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Syntaxonomy, synecology and potential distribution of *Campanula elatinoides* cliff communities in Northern Italy: resolving a botanical debate spanning more than 70 years

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Abstract

The phytosociological classification of the cliff plant communities of *Campanula elatinoides* Moretti, a chasmophyte endemic species of the Lombardy pre-Alps (Northern Italy), has been the subject of an unresolved debate since 1955. This study fills this gap by analyzing 65 phytosociological relevés of *C. elatinoides* communities (on both natural limestone-dolomite cliffs and anthropogenic stone walls) and comparing them with those carried out to define the *Potentillo caulescentis-Telekietum speciosissimae* association (*Potentillion caulescentis* alliance). The results of the multivariate and synecological analyses disproved the historical hypothesis that natural cliff face communities of *C. elatinoides* and those of *Potentillo-Telekietum speciosissimae* could be facies of the same association. Consequently, the new association *Potentillo caulescentis-Campanuletum elatinoidis* of *Potentillion caulescentis* is

formally described; it occupies dolomitic cliffs, crevices and nooks that are more shaded and warmer, with substrates that are less basic and richer in nutrients compared to the *Potentillo-Telekietum speciosissimae*. Furthermore, *C. elatinoides* behaves as a transgressive species, colonizing historic stone walls to form synanthropic communities of *Tortulo-Cymbalarietalia* that act as extra-zonal conservation refugia. Species distribution models (MaxEnt) demonstrated that while wall communities are restricted to low-altitude valley floors, the potential distribution of *Potentillo-Campanuletum elatinoidis* broadly overlaps with *Potentillo-Telekietum speciosissimae*. This confirms that the separation between these two cliff associations is driven by micro-ecological niche partitioning rather than macro-geographic segregation. This research demonstrates the efficacy of modern floristic-vegetational analyses in settling historical botanical debates and provides key predictive tools (habitat suitability maps) to guide the conservation of endemic species and their plant communities.

Keywords: Endemic species; Ecological indices; Phytosociology; Species distribution models; Chasmophytic vegetation; *Potentillion caulescentis*

Introduction

The endemic vascular flora of Northern Italy comprises 447 taxa, primarily concentrated in habitats characterized by open, primary substrates such as rocky outcrops, screes, and grasslands (Bertolli et al. 2024; Tomasi et al. 2026). Among the Italian Alpine regions exhibiting a pronounced occurrence of endemism are the carbonate pre-Alps of Lombardy (Blasi et al. 2011; Andreis et al. 2017), where individual areas (grid cells) may harbour over 50 endemic taxa (Tomasi et al. 2026).

The stenoendemic flora associated with the calcareous-dolomitic cliff and scree communities of the Lombardy pre-Alps (and limited contiguous areas outside the regional administrative border) includes several species of the genus *Campanula* (Campanulaceae), such as *C. raineri* Perp., *C. martinii* F.Fen., Pistarino, Peruzzi & Cellin., *C. bergomensis* F.Mangili & L.Mangili and *C. elatinoides* Moretti (Martini et al. 2012; Fenaroli et al. 2013; Giupponi and Giorgi 2017; Pignatti et al. 2017-2019; Giupponi 2020; Valle et al. 2024). The latter is a scapose hemicryptophyte and an obligate chasmophyte, with an ecological optimum restricted to niches, overhanging crevices, and rock shelters on calcareous-dolomitic cliffs, where it is sheltered from direct rainfall and interstitial water percolation (Arietti et al. 1955; Ferlinghetti 2011). In addition to natural cliff habitats, *C. elatinoides* exhibits a marked synanthropic

tendency, stably colonizing vertical anthropogenic surfaces such as historical stone walls. These structures, often associated with historic and religious buildings, represent microhabitats of significant biocultural conservation interest (Ferlinghetti 2011). Although the species is currently classified as "Least Concern" (LC) in the Red List of the Italian Flora (Rossi et al. 2020), the intrinsic vulnerability of its sites, particularly those located on man-made structures susceptible to building renovation works, has led to its inclusion among the strictly protected species of the Lombardy Region (Regional Law no. 10/2008).

The distribution range of *C. elatinoides* is restricted to the Lombardy Prealpine geobotanical district (Andreis 2002), between Lecco Lake and Garda Lake (Insubric area) (Martini et al. 2012), belonging to the Central and Eastern Alps ecoregional section (Alpine Province) (Blasi et al. 2014). This area is characterized by a Prealpine sub-litoranean climate with abundant annual precipitation (>1000 mm), mostly concentrated during the equinoctial periods. Furthermore, *C. elatinoides* occurs across an altitudinal range between 150 m and 2040 m a.s.l., although most populations thrive within the 400-1300 m a.s.l. range (Martini et al. 2012). The ecological (and morphological) plasticity of this species was confirmed by Giupponi (2020), who highlighted significant variability in Grime's (2001) Competitor, Stress-tolerator, Ruderal (CSR) functional strategy, as well as in leaf blade shape among populations growing in areas with differing environmental features.

From a phytosociological perspective, *C. elatinoides* forms communities of *Potentillion caulescentis* alliance (*Potentilletalia caulescentis* order, *Asplenietea trichomanis* class) (Arietti et al. 1955; Mucina et al. 2016; Pignatti et al. 2017-2019), and the debate regarding the formal description of a dedicated plant association is open. In a comprehensive essay on the distribution, ecology, and variability of this endemic species, Arietti et al. (1955) provisionally proposed the *Campanuletum elatinoidis* (nom. inval.), designating *C. elatinoides* as its sole characteristic species. However, the authors deferred the description/formalization of the association pending further in-depth studies aimed at comparing the floristic data of *C. elatinoides* communities occurring on natural cliff faces with those on artificial walls, as well as with other endemic cliff associations in the same geographical area - studies that were never undertaken.

In 1962, Sutter described the *Potentillo caulescentis-Telekietum speciosissimae* (*Potentillion caulescentis*) (Sutter 1962), a calcicolous sunny cliff face association of the Insubrian region comprising several chasmophytic species endemic to the Southern Alps, including *Xerolekia speciosissima* (L.) Anderb. (Biondi et al. 1997; Leuschner and Ellenberg 2017). The latter is a basiphilous plant whose geographical distribution, extending from Lombardy to Trentino-

Alto Adige region, largely overlaps with that of *C. elatinoides* (Martini et al. 2012; Bertolli et al. 2024). Subsequently, Fenaroli (1965), in a publication on the history, ecology, and distribution of *X. speciosissima*, hypothesized (owing to the lack of exhaustive vegetation relevés) that *Campanuletum elatinoidis* and *Potentillo caulescentis-Telekietum speciosissimae* might be interpreted as local facies of a single association. A few years later, this hypothesis was refuted by Sutter (1969), who argued that there is only a slight similarity between the *Campanuletum elatinoidis* and the *Potentillo caulescentis-Telekietum speciosissimae*. In support of his thesis, he provided additional floristic data and photographs regarding the *Potentillo caulescentis-Telekietum speciosissimae*. However, he did not perform numerical/statistical analyses to compare the two cliff associations from a floristic and/or synecological perspective, which could have unequivocally resolved the issue.

Since 1969, the *Campanuletum elatinoidis* has been absent from subsequent phytosociological literature. Indeed, in the syntaxonomic revision of the vegetation of the order *Potentilletalia caulescentis* in Italy (Biondi et al. 1997), no record of this association appears, whereas *Potentillo caulescentis-Telekietum speciosissimae* is reported. This omission likely stems from the fact that *Campanuletum elatinoidis*, as hypothesized in 1955, was never formally defined nor sufficiently described with a designated type relevé (*holotypus*), mandatory requirements under the International Code of Phytosociological Nomenclature (Theurillat et al. 2021). Furthermore, *Campanuletum elatinoidis* is omitted from the most recent syntaxonomic overviews of both Italian (Biondi and Blasi 2014) and European vegetation (Mucina et al. 2016), as well as from their associated, periodically updated online databases (www.prodromo-vegetazione-italia.org; www.floraveg.eu, Chytrý et al. 2024). Consequently, this proposed association has effectively fallen into oblivion, leading to a general lack of floristic, ecological, and syntaxonomic studies focusing on *C. elatinoides* communities, and leaving the questions raised since the 1950s unaddressed.

