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Tracking plant diversity and phenology by high-altitude aerobiology in Alpine Natura 2000 sites

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Abstract

Airborne pollen is increasingly recognized as a valuable tool for assessing plant biodiversity in mountain ecosystems where traditional field surveys are logistically challenging. In Alpine bioregions, pollen data can provide critical insights into vegetation dynamics, climate change impacts, and conservation priorities. However, the relationship between modern airborne pollen and local plant biodiversity remains understudied in high-altitude ecosystems.

This study investigates the pollen–plant biodiversity relationship across four protected high-altitude sites in Trentino (2022–2024). Airborne pollen was sampled using Sigma-2 passive traps, while plant biodiversity was quantified via multi-scale vegetation surveys (10 m, 100 m, and 1000 m radius). Data were analyzed using Jaccard similarity indices, non-metric multidimensional scaling (NMDS), and Pollen-Vegetation ratios (R-values) across separate plant growth forms.

A total of 53 pollen taxa and 306 plant species (corresponding to 38 pollen-equivalent plant taxa) were identified across the sites. Herbaceous pollen richness selectively captured fine-scale local plant diversity of open alpine habitats; woody pollen reflected broader, landscape-level downslope forest belts. Anemophilous arboreal taxa (e.g., *Alnus*, *Pinus*) yielded high R-values (pollen-to-vegetation abundance ratios > 1), while entomophilous herbs scored significantly lower. High-resolution aerobiological data demonstrated a 2-week lag in Poaceae flowering between 1900 and 2600 m a.s.l.

Airborne pollen data obtained via gravitational deposition offer a cost-effective, scalable, and non-invasive approach to complement traditional field-based plant biodiversity metrics. Integrating modern aerobiological data with multi-scale vegetation data provides a reliable environmental baseline for tracking climate-driven changes, such as in plant phenology and biodiversity in vulnerable mountain ecosystems.

1. Introduction

Pollen grains are biological particles that, along with fungal spores, bacteria, viruses, algae, and fragments of lichens, plants, and animals, constitute the bioaerosol (Robinson and Breed 2023). Their study enables the characterization of airborne plant biodiversity and provides proxies for major vegetation cover and land use (Stivrins et al. 2021; Hornick et al. 2022).

Aerobiology, traditionally associated with allergenic pollen monitoring in urban areas (e.g., ZAUM map; Buters et al. 2018), holds significant potential for biodiversity research and conservation (Fernández-Llamazares et al. 2014; Leontidou et al. 2021; Hornick et al. 2022). A key mission of protected areas is to warrant plant biodiversity conservation by means of research and monitoring. Assessing the role of plant diversity in ecosystem functioning over extended timescales is challenging, and pollen analysis is, in principle, a suitable method for conducting such studies (Matthias et al. 2015).

The presence of pollen in the air depends on its production and subsequent release by the floral organs of plants. Among the various pollination strategies, anemophily is the one that contributes the highest amounts of airborne pollen. Anemophilous plants (gymnosperms, grasses, many temperate deciduous trees, herbaceous weeds, and shrubs) rely on massive production of pollen to overcome the dilution effect of the air used as a pollination vector. Entomophilous plants, on the other hand, lure insects to ensure sexual reproduction. When insects carry pollen from plant to plant, they may lose some while in action.

Airborne pollen at a given site and time reflects: (i) vegetation composition and structure; (ii) flowering phenology; (iii) pollen transport across varying distances driven by air mass movements.

In paleoecology, fossil pollen richness and abundance are widely used as indicators of plant diversity, climate variability, and human activity (Bunting et al. 2013; Birks et al. 2016; Giesecke et al. 2019; Fekadu et al. 2025). Pollen–plant relationships differ across ecological settings and the spatial scale of vegetation surveys (Abraham, 2022). The correlations between pollen and plant richness are generally positive in heterogeneous landscapes that include both open habitats (e.g., alpine areas, grasslands, peatlands) and forests in Central Europe (Abraham, 2022), although shaped by multiple ecological and methodological factors (Birks et al. 2016; Reitalu et al. 2019; Abraham et al. 2022). Similarly, the pollen-plant relationship along elevational gradients in Northern Europe was linear across vegetation zones (Felde et al. 2016). Pollen richness in open landscapes tends to reflect ecosystem diversity rather than strictly local vegetation (Reitalu et al. 2019; Giesecke et al. 2019; Pardoe 2021). However, at small spatial scales (0.5–6 m radius) in open habitats such as fens, herbaceous pollen richness can be a reliable proxy for local plant diversity. In contrast, woody pollen taxa correlate more strongly with vegetation at larger spatial scales (6–100 m radius), suggesting that woody pollen reflects broader landscape patterns (Bunting et al. 2013).

The interpretation of the pollen signal improves when pollen data are analyzed in terms of growth forms (herbaceous vs. woody taxa) and spatial integration. Herbaceous pollen more accurately captures fine-scale vegetation patterns, whereas woody taxa integrate signals across broader spatial extents (Blaus et al. 2020). Pollen diversity is a robust measure of vegetation structure and landscape heterogeneity and is suited for between-site comparisons. In combination with pollen richness and evenness, it provides a powerful framework for evaluating long-term changes in vegetation structure related to climate and land use (Matthias et al. 2015).

Classes of Essential Biodiversity Variables (EBVs) have been proposed to streamline biodiversity data for comparison at national and global scales, essential to detect changes in time and space, and to set management priorities (Jetz et al. 2019; Schmeller et al. 2024; Kissling et al. 2026; Kim et al. 2026). Community composition and abundance could be derived from pollen data. Repeatedly detected pollen taxa during the flowering season serve as indicators of flowering phenology in anemophilous plants such as graminoids, shrubs, and trees (García-Mozo et al. 2014; Ghitarrini et al. 2017; Zemmer et al. 2024). Growth forms are closely linked to community structure, for example in mountain ecosystems: graminoids characterize open habitats, while shrub and tree communities define downslope vegetation belts along temperature gradients (Markgraf 1980; Zhang et al. 2017, 2021). In sum, pollen provides high-resolution data on flowering phenology and species composition across broad spatial and temporal scales (Mercuri et al. 2016; Gehrig and Clot 2021; Cristofolini et al. 2024; Ščevková et al. 2024), which are otherwise difficult to capture through field surveys. Protected alpine sites serve as biodiversity refugia and reference systems for conservation. Monitoring airborne pollen biodiversity in such highly natural environments strengthens our ability to disentangle climatic signals from anthropogenic pressures on plant communities. As emphasized by Zemmer et al. (2024), there is a need to deepen understanding of pollen biodiversity in alpine environments and its relationship with local vegetation to unlock the full potential of aerobiology for conservation and monitoring.

The present study focuses on protected Alpine sites in Trentino (Eastern Alps, Italy). We aim to

1. to characterize high-altitude airborne pollen diversity and phenology across a three-year monitoring campaign (2022–2024) to establish an environmental baseline to integrate in estimations of global change–driven variations in mountain vegetation across time and space;
2. to evaluate the potential of airborne pollen biodiversity as a proxy for plant biodiversity across different spatial scales.

2. Materials and Methods

2.1 Study sites

The study was conducted in the surroundings of four Alpine refuges located in protected areas of the Natura 2000 network in Trentino, Northern Italy: Rifugio Val di Fumo (FUM; Adamello Brenta Natural Park), Rifugio Altissimo (ALT; Monte Baldo Local Natural Park), Rifugio Rosetta (ROS; Paneveggio Pale di San Martino Natural Park), Rifugio Larcher al Cevedale (CEV; Stelvio National Park) (Fig. 1; Table 1). The vegetation at the regional level is characterized by a pronounced altitudinal zonation, transitioning from Mediterranean-influenced communities on the valley floors to expansive montane forests — primarily composed of *Picea abies*, *Pinus sylvestris*, *Fagus sylvatica*, and *Larix decidua* — which occupy over 60% of the provincial territory. At higher elevations, this gradient shifts toward subalpine stands of *Larix decidua* and *Pinus cembra*, eventually giving way to alpine meadows and specialized lithophilic flora.

