRE, LECH, PMZ, LAOU3 and PTZ).

3.2. Spatial extent of the REVEALS estimates (Zmax)

We conducted a Dirichlet regression analysis (Appendix B, Figure B2) to assess the extent to which different Zmax values (from 20 km to 50 km with 5 km intervals) impact the REVEALS outcomes. Generally, the abundance of plant taxa remains relatively stable with various Zmax values. The results of the Dirichlet regression indicate that variations in the proportions of each taxon obtained with REVEALS for different Zmax distances are not statistically significant. The spatial extent thus appears to have minimal effect on the REVEALS results. This finding is consistent with observations from previous studies and agrees with the observed vegetation. Indeed, for the REVEALS runs and therefore for the transformed pollen data, no pollen type appears to have abundances that change significantly (p-value >0.05) across the different Zmax values. However, the abundances of certain pollen types change significantly in the vegetation observed (MAP) across the radii selected (corresponding to the Zmax values). For only two pollen types (*Chenopodiaceae, Cerealia*) the variations are very significant (p-value <2.5e-4) but their abundances are quite low (<2%). However, for eight other pollen types (*Abies*, Ericaceae, *Fagus, Corylus, Carpinus, Plantaginaceae*, *Plantago lanceolata, Quercus)*, with higher abundances, the results are still significant but less so, with p-values between 0.05 and 0.01 (Appendix B, Table B1). Based on these results, and in line with several previous studies (Marquer et al., 2020a; Mazier et al., 2012, 2015), we selected the Zmax value at 50 km for the next analysis.

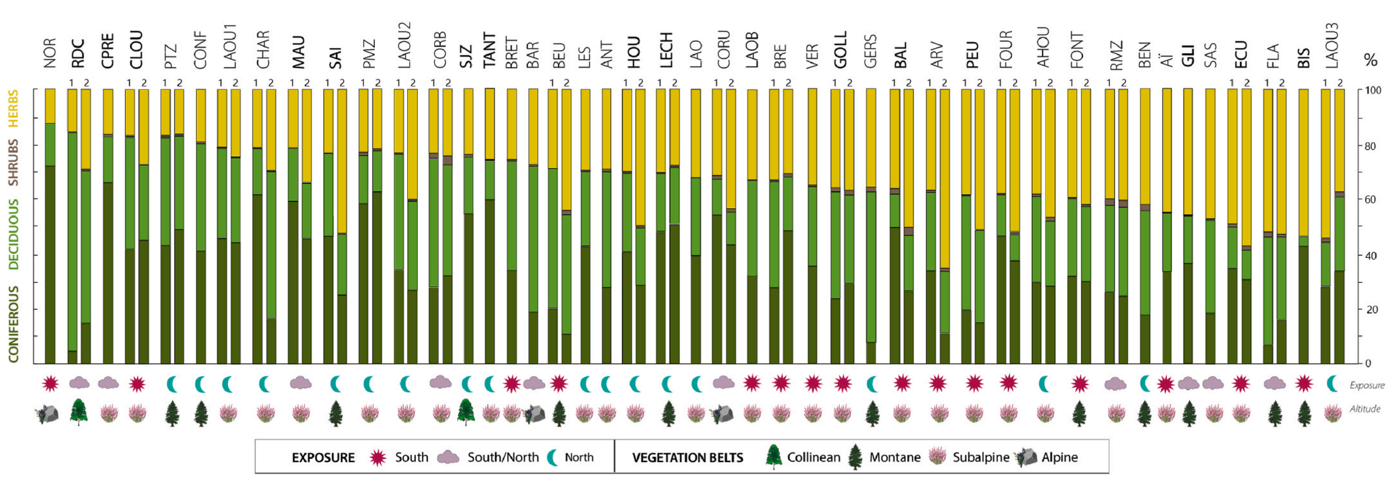

Fig. 4. Simplified pollen composition for each site.
The pollen results are grouped into different categories: coniferous, deciduous, shrubs, and herbs. Sites in bold font represent peat bogs, while sites in standard font represent lakes. Two assemblages for each site are compared (1: post 1970 CE; 2: 1970–1950 CE).

3.3. Effect of wind speed on REVEALS estimates

As mentioned above, the REVEALS (RV) results were tested with different values of wind speed (3, 3.5, 4, 4.5, 5, 5.5, 6 m s^{-1}). Fig. 5 illustrates the variation in REVEALS results for each taxon according to the wind speed values, compared to the Pollen Proportions (PP) values. Two distinct trends emerge across different taxa. The abundance of pollen types such as Ericaceae, Poaceae, *Pinus*, *Corylus*, *Betula* and *Alnus*