This research aims to collect and statistically analyze the floristic-vegetational data of *C. elatinoides* plant communities on cliff faces and walls. It considers both data published in the recent literature (Giupponi 2020) and those from original relevés, comparing them with data from *Potentillo caulescentis-Telekietum speciosissimae* (Sutter 1962, 1969) in order to highlight floristic and ecological similarities and differences, and to define their syntaxonomic framework. Furthermore, using species distribution models, it aims to provide an overview of the potential distribution of *C. elatinoides* in Lombardy, as well as the key diagnostic species of its plant communities and those of *Potentillo caulescentis-Telekietum speciosissimae*, to

better clarify their ecology and identify geographic areas where the different associations/communities may co-occur.

Materials and Methods

Sampling areas and data collection

Floristic-vegetational data of *C. elatinoides* communities were collected by integrating both recently published literature and new phytosociological relevés. Specifically, 31 relevés from Giupponi (2020) representing *C. elatinoides* communities on cliff faces were included, along with 34 original relevés carried out on rock walls hosting *C. elatinoides*. Relevés of wall vegetation were carried out between 2020 and 2025 (during June, July, and August) following the same methodological procedure used by Giupponi (2020). Relevé area ranged from 2 to 16 m² depending on wall size and extent, across 8 sites distributed throughout the range of the species in the Lombardy pre-Alps (Fig. 1). Site selection was primarily based on presence records of *C. elatinoides* reported by Arietti et al. (1955) and Ferlinghetti (2011), as well as on the authors' field knowledge and observations.

Vascular plants (tracheophytes) were identified using the dichotomous keys of Pignatti (2017-2019). For each species, percentage cover was estimated by assigning an abundance-dominance index according to the Braun-Blanquet scale: r, rare species in the relevé; +, cover < 1%; 1, cover 1-5%; 2, cover 5-25%; 3, cover 25-50%; 4, cover 50-75%; 5, cover 75-100% (Braun-Blanquet 1964). Data regarding life forms and chorotypes for each species were extracted from Pignatti (2017-2019).

In order to define the syntaxonomic position of *C. elatinoides* plant communities and perform a synecological comparison with *Potentillo caulescentis-Telekietum speciosissimae*, data from the 7 phytosociological relevés conducted by Sutter (1962, 1969) to describe and define the aforementioned association were also included in the statistical analyses (Fig. 1).

Scientific names of species follow Pignatti (2017-2019).

Phytosociological and synecological analysis

Data from literature and newly collected relevés were compiled into a relevé x species matrix, in which Braun-Blanquet abundance-dominance cover indexes were transformed according to the ordinal scale proposed by van der Maarel (1979) (r = 1; + = 2; 1 = 3; 2 = 5; 3 = 7; 4 = 8; 5 = 9) to enable statistical analysis. Subsequently, a power transformation with an exponent of 0.3 was applied to these values following Tichý et al. (2020) to improve vegetation

classification at the plant association level. The data matrix was then imported in R 4.4.1 software (R Development Core Team 2025) and used for statistical analyses.

Cluster analysis was performed using the group average method (Unweighted Pair Group Method with Arithmetic Mean, UPGMA) and chord distance coefficient (Legendre and Gallagher 2001), in order to highlight floristic-physiognomic similarities and differences among relevés. Relevés were also ordered using detrended correspondence analysis (DCA) to reveal potential floristic and ecological gradients. Cluster analysis and DCA were carried out using the 'vegan' package (Dixon 2003) in R.

Pearson's phi coefficient (Φ) was used to identify the diagnostic species (plants significantly associated with the different types of vegetation) of each cluster of vegetation as proposed by Chytrý et al. (2002) and Tichý and Chytrý (2006). The coefficient Φ was calculated using the 'indicspecies' R package, considering the following formula:

$$\Phi = \frac{N \cdot n_p - n \cdot N_p}{\sqrt{n \cdot N_p \cdot (N-n) \cdot (N-N_p)}}$$

where N is the number of relevés in the data set, N_p is the number of the relevés in a target group of relevés equalizing the size of relevés groups, n is the number of occurrences of the species in the dataset and n_p is the number of occurrences of the species in the target group of relevés.

The vegetation groups identified by the cluster analysis were analysed from a phytosociological perspective. Phytosociological analysis of the vegetation was performed following the hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities of European vegetation (Mucina et al. 2016; Chytrý et al. 2024), the 'Prodrome of the Italian Vegetation' (Biondi and Blasi 2014), and specific literature concerning the vegetation of limestone-dolomite cliffs and wall communities in the Alps and neighboring areas (Sutter 1962, 1969; Poldini 1978; Mucina et al. 1993; Poldini and Vidali 1994; Teurillat et al. 1994; Allegrezza et al. 1997; Biondi et al. 1997; Brullo and Guarino 1998, 2002; Poldini et al. 2009; Tomaselli et al. 2019). The names of syntaxa (from class to alliance level) are in accordance with Mucina et al. (2016).

Landolt ecological indicator values (Landolt et al. 2010) were used to analyze ecological differences among vegetation types. In particular, the following indicators were considered: temperature index (T), continentality index (K), light index (L), soil moisture index (F), substrate reaction index (R), nutrient index (N), humus index (H), and substrate aeration index

(D). For each relevé, mean values for each ecological index were calculated weighted by species cover-abundance. Synecological data were analyzed using a one-way ANOVA to evaluate significant differences (p<0.01) among vegetation groups. When significant ecological differences were identified among groups, Tukey's post hoc test was applied to detect pairwise differences between vegetation types.

Potential distribution analysis

For *C. elatinoides* and other representative/abundant diagnostic species of each vegetation type, the geographical distribution of their suitable habitats was modelled to evaluate the potential distribution of each plant community and identify geographic areas where different vegetation types may coexist. This analysis was carried out using the presence records of each target species, the corresponding climatic data, and the maximum entropy algorithm (MaxEnt) for species distribution modelling.

Geographic coordinates for the Lombardy occurrences of *C. elatinoides* and the key diagnostic species of each vegetation cluster were downloaded from the Global Biodiversity Information Facility (GBIF) database (https://www.gbif.org), an international network and data infrastructure funded by the world's governments aimed at providing open-access data on all types of life on Earth (Flemons et al. 2007; Ivanova and Shashkov 2021).

For the habitat suitability analysis, 19 bioclimatic variables were considered (Table S1). Bioclimatic layers were obtained from the WorldClim 2.1 dataset (http://worldclim.org) at a spatial resolution of 2.5 arc-minutes (~20.25 km²) under current climatic conditions. In addition, a shapefile representing the areas of Lombardy characterized by calcareous-dolomitic geological substrates was generated using QGIS 3.40 software, derived from the 1:250,000 geological map of Lombardy retrieved from the Lombardy Geoportal (www.geoportale.regione.lombardia.it).

The MaxEnt algorithm was executed within the R environment (Hijmans et al. 2026) to predict species distributions, an approach particularly well-suited for presence-only data (occurrence records) (Phillips et al. 2006). The relative contribution of each bioclimatic variable generated by the MaxEnt model was extracted, and model accuracy was evaluated by computing the Area Under the Curve (AUC) of the Receiver Operating characteristic Curve (ROC). AUC values range from 0 to 1, where higher values indicate superior model performance.