The study sites cover an altitudinal range of about 700 m, from 1,918 m a.s.l. (FUM) to 2,609 m a.s.l. (CEV). The sites represent a phytoclimatic north-south gradient from the continental, inneralpine CEV, FUM, and ROS at the verge to prealpine submediterranean vegetation at ALT (Gandolfo and Miori 2018). The average annual rainfall at FUM, ALT, ROS, and CEV is 1,446 mm, 1531 mm, 1349 mm, and 887 mm, respectively. The mean minimum and maximum monthly temperatures at FUM range from 0.1°C to 9.8°C, at ALT from 2.1°C to 10.1°C, at ROS from −0.5°C to 6.6°C, and at CEV from − 3.8°C to 3.0°C. Meteorological data were retrieved from the nearest weather station (Provincia Autonoma di Trento 2026). FUM lies in a granitoid glacial valley with subalpine shrubs of *Rhododendron* spp., *Juniperus communis*, and *Pinus mugo.* The vegetation corresponds to the Natura 2000 habitat code 4060. Further on, respective habitats are reported as number code in brackets. *Carex nigra* fens and transition fens (7140) occur along alluvial areas alternating with *Nardus stricta* pastures (6230); *Alnus viridis* is frequent. ALT, on Monte Altissimo in the Monte Baldo range, features alpine and subalpine calcareous grasslands (6170) interspersed with montane and thermophilous screes (8120 and 8130). ROS, on the Pale di San Martino plateau, is characterized by limestone pavements (8240), calcareous rocky slopes with chasmophytic vegetation (8210) and screes (8120) with sparse alpine and snowbed vegetation (6170). CEV, on metamorphic rock with siliceous screes (8110), supports alpine grasslands with *Nardus stricta* and *Festuca halleri* (6150), and patches of wind-exposed *Carex curvula–Juncus trifidus* vegetation (8220).

Table 1
Overview of the sampling sites: location, Natura 2000 Habitat codes within 1,000 m of the aerobiological sampler (https://natura2000.eea.europa.eu/), geographical coordinates, elevation, sampling periods, and number of samples collected.

Site	Natura 2000 site	Natura 2000 Habitat code	Lat, Long	Elevation (m a.s.l.)	Sampling year	Start date	End date	Sample, n
FUM	Adamello (IT3120175)	4060	46.0847, 10.5628	1918	2022	24/6/2022	28/9/2024	15
		6230			2023			16
		7140			2024			14
ALT	Monte Baldo di Brentonico (IT3120173)	6170	45.8105, 10.8906	2057	2022	7/7/2022	25/10/2024	12
		8120			2023			16
		8130			2024			6
ROS	Pale di San Martino (IT3120178)	6170	46.2672, 11.8388	2577	2022	22/06/2022	25/09/2024	13
		8120			2023			11
		8210						
		8240			2024			3
CEV	Stelvio (IT3120157)	6150	46.4367, 10.6664	2609	2022	21/6/2022	20/9/2022	13
		8110			2023	21/6/2023	20/9/2023	12
		8220			2024	21/6/2024	7/9/2024	11
Total								142

2.2 Pollen sampling and identification

Passive Sigma-2 samplers (https://www.passam.ch/particles) for standardized ambient air sampling (VDI2119) were employed in the aerobiological study; they are based on the principle of gravitational sedimentation for capturing particles from the atmosphere, which is especially suited for remote, hard-to-reach locations without power sources.

The sampling surface consisted of a microscope slide coated with an adhesive medium (silicone). Sampled slides were removed and replaced with new ones, weekly to monthly, mainly during spring and summer (Table 1), and stored at 4°C until their preparation for the microscopic analysis by adding fuchsin-stained Poly(vinyl alcohol) (Merck Life Science S.r.l., Milano, Italy). Overall, 142 aerobiological samples were collected during the three-year survey (Table 1). Pollen sampling at CEV was suspended between the end of September and the 21st of June of the following year due to meteorological constraints.

For each sample, a surface area of 94.08 mm² (corresponding to four sweeps of 0.48 × 48 mm) was analyzed. Pollen grains were identified at the taxonomic level, counted, and quantified. Expert operators conducted the analysis using an optical microscope (Leitz Diaplan, Ernst Leitz Wetzlar, Wetzlar, Germany) at 400× magnification. Pollen reference slides derived from the vegetation survey (see Section 2.3) and standard identification manuals (Smith 1984; Fægri et al. 2007; Beug 2021) supported taxonomic identification. Non-identified pollen taxa were

recorded as “other pollen”. Pollen data is reported as the pollen sedimentation rate for each taxon, i.e. the number of pollen grains per unit of surface area and time ($P \bullet cm^{-2} \bullet d^{-1}$). We apply the term Annual and Seasonal Pollen Integral (APIn and SPIn) by summing the daily sedimentation rates over the year and the pollen season (i.e., a common period for all the sites, from week 25 to week 38) instead of the daily pollen concentration sensu Galán et al. (2017).

Three categories of total pollen load were defined for each site based on the mean weekly sedimentation rates: low pollen load (values below the first quartile), medium pollen load (values between the first and third quartiles), and high pollen load (values above the third quartile). These values were used to graphically represent the pollen load levels during the main flowering season.

2.3 Vegetation survey

At each study site, the flora and vegetation were visually assessed as follows: i) all vascular plant taxa in a circle of 10 m radius from the aerobiological sampler; ii) all vascular plant taxa and abundance (%) in five randomized plots of 2x2 m within the radius of 100 m from the aerobiological sampler; iii) all vascular plant taxa in a 1000x2 m transect following the main wind direction of the valley (Fig. 2). An individual-based approach was applied at the 10 m and 1000 m radius, recording the species identity of one plant sequentially after another, while a sample-based assessment protocol, based on the evaluation of replicated, multi-individual samples, was applied at the 100 m radius survey (Gotelli and Colwell 2001). For the identification of plant species, we used the Flora del Trentino (Prosser et al. 2019), Flora Helvetica (Lauber and Wagner 2009) and Exkursionsflora für Österreich, Liechtenstein und Südtirol (Fischer et al. 2005).

2.4 Data analysis

Pollen taxa and plant species were all categorized for their growth form (i.e., herbs, graminoids, shrubs, dwarf-shrubs, trees, and climbers; see Table S1 for pollen and Table S2 for plants in Online Resource 1). For comparison with pollen data, each plant species was aligned to the corresponding pollen-equivalent taxon (Table S2).

The Jaccard index (Ji; Eq. 1) was calculated to evaluate the similarity between the pollen taxa list (A) and the pollen-equivalent plant taxa list (B). Ji is calculated as the number of taxa in the intersecting set of the two taxa lists divided by the number of taxa in the union of the two data sets (A, B):

$$Ji\,(A,B) = \frac{|A \cap\ B|}{|A \cup\ B|}$$

1

Ji was applied between the pollen taxa list and the pollen-equivalent taxa assessed at three distances from the pollen sampler (i.e., 10, 100, 1000 m); values range from 0 (no pollen and plant taxa shared) to 1 (all pollen and plant taxa shared).

To test for the compositional difference of pollen spectrum and plant abundance on the four sampling sites, Semi-Parametric Permutational Multivariate Analysis of Variance (PERMANOVA) was run using the standard Bray-Curtis dissimilarity matrix (Anderson 2017). To test for false positive results, given the unbalanced sample sizes, the Bonferroni correction was used for pairwise comparisons of sites. Moreover, the alternative non-parametric test Analysis of Similarities (ANOSIM) was performed based on abundances and taxa to test for differences in

dispersions among groups. The ANOSIM test statistic (R) ranges between − 1 and + 1, where values close to + 1 indicate strong separation between groups, while values near 0 indicate that the groups are completely overlapping. Non-Metric Multidimensional Scaling (NMDS) was used to visualize the degree of similarities among pollen samples of the four alpine sites in the space of the dissimilarity measure. It is based on a multivariate composition vector of length, where each pollen taxon present in the sample contributes to the pollen signature of that sample. For the NMDS analysis of the vegetation, only plant species occurring in at least two plots per site were included in the analysis to emphasize site characteristics. Plant abundance data were Hellinger transformed to standardize species abundance data (Legendre and Gallagher 2001). We report the stress value for the goodness of fit of the 2-dimensional representation in the NMDS ordination plots, whereby values of < 0.20 are generally an acceptable representation of distances (Anderson 2017).

The R-value (R; Eq. 2) was calculated to give insight into the contribution of individual plant taxa to the pollen sample, as follows:

$$R = P/V$$

2

where P represents the pollen sedimentation rate percentage of a specific taxon (i.e., APIn %), and V is the mean cover percentage of the respective pollen-equivalent plant taxon assessed in the five 2x2 m quadrats within the 100 m radius area from the pollen sampler at each site. Well-represented plant taxa in the pollen sample have a value close to 1, while overrepresented plant taxa score > 1, and underrepresented plant taxa score < 1 (Charalampopoulos et al. 2013; van der Sande et al. 2021). To improve the readability of graphs, values were log-transformed.

