



Review

Aerobiology in alpine environments: Exploring pollen biodiversity and its impacts on human health[☆]

Franziska Zemmer^{a,b,*}, Antonella Cristofori^{a,b}, Fabiana Cristofolini^a, Elena Gottardini^{a,b}

^a Fondazione Edmund Mach, Research and Innovation Centre, Via Mach, 1, 38098 San Michele all'Adige, Italy

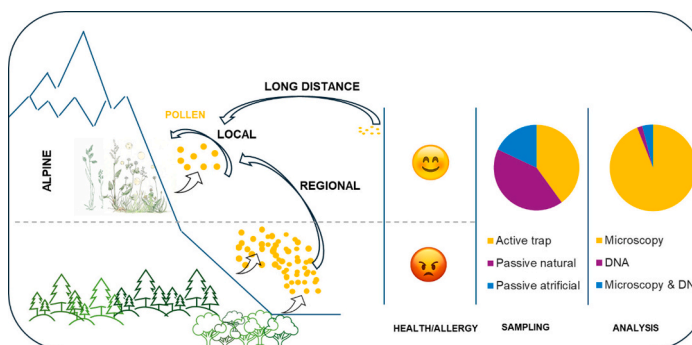
^b National Biodiversity Future Centre, Piazza Marina, 61, 90133 Palermo, Italy



HIGHLIGHTS

- Alpine sites are receptors of local to distant airborne pollen sources.
- Pollen sources are identified by vegetation data from the same scale.
- Deposition sampling of pollen is the method of choice in alpine sites.
- Land-air relationships in alpine biomes mirror the effects of global change.
- Low allergenic pollen load of the alpine air is beneficial for human health.

GRAPHICAL ABSTRACT



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ABSTRACT

This review summarizes methods and relevant outcomes of aerobiological studies carried out in the alpine biome worldwide impacting the knowledge on the occurrence of airborne pollen and their origin, for biodiversity studies, models of transport, forecasts, and climate change scenarios, for the reconstruction of past vegetation, and the potential impacts on human health. Deposition sampling is the method of choice, while volumetric sampling is mostly performed in densely populated mountain ranges.

Conventional microscopic identification of pollen of alpine environments is rarely complemented or replaced by molecular methods. The pollen bioaerosol mirrors the surrounding vegetation but includes components from medium and distant source locations. However, there is no uniform understanding on the definition of source-scales – crucial for the interpretation of the bioaerosol constituents – to which we propose an answer.

Alpine habitats, with their cold-adapted plant communities, may react to increasing temperatures with shifts in their range. The potential of using pollen as a proxy to monitor such changes in alpine biomes has been exploited in paleoecology but rarely in aerobiology.

☆

The air was delightful pure, dry, clear, sun-drenched, filled with a symphony of blithe wildflower fragrances.

Thomas Mann, The Magic Mountain

* Corresponding author at: Fondazione Edmund Mach, Research Innovation Centre, Via Mach, 1, 38098 San Michele all'Adige, Italy.

E-mail address: franziska.zemmer@fmach.it (F. Zemmer).

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Health impacts are linked to the low allergen load in the bioaerosol and the overall effect of the alpine climate in a highly natural environment. Generally, the soothing effect is reported for respiratory allergy patients, which may be jeopardized by seasonality and allergens transported from outside. The complex topography of mountain ranges does not allow for general assumptions on the quality and quantity of bioaerosol in alpine environments. We emphasize the importance of monitoring the bioaerosol in alpine environments to evaluate the effects of global change, and to optimize the management of respiratory health issues.

Definitions

- **Actuopalynology** is the study of modern pollen and spores to understand current ecological and environmental conditions, plant distribution, richness, and vegetation dynamics.
- **Aerobiology** deals with the study of bioaerosols, and how they interact with the atmosphere, including the dispersal, transport, and impact on the environment (Burge, 1995; Mandrioli et al., 1998; Lacey and West, 2006).
- **Atmospheric boundary layer (ABL)** refers to the lowest part of the Earth's atmosphere extending from the Earth's surface to around 1 to 3 km above. It is characterized by turbulent mixing of air exchanged between the Earth's surface and the atmosphere above (Stensrud et al., 2015; Collaud Coen et al., 2017).
- **Diversity indices** quantify the variety of taxa (i.e., the number of different species present) and the relative abundance of each species within a given ecological community or area.
- **DNA barcoding** is a molecular technique used to identify and classify a single unique individual based on short, species-specific DNA sequences.
- **DNA metabarcoding** is a high-throughput DNA sequencing technique used to identify and classify multiple species present in complex environmental samples.
- **Non-Pollen Palynomorphs (NPPs)** refer to microscopic organisms other than pollen and their remnants but similar in size (10–250 μm) (Kuoppamaa, 2023).
- **Palynology** deals with the examination of pollen, spores, dinoflagellates, and similar microscopic biological particles (<https://palynology.org/>).
- **Palynomorphs** include organic particles such as pollen grains, spores, and certain algae and fungal structures. These particles are often resistant to decay and can be well-preserved in sedimentary records.
- **Phenology** is the study of cyclic and seasonal natural phenomena in living organisms, such as flowering and leaf emergence in plants, in relation to climate and other environmental factors.
- **Taxon** (plural: taxa) is a group of organisms that are hierarchically classified in ranks based on shared characteristics. Commonly recognized taxa, in descending order of inclusiveness, are kingdom, phylum, class, order, family, genus, and species.
- **Taxonomic assignment** is the process of classifying or assigning DNA sequences to taxonomic categories, such as species, genera, families, or higher taxonomic groups.

1. Introduction

Among the components of the bioaerosol, pollen assumes a primary role in seed plant reproduction, and is highly relevant for the environment and health (Hornick et al., 2022). Pollen may cause respiratory allergies, act as a vector for endotoxins (Oteros et al., 2019), and particulate matter (Visez et al., 2020), affect the chemical composition of precipitation (Verstraeten et al., 2023), be a source of macromolecules responsible for ice nucleation (Pummer et al., 2012; Seifried et al., 2021).

The alpine biome typically is an open landscape situated above the treeline, where the natural absence of trees is primarily driven by low temperatures (Körner, 1998; Grabherr et al., 2010; Körner, 2021). It

covers 3.56 Mkm² (2.64 % of the world land masses, excluding Antarctica), stretching over all continents and latitudes, with an annual mean temperature below 5.9 °C (Testolin et al., 2020). Apart from temperature, macroclimatic features of the alpine life zone are difficult to generalize at a global scale (Körner, 2021). A common trait is reduced air humidity connected to low temperature. High intensity of solar radiation due to altitude holds true when skies are clear. Atmospheric pressure, as well as partial pressure of atmospheric gasses, linearly decreases with altitude but not with latitude (Körner, 2021). In arctic tundras, permafrost is widely present, precipitation is low and long day lengths characterize the growth season (Billings and Mooney, 1968). Decreasing temperatures with increasing height and latitude together with the length of the growth season determine the lower alpine, upper alpine and nival thermal belts. Such division facilitates the comparison of biodiversity of alpine biomes (Körner et al., 2011). Around the tree line in the lower alpine belt, ordinary shrubs can still grow, while trees assume a twisted shrub-like form, also referred to as *krummholz* (Billings and Mooney, 1968; Körner, 2021). The colder it gets, dwarf shrubs, herbaceous perennial plants, mosses, and lichens become more abundant (Billings and Mooney, 1968). The vegetation in the alpine biome is patched due to local climatic and topographic features forming micro-environments (Grabherr et al., 2010).