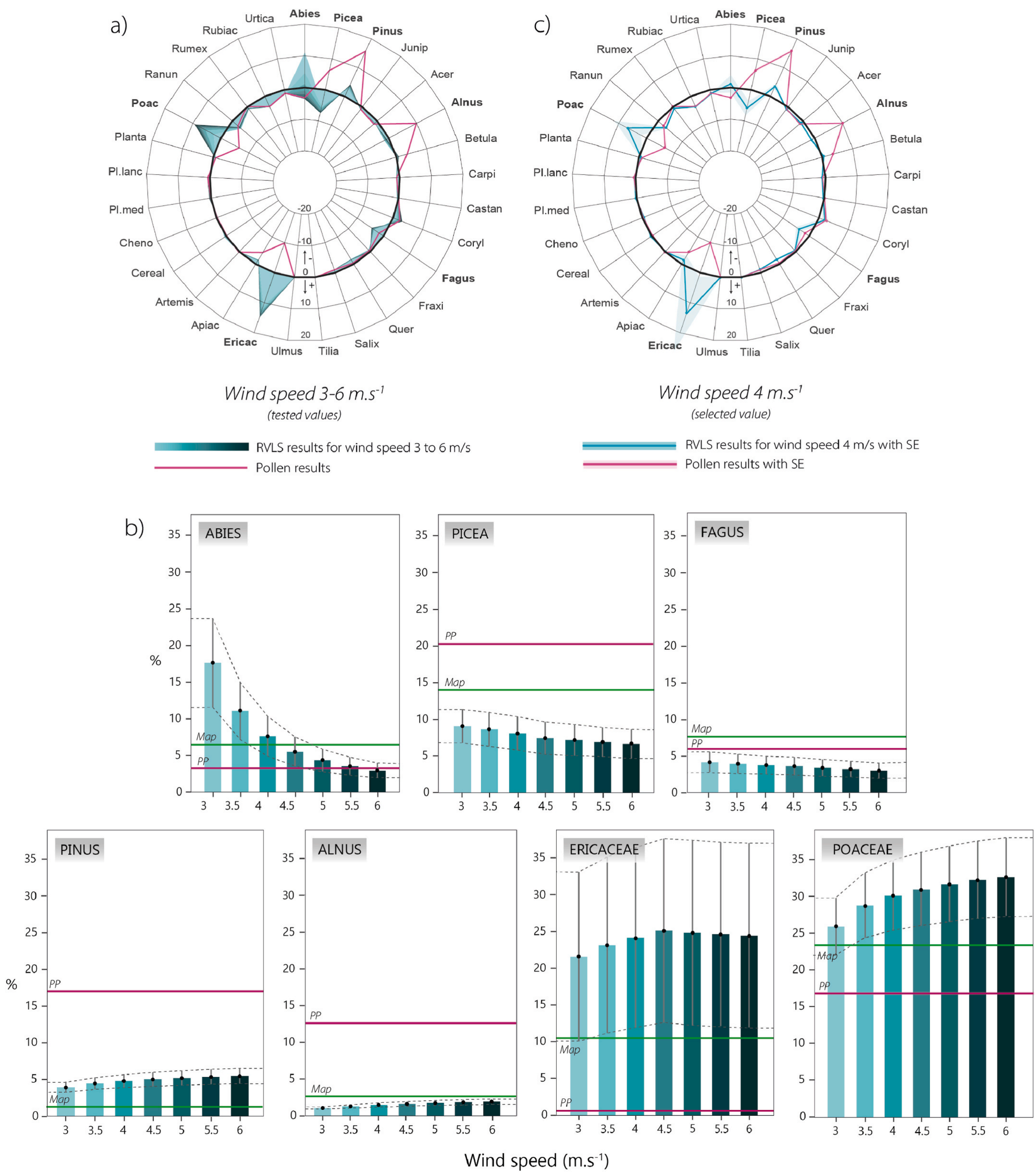

Fig. 5. Wind speed influence on REVEALS estimates.
a) Differences between the REVEALS (RV) results and MAP (vegetation observed, dark circle) for wind speed increasing from 3 to 6 m s^{-1}. b) The abundances of 7 pollen types (*Abies, Picea, Pinus, Fagus, Alnus*, Ericaceae, Poaceae) as a function of wind speed. c) Differences between the RV results with standard errors (SE) and MAP, for a wind speed of 4 m s^{-1}.

increases with increasing wind speed (Fig. 5a and b). In contrast, the abundance of other pollen types such as *Abies, Fagus* and *Picea* decreases with increasing wind speed (Fig. 5a and b). Another interesting observation is that for *Abies,* Poaceae, Ericaceae*, Picea* and *Alnus*, the trends between RV and PP are not the same. The REVEALS model tends to overestimate the proportions of *Abies,* Poaceae and Ericaceae, while the pollen proportions underestimate their abundance. Conversely, REVEALS underestimates the abundance of *Picea* and *Alnus*, while pollen proportions overestimate them.

Among the 29 pollen types, seven show a difference of more than 5% between PP and RV (but not necessarily for all wind speeds for some taxa) with MAP (Fig. 5a); the pollen types in question are Ericaceae, Poaceae*, Abies, Picea, Pinus*, *Fagus* and *Alnus*. Their abundance trends with different wind speeds were observed in detail to determine the most appropriate wind speed value to use. *Abies* has an optimal value, considering the standard errors, between 4 and 4.5 m s^{-1}. *Fagus* and *Picea* are underestimated for all wind speed values but the closest values to those of the MAP are for 3 m s^{-1}. *Pinus,* Ericaceae and Poaceae are always overestimated, but the closest values to those of the MAP are also for 3 m s^{-1}. *Alnus* is always underestimated and the best value is for 6 m s^{-1}. However, it is important to mention that the different REVEALS scenarios depending of the wind speed do not show a lot of variation (<3%). Only *Abies* and Poaceae seem to have significant variations in their abundances among the different wind speeds, 15% and 7% respectively. The variation of REVEALS abundances according to the wind speed for *Abies* is therefore much higher than the variations of the other taxa. In fact, considering the standard errors, the abundances of Ericaceae, Poaceae and *Picea* do not vary much between 3 and 4 m s^{-1} (<5%). The calculated dissimilarity index considering all the pollen types (Table 3) is the lowest for 3.5 m s^{-1} and 4 m s^{-1}, i.e. 0.14394 and 0.14390, respectively. Based on these results, we selected 4 m s^{-1} as the value of wind speed to favour a good estimation of *Abies* (difference between 3 and 4 m s^{-1} >10%). Differences between the MAP and RV (including the standard error associated with the model) for this specific wind speed and for all pollen types are represented in Fig. 5c and can be compared with the differences between the MAP and PP. The REVEALS model provides plant abundances closer to those estimated in the observed vegetation (MAP) than PP, especially for *Pinus, Alnus,* Ericaceae, Poaceae and *Picea* (Fig. 5c). However, the difference between the REVEALS results and the MAP is still very high for Ericaceae (13.7%, i.e. higher than from PPs) and to a lesser extent for Poaceae (6.8%) and *Picea* (5.9%). We can note that for a number of taxa (*Abies, Alnus, Betula*), RV outputs are very close to the MAP, while for some (*Quercus*) PP are better than RV and very close to the MAP. In some cases (*Salix, Tilia, Ulmus, Artemisia, Cerealia*, Chenopodiaceae*, Plantago media, Plantago lanceolata, Plantaginaceae*, *Rumex, Urtica*) the RV and PP outputs are all very close to the MAP. These latter taxa are present in the area in proportions of less than 2% (except *Quercus*).

The NMDS analysis for wind speed can be found in Appendix B (Figure B7), as this analysis is not the best for visualising the results of the influence of this variable. The impact of wind speed on the REVEALS results is not very visible because it only affects certain taxa and only a small portion of the assemblage as a whole, and it is therefore complicated to assess quantitatively the impact of wind speed on the taxa concerned.

3.4. Altitudinal influence on REVEALS estimates

Carpi: *Carpinus*, Cheno: *Chenopodiaceae*, Junip: *Juniperus*, Pl. lanc: *Plantago lanceolata*, Pl. med: *Plantago media*, Poac: Poaceae, Ranun: Ranunculaceae.

The influence of altitude on the REVEALS estimates has been tested based on a non-metric multidimensional scaling (NMDS) including datasets of PP and RV clustered by vegetation belt and the MAP dataset for comparison (Fig. 6a). The RV results are closer to the MAP than the PP results for each altitudinal belt. On the NMDS analysis plot, we can see that the RV, MAP and PP results are distributed along axis 2. The REVEALS and MAP results cluster in the lower part of the plot, where the scores of the axis are negative, while they are distinct from the PP results, which are situated in the upper part with positive scores. The PP results are clearly characterised by an overestimation of the abundances of *Alnus, Pinus, Artemisia* and *Betula,* whereas the RV results demonstrate a better estimation of these taxa and a higher abundance of Ericaceae. However, a similar trend along the altitudinal gradient can be observed for the PP and RV results (black line Fig. 6a). This altitudinal gradient follows axis 1 of the NMDS plot, with the negative values characterised by the lower belts (collinean, montane), i.e. areas dominated by forests. On the contrary, the positive values are characterised by the upper belts, dominated by open land. The MAP vegetation composition falls close to 0 on axis 1, indicating that each altitudinal belt makes a roughly equal contribution to the landscape within the study area. RV outputs from sites in the collinean belt and on the opposite in the alpine belts are the most distant from the MAP. However, it should be noted that these two categories have the lowest number of sites (3 and 2 respectively). The closest results are obtained first for the montane sites with a dissimilarity index value of 0.110 and then for the subalpine sites with a dissimilarity index value of 0.158 (Table 3). The overall results with all sites combined are closer to the subalpine than to the montane sites.