3. Results

3.1 Pollen and plant richness, and growth forms

Overall, in the 142 aerobiological samples collected in the four alpine sites in 2022–2024, 53 pollen taxa were identified (Table 2; Table S1 in Online Resource 1). The highest richness was evidenced at the ALT site with 49 pollen taxa, followed by FUM and ROS (39), and CEV (28).

A total of 306 plant species (excluding cryptogams) were identified across the four sites within 1 km from the aerobiological samplers (Table 2; Table S2). As with pollen, ALT displayed overall the highest species richness also for plants (141), while the ROS site had the lowest (56). Considering the three distances from the aerobiological sampler, an overall increase of approximately 70 (+ 23%) plant species occurred from 10 to 100 m, and of 100 (+ 33%) plant species from 100 to 1000 m. The 306 plant species identified resulted in 38 pollen-equivalent plant taxa. Overall, 25 taxa were common between pollen and pollen-equivalent plant taxa. Among the 28 exclusive pollen taxa (i.e., those for which the corresponding pollen-equivalent plant taxon was missing), 68% belonged to (anemophilous) trees; all 13 exclusive pollen-equivalent plant taxa were (entomophilous) herbs.

Table 2
Pollen taxa, plant species, and pollen-equivalent plant taxa richness identified during the 2022–2024 field surveys at each site. Plant richness was assessed at different distances from the aerobiological sampler. (1) Sampling at CEV was discontinued during winter.

Pollen richness	**FUM**	**ALT**	**ROS**	**CEV**	**tot**
	39	**49**	**39**	**28**(1)	**53**
Plant richness					
Distance from aerobiological sampler (m):					
0–10	37	50	34	49	129
0-100	60	83	41	68	199
0-1000	113	141	56	102	306
Pollen-equivalent plant richness					
Distance from aerobiological sampler (m):					
0–10	12	15	10	14	22
0-100	18	23	12	17	31
0-1000	31	31	14	23	38

Considering the growth form, there were more pollen taxa belonging to woody plants (i.e., shrubs, dwarf shrubs, trees, and climbers) than non-woody ones (i.e., herbs and graminoids) at FUM (61% vs. 39%), ALT (59% vs. 41%), and ROS (59% vs. 41%) sites; at CEV site, pollen from woody plants was slightly lower than non-woody ones (46% vs. 54%) (Fig. 3; Table S1 in Online Resource 1). Vice versa, the most abundant plant species at the three distances were non-woody (herbs and graminoids), accounting, on average, for 90% of the total (Fig. 3; Table S2 in Online Resource 1). In total, in all four study sites, five tree species were found; they were always absent within the 10 m radius areas.

By comparing the pollen and pollen-equivalent plant taxa lists, the Jaccard similarity values ranged from 0.13 (ROS; 10 m) to 0.33 (ALT; 1000 m). The ALT site displayed the highest Jaccard values at the three distances (0.29, on average), and ROS the lowest ones (0.14, on average). The mean similarity index calculated for the four sites showed an increase of 38% from the 10 m radius area (Ji = 0.19) to the 1000 m transect (Ji = 0.26); the largest increase (+ 21%) occurred between 10 and 100 m (Table 3).

Table 3
Jaccard similarity indices (Ji) calculated between the pollen taxa and the pollen-equivalent plant taxa lists for three different distances and four sites.

Site	0–10	0-100	0-1000
FUM	0.16	0.22 (+ 38%)	0.30 (+ 36%)
ALT	0.25	0.30 (+ 21%)	0.33 (+ 10%)
ROS	0.13	0.15 (+ 15%)	0.15 (+ 0%)
CEV	0.20	0.22 (+ 10%)	0.24 (+ 9%)
mean	0.19 ± 0.052	0.22 ± 0.063	0.26 ± 0.080

3.2 Pollen and plant abundances

ALT and CEV registered the highest cumulative sedimentation rate (on average, approximately 2,700 and 1,150 pollen grains per square centimeter, respectively), followed by FUM with approximately 960 ($P \bullet cm^{-2} \bullet d^{-1}$), and ROS with 420 ($P \bullet cm^{-2} \bullet d^{-1}$) (Fig. 4). In all the four sites, the most abundant pollen taxa belonged to Poaceae family (min 17%, max 66%), followed by Urticaceae in ALT and ROS, by Cupressaceae in FUM, and by *Pinus* in CEV (Fig. 4). *Pinus* was the third most abundant pollen at FUM and ROS; at CEV *Juncus* ranked third, and at ALT *Ostrya carpinifolia*. Besides *Ostrya carpinifolia*, other pollen taxa from the Fagales order, including *Castanea*, *Alnus*, *Betula*, and *Corylus*, were relatively abundant in the pollen spectrum of all sites (Fig. 4).

To test for the similarity of the pollen spectra at the regional scale, we compared temporal pollen samples of FUM (n = 44), ALT (n = 34), ROS (n = 24), and CEV (n = 32) in terms of richness and abundance. The iteration resulted in a significant PERMANOVA test (p = 0.0326) for the separation of the pollen communities of the sites. The NMDS ordination (Fig. 5) visualizes the structure of the distinct pollen communities. While there is an overlap among the ellipses of the four sites (ALT, CEV, FUM, and ROS), the centroids are separated particularly along the NMDS axis. The stress value of 0.193 represents the two-dimensional configuration of the multi-dimensional distances well enough, staying within the conventional threshold of 0.20 for ecological data reliability (Souza, 2025). Specifically, the site ROS exhibits the widest dispersion, suggesting a higher internal variability in pollen composition compared to ALT, which appears more tightly clustered. The ANOSIM R = 0.041 further supports these findings, reflecting that while inter-site differences (4%) are statistically significant, the similarities within the alpine context remain relatively high (96%).

The plant communities of our study sites, on the other hand, are clearly different according to the results of PERMANOVA (p = 0.001) and ANOSIM R = 0.821. The stress value for the NMDS site separation was 0.099. *Nardus stricta*, *Rhododendron ferrugineum* and *Larix decidua* are characteristic for FUM; *Carex sempervirens, Festuca norica*, and *Helianthemum alpestre* for ALT; polsters of *Silene acaulis* and *Saxifraga sedoides* along with *Carex firma* represent the environs of ROS, while *Elyna myosuroides*, *Agrostis alpina*, and Avenula *versicolor* characterize CEV.

The mean pollen seasons of total pollen data collected between the second half of June (week 25) and the first half of September (week 38) were developed (Fig. 6). The relatively highest abundance of airborne pollen across the region occurred around mid/end of June to mid-July. After that period, and up to mid-August, there was a medium presence of pollen; subsequently, pollen was scarcely present in the atmosphere.

Site-specific flowering phenology is exemplified by the time course of the pollen sedimentation rate (P•cm-2•d-1) of Poaceae and Juncaceae pollen (Fig. 7). The 2022–2024 mean Poaceae pollen curve peaked between week 27 at the lower-elevation site FUM and week 29 at the highest-elevation sites ROS and CEV. At ALT and CEV, the pollen peak values were the highest among sites, and almost the same (ca. 25 P•cm-2•d-1), followed by FUM (3.7 P•cm-2•d-1) and ROS (1.8 P•cm-2•d-1). Juncaceae pollen peak values at CEV were constant at 8 $P•cm^{-2}•d^{-1}$ over three years, occurring between weeks 26 and 27.

Overall, 147 phanerogams were identified in the 20 2x2 m plots within a 100 m radius around the aerobiological samplers (Table S2). Only *Poa alpina* (Poaceae) was found in all four sites, but with a low coverage (on average, 0.4%). *Carex sempervirens* was the most abundant species, covering, on average, 7.4% of the total plot surface. At the pollen-equivalent level, Poaceae and Cyperaceae together covered, on average, about 39% of the plot surface. At FUM, the largest plot portion (28.4%) was covered by *Larix decidua* (just one tree), followed by *Nardus stricta* (Poaceae; 16%) (Fig. 8a). All Poaceae had a total plot cover of 33.8% at FUM. *Carex sempervirens* (Cyperaceae; 24.6%) and *Festuca norica* (Poaceae; 24.1%) dominated the communities at ALT (Fig. 8b), where the Poaceae family covered 46.9% of the plots. At ROS, *Silene acaulis* was the most abundant species with a plot cover of 2.7% (Fig. 8c). Here, Poaceae covered only 0.12% of the plot surface, while about 84% was rocky or bare soil. At the CEV site, *Avenula versicolor* (Poaceae; 8.7%) was the most abundant species (Fig. 8d); the entire Poaceae family covered 29.2% of the plot surface.