Alpine biomes in high latitudes and mid latitudes are particularly affected by global warming (Stanisci et al., 2016; Hagedorn et al., 2019), while the effects in the tropics are less pronounced (Körner, 2021). Important changes are also expected in precipitation distribution and snow cover (Körner, 2021). Warming scenarios of 2 °C–4 °C in mountain environments for the current century indicate a possible upward-shift of 300–500 m of vegetation zones (Hagedorn et al., 2019). Vegetation responds to rising temperatures with an increase in perennial and thermophilic species and the disappearance of cold-adapted species due to habitat loss (Stanisci et al., 2016; Lamprecht et al., 2018; Hagedorn et al., 2019). Most obvious are alterations of the treeline (Grabherr et al., 2010; Noroozi and Körner, 2018).

Besides temperature, elevated concentrations of atmospheric gasses, and land use change strongly impact the plant life of alpine biomes (Körner, 2021).

How such changes in vegetation composition and distribution translate into airborne pollen in the alpine biome remains poorly understood.

The composition of the pollen spectrum in alpine environments is complex. On one hand, it contains background components deposited from the troposphere, on the other hand from the local and regional vegetation. In more detail, the atmospheric boundary layer (ABL) is particularly close to the surface at high elevation (Collaud Coen et al., 2017), an ideal condition for capturing airborne pollen from remote sources (Ghasemifard et al., 2020; Bayr et al., 2023) that has trespassed the ABL.

The high altitude pollen spectrum is further influenced by mesoscale air mass movements through mountain ridges and valleys (Frei, 1997; García-Mozo et al., 2004; Charalampopoulos et al., 2013), as well as by circadian wind currents driven by mountain-valley thermal air convections. As a consequence, pollen assemblages at alpine locations contain information on the plant biodiversity located beyond the investigated area (Pardoe, 2021; van der Sande et al., 2021; Zhang et al., 2021). Therefore, it is especially important to separate local from non-local pollen sources, when attempting to reconstruct past vegetation and/or

to make projections on future changes thereof (van der Knaap et al., 2001; Quamar et al., 2016; Felde et al., 2015; Zhang et al., 2017; Dubey et al., 2017; Reitalu et al., 2019; Pardoe, 2021).

Moreover, mountainous areas with a high degree of naturality and clean air are of interest for health tourism (Schmude et al., 2021). The clinical impact of alpine climatotherapy on respiratory conditions provides evidence towards the benefits of stays in mountainous areas (Quignon et al., 2021; Cogo et al., 2022; Fieten et al., 2022; Tong et al., 2022). Consequently, studies on pollen diversity in alpine regions have been driven by allergological interest (Davies, 1969; Leuschner and Boehm, 1981; Anderson, 1985; Gehrig and Peeters, 2000; Frei, 1997; Fieten et al., 2023; Bayr et al., 2023; Frisk et al., 2024). However, the question remains whether the alpine destination of choice actually fulfills the promise of healthy air at any place and time, and for anyone.

To our knowledge, this is the first review on aerobiological studies conducted in alpine environments. Through the articles reviewed here, we aim to provide detailed information about aerobiology in the alpine biome, focusing on: (i) sampling and analytical techniques used, (ii) the relationship between airborne pollen biodiversity and source vegetation at different spatial scales, (iii) the impacts of global change on airborne alpine pollen, and (iv) the human health impacts of airborne pollen in the alpine environment.

2. Paper selection process

We have considered research articles and reviews from areas that are geographically located and/or functionally connected to alpine biomes (Testolin et al., 2020). The databases Web of Science (WOS), PubMed, Google Scholar and Google Scholar Alerts (GS) have been consulted for the key words “pollen + alpine”. We also performed a search with the key words “aerobiology + alpine”, and verified that all articles resulting from the search were included in the results retrieved from WOS “pollen + alpine”; conversely one additional article was found in PubMed, and five from GS. Redundant articles, morphological studies, taxonomical studies, honey studies, paleoecological studies without reference to

airborne modern pollen, non-indexed journal articles, and non-English studies were excluded from this review. From the resulting list we selected representative studies (Fig. 1). There are, however, a number of additional articles cited in support of specific topics, e.g. on the impacts of global change. Moreover, studies on automated pollen sampling were not retrieved for high altitude sites from the search criteria applied in this review. Yet, sampling networks for real time observation (EUMETNET <https://autopollen.net/> and SILVA <https://sylva.bioaerosol.eu/>) are currently developing in Europe including the high altitude monitoring site at Zugspitze at an altitude of 2650 m.

3. Alpine aerobiological studies around the world

The articles retrieved from the systematic search are mapped in Fig. 2 and listed in Supplementary Table 1. There is a geographical imbalance in aerobiological studies considered for this review. Of the 52 papers, 36 are from Europe, 12 from Asia, 3 from the Americas, and 1 from Australia. In fact, historically, aerobiological studies in alpine or related environments began in Europe. All clinical studies addressing health effects in relation to aerobiological data come exclusively from the densely populated Alps. In contrast, the selected studies from Asia primarily focus on actuoapalynological research.

4. Assessing airborne pollen in alpine environments

4.1. Sampling

In aerobiological studies, two main methods are used for sampling bioaerosols: gravimetric (passive) methods, primarily for pollen biodiversity assessments, and volumetric (active) air sampling, mainly in allergological studies. Deposition sampling is especially suited for remote, hard-to-reach locations without power sources, like the alpine biome. Natural traps, including mosses, lichens (Caramiello et al., 1991; Court-Picon et al., 2006), soil (Caramiello et al., 1991; Dubey et al., 2017), lacustrine sediments (Jackson and Smith, 1994; Finsinger et al.,