3.5. Influence of the sedimentary basin on REVEALS performance

As previously, an NMDS analysis distinguishing the vegetation compositions obtained from PP and RV on small lakes, small bogs, large bogs, all small sites, all sites and from the MAP has been performed (Fig. 6b). In line with the previous results, the RV outputs are closer than the PP outputs to the MAP. The NMDS plot illustrates that the RV and PP results are divided by axis 1 of the NMDS, with the RV and MAP results located on the negative values. RV results are notably influenced by Ericaceae, Apiaceae, *Abies* and *Plantago media,* which are accurately estimated by REVEALS as shown in Fig. 5c. Conversely, the PP results, located on the positive values, are mainly influenced by *Alnus, Pinus* and *Picea* which is considerably overestimated by the PP (Fig. 5c).

The "Lakes" (28 sites), "All small sites" (41 sites) and "All sites" (44 sites) categories are separated from the bogs along axis 2 for both RV and PP results. Bogs categories are located on the negative values of axis 2, while the other categories are located on the positive values. Furthermore, the results for small sites ("All small sites", "Small bogs", "Lakes") and "All sites" are closest to the MAP.

However, the category "Large bogs" is very different and further away from MAP than the other categories, especially for the RV results. There are only 3 sites in this category. The "large bogs" have a high *Abies* abundance compared to the other categories, which may be related to the proximity of the sites to *Abies/Picea/Fagus* forests, which could contribute to the substantial dissimilarity suggested by the NMDS.

The REVEALS results closest to the MAP are obtained when all small sites (lakes and/or bogs) are used (Fig. 6b–Table 3). The dissimilarity index values are higher for "Small bogs" (0.139) and then "Small lakes and bogs" (0.147) and "Small lakes" (0.158).

Results on the influence of exposure on REVEALS performance do not show specific trends. Therefore, other factors (e.g. land use, altitude) have probably more influence than exposure (Appendix B, Figure B4; see section 3.4).

3.6. Number of sites used for REVEALS reconstructions

The influence of the number of sites (5, 10 or 20) used in REVEALS was randomly tested, and the results are presented in an NMDS analysis in Fig. 6c. When comparing the dissimilarity index values between RV and MAP (Fig. 6d), the median value does not improve as the number of sites increases, but the variability of the results decreases. Specifically, the mean index value improves with an increase in the number of sites. For the "5 sites" category, the range of minimum and maximum values

Table 3
Dissimilarity indexes.

Test		Diss RV with Map	Diss PP with MAP	Diss RV with PP
Wind speed (m.s-1)	3	0,161	0,299	0,393
	3,5	0,14394		0,365
	4	0,14390		0,356
	4,5	0,150		0,356
	5	0,153		0,350
	5,5	0,158		0,348
	6	0,163		0,348
Vegetation belts (3,5 m.s-1)	Collinean	0,383	0,626	0,296
	Montane	0,110	0,234	0,253
	Subalpine	0,158	0,315	0,374
	Alpine	0,223	0,462	0,321
Type of site (lake/bog, small/large) (3,5 m.s-1)	SLB	0,147	0,299	0,357
	AL	0,158	0,296	0,270
	AB	0,150	0,331	0,369
	SB	0,139	0,337	0,277
	LB	0,284	0,361	0,296
Number of sites (3,5 m.s-1)	5.1	0,166	0,394	0,227
	5.2	0,139	0,350	0,231
	5.3	0,199	0,268	0,295
	5.4	0,124	0,317	0,241
	5.5	0,168	0,297	0,369
	5.6	0,180	0,382	0,296
	5.7	0,199	0,460	0,196
	5.8	0,157	0,348	0,252
	5.9	0,169	0,325	0,344
	5.10	0,131	0,242	0,253
	10.1	0,211	0,390	0,438
	10.2	0,205	0,318	0,376
	10.3	0,146	0,320	0,301
	10.4	0,150	0,309	0,260
	10.5	0,137	0,270	0,309
	10.6	0,213	0,377	0,429
	10.7	0,141	0,323	0,215
	10.8	0,137	0,332	0,234
	10.9	0,163	0,277	0,343
	10.10	0,154	0,299	0,293
	20.1	0,170	0,286	0,412

Test		Diss RV with Map	Diss PP with MAP	Diss RV with PP
	20.2	0,154	0,310	0,348
	20.3	0,141	0,317	0,331
	20.4	0,175	0,324	0,399
	20.5	0,157	0,290	0,368
	20.6	0,155	0,293	0,340
	20.7	0,161	0,314	0,347
	20.8	0,156	0,297	0,360
	20.9	0,158	0,298	0,380
	20.10	0,168	0,287	0,370
Land Cover Categories	CDO	0,013	0,091	

The various dissimilarity indexes (Diss) obtained for all the scenarios tested between REVEALS (RV) and observed vegetation (MAP), Pollen Proportions (PP) and MAP or with RV and PP are presented.
The blue cells correspond to the best RV indexes obtained for the best scenarios in each analysis. The pink cells correspond to the best PP indexes obtained for the best scenarios in each analysis.
SLB: Small Lakes and Bogs; AL: All lakes (all small lakes); AB: All Bogs; SB: Small Bogs, LB: Large Bogs, CDO: Coniferous/Open Land/Deciduous.

spans from 0.106 to 0.198, for "10 sites" it extends from 0.121 to 0.210, while for "20 sites" the range narrows to 0.138 to 0.176. The best index value is obtained in the "5 sites" category.

However, when comparing the dissimilarity index values between RV (number of sites) and RV (using all sites), the index progressively decreases with a high number of sites. The variability of the results decreases alongside the index value. Depending on the random selection of sites, the results can be very close to the MAP or deviate significantly from it. The NMDS analysis (Fig. 6c) indicates that the coverage of the ellipse is lowest when 20 sites are used compared to when 10 or 5 sites are used. Furthermore, the results obtained with all sites used (44 sites) fall within the ellipses of the "10 sites" and "20 sites" categories but remain distant from the "5 sites" category. The distribution of points in the "20 sites" and "10 sites" categories are quite similar.