The ratios of pollen to vegetation cover percentages (i.e., R-values) for the taxa concurrently present in both lists are reported in Fig. 9. All the (log-transformed) values greater than zero (i.e., pollen % > plant cover %) referred to anemophilous taxa; R-values for *Alnus*, Cupressaceae, *Pinus*, and *Plantago* were always > 1 (i.e., log R-values > 0). On the contrary, most of the R-values < 1 (i.e., log R-values < 0; 14 out of 19) referred to entomophilous taxa. Plant species belonging to the Juncaceae family were the most over-represented in the aerobiological samples at FUM (log R-value = 1.46) and CEV (log R-value = 0.57) sites. For Poaceae, the pollen fraction largely exceeded the plant cover percentage at the ROS site (log R-value = 1.80) and, to a lesser extent, at the CEV site (log R-value = 0.35).

4. Discussion

4.1 Airborne pollen as a high-altitude environmental baseline

The potential of pollen as a proxy for plant biodiversity has been extensively exploited to reconstruct past biomes and land-use changes, helping validate modern climate-vegetation models (Sugita 2007; Schild et al. 2024). Beyond tracking historical changes, modern pollen rain provides a dynamic diagnostic tool for characterizing actual vegetation and flowering phenology (Connor et al. 2021; Adams-Groom et al. 2022; De Gálvez-Montañez et al. 2026). Changes in pollen composition over time and space reflect changes in plant communities (Connor et al. 2021). Establishing airborne pollen baselines is of pivotal importance in mountain systems, where rising temperatures disrupt plant communities by forcing species to migrate to higher elevations (Stanisci et al. 2016; Lamprecht et al. 2018; Westrich et al. 2026), and where localized land-use shifts, agricultural intensification, or tourism undermine fragile ecosystem boundaries (Schirpke et al. 2013). Thus, efforts to leverage non-destructive airborne pollen monitoring and the resulting variables for plant biodiversity and phenology estimation appear to be especially meaningful in areas designated for conservation, where biodiversity monitoring is an integral part of management practice. To this end, our study sites are located within the Natura 2000 habitat network in bioclimatically (from pre-alpine to alpine) and geomorphologically (limestone vs granitoid rock and ruggedness)

diverse remote mountain ecosystems in the Italian Alps gathering biodiversity signals from different alpine and subalpine Natura 2000 habitats.

To our knowledge, this study provides the first multi-year aerobiological study in the Eastern Alps to pair data from standardized gravitational airborne pollen monitoring with multi-scale vegetation surveys across a network of protected Natura 2000 habitats.

4.2 High-altitude airborne pollen richness integrates the local and regional signals

When testing how accurately a point-receptor gravitational sampler positioned in largely open environments at a height of two meters captures local ground vegetation within 1000 m, we observed a compositional similarity between pollen and pollen-equivalent plant taxa lists (Jaccard index) ranging between 10% and 30%. The Jaccard similarity index only marginally increased with spatial scaling, i.e. increasing distance of vegetation survey from the sampler. This is in contrast with results from heterogeneous or closed canopy landscapes (Connor et al. 2021; Abraham et al. 2022). Targeting calcareous fens, significant positive correlations of herbaceous pollen and plant richness (up to 100 m) were found (Blaus et al. 2020). Because our alpine study sites lack dense canopy barriers, they are susceptible to the influx of regional pollen blown upward from lower elevational belts as well as deposited from the atmospheric boundary layer (Zemmer et al., 2024). At all four sites, pollen from lowland deciduous trees, including *Fagus sylvatica*, *Fraxinus spp*., *Castanea sativa*, and *Ostrya carpinifolia*, was detected. In contrast, pollen from local subalpine species (*Larix decidua, Pinus mugo, Pinus cembra*, and *Alnus viridis*) was detected only at the subalpine site FUM. The presence of pollen from invasive weeds like *Ambrosia ssp.* further underscores this regional signature. What we observe in these alpine environments is that airborne pollen richness integrates the regional community composition of the wider mountain ecosystem catchment area rather than strictly mirroring local-scale floristic richness (Gosling et al. 2009; Abraham et al. 2022; Razafimanantsoa and Razanatsoa 2024). Beyond taxonomic richness, evaluating the airborne pollen spectrum through plant growth forms provides a clearer diagnostic indicator of broad community composition. In our alpine sites, while the local vegetation is strictly dominated by non-arboreal growth forms (graminoids and dwarf shrubs), the airborne spectrum is heavily weighted by regional arboreal pollen (phanerophytes) transported from lower altitudinal belts. This indicates that while airborne pollen may underrepresent the precise taxonomic richness of local alpine plots, it serves as a functional indicator of macro-community composition.

4.3 Pollination strategies and local habitat structures drive discrepancies in pollen–vegetation representation

Evaluating the relationship between airborne pollen abundance and vegetation cover requires accounting for plant pollination strategies. Anemophilous plants dominate the airborne pollen spectrum because they must produce massive, lightweight biological particles to counteract atmospheric dilution and ensure random pollination (Lacey and West 2006). Small, highly buoyant grains—such as those from *Betula*, *Alnus*, *Castanea*, and *Urticaceae*—are structurally optimized for long-range transport (Zemmer et al. 2012; Sofiev 2013; Ghasemifard et al. 2020; Menzel et al. 2021). Conversely, some graminoids produce larger anemophilous grains that tend to settle closer to their source (Frisk et al. 2023). Entomophilous species, by contrast, exhibit specialized floral morphologies and produce much smaller quantities of pollen grains with sculpturing and a sticky substance (pollenkitt), facilitating adhesion to insect hairs. These grains are structurally sequestered within flowers (e.g., Fabaceae) and are rarely released in ambient air. In accordance, our results revealed that anemophilous taxa (e.g., *Alnus*, Cupressaceae, *Pinus*, *Plantago*) were mostly overrepresented (log R > 0), while 14 out of 19 entomophilous taxa were underrepresented (log R < 0).

Furthermore, local habitat structures shaped the pollen-plant abundance relationships. For instance, at the rocky ROS site, where bare ground and rock cover 84% of the plot area, a scarce presence of *Poaceae* plants generated a high R-value (1.80) due to a non-local atmospheric contribution. At FUM, the presence of a single *Larix decidua* tree dominated the in-plot coverage (28.4%) but contributed very little to the sedimented pollen. Across all sites, *Urticaceae* pollen was highly abundant, particularly at ALT, despite the plants being not locally detected, signaling anthropization and livestock grazing near the sampling perimeters.

4.4 Airborne pollen provides a spatial synthesis at the ecosystem level

When scaling our analysis from site-specific metrics to a regional alpine synthesis, NMDS ordination revealed shared ecological characteristics alongside localized differences. Although PERMANOVA confirmed that the separation of the four pollen and plant communities was statistically significant ($p = 0.0326$), the high degree of ellipse overlapping and a low ANOSIM value ($R = 0.041$) demonstrate that regional similarities among pollen spectra across the Trentino alpine cluster are remarkably high (96%). This homogeneity reflects the widespread distribution of subalpine *Rhododendron*-scrub, *Pinus mugo* formations, and montane conifer forests throughout the regional valleys. Localized exceptions, such as the absence of thermophilous Fagales (*Fagus sylvatica, Ostrya carpinifolia*, *Fraxinus ornus*) at the strictly inner-alpine, high-elevation CEV site, demonstrate that modern pollen rain can differentiate distinct regional climatic zones based on the presence or absence of diagnostic indicator taxa (Gosling et al. 2009; Ortuño et al. 2011).

While vegetation assessed in randomized plots captured the mosaic of local habitats, airborne pollen provided a spatial synthesis at a broader ecosystem level, in alignment with previous studies in different bioclimatic settings (Gosling et al., 2009; Abraham et al., 2022; Razafimanantsoa & Razanatsoa, 2024).