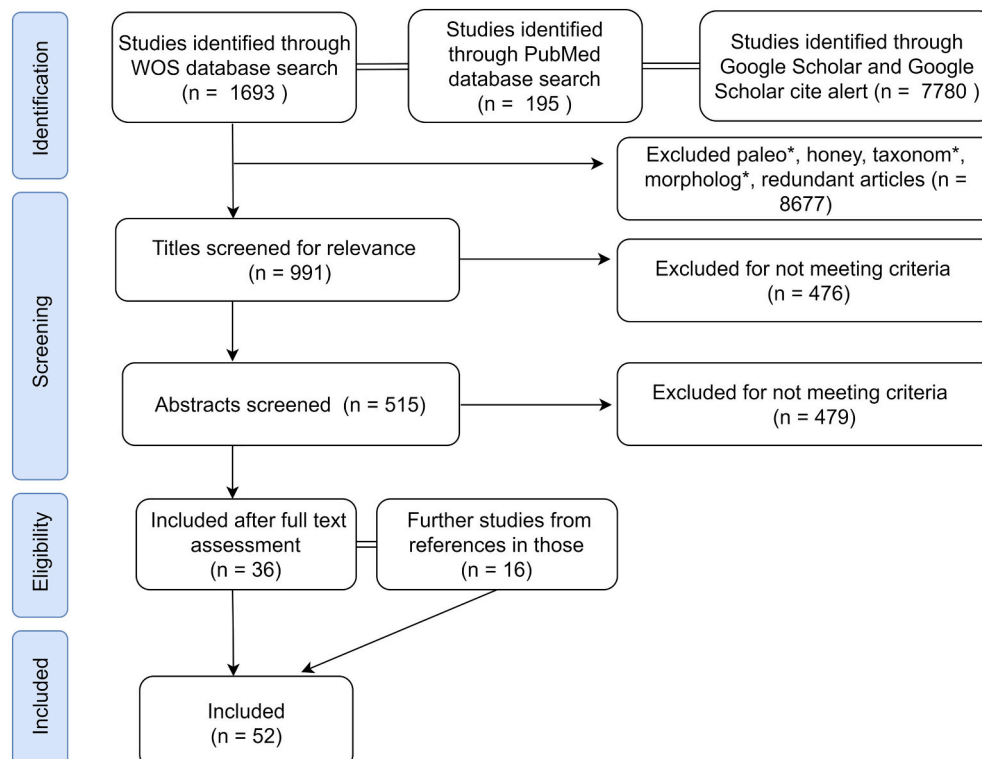


Fig. 1. The paper selection process.

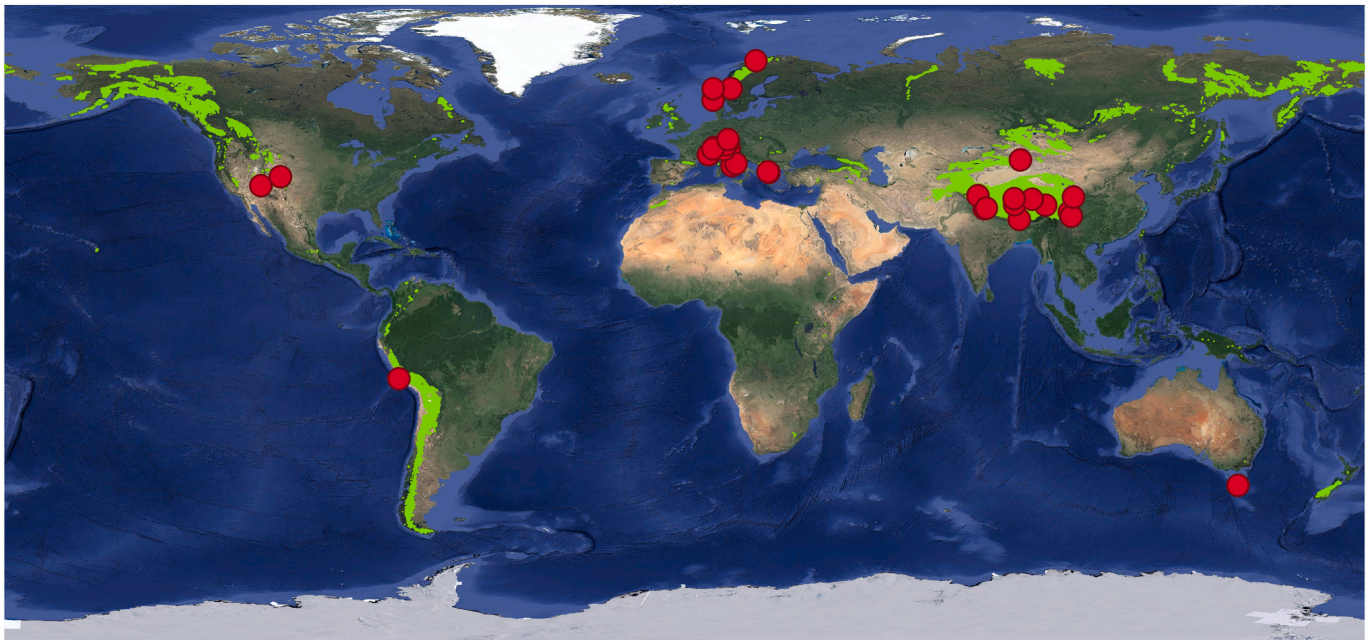


Fig. 2. Aerobiological study locations. $N = 52$ reviewed articles (red dots), and alpine environments (green areas) around the globe (Testolin et al., 2020). Click [here](#) for the interactive map.

2007; Herzschuh and Birks, 2010), snow and ice (Varotto et al., 2021), and artificial traps (Tauber, Durham) (Markgraf, 1980; van der Knaap et al., 2001), are commonly used.

The effectiveness of natural traps varies based on region and matrix. To address high variability in pollen samples from moss, at least 20 samples are recommended (Pardoe et al., 2010). Studies indicate that moss patches and the first layer (ca. $0 < 4$ cm) of lake sediments provide a sampling resolution of about 10–15 years (Felde et al., 2015; Quamar et al., 2016; Pardoe, 2021). Mosses, which are lighter than soil, may contain more pollen when an equal weight of both matrices is used (Caramiello et al., 1991). For alpine vegetation reconstruction, lake sediments are often preferred (Liu et al., 2023). Natural traps, compared to artificial traps, provide a better match to vegetation composition, with artificial traps more likely to overrepresent woody plants (Yu et al., 2001).

Artificial traps capture bioaerosol on an adhesive surface or in liquid. Durham samplers (Durham, 1946) are suitable for studying bioaerosol biodiversity, the intensity and timing of plant reproductive phenophases. For example, Durham traps were used at 3600 m altitude in the Himalayan alpine zone to measure daily airborne pollen (Gaur and Kala, 1984). Similarly, modified Durham traps were used to assess weekly birch pollen sedimentation in the Bavarian Alps (Wörl et al., 2022).

Tauber traps (Tauber, 1974), used for studying pollen dispersal, were employed by Markgraf (1980) to analyze spatiotemporal dispersal patterns in a Swiss valley-mountain system. These traps also help estimate pollen productivity for individual taxa, improving pollen diagram accuracy. For instance, Sjögren et al. (2008) used Tauber traps to calculate Absolute Pollen Productivity (APP) values for various taxa in the Swiss Alps. Tauber traps are also useful for collecting pollen for environmental DNA (eDNA) analysis, as shown by alpine biodiversity assessments (Leontidou et al., 2021).