3.7. REVEALS performance in reconstructing plant abundances

As mentioned above, there is no linear relationship between pollen and vegetation (Prentice and Webb III, 1986; Serge et al., 2023; Sugita, 2007a), which the REVEALS attempts to correct. By comparing the linear regressions of REVEALS and PP (Fig. 7), the results indicate that the linearity of the REVEALS results with observed vegetation is significantly better ($R^2 = 0.78$) than that of the PP ($R^2 = 0.40$). The RV results are therefore closest to a linear relationship where 1% of the predicted pollen data corresponds to 1% of the corresponding taxa in the observed vegetation. Pollen types with observed values below 3% have very similar RV and PP results, but are mainly underestimated by RV and overestimated by PP. The largest disparities are observed for pollen types with proportions above 3%. RV tends to overestimate these plant abundances, especially Poaceae and Ericaceae, while PP tends to underestimate them. However, *Picea* is underestimated by RV and *Picea, Pinus* and *Alnus* are overestimated by PP. Finally, it is the values of Poaceae, Ericaceae that mainly drive the lines of the linear regressions for both PP and LV.

The relationship between pollen and observed vegetation is non-linear. However, the LRA model attempts to correct this into a linear relationship by considering the production, dispersal, and deposition of pollen grains (Sugita, 2007a; Prentice and Webb III, 1986; Serge et al., 2023). The linear regression curves of RV (predicted) and PP (counted) with the observed vegetation (MAP) are shown, along with their respective R^2 values.

Carpi: *Carpinus*, Casta: *Castanea*, Cheno: *Chenopodiaceae*, Fraxi: *Fraxinus*, Junip: *Juniperus*, Pl. *Plantaginaceae*, Pl. lanc: *Plantago lanceolata*, Pl. med: *Plantago media*.

3.8. REVEALS performance in reconstructing land cover categories

Based on all our datasets, i.e. all 44 sites, we assessed the performance of the REVEALS model in assessing the three main Land Cover Categories (LCC), i.e. (semi)open lands (12 herbaceous taxa and 2 shrubs taxa), coniferous forests (3 taxa) and deciduous forests (12 taxa) (Fig. 8, Table 2). The proportions of the different LCCs in the observed vegetation (MAP) do not vary by more than 20% across the 50 km. Open lands are more abundant than coniferous or deciduous forests, but tree cover in general (coniferous and deciduous forests) is relatively equal to open lands. At a distance of ca. 25–30 km, open lands increase as the coniferous forests decrease. The deciduous forests are quite stable and do not vary by more than 5%.

Overall, the results from REVEALS Land Cover Categories (RV.LCC) are closer to the vegetation observed (MAP) than those from Pollen Proportions Land Cover Categories (PP.LCC). The RV. LCC results are better than for the individual taxa (RV). The dissimilarity indexes are the lowest (<0.02 for RV and <0.1 for PP, Table 3) indicating higher efficiency with REVEALS. Looking at the standard errors, the RV results are even closer and include the regional variations for the 50 km radius area.

The RV. LCC results for coniferous forests are very close to the MAP (1.3% difference), whereas the PP. lcc tends to overestimate the proportions (18.72% difference). The results for (semi)open lands are also very close to the MAP. Indeed, the difference between the MAP and RV. LCC results is only 9.54%, compared to 28.82% for the PP. LCC, which underestimates the proportions. The standard errors for open lands are quite high. This is also observed by Marquer et al. (2020a) in the Pyrenees. The overestimation of Ericaceae and these high standard errors (Fig. 5) may account for the overestimation of open land compared to coniferous forest by REVEALS. Lastly, the results for broadleaved trees are less consistent with the MAP than for the previous land covers, yet REVEALS still provides better estimates than Pollen Proportions. REVEALS tends to underestimate their abundance (8.25% difference), while PP overestimates them (10.1% difference). These discrepancies for broadleaved trees are likely due to the important underestimation of *Fagus* by the REVEALS model (Fig. 5).