Model outputs were expressed as continuous suitability maps ranging from 0 (unsuitable) to 1 (highly suitable). To convert continuous predictions into binary suitability maps, a threshold was applied based on the maximum sensitivity plus specificity criterion, which maximizes the

sum of sensitivity (true positive rate) and specificity (true negative rate) (Liu et al. 2005). Areas with suitability values exceeding this threshold were classified as climatically suitable for the target species. Finally, the areas in Lombardy displaying suitable climatic conditions for *C. elatinoides* and the other diagnostic species of the vegetation clusters were masked in QGIS using the calcareous and dolomitic rock layers. This integration of both climatic and geological substrate data allowed for a more refined definition of the potential distribution of these species and their associated plant communities.

Results

Floristic and vegetational features

Figure 2 shows the dendrogram of relevés generated by the cluster analysis and the DCA biplot. The dendrogram reveals two main clusters of relevés (A and B), corresponding to plant communities growing on calcareous-dolomitic cliffs (A) (*Potentillion caulescentis*) and synanthropic communities growing on anthropogenic walls (B) (*Cymbalario-Parietarietea diffusae*) (Table 1). Cluster A is further divided into two well-defined subclusters: one grouping the relevés of plant communities where *C. elatinoides* grows on cliff faces (A1), and the other comprising the relevés of *Potentillo caulescentis-Telekietum speciosissimae* (A2). The synoptic table (Table 1) highlights the diagnostic species for each subcluster (or group of subclusters) identified via Φ coefficient calculation and analysis (for which values and statistical significance are provided in Table S2), and the complete phytosociological table of the relevés is presented in Table S3.

The high number of diagnostic species differentiating *Potentillo caulescentis-Telekietum speciosissimae* from cluster A1 rules out the possibility that the two vegetation types represent mere facies of the same association, indicating instead that they are two distinct associations, of which the new (corresponding to cluster A1) is formally defined below:

- *Potentillo caulescentis-Campanuletum elatinoidis* ass. nova hoc loco
  Suppl. material, Table S3: rels Gi1-Gi31; *typus* rel. Gi6: gorge of Enna stream (Taleggio municipality, Bergamo province); Elevation (532 m a.s.l.); Aspect (216°); Slope (90°); Area (16 m^2); Cover (20%). Diagnostic and differential species of the association: *Campanula elatinoides* (dominant), *C. carnica* Schiede ex Mert. & W.D.J.Koch subsp. *puberula* Podlech, *Physoplexis comosa* (L.) Schur. A representative photograph of the association is provided in Figure S1.

This new association includes only *C. elatinoides* communities of natural calcareous-dolomitic cliff faces in the hilly and mountain belts. Indeed, in addition to lacking the more microthermic

species of *Potentillion caulescentis* and *Potentilletalia caulescentis* (such as *Bupleurum petraeum* L., *Rhamnus pumila* Turra, *Cystopteris alpina* (Lam.) Desv., *Saxifraga vandellii* Sternb., and *Campanula raineri* Perp.), it exhibits a well-represented component of scree species (*Thlaspietea rotundifolii*) as well as species of mesic and warm deciduous forests (*Carpino-Fagetea sylvaticae* and *Quercetea pubescentis*) (e.g., *Achnatherum calamagrostis* (L.) P.Beauv., *Fraxinus ornus* L., *Ostrya carpinifolia* Scop., *Hedera helix* L. and *Emerus major* Mill.). This feature further distinguishes it from *Potentillo caulescentis-Telekietum speciosissimae* (Table 1).

This difference is also reflected in the graph comparing the biological spectra of the clusters (Fig. 3a), where phanerophytes in *Potentillo caulescentis-Campanuletum elatinoidis* exceed 13%, whereas they are absent in *Potentillo caulescentis-Telekietum speciosissimae*. Furthermore, the new association displays higher species richness (19.7 ± 4.95 *vs.* 11.7 ± 5.53 in A2) and a larger proportion of Mediterranean (15.1%), European (26.4%), and exotic (2.8%) species compared to *Potentillo caulescentis-Telekietum speciosissimae*, which completely lacks European and exotic species but has an orophytic component exceeding 50% (Fig. 3b).

Xerolekia speciosissima is present in all relevés of *Potentillo caulescentis-Telekietum speciosissimae*, for which it serves as a diagnostic species. It also occurs in *Potentillo caulescentis-Campanuletum elatinoidis*, but in fewer than 40% of the relevés and with low cover values (Table 1 and Table S3).

Regarding the communities in which *C. elatinoides* grows on man-made walls (cluster B) (Fig. 2), these differ considerably from *Potentillo caulescentis-Campanuletum elatinoidis* (and from *Potentillo caulescentis-Telekietum speciosissimae*) due to the absence of most *Potentillion caulescentis* and *Potentilletalia caulescentis* species of cluster A1 (and A2) (Table 1), as well as a overall lower species richness (B1 = 6.88 ± 2.74; B2 = 9.33 ± 4.47). Cluster B also lacks most of the basophilic grassland species present in cluster A (such as *Sesleria caerulea* (L.) Ard.), while harboring species typical of wall habitats (*Tortulo-Cymbalarietalia* and *Cymbalario-Parietarietea diffusae*) (completely absent in cluster A2) along with various synanthropic and ruderal species (exclusive to cluster B), many of which are annual/ephemeral (therophytes) and/or cosmopolitan or exotic (Fig. 3 and Table S3).

Cluster B1 differs from B2 mainly in having a lower proportion of Mediterranean species and a higher proportion of European species (Fig. 3a). Furthermore, Table 1 highlights two *Cymbalario-Parietarietea diffusae* species with a frequency exceeding 70%, *Cymbalaria muralis* G.Gaertn., B.Mey. & Scherb. and *Parietaria Judaica* L., which serve as diagnostic species for clusters B1 and B2, respectively. It was not possible to assign these two

communities at the alliance level, let alone at the association level, mainly due to the lack of data on wall-dwelling bryophyte species; therefore, a generic name was assigned to each community: *Cymbalaria muralis-Asplenium trichomanes* community (B1) and *Parietaria judaica-Centranthus ruber* community (B2).

The DCA biplot confirms the grouping of relevés generated by the cluster analysis and highlights two main floristic-ecological gradients corresponding to axes DCA1 and DCA2 (Fig. 2b). Along the first axis, synanthropic species of wall communities decrease, while species of rock/cliff (minimally disturbed by human activity) increase. Instead, the vertical axis (DCA2) separates the two communities of cluster B as Mediterranean species decrease and European species increase.

Synecology and potential geographical distribution

Figure 4 shows the ecological features of the four vegetation types, which differ significantly for all Landolt indicator values except for F (Table 2). In particular, the Tukey test revealed significant differences among all vegetation types only for T: *Potentillo caulescentis-Telekietum speciosissimae* is composed of the least thermophilic species, followed by *Potentillo caulescentis-Campanuletum elatinoidis*; wall communities, on the other hand, are more thermophilic than cliff face communities, with cluster B2 being significantly more thermophilic than B1. Wall communities also differ from cliff communities (A1 and A2) in having more nitrophilous species and occurring in less continental climates.

Synecological analysis highlights further differences between *Potentillo caulescentis-Telekietum speciosissimae* and *Potentillo caulescentis-Campanuletum elatinoidis*. The latter association is indeed composed of less heliophilous and less basophilic species that require rock crevices/nooks that provide a slightly higher (though still limited) availability of fine earth, nutrients, and organic matter.

Figure 5 presents the MaxEnt model outputs, showing the macroclimatically suitable areas in Lombardy for *C. elatinoides* (diagnostic/differential species of cluster A1) and three other key diagnostic species: *Xerolekia speciosissima*, *Cymbalaria muralis*, and *Parietaria judaica*. These three species represent *Potentillo caulescentis-Telekietum speciosissimae* (A2), the *Cymbalaria muralis-Asplenium trichomanes* community (B1), and the *Parietaria judaica-Centranthus ruber* (B2) community, respectively (Table 1). All models exhibited high accuracy, with AUC values exceeding 0.95 (Fig. 5b); the relative contribution of each climatic variable is detailed in Table S4.