Volumetric Hirst-type traps (Hirst, 1952) are less common in alpine regions but are useful for studying pollen biodiversity's potential impact on allergies. Data from Swiss and German alpine sites validated the COSMO ART pollen forecast model (Pauling et al., 2020). Time-series data from Hirst-type traps, such as those collected at the Gran Sasso mountain massif in Italy, also help analyze the effects of meteorological factors on pollen distribution (Pace et al., 2018). Long-term Hirst-type trap data can model the impact of global warming on pollen seasons

(Rojo et al., 2021b). Altitudinal gradient studies further track flowering phenology changes linked to temperature variations (Jochner et al., 2012). Volumetric samplers primarily catch wind-pollinated pollen (anemophilous), though insect-pollinated pollen (entomophilous) is occasionally found, such as in the Austrian Northern Limestone Alps (Bastl et al., 2020). While pollen biodiversity studies are limited by microscopic analysis, eDNA metabarcoding offers higher taxonomic resolution (Després et al., 2007). Table 1 outlines the pros and cons of passive and active sampling methods.

Table 1

Advantages and disadvantages of deposition (natural and artificial) and volumetric sampling.

Sampling method	Advantages	Disadvantages
Deposition (passive)	Low costs; suitable for remote locations; allows intense, large-scale and/or long-term studies. <i>Natural traps</i> : suitable for locations without infrastructures; available in situ; no set up required; quantitative and qualitative assessment of palynomorphs. <i>Artificial traps</i> : suitable for locations without infrastructure; controlled temporal sampling; easy management and sample preparation (except Tauber traps).	Standard operational Procedures (SOPs) not available; coarse temporal resolution of data; data not directly comparable to those from volumetric sampling. <i>Natural traps</i> : uncertainty on temporal resolution; pollen seasons cannot be determined (except for snow); laborious sample preparation; high data variability depending on the sampled matrix. <i>Artificial traps</i> : set up required; risk to be destroyed.
Volumetric (active)	SOPs available (EN 16868:2019, 2019); air concentration values obtained, with high temporal resolution (2 h to 1 day); allergy services in support for public health feasible; long time data series (>5 yrs) allow to build pollen calendars and detect temporal trends.	Infrastructures and electricity (or solar panel) required; (high) costs for the devices; (laborious and) recurrent (at least weekly) sampler management and samples handling required; risk of failure and malfunction.

Table 2
Advantages and disadvantages of the main analytical methods of aerobiological samples.

Analytical method	Advantages	Disadvantages
Optical microscopy	Standard methodology available (for Hirst-type samples); Largely adopted method, it allows data comparability in time and space; Easy pollen quantification (i.e., number of pollen grains per volume or surface unit)	Time-consuming method; Specific knowledge on morphological features of pollen taxa required; Quality of results depending (also) on operator capabilities; results are limited by shared pollen morphology of different taxa
eDNA metabarcoding	Highly specific taxonomic assignment; It allows to concurrently analyze a large number of samples; molecular techniques in continuous evolution	Standard procedures not available; Pollen quantification hardly feasible; Highly specialized technological facilities required

of the relationship between pollen and floristic diversity (Pardoe, 2021). Alternatively, in alpine pastures and grasslands, taxon coverage was categorized according to Braun-Blanquet (Caramiello et al., 1991; Court-Picon et al., 2006). Felde et al. (2015) assigned frequency codes to species within 500 m of lake sediment sampling sites and converted these into coverage abundances (i.e. code 1 = 0.5 %, 2 = 12.5 %, 3 = 37 %, 4 = 62.5 %, and 5 = 87.5 %). Floristic observations were used to assess pollen dispersal in relation to vegetation communities in mountain/valley systems (Markgraf, 1980), and pollen productivity was estimated based on vegetation data from gradually increasing concentric rings around sampling points (van der Knaap et al., 2001; Sjögren et al., 2008, 2015; Qin et al., 2020).

5.2. Pollen biodiversity sources

“Remote biodiversity,” originally coined by Bayr et al. (2023) to describe pollen from long-distance sources, highlights the importance of non-local pollen in open, high-altitude environments. Aerobiological samples along altitudinal vegetation gradients consistently show an overlap of pollen from different vegetation belts (Markgraf, 1980; Fletcher and Thomas, 2007; Yang et al., 2016; Ali et al., 2020; Pardoe, 2021; van der Sande et al., 2021). Fig. 4 illustrates examples from around the globe regarding the distribution of pollen taxa along mountain gradients from vegetation at different elevations. At Niederhorn in the European Alps, *Quercus robur*, *Q. petraea*, *Pinus sylvestris*, and *Fagus sylvatica* from the colline and montane belts were identified as pollen sources in the subalpine environment. *Pinus montana arborea* (*Pinus mugo* subsp. *uncinata* according to current taxonomy) represented

a local source at high elevations. Poaceae pollen originated from grassland communities in forest clearings, meadows and pastures along the gradient with *Nardus stricta* being the dominant Poaceae source in alpine grasslands above the timberline (Markgraf, 1980). At high latitudes in arctic tundras as in Norway, the altitudinal gradient effect for pollen apportionment of anemophilous trees appears of minor importance than horizontal airstreams carrying pollen from regional and extra regional sources.

For example, in treeless glacier forefields, arboreal pollen comprised over 80 % of samples, mainly from *Betula* (Betulaceae), and *Pinus* (Pinaceae). *Betula pubescens*, *B. pendula*, and *Pinus sylvestris* are widely present in the regional vegetation. While *Betula pubescens* was the local source at the lowest site (400 m a.s.l.), Poaceae pollen from pioneer species like *Poa alpina* was common in alpine habitats.

In high mountain ranges like the Middle Tianshan Mountains in the Himalayas and the Amazonian Andes, upslope and downslope winds play a significant role in the mixing of pollen (Yang et al., 2016; van der Sande et al., 2021). For instance, *Picea* (Pinaceae) pollen was detected beyond and below vegetation belts hosting Tianshan spruce (*Picea schrenkiana*). *Artemisia rupestris* (*Artemisia alba* according to current taxonomy) and several species of Amaranthaceae, including *Haloxylon ammodendron*, *Salsola* spp., *Petrosimonia sibirica*, *Suaeda physophora*, are dominant components of the desert vegetation at the bottom of the gradient, providing pollen found throughout the elevational gradient (Yang et al., 2016).

In the case of *Pinus* ssp., the problem for aerobiologists is distinguishing local from non local pollen, since Pinaceae pollen is present in the alpine open space (Markgraf, 1980; Gerasimidis et al., 2006; Pardoe, 2021).