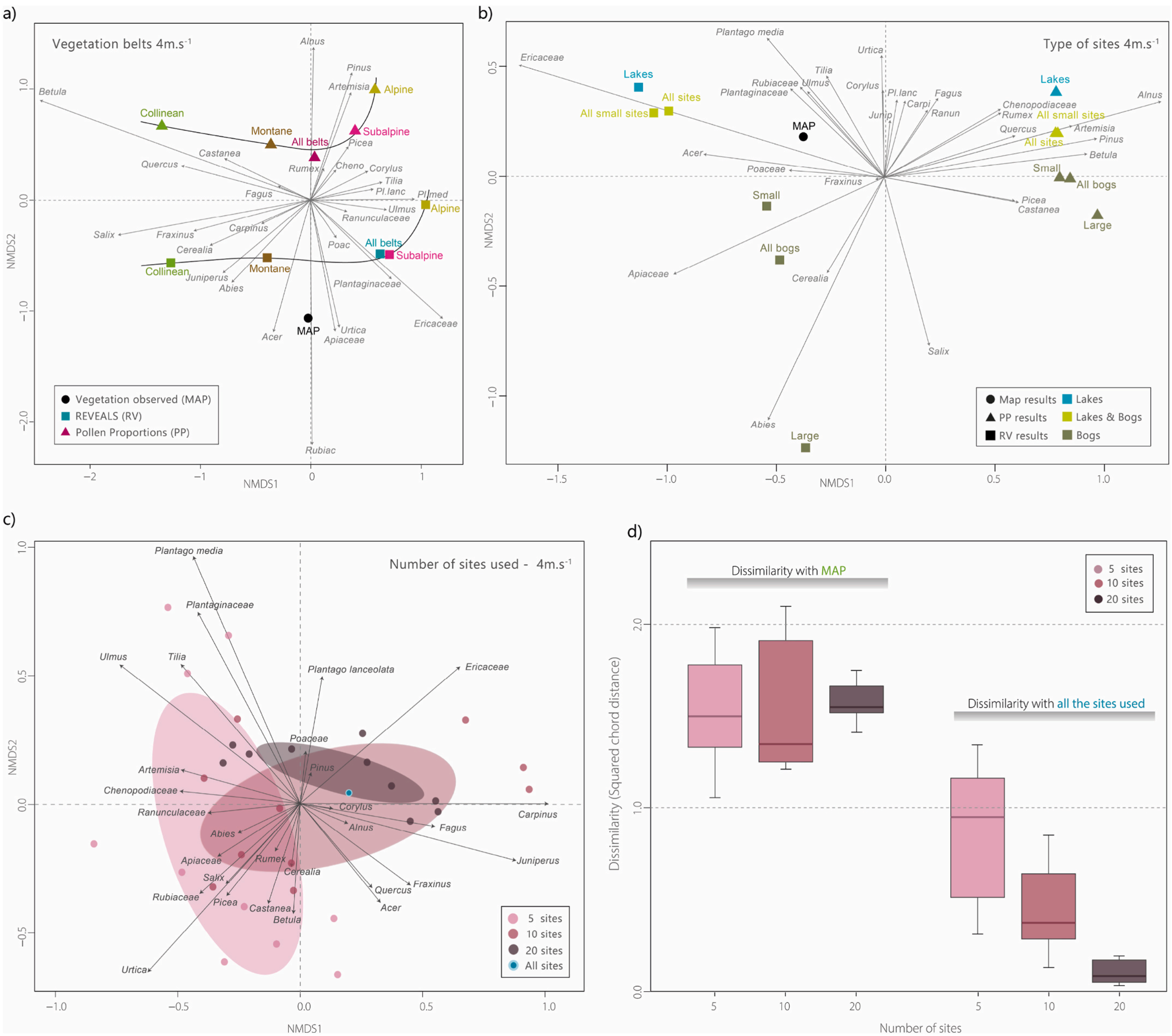

Fig. 6. Effect of different variables (vegetation belts, type and number of sites used) on REVEALS by using non-metric multidimensional scaling (NMDS) analysis. a) Distribution of RV and PP results for each vegetation belt compared to the observed vegetation (MAP). b) Distribution of RV and PP results for each type of site compared to the observed vegetation (MAP). c) Distribution of random RV runs for each category of number of sites (5, 10 and 20) compared with RV results (using all 45 sites). The ellipses represent the standard deviation of the dots for each group (5 sites, 10 sites and 20 sites used). d) The dissimilarity indexes for each of the 10 runs for each category of sites are shown. On the left is the dissimilarity index between the RV and MAP results. On the right, the dissimilarity index between the RV results of each category and the RV results using the 45 sites.

4. Discussion

4.1. The effect of pollen dispersal on REVEALS

4.1.1. Effect of wind speed

In previous studies the wind speed is commonly set at 3 m s^{-1} as a default parameter (Hellman et al., 2008b; Hjelle et al., 2015; Marquer et al., 2020a; Sugita, 2007a; Sugita et al., 2010). Furthermore, neutral atmospheric conditions are usually considered for the REVEALS runs. However, due to the complexity of the atmospheric conditions in mountainous areas, wind speed and atmospheric conditions are likely variable. Wind speed is an important parameter for the model runs as it could influence the simulations of pollen dispersal.

The dissimilarity index analysis shows that the best results are obtained with a wind speed value of 4 m s^{-1} (Table 3). As mentioned above, the dissimilarity indexes are quite similar between wind speed set at 3.5 and 4 m s^{-1}. These results are consistent with the actual current wind speed values, with the mean of the maximum and minimum values being between 3.5 and 4.6 m s^{-1} (from January to September), depending on the averaging calculations (mean of maximum and minimum values vs. mean of maximum and minimum averages) (Appendix A, Figure A5). However, our results also show that generally selecting different wind speed values has minimal effects on REVEALS (Fig. 5). This is true for most taxa individually, except for *Abies*, Poaceae and to a lesser extent Ericaceae, *Picea* and *Fagus*. This was also observed by Zhang et al. (2021) and by Soepboer et al. (2010) who tested the effect of wind speed on the REVEALS results and on Relative Pollen Productivities (RPP) calculations, respectively.

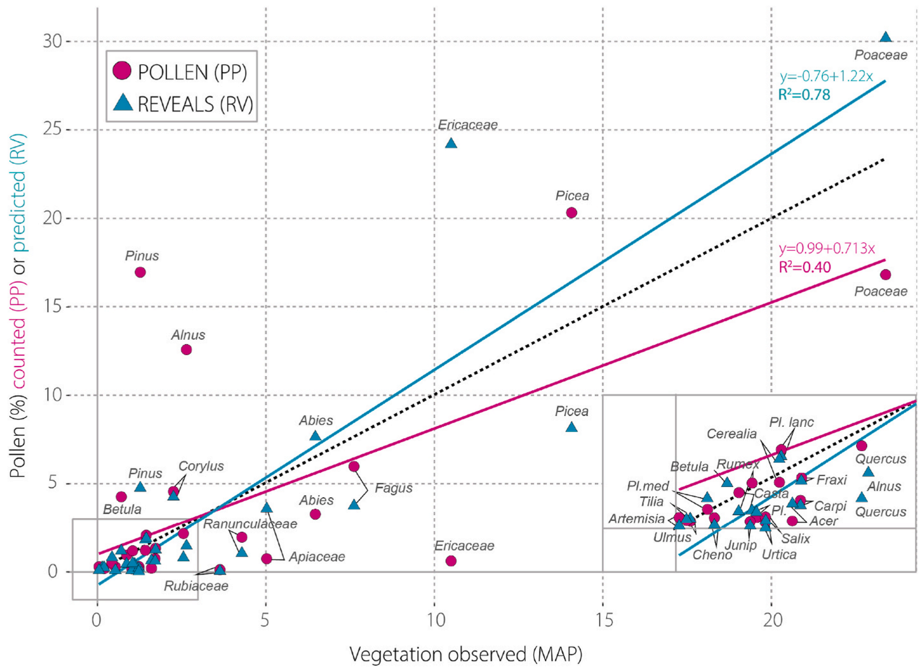

Fig. 7. Linear regression of REVEALS and Pollen Proportions results with observed vegetation.

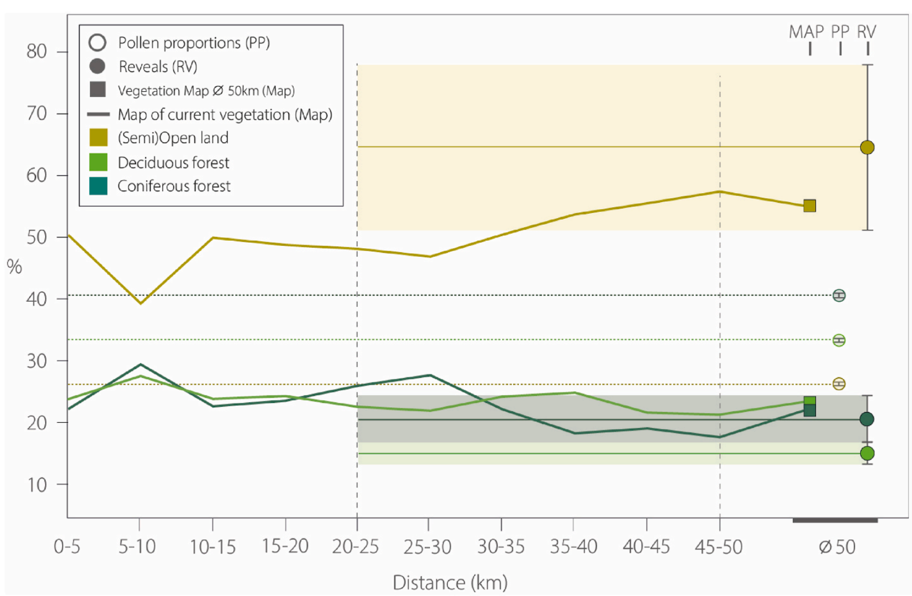

Fig. 8. Land Cover Categories results (LCC).
a) This figure shows the results for three LCCs: coniferous forest, deciduous forest and (semi)open land. The MAP proportions of each of these LCCs are represented by the curves along the distance and the global proportions for the 50 km radius area are represented by the square dots. The REVEALS LCCs (RV.LCC) results are represented by the lines and solid circle dots, while the Pollen Proportions LCCs (PP.LCC) results correspond to the dotted lines and hollow circle dots. The vertical dashed lines represent the minimum and the maximum spatial extent of the REVEALS reconstructions in our study area.