The maps in Figures 5b and 5c confirm that the wall communities of *C. elatinoides* are generally more thermophilic. Indeed, climatically suitable conditions for both *Cymbalaria muralis* and, to a greater extent, *Parietaria judaica* occur in low-elevation areas of Lombardy, specifically within hilly areas and the upper Po Plain. Conversely, areas climatically suitable for *Xerolekia speciosissima* and *Campanula elatinoides* are concentrated in the mountainous sectors of Lombardy, particularly across the pre-Alps. Furthermore, when restricting the analysis strictly to areas with calcareous-dolomitic geological substrates (Fig. 5c), the potential distribution ranges of *Campanula elatinoides* and *Xerolekia speciosissima* appear similar, albeit with differences. The main distinction lies in the easternmost and westernmost calcareous-dolomitic mountain ranges of the region, where suitable climatic conditions are present for *Xerolekia speciosissima* but not for *C. elatinoides*.

Figure 6a displays the suitable habitat (considering both climate and geological substrate) for *Campanula elatinoides*, representing the geographical areas where the species finds suitable conditions to grow and form its plant communities. Figure 6b shows the geographical areas with shared macroclimatic and geopedological conditions for *C. elatinoides* and *X. speciosissima*, indicating where the two associations (*Potentillo caulescentis-Campanuletum elatinoidis* and *Potentillo caulescentis-Telekietum speciosissimae*) could geographically coexist. Comparison of Figures 6a and 6b reveals that almost all areas suitable for *C. elatinoides* overlap with the potential distribution of *Potentillo caulescentis-Telekietum speciosissimae*. Conversely, the geographical areas where the wall communities of *C. elatinoides* (cluster B1 and B2) can potentially occur (Fig. 6c and 6d) are far more restricted compared to the overall potential distribution of *C. elatinoides*, being mainly concentrated at lower elevations (valley floors) within the pre-Alps. Finally, Figure 6e shows that only a limited number of geographical areas in Lombardy provide conditions suitable for the potential co-occurrence of all four analyzed vegetation types.

Discussion

The results of the multivariate analysis demonstrate that the *C. elatinoides* plant communities (occurring on both natural rock faces and walls) are floristically distinct from those of the *Potentillo caulescentis-Telekietum speciosissimae* as formalized by Sutter (1962, 1969). Furthermore, the communities of the latter association exhibit a substantially higher floristic similarity to the chasmophytic *C. elatinoides* communities of *Potentillo caulescentis-Campanuletum elatinoidis* than to those occurring on anthropogenic walls, largely driven by the shared presence of *Potentillion caulescentis* species (Fig. 2, Tab. 1). Consequently, the cliff

face *C. elatinoides* communities were correctly assigned to the alliance level by Arietti et al. (1955). From both a floristic and ecological perspective, the recognition of a distinct association grouping these communities (namely, *Potentillo caulescentis-Campanuletum elatinoidis*) and differentiating them from *Potentillo caulescentis-Telekietum speciosissimae* is well-founded. This association likely corresponds to the informal *Campanuletum elatinoidis* hypothesized by Arietti et al. (1955), the name of which is here emended and formalized since it was never validly published. Furthermore, in accordance with modern phytosociological nomenclature rules aimed at preventing homonymy and vague syntaxonomic descriptions, current nomenclatural practice for describing a new association (or validating a *nomen nudum*) requires the designation of two name-giving taxa (Theurillat et al. 2021). In this specific case, *Potentilla caulescens* was selected to reflect the higher-level phytosociological and ecological framework of alpine and prealpine calcicolous chasmophytic vegetation (*Potentilletalia caulescentis* and *Potentillion caulescentis*), whereas *C. elatinoides* defines the local, stenoendemic identity of the phytocoenosis. Furthermore, the *Potentillo caulescentis-Campanuletum elatinoidis* is the result of a statistical analysis and comparison of relevés from different *C. elatinoides* communities (both cliff faces and anthropogenic walls) alongside those of the *Potentillo caulescentis-Telekietum speciosissimae*.

Such a comparative analysis had never been undertaken, despite decades of syntaxonomic debate among past authors (e.g., Fenaroli 1965; Sutter 1969). This historical knowledge gap likely stems from the fact that 20th-century researchers lacked the computational power, software, and multivariate algorithms required to efficiently process complex vegetation datasets (Mucina and van der Maarel 1989; Podani 2000). In classical phytosociological studies, classification and the resolution of nomenclatural disputes relied almost exclusively on manual tabular sorting and subjective, qualitative expert judgment (Kent 2012). Consequently, even intuitive syntaxonomic hypotheses, such as those proposed by Arietti et al. (1955), Fenaroli (1965), and Sutter (1969), remained without objective, reproducible statistical validation, leading to prolonged and often inconclusive interpretative debates.

In recent decades, the rapid advancement of computational technology and the widespread adoption of dedicated statistical software, such as the R environment for community ecology, have marked a major paradigm shift in vegetation science and phytosociology (Dengler et al. 2008; Biondi 2011; Borcard et al. 2018). The speed and efficiency with which multivariate analyses can now be performed, particularly hierarchical cluster analysis and ordination techniques, have freed the discipline from observer subjectivity (Wildi 2021). Applying these statistical tools to vegetation relevé data not only helps resolve historical debates and redefine

syntaxonomy on empirical and mathematical grounds (Chytrý et al. 2020), but also serves as a fundamental pillar for understanding their ecological relationships.

Although multivariate analyses (particularly cluster analysis) gained traction in ecological and botanical research as early as the 1970s and 1980s (Orlóci 1978; Whittaker 1978; Gauch 1982) before becoming standardized tools in subsequent decades, the syntaxonomic debate surrounding *C. elatinoides* communities remained unresolved for over half a century without being subjected to a decisive statistical approach. The primary reason for this scientific inertia likely lies in the gradual oblivion into which the *Campanuletum elatinoidis* controversy fell in the decades following its emergence. This was probably driven by the fact that foundational historical contributions on the topic (e.g., Arietti et al. 1955; Fenaroli 1965; Sutter 1969) remained confined to non-digitized print publications, archived solely in physical scientific/specialized libraries, and were thus far less accessible than digital literature. Over recent decades, the literature search paradigm has shifted radically, with researchers relying almost exclusively on academic search engines and indexed digital databases such as Scopus, Web of Science, Google Scholar and ResearchGate (Gusenbauer and Haddaway 2020). Consequently, older non-digitized literature (often non-English) suffers from a pronounced digital blind spot, facing the risk of being overlooked in modern scientific studies, including syntaxonomic syntheses and systematic reviews (Amano et al. 2016).

This case study demonstrates the urgent need to accelerate the digitization of historical bibliographical heritage. Retrieving, digitizing, and indexing botanical research from past decades, and integrating these works into digital libraries and open-access vegetation databases such as the European Vegetation Archive (EVA; Chytrý et al. 2016), represents a crucial step for knowledge dissemination and the advancement of the discipline. In doing so, we would not only avoid redundant effort in vegetation science (and beyond), but also unlock valuable historical floristic and phytosociological insights that, when reanalyzed using modern tools, can finally reach a definitive scientific resolution.

An additional methodological constraint that historically hindered the resolution of the syntaxonomic controversy surrounding *C. elatinoides* communities lies in the difficulty faced by early authors in conducting quantitative synecological and functional-ecological comparisons (such as the one carried out in this study) between the various *C. elatinoides* communities and related syntaxa. Indeed, the first structured systems of ecological indicator values, applicable mainly to Central European vegetation (and only to a limited extent to the Alpine belt), were formalised only from the 1950s and 1970s onwards by Ellenberg (1950, 1974; Pignatti 1995). It was not until the late 1970s that Landolt (1977) proposed a system of

ecological indices specifically tailored to the Swiss flora applicable to various sectors of the Italian Alps, albeit with limitations due to the absence of Alpine species not present in Switzerland, such as Italian endemics that characterise many of the communities analyzed here. This system was subsequently expanded and refined for the entire Alpine chain in "Flora Indicativa" (Landolt et al. 2010), which serves as the framework used in this study and in much of the ecological research dealing with plant communities of the Alps (Ivanova and Zolotova 2023).