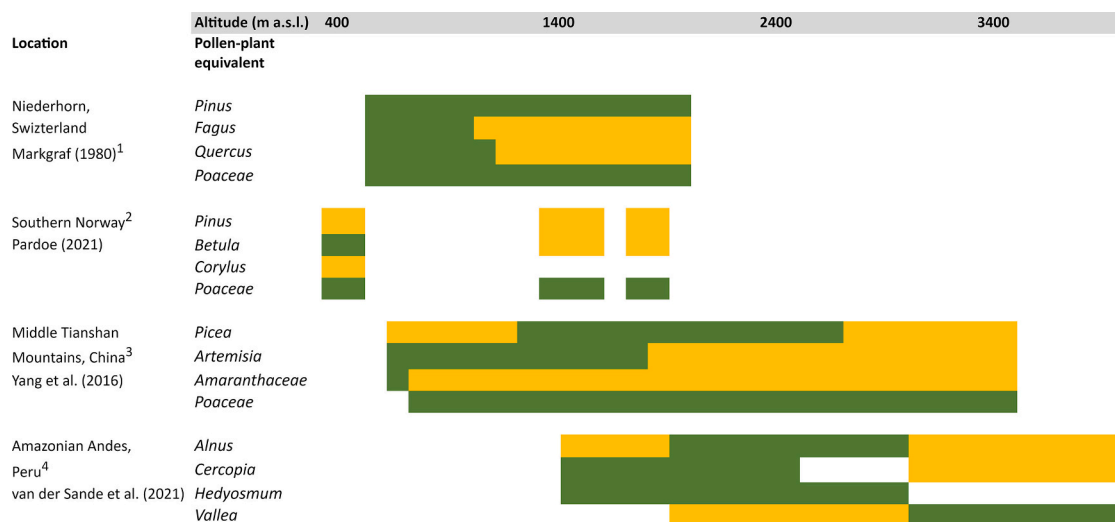


Fig. 4. Pollen and plant biodiversity on altitudinal gradients. Plant taxa on site and in deposition pollen samples on mountain gradients around the world. The top bar shows the elevation. Okra bar: pollen taxon only; dark green: pollen and plant taxon; white: not applicable. ¹) 500–1200 m a.s.l.: mixed oak forests; xeric pine forest; beech - maple forest; 1500–2000 m a.s.l.: subalpine spruce-mountain pine; grasslands; ²) 400 m a.s.l.: Glacier forelands with moss vegetation, heat shrubs, birch and salix scrubs; 1400 m a.s.l.: Glacier forelands with moss, pioneer, and snowbed vegetation, heat shrubs; 1800 m a.s.l.: Glacier forelands with lichens, moss, and pioneer vegetation; ³) 700–1230 m a.s.l.: *Artemisia* desert, 1300–1720 m a.s.l.: Forest - steppe, 800–2600 m a.s.l.: Tianshan spruce forest, 2600–3390 m a.s.l.: Alpine and subalpine grassland, 3500–3900 m a.s.l.: Alpine cushion; ⁴) Plant occurrences in elevational belts of a tropical forest gradient.

Deposited stomata can, thus, complement pollen samples to detect alterations in the tree line (Li and Li, 2015).

Overall, pollen at the receptor site originates from a complex mixture of sources at different scales (Janssen, 1966).

5.2.1. A matter of spatial scale

However, interpretation of scales related to pollen source areas in the reviewed literature are subjective, if not contradictory (Table 3). Menzel et al. (2021) argue: “There is no generally applicable definition of medium- and long-range transport”. Nevertheless, there is a clear need to define scales for pollen source areas when components of the bioaerosol are used in an ecological research context or to predict the effects of global change on vegetation (Sugita, 1994).

Since the transport of airborne pollen depends on atmospheric processes (Rantio-Lehtimäki, 1994), we suggest standardizing scale definition following Orlandi (1975) (Fig. 5):

- i) local sources (0–2 km) where airborne pollen is carried by micro-scale air currents (short distance), such as wind gusts and plumes;
- ii) regional sources with meso- γ and β scale air currents (medium distance, or medium range) (2–200 km), which include topography-driven convections, thunderstorms, and nighttime depositions;
- iii) long-distance sources (200–2000 km) with meso- α scale currents, including weather fronts and hurricanes.

Examples of this alignment are as follows:

(i) Local sources

Plant taxa in the immediate vicinity of the receptor site in open alpine spaces of the Northern Hemisphere are represented in the pollen spectrum, with anemophilous herbaceous taxa such as Poaceae, Cyperaceae, and Juncaceae dominating. Entomophilous taxa are quantitatively less present but act as indicators of the local flora (Markgraf, 1980; Ali et al., 2020).

Table 3

Scales for bioaerosol source areas according to example references reviewed. Definitions are direct quotes from the articles.

Scale	Definition	Reference
Local	Within sampling site	Dubey et al., 2017
	Herbs within 46.6 m, trees within 100 m	van der Knaap et al., 2001
Extra-local	Surrounding 100 m ²	Pardoe, 2021
	A few hundred meters from site	Dubey et al., 2017
Regional	Beyond a few hundred meters	Dubey et al., 2017
	Trees within 0.1–4.64 km	van der Knaap et al., 2001
	Not defined	Pardoe, 2021
Medium range	Particle transport with the wind, mixing inside the atmospheric boundary layer, as well as dry and wet removal at the regional scale	Menzel et al., 2021
	1° × 1° for regional circulation patterns (each degree latitude corresponds to ca. 110 km)	Bayr et al., 2023
	Pollen transport of up to 100 km	Frei, 1997
Extra-regional	Beyond the area of vegetation formation	Dubey et al., 2017
	>4.64 km, across the Alps	van der Knaap et al., 2001
Long distance	Long distance from lower down the valley	Pardoe, 2021
	Dispersion with synoptic (large) scale wind plus exchange between the boundary layer and the free troposphere	Menzel et al., 2021
	>100 km	Bayr et al., 2023
	Taxa that do not live in the study area	Pace et al., 2018

The pollen spectrum detected above the treeline (extra-local) contains taxa from vegetation at lower elevations. These are carried by micro-scale air currents, including thermic upward air mass movements from the valleys, as seen with *Pinus* (Pinaceae) (Markgraf, 1980; Ali et al., 2020; Pardoe, 2021) or *Artemisia* (Asteraceae) (Yang et al., 2016).

(ii) Regional sources

Pollen from regional sources represents the background pollen signal of a region (Sjögren et al., 2008). For instance, *Picea* (Pinaceae) pollen found in Norwegian glacier forelands was linked to spruce forests at least 100 km away (Pardoe, 2021). Wind patterns and topography facilitated the influx of *Castanea* (Fagaceae) pollen from the southern foothills of the Alps to the Central Alps, providing evidence for medium-range transport (Frei, 1997).