In theory, the GPM model would not provide a reliable correction for the REVEALS estimates of *Abies* because the GPM model places more emphasis on short-distance transport, which particularly affects the heavier pollen grains, such as those of *Abies,* because they have high fall speed of pollen. Fall speeds of pollen are calculated based on pollen grain size. On the one hand, larger pollen grains are heavier and are therefore assumed to have a higher fall speed and then fall close to the source of emission (Theuerkauf et al., 2016). On the other hand, the smaller pollen grains, which are lighter, may disperse further away from the pollen sources. Pollen grain velocity or fall speed equation is also calculated based on the density of pollen grains, density of the air, acceleration due to gravity and air viscosity. All these variables determine the speed at which the pollen grain falls (Gregory, 1973; Sugita, 2007a). Therefore, the fall speed values have direct influences on dispersal modelling schemes used to calculate the probability of pollen coming from a short or long distance.

The RPP equation is also based on the Fall Speed of pollen value. A high FSP value associated with a high RPP value for *Abies* results in the assumption by the GPM that *Abies* produces a large amount of pollen grains that fall not far from the source of emission. The overestimation of *Abies* proportions by the GPM model for low wind speeds (<4 m s^{-1}) can therefore be mainly attributed to its high fall speed of pollen, when it has the potential to be dispersed over longer distances than those assumed by the modelling scheme because of its characteristic pollen morphology (i.e. presence of air bladders adapted for wind dispersal). Note that the Fall Speed value only considers the density and size of the pollen grains and does not consider the morphology of conifer pollen grains. Furthermore, the GPM model overestimates the proportions of *Abies* when low wind speed values are used. As wind speed increases, pollen grains regardless of their size or density are carried higher into the atmospheric layers, allowing them to travel greater distances. At higher wind speeds, the influence of pollen grain size and density becomes less significant compared to lower wind speeds, which mainly explains our results.

Fagus and *Picea* also have heavy pollen grains (and air bladders in the case of *Picea*), but their fall speed values are lower than that of *Abies* although it is still higher than the other taxa; *Fagus* and *Picea* pollen types are smaller than *Abies* type. This leads to the underestimation of these taxa whereas *Abies* is overestimated. As we have mentioned above, prior research shows that increasing wind speed influences the long-distance transportation of pollen (see also Nielsen and Sugita, 2005); this is likely to explain the decrease in *Abies, Picea* and *Fagus* abundances when the wind speed increases.

In a mountain context, such trends with an overestimation of *Abies* have also been observed by Zhang et al. (2021; China). In the French Alps, a reliable estimation of *Abies* abundance would be for a wind speed of 4 m.s-^{1}, however this results in an overestimation of Poaceae and Ericaceae. However, in the case of the Ericaceae, the plants are insect pollinated plants (like also Rubiaceae and Apiaceae) and this type of pollen transportation is not considered by the model, so far. It is well-known that pollen grains from entomophilous plants are usually underestimated in pollen archives. However, REVEALS overestimates the plant abundance for this pollen type. The morphology of Ericaceae flowers may explain some of the differences between REVEALS estimates and the observed map. Ericaceae species presents in the area, such as *Rhododendron ferrugineum*, have exserted stamens that can favour anemophilous transport of pollen (Serge et al., 2023). This is different from other Ericaceae species, such as *Calluna vulgaris* or Vaccinium species (e.g. *Vaccinium myrtillus, Vaccinium uliginosum*, and *Vaccinium vitis-idaea*), also present in the area. The different flower morphologies of these species, particularly between *Rhododendron ferrugineum* and *Vaccinium myrtillus*, which are the most abundant Ericaceae species in the region, may therefore affect the REVEALS outcomes. In addition, Ericaceae pollen grains can also be transported by water due to the buoyancy and hydrodynamic characteristics of its pollen morphology (e.g tetragonal tetrads) (Castro-Parada and Muñoz Sobrino, 2022). This means that in some cases, pollen grains can be transported by insects, wind and/or water. Consequently, as the GPM model does not consider any types of transport other than wind, it only treats Ericaceae and other entomophilous pollen types on the basis of their RPP and FSP values. It should be mentioned that the RPPs for Ericaceae available for pollen-based modelling are not based on mountain Ericaceae species. This underlines the need of calculating a new set of RPPs specifically for the application of REVEALS in mountain regions.

Finally, the GPM modelling scheme puts more emphasis on short-distance pollen transport, leading to the overestimation of heavy taxa. In contrast, the LSM model might better estimate long-distance pollen transport (Marquer et al., 2020a; Theuerkauf et al., 2013, 2016; Theuerkauf and Couwenberg, 2021) because it considers the turbulence conditions (Kuparinen et al., 2007). The LSM model could be better than the GPM for mountain regions. But this model has only been applied in a few contexts that are limited in terms of plant cover (Finnish pine forests) and topographies (lowlands) (Kuparinen et al., 2007). This means that the LSM modelling scheme needs to be developed for mountain contexts (Marquer et al., 2020b). However, the current availability of RPP values based on LSM is not sufficient to use this model in mountain areas for now.

4.1.2. Effect of the altitudinal gradient

Another assumption of REVEALS is that vegetation should be homogeneous without geographical gradients. Applying REVEALS in mountainous areas involves a breach of this condition, in particular the altitudinal gradient of mountain landscapes and various exposures result in vegetation patches/mosaics. Pollen production, dispersion and deposition in sedimentary basins (i.e lakes and bogs) further vary with altitudes. Markgraf (1980) observed in the Swiss Alps that pollen from the lowlands is not deposited above 1200 m due to wind directions. However, in general, pollen grains from the lowest altitudes (collinean and montane belts) are transported to the upper belts, masking the local pollen signal of subalpine/alpine grasslands or heathlands (David, 1993, 1997; Fall, 1992; Markgraf, 1980; Marquer et al., 2020a; Ortu et al., 2006; Randall, 1990; Zhang et al., 2017). Pollen proportions (PPs) in the present study confirm this statement as the sites in the upper belts have high abundances of *Abies, Picea, Pinus* and *Alnus* (>65%) when these plant taxa are generally located at lower altitudes (Appendix B, Figure B3). Furthermore, in the upper belts, the stronger winds bring greater contributions of regional pollen loads compared to the local ones (Markgraf, 1980).