Floristic-ecological indicator systems are particularly useful in vegetation science as they allow researchers to define and compare the ecological requirements of plant communities/associations, highlighting microenvironmental niches and ecological gradients that would otherwise be difficult to discern through floristic-structural analysis alone. The effectiveness of this approach is demonstrated by the fact that Landolt's indices, alongside many others developed across various European geographic contexts, have recently been integrated into the architecture of advanced continent-wide bioindication systems, such as the standardized indicator values for European vascular flora proposed by Tichý et al. (2023) and the European Ecological Indicator Values System (EIVE 1.0; Dengler et al. 2023).

The ecological indicator values of Landolt et al. (2010) proved particularly useful in this study, as they allowed us to define the ecological profiles of the vegetation types identified by the cluster analysis (summarized in Fig. 7). Specifically, the application of Landolt's indices provided further clarity on the factors differentiating *Potentillo caulescentis-Telekietum speciosissimae* from *Potentillo caulescentis-Campanuletum elatinoidis*. The latter is characterized by species that are more sciaphilous, more thermophilous, and adapted to less basic, more nutrient-rich substrates. Indeed, *Potentillo caulescentis-Campanuletum elatinoidis* communities occur in shade-sheltered microhabitats (gorges, crevices, cave entrances) compared to those of *Potentillo caulescentis-Telekietum speciosissimae*. In these settings, increased shading is driven by both (micro-)geomorphology and the canopy cover of thermophilous trees such as *Ostrya carpinifolia* and *Fraxinus ornus*, species typical of rupicolous forest communities (*Fraxino orni-Ostryion*) in the hilly-submontane belt of the Lombardy Prealps (Del Favero 2002; Verde et al. 2010). The lower proportion of basiphilous species in *Potentillo caulescentis-Campanuletum elatinoidis* communities is likely due to their primary occurrence on dolomitic bedrock (Arietti et al. 1955). Conversely, *Potentillo caulescentis-Telekietum speciosissimae* communities grow mainly on pure, massive limestones (Sutter 1962, 1969), where the formation of rock crevices and pockets capable of accumulating fine soil and nutrients is less frequent. Furthermore, *Potentillo caulescentis-Campanuletum*

elatinoidis exhibits a higher richness of basiphilous grassland species with broad ecological plasticity, such as *Sesleria caerulea*. In addition to its occurrence in primary alpine grasslands, *S. caerulea* reaches its ecological optimum also in Prealpine gorges (Poldini et al. 2009). In these habitats, microclimatic conditions, characterized by summer cool-moist air and high atmospheric humidity, promote its growth, as well as that of *C. elatinoides*.

The multivariate and synecological analyses also revealed that *C. elatinoides* forms plant communities on stone walls that are floristically, physiognomically, and ecologically distinct from those of *Potentillo caulescentis-Campanuletum* elatinoidis. These wall-dwelling communities - composed of species that are more thermophilous and heliophilous than those in *Potentillo caulescentis-Campanuletum elatinoidis*, along with a higher proportion of exotic and synanthropic species - belong to *Tortulo-Cymbalarietalia* order (*Cymbalario-Parietarietea diffusae* class). Consequently, *C. elatinoides* acts as a transgressive species, also penetrating man-made communities of thermophilous wall chasmophytic vegetation.

It was not possible to assign the wall-dwelling *C. elatinoides* communities to the alliance and association levels, both because this study focused exclusively on tracheophytes (excluding bryophytes) and due to the complex and debated syntaxonomic framework of *Cymbalario-Parietarietea diffusae* class. Historically, several authors have not considered wall vegetation to be an autonomous class, treating it instead as a derived and ecologically contiguous subset of *Asplenietea trichomanis*. Specifically, across Central Europe and Northern Italy, wall vegetation has often been assigned to the class of natural rock communities, restricting the classification within *Cymbalario-Parietarietea diffusae* solely to Southern Italian and Mediterranean communities (Mucina et al. 1993; Poldini and Vidali 1994; Teurillat et al. 1994; Leuschner and Ellenberg 2017).

Based on current phytosociological knowledge and the analyzed relevé data, it is nevertheless likely that the two wall-dwelling communities of *C. elatinoides* belong to *Cymbalario-Asplenion* (*Tortulo-Cymbalarietalia*), the only temperate European alliance whose presence in the Alps was confirmed by Mucina et al. (2016). However, it cannot be ruled out that the more thermophilous community (*Parietaria judaica-Centranthus ruber* community) may be assigned to *Galio valantiae-Parietarion judaicae*, a Mediterranean alliance capable of penetrating temperate macroclimates (Brullo and Guarino 1998, 2002; Biondi and Blasi 2014; Mucina et al. 2016). Targeted future studies will be required to resolve this issue. Nevertheless, man-made walls (constructed to retain roads or embankments, as well as those of historic buildings) built with local calcareous-dolomitic stone can serve as extra-zonal conservation refugia for *C. elatinoides*. Particular attention should therefore be paid to their maintenance

and restoration by developing targeted protocols that respect local rupicolous biodiversity. This is fundamental to prevent the loss or decline of *C. elatinoides* populations, as previously documented by Ravazzi and Marinoni (2004) during the restoration of the historic walls of "Piazza della Rocca" in Clusone (Bergamo province), and by Ferlinghetti (2011) following the cleaning of the bell tower walls in Premolo (Bergamo province).

The results of the habitat suitability analysis for the main diagnostic species of the vegetation clusters (Fig. 5 and Fig. 6) provided spatial confirmation of the floristic and synecological findings, allowing us to map the potential distribution of *C. elatinoides* communities and assess the areas of actual coexistence with the *Potentillo-Telekietum speciosissimae*. Habitat suitability maps highlighted a marked macro-geographic overlap between the potential ranges of *C. elatinoides* and *X. speciosissima* in Lombardy (Fig. 6b), confirming the strong affinity of both species for the carbonate Prealps. At the macroclimatic and geological levels, nearly the entire area suitable for the development of the *Potentillo caulescentis-Campanuletum elatinoidis* falls within the potential area of the *Potentillo caulescentis-Telekietum speciosissimae*. However, *X. speciosissima* exhibits climatic suitability extending into the easternmost and westernmost limestone-dolomite cliff face systems of Lombardy, where climatic conditions are unsuitable for *C. elatinoides*. The broader ecological tolerance (euryoecy) of *X. speciosissima* is reflected in its wider geographical range: both the species and the *Potentillo caulescentis-Telekietum speciosissimae* occur across Lombardy and the Trentino-Alto Adige region, whereas *C. elatinoides* is restricted to a narrow geographic sector of Lombardy between Lecco Lake and Garda Lake (Bertolli et al. 2024). The potential distribution results thus confirm that the clear floristic and syntaxonomic difference between these two *Potentillion caulescentis* associations is not driven by macro-scale geographical segregation, but rather by precise meso- and micro-ecological niche partitioning within the same territory (Fig. 7), in line with micro-habitat segregation patterns observed in other rocky plant communities (Tomaselli et al. 2019).

Regarding the habitat of synanthropic wall communities, spatial modelling restricted their suitability to much narrower portions of the territory compared to the overall potential distribution of *C. elatinoides*, concentrating them mainly in Prealpine valley bottoms, hilly areas, and in the upper Po Plain. Marked thermophily and the presence of nitrophilous/ruderal species limit these communities to low elevations where man-made structures built with local calcareous-dolomitic stone are present. Consequently, the geographic areas in Lombardy where conditions are suitable for the simultaneous coexistence of all four vegetation types analyzed in this research are extremely localized (Fig. 6e). A notable setting where such coexistence can

occur is represented by deep carbonate gorges intersected by roads (Fig. 7) or other man-made structures. Here, pronounced altitudinal gradients and sharp variations in shading and solar radiation across steep cliffs can generate marked microclimatic gradients, while the presence of old walls (along roadsides, embankments, or other structures) can provides artificial substrates with varying exposure/insolation and temperature regimes.