(iii) Long distance sources

In the Himalayan alpine zone, temperate and subtropical pollen outnumbered local taxa at Rudranath (Gaur and Kala, 1984), and similarly small amounts of *Syzygium* and *Ailanthus* pollen from tropical areas were found in the Kalla glacier valley (Ali et al., 2020). Pollen from long-range air mass movements, attributed to “remote biodiversity,” was possibly responsible for 87 % of allergenic symptoms at an alpine receptor site at 2600 m a.s.l. in South Bavaria (Bayr et al., 2023). Moreover, bioaerosol apportionments from remote sources can lead to a mismatch between the onset of local flowering and the temporal distribution of pollen, as demonstrated by back-trajectory models and phenological observations at the pollen monitoring station in Oberjoch, Germany. Only 13 % of the pollen spectrum could not be explained by back-trajectory models (Menzel et al., 2021).

5.3. Towards a pollen-plant relationship

Modern aerobiological data facilitate the interpretation of fossil pollen data when reconstructing past vegetation and climate (Caramiello et al., 1991; van der Knaap et al., 2001; Fletcher and Thomas, 2007; Sjögren et al., 2008; Li et al., 2012; Felde et al., 2015; Zhang et al., 2017; Dubey et al., 2017; Reitalu et al., 2019; Pardoe, 2021). To this end, pollen-vegetation relationships are extensively studied for paleoecological purposes in the alpine biome of Europe ($n = 10$ papers analyzed) and high-altitude mountain systems in Asia ($n = 12$). From other regions, only one study from the Andes (van der Sande et al., 2021) and one from Tasmania (Australia) (Fletcher and Thomas, 2007) were found eligible (Fig. 2). When quantifying the relationship between pollen and vegetation, several biases need to be considered.

One key bias is the difference in pollen production among source plants. Qin et al. (2020) estimated the relative pollen productivities (RPP) of 15 non-arboreal taxa compared to Cyperaceae, which was found to be the most suitable taxon for calibrating pollen-vegetation models (Li and Li, 2015). The representation of a pollen taxon in the sample depends on how much and how far pollen is dispersed. Pollen accumulation rates (PAR) can be used in dispersal models, together with the cover of a taxon in a specific area, to calculate Absolute Pollen Productivity (APP) values (pollen * cm⁻² * yr⁻¹) for that taxon. The advantage of APP is that it is a taxon-specific value that can be used to reconstruct its cover independently of other taxa. APP values were calculated for the woody taxa *Larix*, *Picea*, *Pinus* total, *Pinus cembra*, *Pinus mugo* (Pinaceae), *Alnus alnobetula* (Betulaceae), and later for the herbaceous Poaceae and Cyperaceae (Sjögren et al., 2008, 2015).

Moreover, vectors for sexual reproduction (wind or insects), the buoyancy of pollen depending on the morphological traits of the pollen grain, and the spatial scale (see Section 5.2) must be considered in the evaluation. Plant species that produce pollen grains with similar traits are often grouped at the genus or family level, which reduces taxonomic resolution (Birks et al., 2016; Felde et al., 2015; Reitalu et al., 2019).

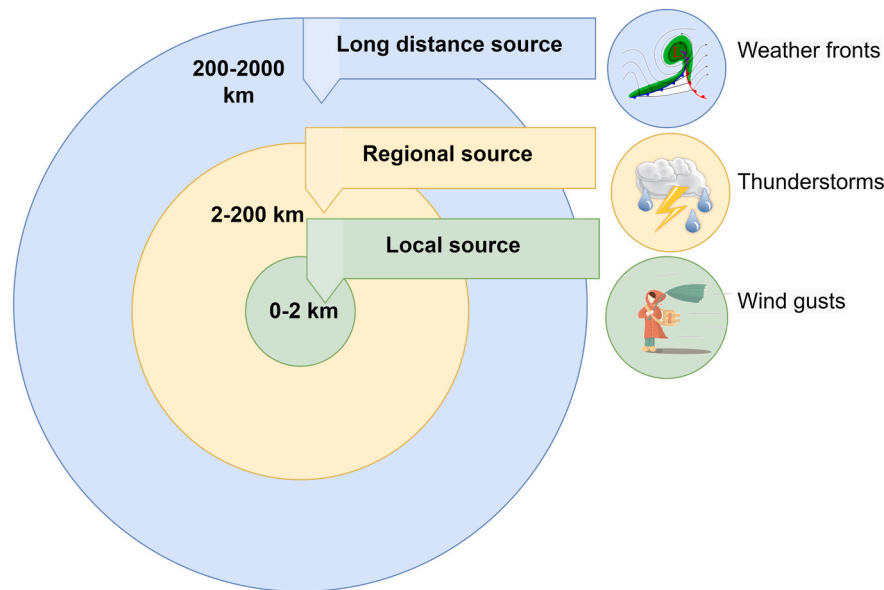


Fig. 5. Scales of source areas for an aerobiological sampling point and exemplary atmospheric processes.

However, this step is essential to establish a pollen-vegetation ratio. The R-value, a simple pollen-vegetation ratio ($R = P/V$), where P is the percentage of a pollen taxon relative to total pollen, while V refers to the percentage of plant cover relative to a given area, gives insight into the contribution of individual plant taxa to the pollen sample. Well-represented plant taxa in the pollen sample have a value close to one, while overrepresented taxa score above one and underrepresented taxa score below one (Charalampopoulos et al., 2013; van der Sande et al., 2021).

Richness, the total number of taxa (α biodiversity) identified in samples, is another critical measure (Felde et al., 2015; Reitalu et al., 2019; Pardoe, 2021). Indices for richness are reviewed in Birks et al. (2016). Promising results in using pollen to estimate plant biodiversity stem from DNA metabarcoding studies. DNA metabarcoding results of air samples by Leontidou et al. (2021) corresponded with the plant species of a protected site and showed a temporal alignment with flowering phenophases. Furthermore, pollen α -biodiversity along elevational gradients was aligned with plant records from the same site. However, the estimation of plant abundance by microscopic analysis of pollen and DNA metabarcoding differed. For example, *Pinus* was the main taxon found by both microscopy and eDNA, but was proportionally higher in DNA reads than pollen on microscopic slides (Leontidou et al., 2021).

In conclusion, when assessing plant biodiversity from pollen-vegetation relationships, it is essential to address pollen production, pollination mode, plant abundance, richness, and the identification methodology used.

5.4. Drivers of change in airborne pollen assemblages and phenology

Modifications in pollen assemblages and phenology in the alpine biome may reflect the impact of global change on the ecosystem in general and alpine flora in particular. In alpine environments, plant growth depends on temperature (Rixen and Wipf, 2017), rain, snow cover (Grytnes et al., 2014), atmospheric CO_2 and N concentrations, as well as non-climatic factors such as land use (Rixen and Wipf, 2017; Vanneste et al., 2017; Körner, 2021).