When using REVEALS, it turns out that montane and subalpine sites yield the best results and therefore they seem to better represent the regional vegetation than the sites located in other belts (Table 3). The montane belt has a better estimate of (semi)open land and therefore of Ericaceae but conifers, particularly *Abies,* are overestimated. However, this overestimation of conifers by montane sites seems less important for the RV results (all sites and vegetation belts included) than those of Ericaceae and Poaceae by the subalpine sites. In addition, the diversity of sites in the montane and subalpine belts (open, forested, semi-open) lead to more homogeneous results that are closer to the results for the whole region. The results for the alpine belt reveal an assemblage that differs little from that of the subalpine belt, apart from a significant underestimation of *Fagus* and an overestimation of *Pinus* and Poaceae (Appendix B, Figure B3).

All of these results are not very surprising, as the REVEALS was not initially designed to correct pollen dispersal in complex topographies, and the current version of REVEALS does not consider heterogeneous vegetation conditions. The best way to overcome the problem of heterogeneous vegetation patches in mountain areas (Hellman et al., 2008b; Marquer et al., 2020a) is therefore to have this heterogeneity represented in the sample sites. This shows once again that the best way of estimating regional vegetation in mountain contexts is to have a large selection of pollen sites in a large range of environmental contexts.

4.2. The influence of site characteristics in the application of REVEALS in a mountain context

4.2.1. Sedimentary basin characteristics

REVEALS was initially designed to be applied to pollen records from large lakes and to simulate pollen dispersal for circular basins. However, many of the mountain lakes we have used in the present study are small and non-circular. These differences in shape characteristics may affect the REVEALS outputs. As an example, for elongated and non-circular sites, the calculated area of a site may be greater than the real area. However, we have compared the outcomes from various REVEALS runs considering different areas. The results do not show significant differences based on our pollen sites (Appendix B, Figure B5).

Regarding the use of small pollen sites, several studies have demonstrated that using numerous small sites is a reliable alternative (Hjelle et al., 2015; Fyfe et al., 2013; Marquer et al., 2017; Mazier et al., 2012; Trondman et al., 2016). Trondman et al. (2016) and Fyfe et al. (2013) highlight that the use of several small bogs has a greater effect on the REVEALS estimates than the use of several small lakes. In the present study, small sites selected in various contexts yield the best results, first for a combination of small bogs (independently of the number of bogs), second for a combination of small bogs and lakes, and then for groups of small lakes.

Considering the type of pollen site (i.e. bogs versus lakes), Fyfe et al. (2013) and Trondman et al. (2016) have shown that the type of site has a greater influence on REVEALS estimates than the size of the basin However, our study nuances this statement, as small bogs give similar results to those of small lakes. On the contrary, bogs classified as large sites give results that are far from the vegetation observed and from the results of other site types and sizes. One should mention that the REVEALS scenario using large bogs only grouped three sites. Finally, Hjelle et al. (2015) compared the results obtained using small lakes and large lakes with observed vegetation (Corine Land Cover, 8 categories) in a complex topographic context. Their study suggests that the use of a large number of small lakes provides results that are as reliable as those obtained using a large lake, and all results are close to the observed vegetation. Our results support these findings, and we have been one step further by adding bogs in the comparison and a more complex topographical context.

4.2.2. Site selection for REVEALS application

As previously mentioned, the type of sites and their altitude (i.e. vegetation belt) as well as the wind speed affect the REVEALS outcomes. Although REVEALS significantly corrects for the biases related to the basin type, a correction of the influence of the altitude in the REVEALS results is less obvious. Similar spatial patterns are observed between PP and RV estimates across different altitudinal belts. However, altitude and type of sites, though studied independently, are likely to be interrelated. The impact of the basin type (i.e. small or large, and bog or lake) also depends on site altitude and, above all on the exposure of the site's catchment area (north face, south face, intermediate face), which can lead to different vegetation and land use. Similarly, wind speed does not have the same effect on sites with different basin types and altitudes. It was noted above (section 4.1) that the source of the pollen grains is not homogeneous for each altitudinal belt and for each type of basin (lakes or bogs). This can be seen in Fig. 4, where the NAP (Non-Arboreal Pollen) versus AP (Arboreal Pollen) values are not completely homogeneously distributed along the altitudinal and exposure gradients. This highlights the influence of intra-site variables such as anthropogenic activities (pastures, lake development activities, ski slopes, etc …) and topographic variables (steep landscapes, slopes, etc.).

To improve the effectiveness of REVEALS, it is therefore necessary to reflect on the selection of the sites and/or potential influences related to the site characteristics. However, several studies (Hellman et al., 2008a, 2008b; Hjelle et al., 2015; Trondman et al., 2016) suggest that the main limiting factor when working with small sites in areas with heterogeneous and stratified vegetation (with numerous land covers such as deciduous forests, arable lands, heathlands, grasslands, coniferous forests, and mixed forests) is the number of sites used for REVEALS application. The use of more sites results in smaller standard errors (Hjelle et al., 2015; Trondman et al., 2016). Currently, there is no research in mountain areas that shows the minimum number of sites required to obtain robust REVEALS results, and how they should be selected. Our study suggests that the type and altitude of the sites have the most significant impact on the results when using 10 or fewer sites. This means that if we use a low number of sites, it important to select them by considering a variety of sites and land covers, as well as a large range of altitudes and exposures as it has been already suggested by Marquer et al. (2020a). The best choice would be to use more than 10 sites, because this considers the local variability of site characteristics due to the mountain context.

4.3. Performance of REVEALS in mountain context

This figure summarizes the main results of the different analyses, illustrating the dissimilarity indexes between the RV results and MAP, and between the PP results and MAP. The RV/MAP and PP/MAP indexes are presented for the different analyses:

(a) Results of the wind speed analysis (ranging from 3 to 6 m.s-1). The 4 m s^{-1} speed appears to be the least dissimilar to MAP.
(b) (b) Results of the altitude analysis. Colli: Collinean, Mont: Montane, Sub: Subalpine, Alp: Alpine. Sites in the montane and subalpine belts appear to be the least dissimilar to MAP.
(c) (c) Results of the site type analysis. LB: Large bogs, SB: Small bogs, AB: All bogs, AL: All lakes, SLB: All small lakes and bogs. SB, followed by SLB and AL, appear to be the least dissimilar to MAP.

The results for a wind speed of 4 m s^{-1} have a dissimilarity index almost 2.1 times lower than that of the PP (Fig. 9, Table 3). Regardless of the tested scenarios, such as wind speed, altitude, or site type, the dissimilarity index consistently yields results 1.6 to 2.4 times better than those of the PP, except for large bogs. In the case of large bogs, the results are similar between PP and RV (Fig. 9), showing that REVEALS does not correct much the biases in pollen dispersal, production and deposition for such sites (see section 4.2).

In addition, at the pollen type levels, REVEALS estimates are more similar between MAP and RV compared to PP and MAP, except for Poaceae, Ericaceae and *Picea* (Fig. 7). Regarding the land cover types (LCC), the results (Fig. 8) are better than those obtained at the pollen type levels; this supports previous findings, see (Hellman et al. (2008a) and Trondman et al. (2016). Note that the standard errors is high for the open land category.