Although a much more detailed and accurate floristic-distributive knowledge is available today for *C. elatinoides* and the other diagnostic species considered (Martini et al. 2012; Stinca et al. 2021; Bertolli et al. 2024) compared to that possessed by last century's botanists, the application of species distribution models retains fundamental relevance. Indeed, the utility of this approach lies not in merely mapping known occurrences, but in its ability to delineate and delimit the bioclimatic space theoretically suitable for each taxon. In this study, such an approach allowed us to uncouple the analysis from the observed actual distribution, often influenced by geographic barriers, dispersal dynamics, or anthropogenic pressure, thereby providing a predictive cartographic foundation essential for evaluating the potential coexistence of species/communities, which may prove valuable for planning their future conservation strategies across the Lombardy region.

Conclusion

This research resolves the long-standing syntaxonomic debate regarding cliff-dwelling *C. elatinoides* communities, overcoming an impasse that has persisted for over seventy years. Statistical analyses disproved the hypothesis that communities of *C. elatinoides* established on calcareous-dolomitic cliff faces and those of *Potentillo caulescentis-Telekietum speciosissimae* are mere facies of a single association. Instead, they confirmed the floristic and ecological autonomy of both units, leading to the formal definition of the new Lombardy endemic association: *Potentillo caulescentis-Campanuletum elatinoidis*. From a synecological perspective, this new association differs from *Potentillo caulescentis-Telekietum speciosissimae* by occupying more shaded, warmer habitats with less basic and more nutrient-rich substrates, such as those of dolomitic crevices and nooks. Concurrently, *C. elatinoides* was shown to act as a transgressive species, also colonizing man-made stone walls to form synanthropic communities of *Cymbalario-Parietarietea diffusae* that are distinctly separated from cliff face vegetation. Finally, potential distribution modelling of diagnostic species revealed that the differentiation between the two cliff associations (*Potentillo caulescentis-Telekietum speciosissimae* and *Potentillo caulescentis-Campanuletum elatinoidis*) is not driven

by macro-scale geographical separation, but rather by precise ecological niche partitioning within the carbonate pre-Alps of Lombardy.

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Appendix

Syntaxonomic scheme:

Asplenietea trichomanis (Br.-Bl. in Meier et Br.-Bl. 1934) Oberd. 1977

Potentilletalia caulescentis Br.-Bl. in Br.-Bl. et Jenny 1926

Potentillion caulescentis Br.-Bl. in Br.-Bl. et Jenny 1926

Potentillo caulescentis-Telekietum speciosissimae Sutter et Pirola in Sutter 1969

Potentillo caulescentis-Campanuletum elatinoidis ass. nov.

Cymbalario-Parietarietea diffusae Oberd. 1969

Tortulo-Cymbalarietalia Segal 1969

Other syntaxa quoted in the text: *Artemisietea vulgaris* Lohmeyer et al. in Tx. ex von Rochow 1951; *Carpino-Fagetea sylvaticae* Jakucs ex Passarge 1968; *Cymbalario-Asplenion* Segal 1969; *Elyno-Seslerietea* Br.-Bl. 1948; *Festuco-Brometea* Br.-Bl. et Tx. ex Soó 1947; *Fraxino orni-Ostryion* Tomažič 1940; *Galio valantiae-Parietarion judaicae* Rivas-Mart. ex O. de Bolòs 1967; *Papaveretea rhoeadis* S. Brullo et al. 2001; *Quercetea pubescentis* Doing-Kraft ex Scamoni et Passarge 1959; *Thlaspietea rotundifolii* Br.-Bl. 1948.

Electronic supplementary material

Table S1 Bioclimatic predictors (BIO1-19) and their importance in the distribution model of the four species (*Campanula elatinoides*, *Xerolekia speciosissima*, *Cymbalaria muralis* and *Parietaria judaica*), expressed as percentage of contribution.

Table S2 Diagnostic species of each vegetation cluster. Pearson's phi coefficient (Φ) and *p*-value of each diagnostic species are reported.

Table S3 Phytosociological table of relevés. The relevés are listed according to the sequence given by the cluster analysis. Cover indices refer to the Braun-Blanquet (1964)

abundance/dominance scale: r, rare; +, <1%; 1, 1-5%; 2, 5-25%; 3, 25-50%; 4, 50-75%; 5, 75-100%.

Figure S1 Representative aspect of *Potentillo caulescentis-Campanuletum elatinoidis* (calcareous-dolomitic cliff of Camerata Cornello, Brembana Valley, Bergamo province).

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Tables

Table 1 Synoptic table of the four vegetation types: A1, *Potentillo caulescentis-Campanuletum elatinoidis*; A2, *Potentillo caulescentis-Telekietum speciosissimae*; B1, *Cymbalaria muralis-Asplenium trichomanes* community; B2, *Parietaria judaica-Centranthus ruber* community. Values are expressed as percentage frequencies. Species with statistically significant *Φ*-coefficient values, as determined by Fisher's exact test, are highlighted: *, $p < 0.05$; **, $p < 0.01$ (see also Table S2).

Vegetation type (cluster code)	A1	A2	B1	B2
No. of relevés	32	7	24	9
***Potentillo caulescentis-Campanuletum elatinoidis* ass. nova**				
Campanula elatinoides Moretti	100**	.	100**	100**
Campanula carnica Schiede ex Mert. & W.D.J.Koch subsp. *puberula* Podlech	40**	.	.	.
Physoplexis comosa (L.) Schur	25**	.	.	.
Potentillo caulescentis-Telekietum speciosissimae				
Xerolekia speciosissima (L.) Anderb.	38	100**	.	.
Phyteuma scheuchzeri All. subsp. *columnae* (Gaudin) Bech.	75*	29	.	.
Campanula raineri Perp.	.	42**	.	.
Potentillion caulescentis* and *Potentilletalia caulescentis				
Potentilla caulescens L.	75**	100**	4	.
Carex mucronata All.	37*	28*	8	.
Kernera saxatilis (L.) Sweet	13	42**	.	.
Globularia cordifolia L.	18*	28*	.	.
Saxifraga caesia L.	3	42**	.	.
Moehringia insubrica Degen	3	42**	.	.
Valeriana saxatilis L.	6	28**	.	.
Valeriana tripteris L.	9	14	.	.
Primula auricula L.	3	14	.	.
Adiantum capillus-veneris L.	19	.	.	11
Bupleurum petraeum L.	.	57**	.	.
Arabis bellidifolia Crantz subsp. *bellidifolia*	.	28**	.	.
Rhamnus pumila Turra	.	28*	.	.
Cystopteris alpina (Lam.) Desv.	.	28*	.	.
Saxifraga vandellii Sternb.	.	28*	.	.
Asplenium viride Huds.	.	28**	.	.
Asplenietea trichomanis				
Asplenium ruta-muraria L.	63	100	70	44
Asplenium trichomanes L.	59**	85**	58**	.
Phyllitis scolopendrium (L.) Newman subsp. *scolopendrium*	19	.	8	.
Hieracium amplexicaule L.	.	28*	.	.
Heliosperma pusillum (Waldst. et Kit.)	13	.	.	.
Sedum dasyphyllum L.	6	.	.	.
Thlaspietea rotundifolii				
Achnatherum calamagrostis (L.) P. Beauv.	53*	.	21	33*
Hieracium glaucum All.	38	.	21	11
Aquilegia confusa Rota	19	14	.	.
Adenostyles alpina (L.) Bluff et Fingerh.	25*	.	.	.
Polystichum lonchitis (L.) Roth	6	.	.	.
Tortulo-Cymbalarietalia* and *Cymbalario-Parietarietea diffusae				
Parietaria judaica L.	25	.	29	89**
Centranthus ruber (L.) DC.	13	.	4	22
Cymbalaria muralis G. Gaertn., B. Mey et Scherb.	9	.	75**	.
Ficus carica L.	22	.	4	.
Sedum album L.	.	.	.	11*
Erigeron karvinskianus DC.	9	.	.	.