Alpine environments are among the habitats most strongly affected by climate change (Engler et al., 2011). Time-scale studies show the complex relationship between climate change, vegetation phenology (Dorji et al., 2020; Chen et al., 2023), and the amount of airborne pollen

(Simoleit et al., 2016; Rojo et al., 2021a). Over a 30-year period (1982–2014), an earlier start and peak trend of the *Fagus* (Fagaceae) main pollen season, as well as an increase in pollen amounts, significantly correlated with increased temperatures at a German alpine site (Simoleit et al., 2016). Century-old vegetation records show considerable upward migration of species towards mountain summits, caused by the alteration of the optimum elevation for plants due to climate warming (Lenoir et al., 2008; Rixen and Wipf, 2017). A consistent signal of altitudinal expansion in birch tree distribution, and subsequent increases in airborne *Betula* (Betulaceae) pollen, due to climate change was reported for the Bavarian Alps (Rojo et al., 2021a), affecting the pollen season at altitudes above 800 m a.s.l. (Rojo et al., 2021b). Although *Alnus viridis* (*Alnus alnobetula* according to current taxonomy) is in decline in the Alps, linked to the reduction of snow cover and increasing temperatures (Pisetta et al., 2012), earlier and more intense pollen seasons at higher altitudes were predicted for *Alnus* (Rojo et al., 2021b), likely favored by the expansion of *Alnus incana*, *A. glutinosa*, which have their growth optimum at lower elevations.

Snow cover determines the length of the vegetation period in alpine environments (Körner, 2021). Pollen concentrations in high mountain Mediterranean grasslands in the Sierra Nevada (Spain) were mostly influenced by temperature, which alters snow cover, but also by land use change. As a result, Poaceae pollen abundance was shown to be a useful indicator of global change, given its sensitivity to both anthropic and hydro-meteorological changes (Algarra et al., 2019).

Changes in grazing practices and land exploitation for tourism or recreational use in alpine contexts may further complicate biodiversity modifications expected due to climate change (Bhatta et al., 2018; Wei et al., 2020; Peringer et al., 2022). Decreased grazing intensity, along with increased temperatures and precipitation, has led to significant changes in the frequency and relative abundance of alpine plant species. These variations might be driven by alterations in N availability due to grazing, changes in the N/P ratio, and soil moisture levels (Zhang and Fu, 2021). Aerobiology is capable of distinguishing natural vegetation from human-modified vegetation through characteristic pollen markers. In the alpine and subalpine environments of the French Alps, *Rhinanthus* type (Orobanchaceae), Apiaceae, and Dipsacaceae are indicators of mown meadows, while *Urtica* type (Urticaceae), *Plantago media/major* (Plantaginaceae), *Trifolium* type (Fabaceae), and *Potentilla* type (Rosaceae) indicate grazed areas. This is important for the reconstruction of past land use (Court-Picon et al., 2006). As vegetation changes, it is

plausible to expect qualitative and quantitative changes in airborne pollen spectra. Pace et al. (2018) detected a high abundance of Cupressaceae/Taxaceae pollen in an Apennine alpine site (2117 m a.s.l.), linked to the expansion of heliophilic *Juniperus* (Cupressaceae) due to global change. As a colonizer of disturbed, poorly developed soils with a wide temperature range (Enescu et al., 2016), *Juniperus* (Cupressaceae) has been favored by anthropogenic disturbances (Pearman et al., 2008).

Elevated CO₂ concentrations augments photosynthetic efficiency, which could influence growth rates and biomass production (Körner, 2021), potentially altering pollen production in alpine plant communities. Due to the atmospheric fertilizer N, nitrophilic taxa (e.g. Amaranthaceae, Urticaceae), will be more abundant. The airborne pollen spectra of the alpine environment also contain pollen from lowland species due to medium- and long-range transport (Ghasemifard et al., 2020; Bayr et al., 2023) (see Section 5.2). For example, pollen from invasive species such as *Ambrosia* spp. (Asteraceae) was observed in all pollen measurements along an altitudinal gradient of Mt. Olympos, despite no known floristic occurrences in the area (Charalampopoulos et al., 2013).

In conclusion, the peculiarities of alpine areas, including actual vegetation cover and biodiversity, must be considered when interpreting pollen sampled in alpine environments, especially under global change scenarios.

6. Impacts on human health

There is extensive consensus in the literature on a reduced pollen load at medium and high altitudes compared to low elevations (Markgraf, 1980; Leuschner and Boehm, 1981; Gehrig and Peeters, 2000; Jochner et al., 2012; Charalampopoulos et al., 2013; Pace et al., 2018; Damialis et al., 2019; Pauling et al., 2020; Wörl et al., 2022; Bayr et al., 2023), although this is not always evident for all pollen taxa.

Pollen sedimentation studies along mountain gradients support this altitudinal decrease (Fig. 6). A 78 % reduction in the total pollen load was reported from 740 to 1990 m a.s.l. in Niederhorn, Switzerland (Markgraf, 1980). In the Pieria mountains of Greece, pollen load decreased by 45 % at 1990 m a.s.l. compared to 1500 m a.s.l., and by 22 % when comparing the highest site (1990 m a.s.l.) with the lowest (1260 m a.s.l.; Gerasimidis et al., 2006). While the pollen abundances do not gradually decrease along the gradient, they are consistently low at the highest sampling point. For example, on the Zugspitze in the Bavarian Alps, a 91 % decrease in Poaceae and a 76 % reduction in *Betula* pollen were reported at the highest site (2657 m a.s.l.) compared to the lowest (720 m a.s.l.) during 2008–2009 (Jochner et al., 2012). In 2020 (April to May), *Betula* pollen in the same area but with a more detailed elevation gradient showed the highest load at 1616 m a.s.l. and the lowest at the summit (Fig. 6, right; Wörl et al., 2022). In Switzerland (Markgraf, 1980), Poaceae pollen abundance did not follow the same pattern, as the highest site did not record the lowest values, although

three out of four lower elevation sites reported higher values (Fig. 6, central panel).

Airborne allergenic pollen poses a significant burden on allergy sufferers. Therefore, hay fever patients may seek relief in alpine environments, where aeroallergen concentrations and air pollution are low (Leuschner and Boehm, 1981; Buck and Levetin, 1985; Monn et al., 1999).

The benefit of reduced grass pollen exposure was tested in a small controlled study of hay fever patients, involving five grass-sensitized and six non-sensitized adults. A significant decrease in allergy symptoms resulted from a short-term change from an urban environment during the peak grass pollen season to a high alpine environment on the Zugspitze at 2600 m a.s.l. Levels of symptoms correlated significantly with daily grass pollen concentrations monitored on site. During the twelve-day stay, allergy-specific IgE values dropped significantly in the sensitized group (Damialis et al., 2019).