Although REVEALS provides better estimates than PP for most taxa, some taxa such as Ericaceae, *Pinus* and *Fagus* (*Fagus* underestimation leads to an underestimation of deciduous forest) still have less reliable estimates. Ericaceae would be the most problematic taxon, and for this reason several studies have excluded this entomophilous taxon (Githumbi et al., 2022; Mazier et al., 2012), because REVEALS only considering the wind transport of pollen grains as dispersal mechanism. In addition, as already mentioned in section 4.1.1 of the manuscript, Ericaceae, which represent most of the entomophilous plants in our study region, have characteristics that make it difficult for REVEALS to correct biases in dispersal and deposition mechanisms. However, in mountainous areas, and especially in the subalpine belt, these taxa are quite abundant. Therefore it is necessary to include them in the modelling scheme to do not lost an important taxa and land cover category (i.e. heathland) for past vegetation reconstruction (Plancher et al., 2022). Furthermore, (Marquer et al. (2020a), Plancher et al. (2022), and Serge et al. (2023) have shown the relevance of including these taxa in REVEALS reconstructions. The results of the present study indicate a similar outcome than these studies. While the dissimilarity for Ericaceae with MAP is higher with RV (13,7%) than with PP (9.9%), RV is more similar to the MAP than PP when the standard errors are considered. Other entomophilous pollen types are underestimated by both RV and PP, except for Apiaceae, which is well estimated by RV. Despite the over-or-under-estimation of these taxa, it is recommended that the entomophilous taxa, particularly Ericaceae, are included in the REVEALS runs.

In addition, the evaluation of the reliability of the REVEALS estimates is further likely influenced by the limitations of the MAP. While the MAP provides the most detailed data available in the present study region, it certainly does not correctly estimate values for pollen types such as *Pinus,* which is more abundant in the vegetation than the MAP data would indicate. Consequently, the observed proportions of Ericaceae and *Fagus* may also differ from those calculated from the MAP.

Although the total value for RV conifer estimates closely matches the observed proportions, the abundance of *Picea* is still underestimated by 5.9% (and only 3% if standard errors are considered). However, the proportion of *Abies* is accurately estimated and, as in the observed vegetation, *Picea* is more abundant than *Abies*. The landscape dynamics observed between these two taxa therefore remain well represented.

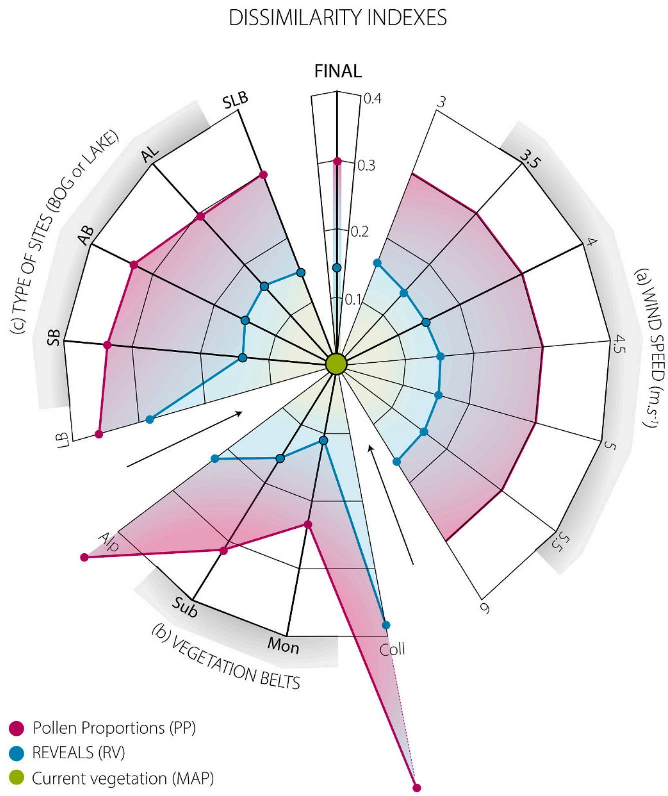

Fig. 9. Summary of dissimilarity index results for all scenarios.

5. Conclusion

This study highlights the potential of applying REVEALS in mountainous regions. However, caution must be exercised due to complex environmental conditions and human activities that result from a variety of local contexts. As expected, the application of the REVEALS model is constrained by various topographical factors, such as altitude gradients and complex atmospheric conditions, which it cannot fully account for. However, the results obtained are satisfactory when compared with both untransformed pollen data and observed vegetation. In addition, our results underline the importance of developing a specific research strategy for the REVEALS runs focusing on site characteristics and pollen dispersal and deposition mechanisms, in particular. In order to consider the variety of local environmental contexts in the regional reconstructions. It is recommended to have a large variety of pollen sites that are representative of the landscape heterogeneity of the study region. Furthermore, one should also be aware of the main limitations of using the REVEALS model because the REVEALS estimates greatly depend on the initial parameters used as inputs (e.g. pollen productivity estimates, fall speed of pollen and basin size characteristics) as well as dispersion modelling schemes. Regarding the dispersal modelling schemes, there is still a need to improve the estimations of some key pollen types such as *Abies, Picea,* Ericaceae and *Fagus*.

Based on the present study, our recommendations for the application of REVEALS in mountain regions are to:

- use as many sites as possible for REVEALS application, and sites should be located in various topographical and environmental contexts (e.g. altitude, nature, exposure, land use etc.).
- do not run REVEALS only on collinean (<800 m) or alpine sites (>2300 m), nor only on large bogs.
- consider wind speed values that are appropriate for the study region during the pollen season.
- include entomophilous pollen types such as Ericaceae that are important for paleoenvironmental reconstructions in mountain regions, by keeping in mind the pros and cons of the entomophilous pollen types in REVEALS applications.
- assess the present "pollen situation" in the study region to understand the site characteristics and dispersal mechanisms affecting pollen dispersal and deposition. Wherever possible, it is recommended that a preliminary calibration study be carried out on the recent period. This would help in adjusting certain parameters used as inputs in REVEALS and the site selection.

The application of REVEALS in mountain areas in general, will provide more accurate palaeoenvironmental reconstructions that can be further compared with other biological proxies such as environmental DNA and tree rings, and information from archaeological and historical archives. The major aim is to assess a long-term perspective of socio-ecosystem changes in relation to climate and anthropogenic forcing in mountain regions.

CRediT authorship contribution statement

Andréa Julien: Writing – original draft, Conceptualization, Investigation, Formal analysis, Visualization, Data curation. **Charline Giguet-Covex:** Writing – review & editing, Conceptualization, Investigation, Formal analysis, Supervision, Funding acquisition. **Erwan Messager:** Writing – review & editing, Conceptualization, Investigation, Supervision, Funding acquisition. **Florence Mazier:** Writing – review & editing, Validation, Methodology. **Laurent Marquer:** Writing – review & editing, Conceptualization, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2024.109089.

Data availability

Data will be made available on request.

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