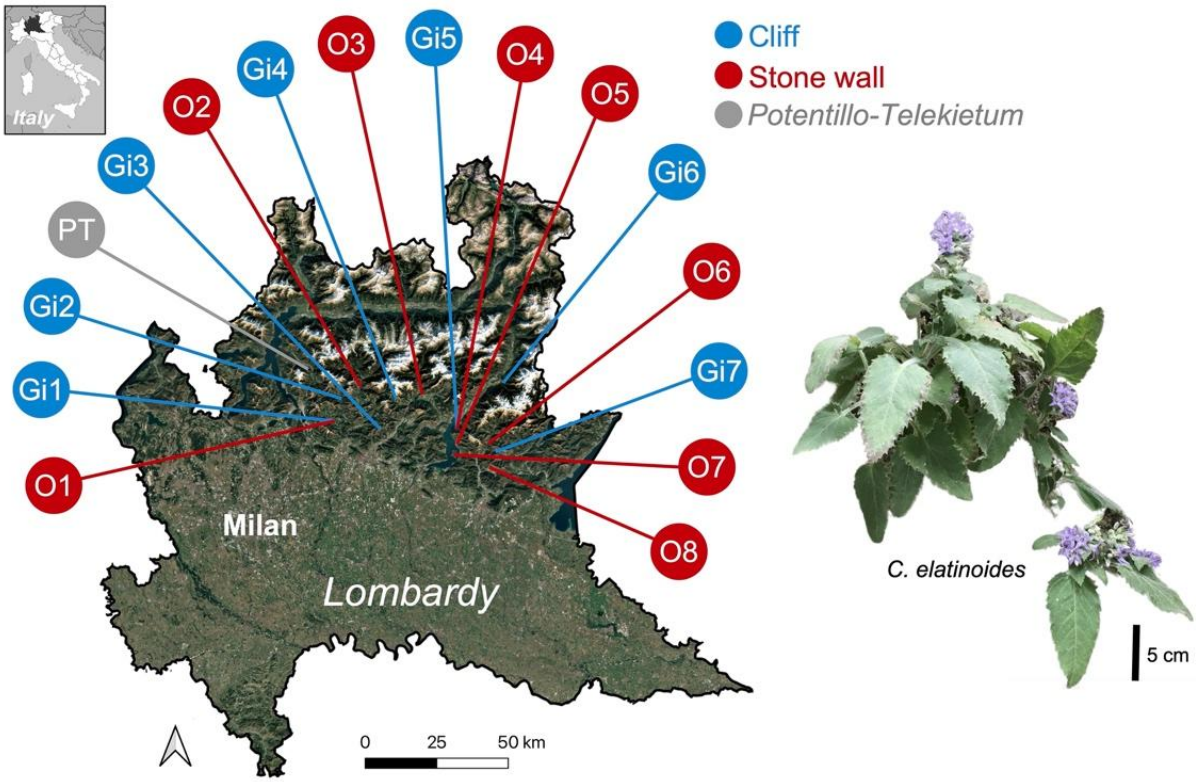
Species of synanthropic, ruderal and nitrophilous vegetation (*Papaveretea rhoeadis* and *Artemisietea vulgaris*)				
Erigeron canadensis L.	.	.	13	67**
Sonchus arvensis L. subsp. *arvensis*	.	.	13	11
Sonchus oleraceus L.	.	.	8	11
Poa compressa L.	.	.	20*	.
Digitaria sanguinalis (L.) Scop.	.	.	17	.
Calystegia sepium (L.) R.Br.	.	.	13	.
Euphorbia peplus L.	.	.	8	.
Galium aparine L.	.	.	8	.
Verbena officinalis L.	.	.	8	.
Species of mesic and warm deciduous forests (*Carpino-Fagetea sylvaticae* and *Quercetea pubescentis*)				
Cyclamen purpurascens Mill.	28	14	13	.
Hedera helix L.	72	.	46	44
Fraxinus ornus L.	65**	.	4	11
Ostrya carpinifolia Scop.	38	.	8	11
Geranium robertianum L.	19	.	13	11
Lactuca muralis (L.) Gaertn.	34*	.	8	.
Veronica urticifolia Jacq.	9	.	8	.
Emerus major Mill.	71**	.	.	.
Arabis turrita L.	.	.	.	44**
Hieracium murorum L. (aggr.)	31*	.	.	.
Galeobdolon flavidum (F. Herm.) Holub	25*	.	.	.
Carex digitata L.	18*	.	.	.
Vincetoxicum hirundinaria Medik.	18*	.	.	.
Gymnocarpium dryopteris (L.) Newman	9	.	.	.
Hepatica nobilis Mill.	9	.	.	.
Laburnum alpinum (Mill.) Bercht. et J. Presl	9	.	.	.
Primula vulgaris Huds.	9	.	.	.
Amelanchier ovalis Medik.	9	.	.	.
Helleborus niger L.	9	.	.	.
Tamus communis L.	9	.	.	.
Carex alba Scop.	6	.	.	.
Daphne mezereum L.	6	.	.	.
Galium sylvaticum L.	6	.	.	.
Geranium nodosum L.	6	.	.	.
Lonicera alpigena L.	6	.	.	.
Melica nutans L.	6	.	.	.
Oxalis acetosella L.	6	.	.	.
Vinca minor L.	6	.	.	.
Aquilegia atrata W.D.J. Koch	6	.	.	.
Clematis recta L.	6	.	.	.
Meso-xerophilous and xerophilous species of basophilic grasslands (*Elyno-Seslerietea* and *Festuco-Brometea*)				
Galium lucidum All.	13	.	4	33*
Sesleria caerulea (L.) Ard.	100**	71**	.	.
Erica carnea L.	68**	14	.	.
Melica ciliata L.	19	14	.	.
Primula glaucescens Moretti	3	14	.	.
Euphorbia cyparissias L.	3	.	.	33**
Leontodon tenuiflorus (Gaudin) Rchb.	.	28*	.	.
Carex firma Host	.	28*	.	.
Brachypodium rupestre (Host) Roem. et Schult.	40**	.	.	.
Laserpitium siler L.	25**	.	.	.
Horminum pyrenaicum L.	16	.	.	.
Centaurea rhaetica Moritzi	13	.	.	.
Buphthalmum salicifolium L.	13	.	.	.
Teucrium chamaedrys L.	13	.	.	.
Fragaria viridis Weston	.	.	8	.
Globularia nudicaulis L.	6	.	.	.
Festuca alpestris Roem et Schult.	6	.	.	.
Teucrium montanum L.	6	.	.	.
Lomelosia graminifolia (L.) Greuter et Burdet subsp. *graminifolia*	6	.	.	.
Tofieldia calyculata (L.) Wahlenb.	6	.	.	.
Fumana ericifolia Walr.	3	.	.	.
Other species				
Buddleja davidii Franch.	3	.	17	11
Rubus ulmifolius Schott	19	.	4	22

Clematis vitalba L.	16	.	17	.
Eupatorium cannabinum L.	13	.	4	.
Salix caprea L.	34**	.	.	.
Pinguicula alpina L.	16	.	.	.
Anthriscus sylvestris (L.) Hoffm.	13	.	.	.
Dianthus sylvestris Wulfen	9	.	.	.
Molinia arundinacea Schrank	9	.	.	.
Anthericum ramosum L.	6	.	.	.
Rhododendron hirsutum L.	6	.	.	.
Ailanthus altissima (Mill.) Swingle	6	.	.	.
Sporadic species	17	3	6	9

Table 2 One-way ANOVA results of plant community effect on ecological indices of Landolt et al. (2010): T, temperature; K, continentality; L, light intensity; F, soil moisture; R, substrate reaction; N, nutrients; H, humus; D, aeration. Key: *, significant ($p < 0.01$); ns, not significant.