4.5 Airborne pollen estimates flowering phenological shifts

Airborne pollen seasonality is regulated by meteorological factors and, in the long term, by climate change (Ziska et al. 2019; Zemmer et al. 2022; Adams-Groom et al. 2022; Cristofolini et al. 2024). Our three-year pollen dataset reveals that in high-altitude alpine ecosystems, the pollen season is highly condensed, with peak atmospheric pollen loads concentrated between mid-June and mid-July. We observed a distinct two-week phenological lag in *Poaceae* pollen release driven by altitude, peaking in week 27 at the lower-elevation subalpine site (FUM, 1,918 m a.s.l.) and in week 29 at the higher alpine sites (ROS and CEV, > 2,500 m a.s.l.). This implies a shift of approximately two days every 100 m of elevation in the regional context. This is partially in line with results for a single mountain ecosystem in the central Alps, where grass flowering phenophases were delayed between 6.3–7.1 days every 100 m, and between 9.3–10.4 days every decreasing unit of temperature (°C) (Jochner et al. 2012).

Tracking the intensity of atmospheric pollen deposition over standardized time intervals provides a framework for assessing flowering phenology across multiple organizational levels, depending on the specific study objective. The pollen signal can be a useful indicator of responses at the level of individual plant species populations to plant communities based on a pollen-plant equivalent taxon.

5. Conclusions and future directions

The three-year aerobiological monitoring campaign presented in this study demonstrates that high-altitude airborne pollen richness and abundance serve as a reliable, standardized metric for characterizing vegetation structure in a mountain ecosystem as well as flowering phenology. While the disproportionate pollen production inherent to

anemophilous strategies affects plot-scale pollen-to-plant ratios (R-values), evaluating the data by structural growth forms (herbs, graminoids, shrubs, and trees) could eliminate localized noise and shed light on the composition of vegetation zones (Xie et al. 2024).

The findings suggest that aerobiological data can supplement classes of EBVs. Tracking the timing and duration of the pollen season offers direct metrics for species traits (flowering phenology) and populations (distribution), while shifting growth-form ratios provide diagnostic indicators for ecosystem structure. This will even more so be the case when the taxonomic resolution of the pollen, here based on morphological features, will improve thanks to eDNA metabarcoding.

Overall, the study highlights the potential of using low-cost, non-invasive gravitational sampling to integrate modern aerobiological monitoring into conservation management and international biodiversity reporting networks.

Declarations

Author Contribution

All authors contributed to the study conception and design, material preparation, data collection, and analysis. The first draft of the manuscript was written by E.G and F.Z, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data Availability

Data supporting the findings of this study are partially available within the paper and its Supplementary Information. The remaining datasets are available from the corresponding author upon reasonable request.

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Figures

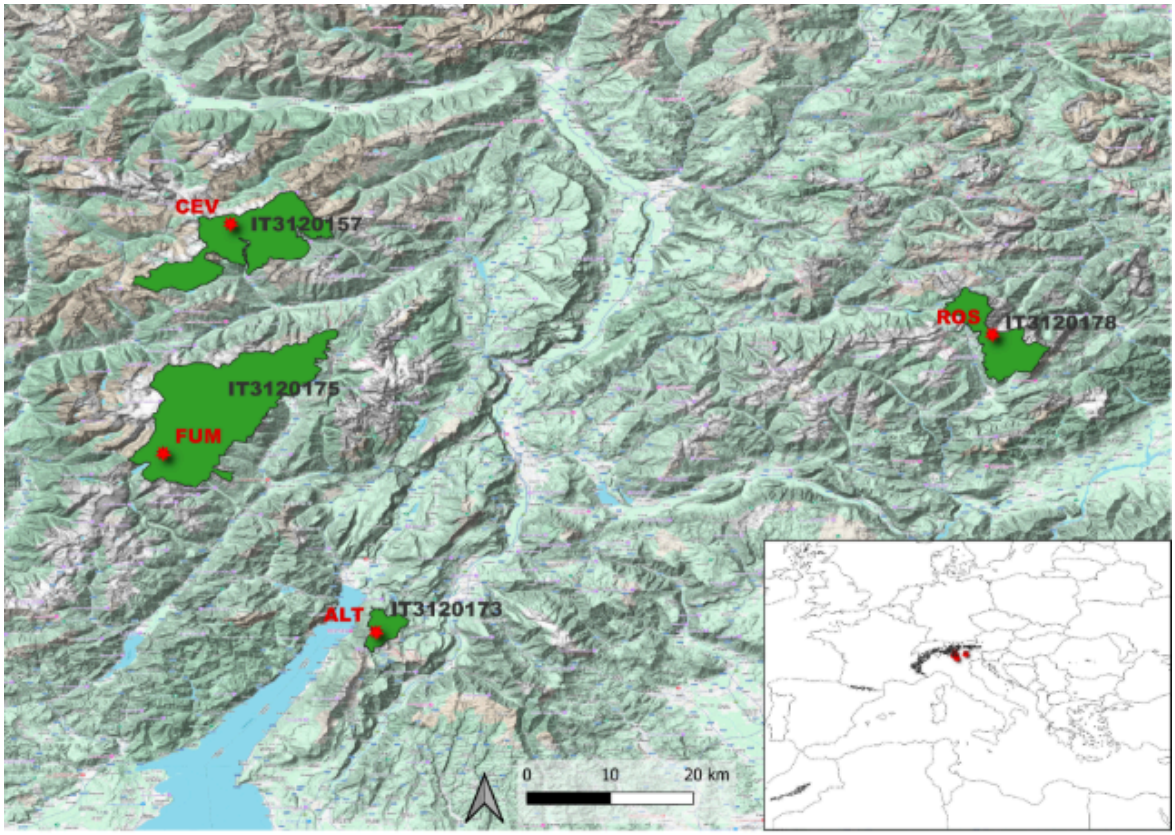

Figure 1

Location of study sites (red stars) within the Natura 2000 sites (green areas and black codes) in Trentino, Eastern Alps, and, in the panel below to the right, within European alpine clusters (black areas) according to Testolin et al. (2020).

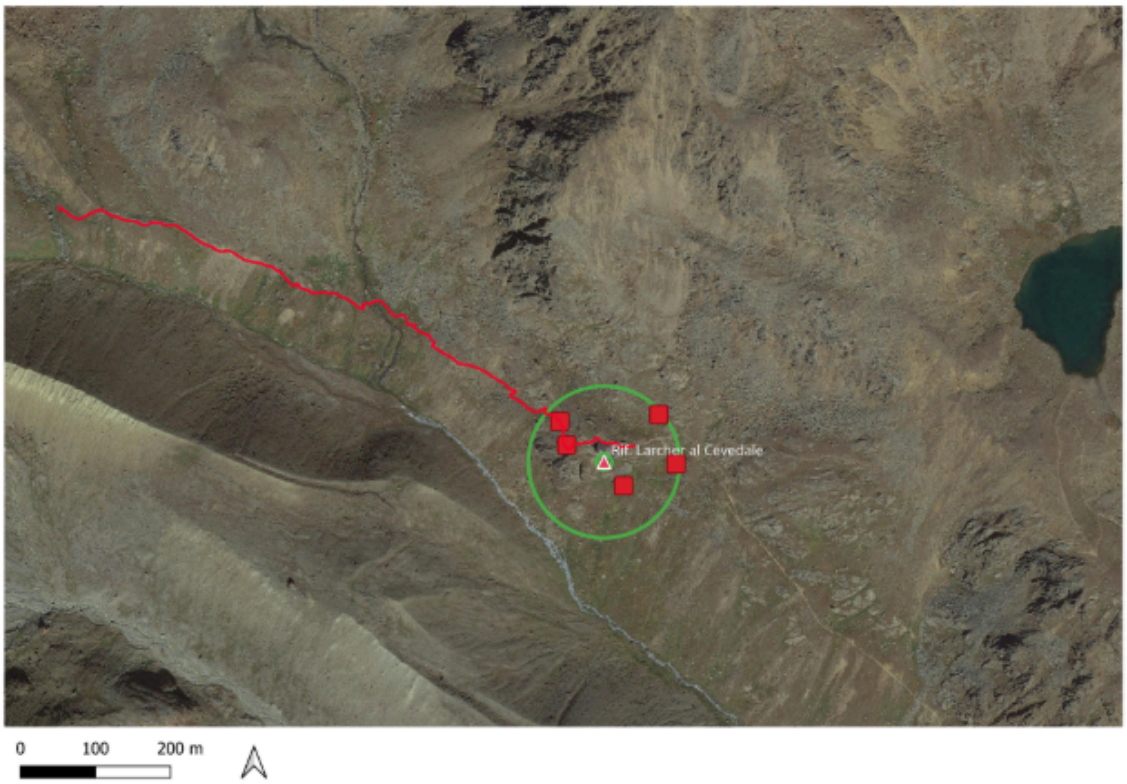

Figure 2

Vegetation sampling design on the example of Rifugio Larcher al Cevedale (CEV). The triangle represents the pollen trap position, the red squares are the randomized 2x2 m vegetation plots within the 100 m radius circle (outer green line), and the red line tracks the 1000 m transect in the main wind direction to the trap. The inner green circle is based on a 10 m radius from the trap.