Considering this, individuals with allergic respiratory conditions benefit from stays at elevated altitudes (Rijssenbeek-Nouwens et al., 2012; Damialis et al., 2019; Quignon et al., 2021; Fieten et al., 2022; Cogo et al., 2022; Tong et al., 2022). In addition to reduced exposure to aeroallergens, levels of irritating pollutants such as NO₂, SO₂, suspended particulate matter, and pollutants (NH₃, HNO₃) are relatively low on average (Monn et al., 1999; Quignon et al., 2021). Moreover, UV radiation (which stimulates vitamin D production) and biogenic volatile organic compounds like tree-emitted terpenes can reduce immune responses, as reviewed by Fieten et al. (2022) and Tong et al. (2022). Clinical cohort studies in Davos (Switzerland), Misurina (Italy), and Briançon (France) have analyzed changes in immunological parameters related to stays at altitude. Both allergic and non-allergic asthmatics showed improved airway inflammation, symptoms, and lung function (Karagiannidis et al., 2006; Rijssenbeek-Nouwens et al., 2012; Cogo et al., 2022).

Regarding the resident population in healthy mountainous environments, pediatric studies from Switzerland and Norway suggest a relatively high aeroallergen sensitization rate (25–39 %) (Njå et al., 2000; Fieten et al., 2023), which was, however, linked to indoor allergen exposure.

Depending on the site, the seasonal course, and transport events, pollen concentrations may still be high enough to trigger allergy symptoms in susceptible individuals. This is due to the allergenic nature of grass pollen, (Damialis et al., 2019; Wörl et al., 2022; Fieten et al., 2023). Poaceae grass was the dominant pollen type in subalpine environments of the Rocky Mountains (Buck and Levetin, 1985) and in Swiss alpine sites (Monn et al., 1999; Gehrig and Peeters, 2000). In fact, meadows and pastures characterize alpine landscapes, explaining the presence of grass pollen in the montane belt. Betulaceae pollen from birch (*Betula*) and alder (*Alnus*) are less prominent, but *Alnus viridis*, which flowers at high altitudes, can release enough pollen to trigger hay fever symptoms (Gehrig and Peeters, 2000).

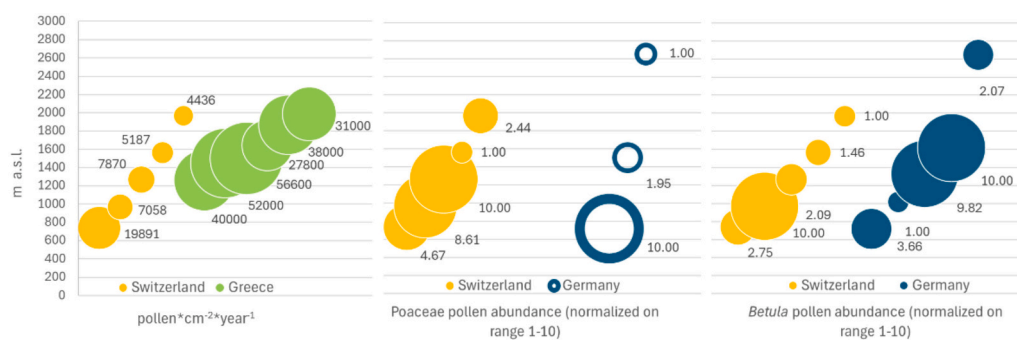


Fig. 6. Pollen abundances on mountain gradients from case studies in Switzerland (Markgraf, 1980); Greece (Gerasimidis et al., 2006) and Germany (Jochner et al., 2012; and Wörl et al., 2022). Abundances are reported as bubble width and labels. Solid filled bubbles refer to data obtained from deposition sampling, circles from volumetric sampling. Left: original values of pollen sedimentation rates; Middle and Left: min-max normalized pollen abundances in a range 1–10.

The duration of the allergenic pollen season at high altitudes and latitudes is largely determined by temperature, as the flowering phenophase starts later in the year leading to a shorter pollen season. However, the climate at high-elevation sites in the European Alps has warmed at a rate of +0.5 °C per decade over the last 30 years (Nigrelli and Chiarle, 2023), and future scenarios of +2°C-4°C will potentially jeopardize the health benefits of alpine stays. Therefore, local pollen information in mountain areas is essential for allergy sufferers to ensure that their stay provides relief when exposure at lower altitudes is especially high (Gehrig and Peeters, 2000).

7. Conclusion and outlook

Climate and socio-economic changes are posing a threat to the alpine environment with impacts on biodiversity and human health. This review aims to shed light on the state of the art regarding aerobiological studies in the alpine environment. The main outcomes are the follows:

- (i) As for the assessment of airborne pollen, deposition sampling, both by natural and artificial traps, results to be particularly suitable for remote areas. Natural traps are already present on site, and for free. Artificial traps, on the other hand, allow for control of the temporal sampling length, and thus the assessment of the seasonal trends.
- (ii) As in aerobiological studies in general, optical microscopy is the most applied method for the quantification and taxonomic identification of pollen grains, based on their micromorphological features. Recent advancements in molecular techniques promise a more specific taxonomic classification compared to microscopic analysis, proving particularly suitable for analyzing biodiversity. This method is up to now scarcely applied in alpine studies.
- (iii) Automated pollen sampling in alpine environments has not (yet) emerged from the search criteria applied in this review. However, automated real time sampling has commenced at high altitude and latitude sites in Europe (<https://www.zaum-online.de/pollen/pollen-monitoring-map-of-the-world.html>.)
- (iv) High elevation sites are receptors for local and non-local pollen bioaerosol and, thus, suitable for measuring a multi-spatial scale biodiversity. Vegetation and/or floristic data at different properly defined spatial scales are useful to establish a pollen-plant relationship. We propose to standardize the definition of source areas in alignment with atmospheric transport processes (Orlanski, 1975) as follows: a) local sources (0–2 km); b) regional sources (2–200 km); c) extra-regional, long distance sources (200–2000 km).
- (v) Climate change is recognized as a factor that impacts on the pollen seasonality as well as on its abundance. Changes in the pollen spectrum may also reflect changes in plant distribution, which in turn can be a consequence of climate or land use changes as, e.g., temperature or grazing practices.
- (vi) Airborne pollen concentration is generally lower at high altitudes than at lowlands, which is beneficial for hay fever sufferers. Low pollen concentrations however, do not always explain allergic symptoms in this environment. Possible causes lay in (indoor) exposure to non-pollen allergens and in long distance transport events.
- (vii) Research gaps related to airborne pollen in the alpine environment concern their trophic role in the alpine ecosystem and their degree of viability, essential for gene dispersal over mountains.

Overall, the need emerges to deepen knowledge on the pollen biodiversity in the alpine environment and the relationships with local vegetation to unleash the potential of aerobiology for conservation and monitoring efforts, as well as for health impacts.

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CRediT authorship contribution statement

Franziska Zemmer: Writing – review & editing, Writing – original draft, Visualization, Methodology, Conceptualization. **Antonella Cristofori:** Writing – review & editing, Writing – original draft. **Fabiana Cristofolini:** Writing – review & editing, Writing – original draft. **Elena Gottardini:** Writing – review & editing, Writing – original draft, Supervision, Conceptualization.

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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Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT in order to rephrase definitions in the glossary, and rarely to paraphrase information taken from the articles reviewed and for a final language proof. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Data availability

No data was used for the research described in the article.

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