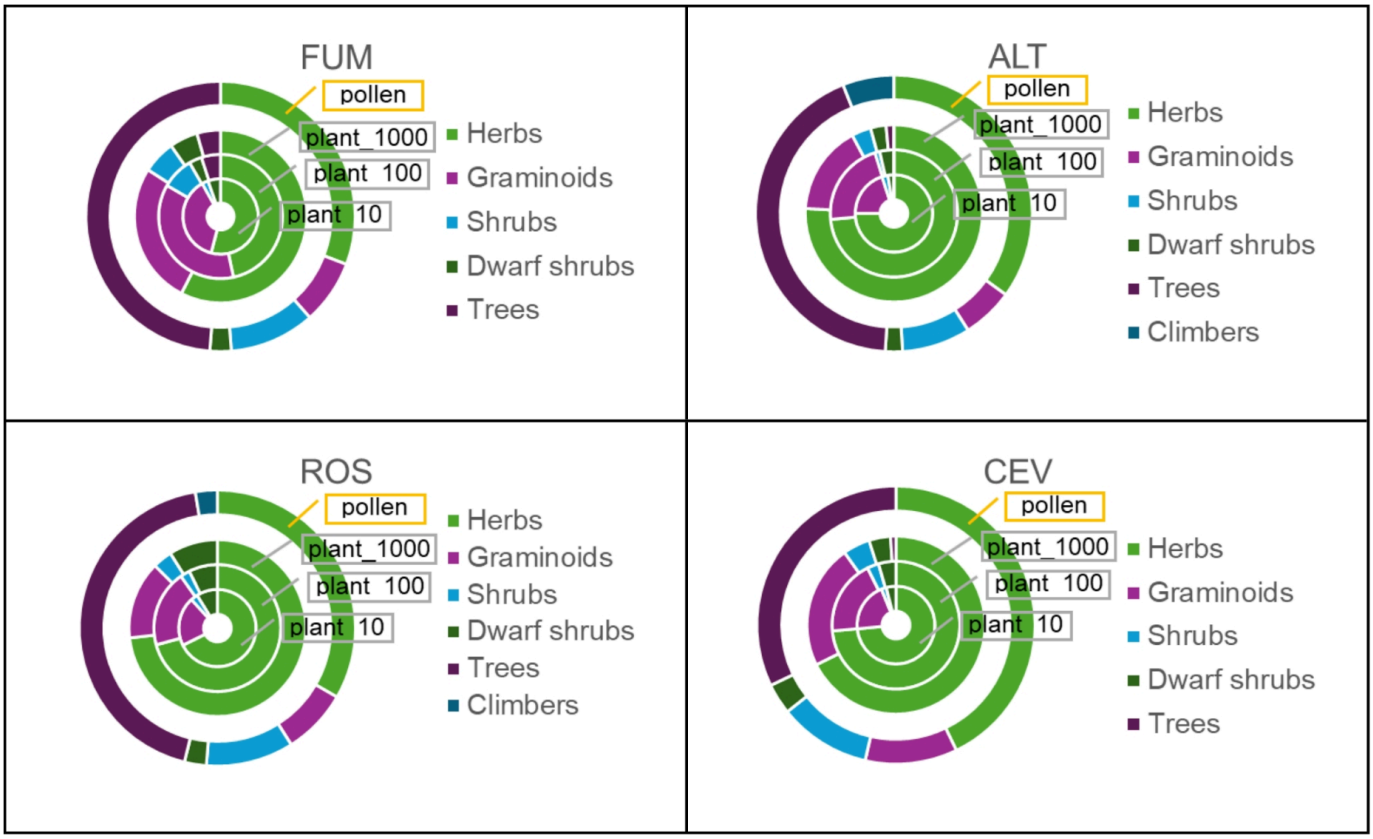

Figure 3

Proportion of pollen taxa and plant species richness detected at 10, 100, and 1000 m from the pollen sampler, aggregated per growth form.

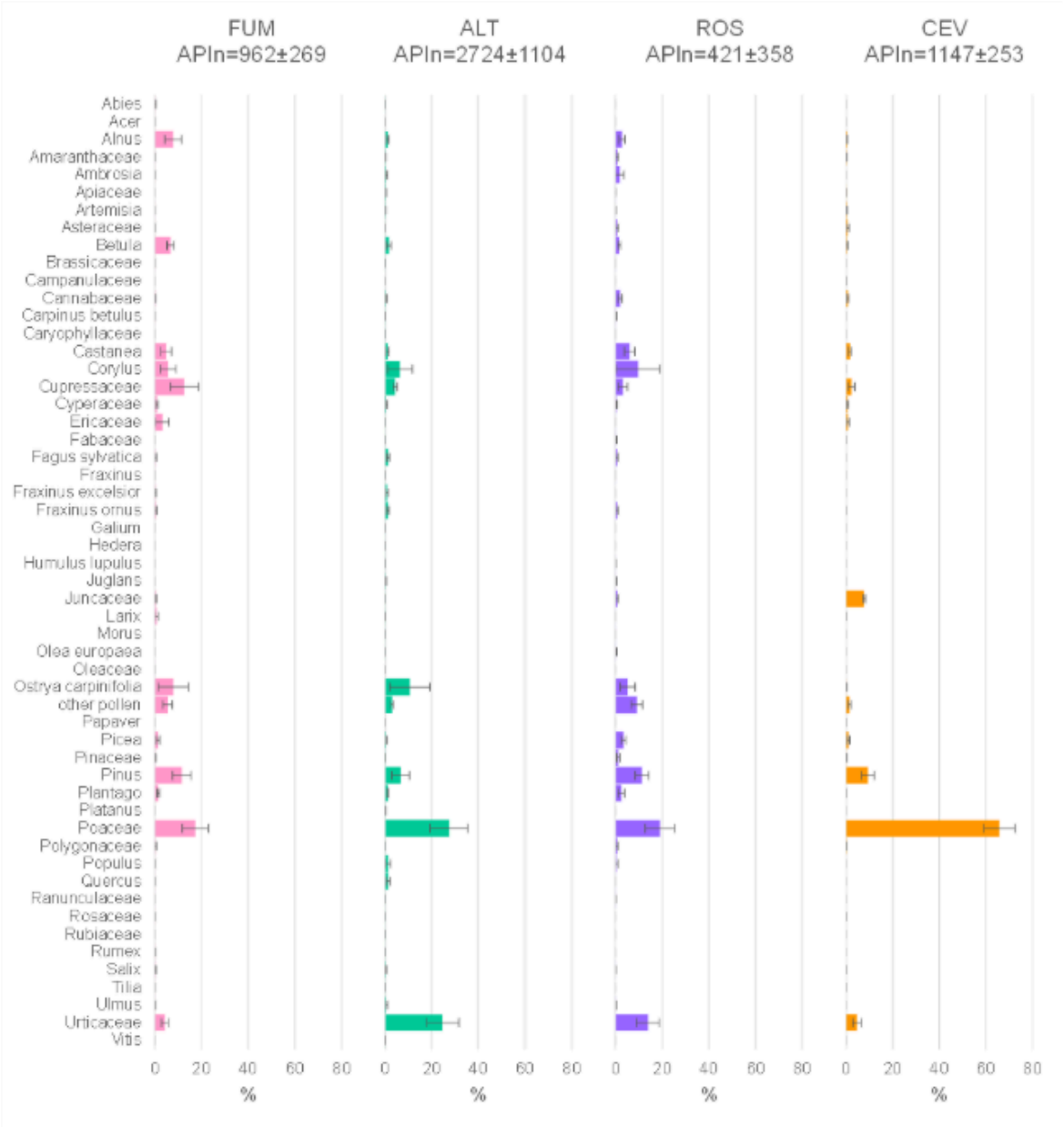

Figure 4

Pollen taxa assessed in the four sites over the years 2022 to 2024 and respective mean annual abundances; bars represent the standard error calculated for the three years. The mean (± SE) annual pollen integral value (APIn; $P \bullet cm^{-2} \bullet year^{-1}$) for each site is also reported. At CEV, the sampling was restricted to weeks 25-37.

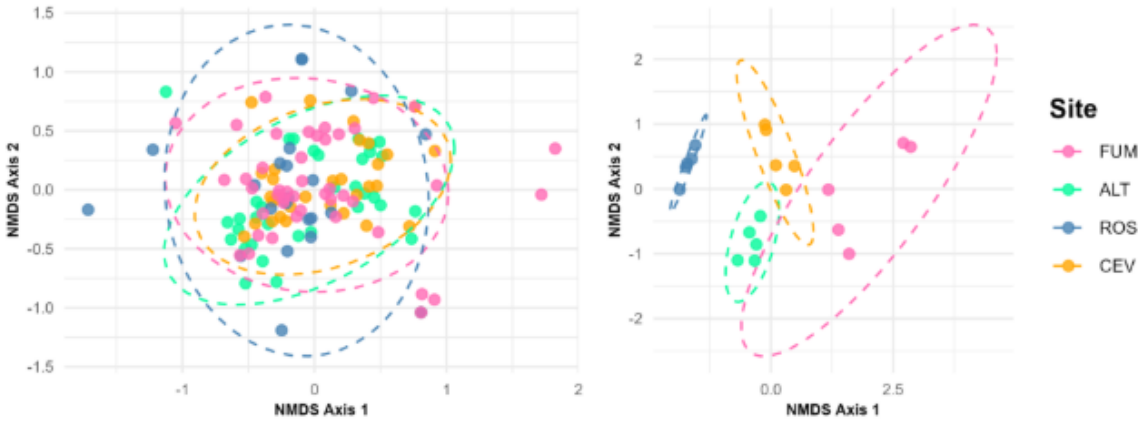

Figure 5

Non-Metric Multidimensional Scaling (NMDS) ordination of pollen (left) and plant composition (right) across four alpine sites. Each colored point represents a vector composed of the taxa in a single sample. The ellipses include the 95% confidence intervals around the centroid for each site group.

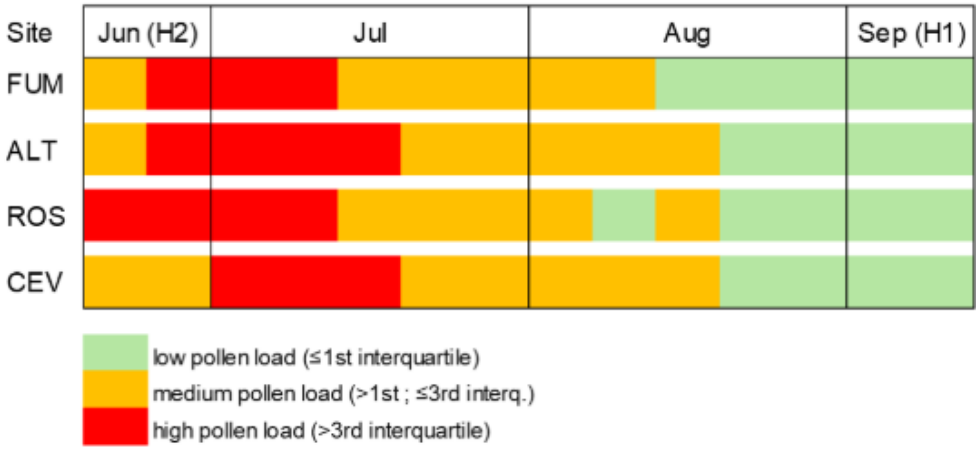

Figure 6

Total airborne pollen levels (high, medium, low) from mid-June (i.e., the second half of the month, H2) to mid-September (i.e., the first half of the month, H1) for the four Alpine sites, based on the mean weekly sedimentation rates between week 25 and 38, obtained during the 3-year aerobiological campaign.

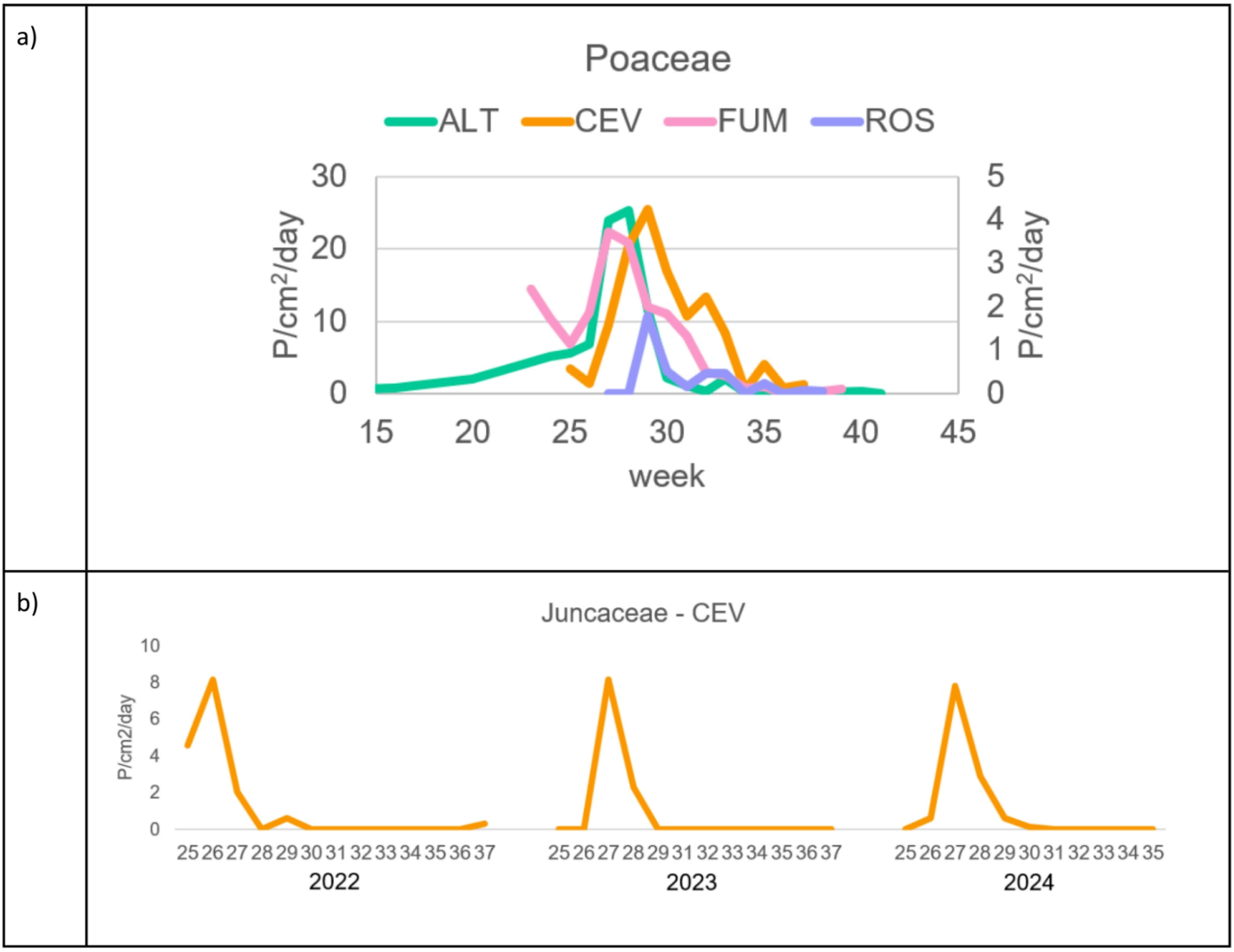

Figure 7

a) Poaceae pollen season based on mean daily sedimentation rates at the four sites, averaged over the three years. ALT and CEV values refer to the primary y-axis (left); FUM and ROS values refer to the secondary y-axis (right). b) Time course of Juncaceae pollen daily sedimentation rates assessed at CEV in the three years of aerobiological monitoring.

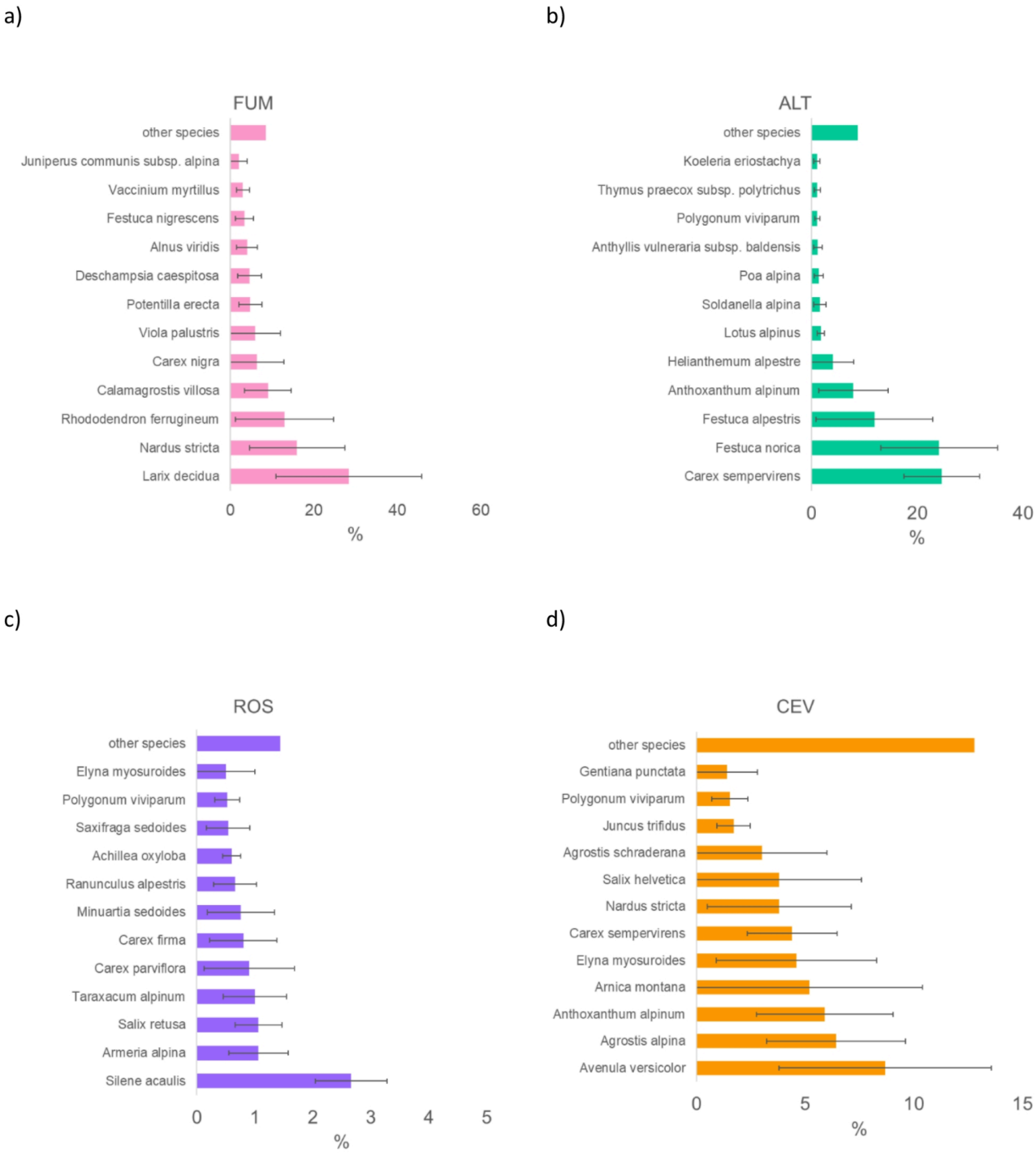

Figure 8

Mean coverage of the 12 most abundant plant species assessed in each site on five 2x2m plots, randomly selected within a 100 m radius area centered on the aerobiological sampler. Bars represent the standard error calculated for the five plots.

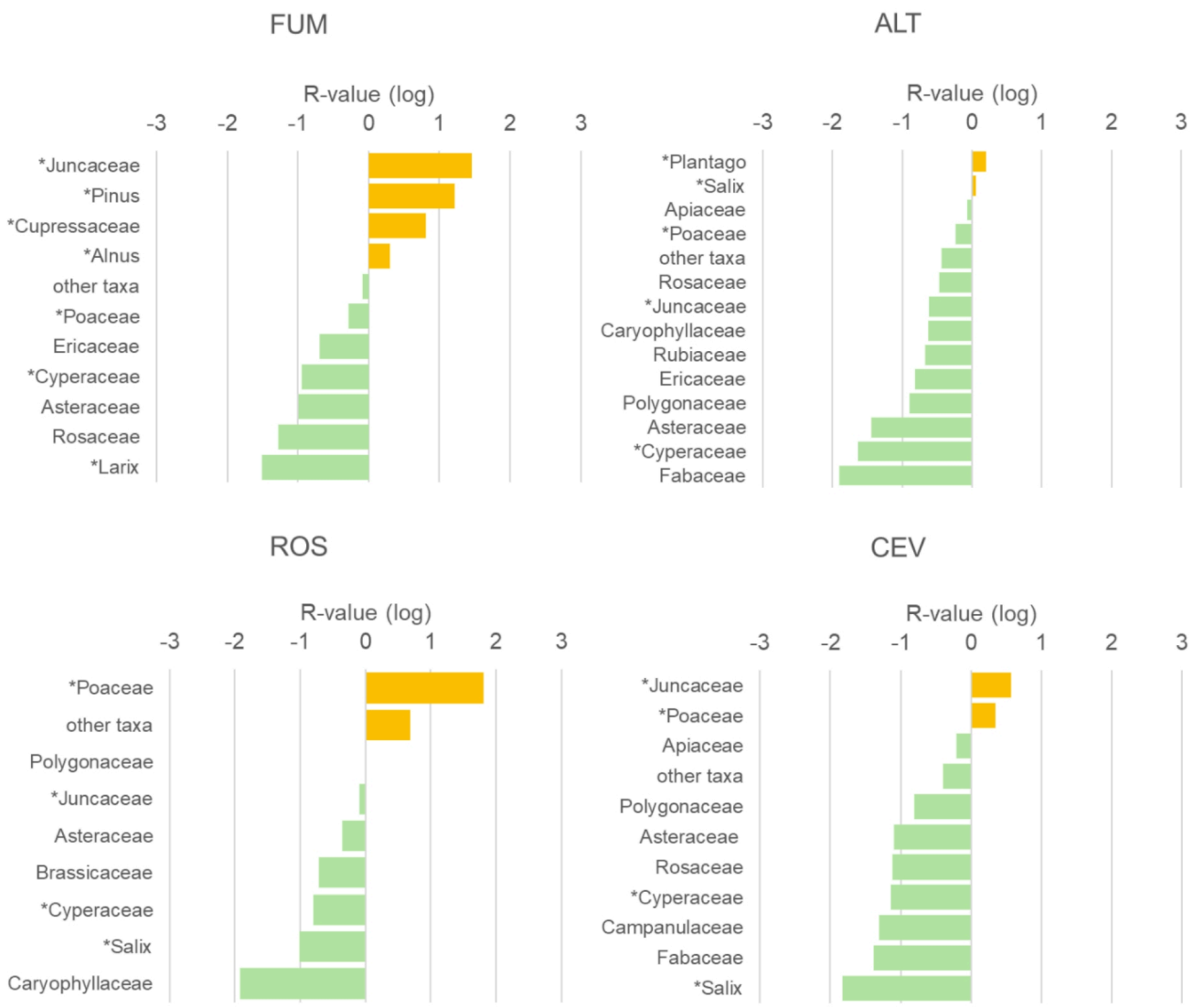

Figure 9

R-values (log-transformed (APIn % / Plant cover %)) for all the taxa with pollen and pollen-equivalent plant data concurrently available, for each study site. Values = 0 indicate the corresponding pollen-equivalent plant is perfectly represented in the pollen spectrum; values > 0 (in orange) indicate the pollen-equivalent plant is over-represented in the pollen spectrum; values < 0 (in green) indicate the pollen-equivalent plant is under-represented in the pollen spectrum. Anemophilous taxa are evidenced with an asterisk.

Supplementary Files

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- AlpBotSupplMat1.docx