Source of variance	Mean square	$F_{3,68}$	P	
T	3.0890	22.88	<0.001	*
K	0.6992	7.812	<0.001	*
L	0.8065	7.753	<0.001	*
F	0.1631	1.539	0.212	ns
R	0.4109	4.405	0.007	*
N	1.2632	17.59	<0.001	*
H	1.7620	14.52	<0.001	*
D	1.3676	7.756	<0.001	*

Figures



Code	Sampling site	Municipality	Elevation (m a.s.l.)	N. of relevés	Data source
O1	Walls of the Cornabusa Sanctuary	Sant'Omobono Terme (BG)	660	3	Original data
O2	Walls of the Church of St John the Baptist and St Barbara	Camerata Cornello (BG)	480	2	Original data
O3	Walls of the Clusone fortress	Clusone (BG)	645	4	Original data
O4	Walls of the Toline railway station	Pisogne (BS)	200	4	Original data
O5	Walls of the Vello railway station	Marone (BS)	190	5	Original data
O6	Walls of the Saint Filastrio cemetery	Tavernole sul Mella (BS)	475	10	Original data
O7	Walls of the Sanctuary of "Madonna della Ceriola"	Monte Isola (BS)	600	5	Original data
O8	Walls of the "El Cuèl" cave	Sarezzo (BS)	430	1	Original data
Gi1	Cliff of Imagna Valley	Sant'Omobono Terme (BG)	675	5	Giupponi (2020)
Gi2	Cliff of Taleggio Valley	Taleggio (BG)	535	5	Giupponi (2020)
Gi3	Cliff of Vertova Valley	Vertova (BG)	565	5	Giupponi (2020)
Gi4	Cliff of Nossana Valley	Premolo(BG)	800	4	Giupponi (2020)
Gi5	Cliff of Iseo Lake	Pisogne (BS)	195	5	Giupponi (2020)
Gi6	Cliff of middle Camonica Valley	Breno (BS)	345	3	Giupponi (2020)
Gi7	Cliff of Trompia Valley	Marcheno (BS)	560	4	Giupponi (2020)
PT	Cliff of Lori Valley and Grigna Massif	Primaluna (LC), Lierna (LC)	750-1730	7	Sutter (1961, 1969)

Fig. 1 Location of the sites where the phytosociological relevés were carried out: O, original relevés; Gi, relevés carried out by Giupponi (2020); PT, relevés carried out by Sutter (1962, 1969) and assigned to the *Potentillo caulescentis-Telekietum speciosissimae*.

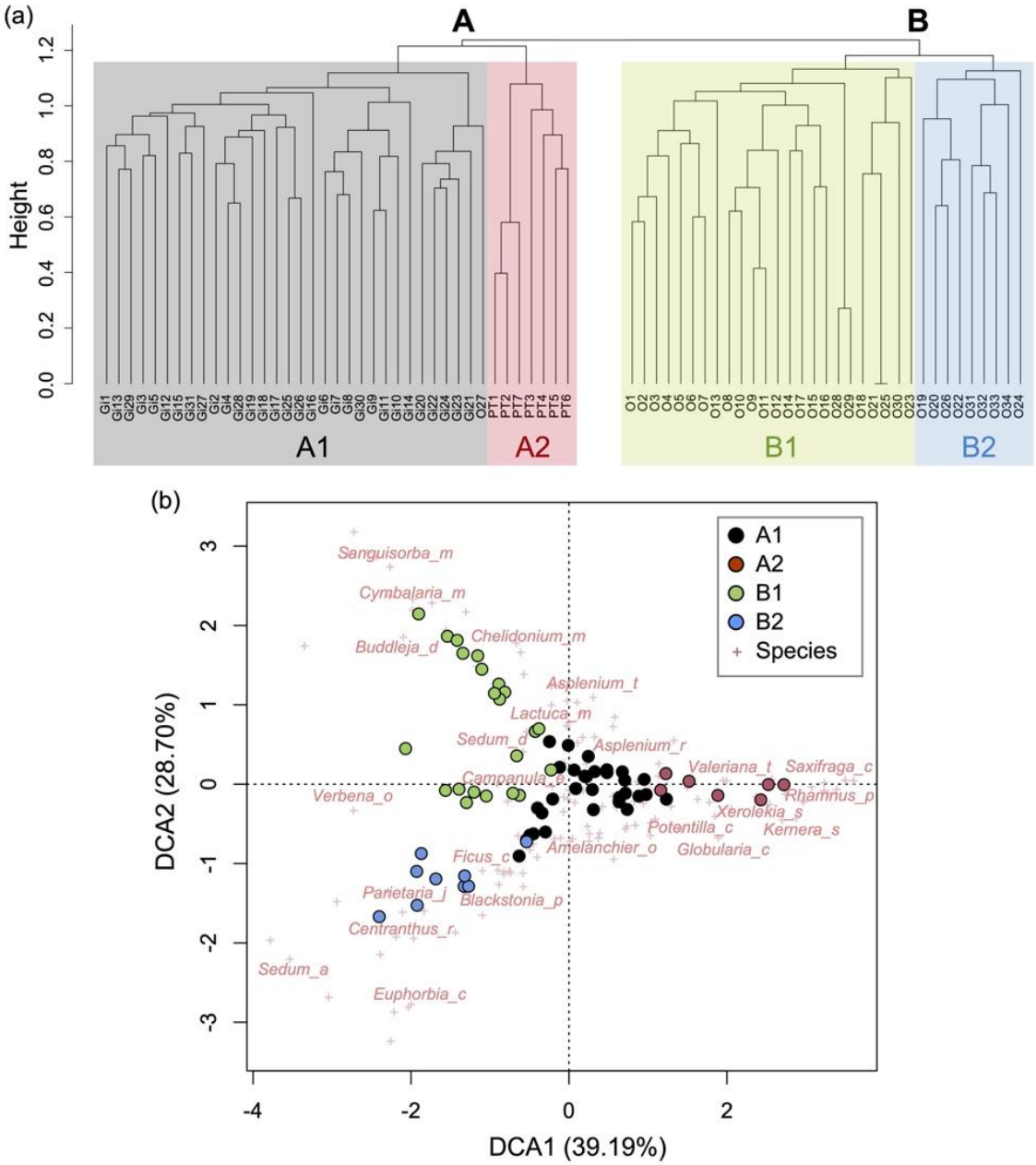


Fig. 2 Dendrogram (a) and DCA biplot (b) of the relevés. The two main clusters (A, plant communities of the calcareous-dolomitic cliffs; B, plant communities of stone walls) and the four subclusters (A1, *Potentillo caulescentis-Campanuletum elatinoidis*; A2, *Potentillo caulescentis-Telekietum speciosissimae*; B1, *Cymbalaria muralis-Asplenium trichomanes* community; B2, *Parietaria judaica-Centranthus ruber* community) are highlighted. Some species are shown in the DCA biplot: Sanguisorba_m, *Sanguisorba minor*; Cymbalaria_m, *Cymbalaria muralis*; Chelidonium_m, *Chelidonium majus*; Buddleja_d, *Buddleja davidii*; Asplenium_t, *Asplenium trichomanes*; Lactuca_m, *Lactuca muralis*; Sedum_d, *Sedum dasyphyllum*; Asplenium_r, *Asplenium ruta-muraria*; Valeriana_t, *Valeriana tripteris*; Saxifraga_c, *Saxifraga caesia*; Campanula_e, *Campanula elatinoides*; Verbena_o, *Verbena*

officinalis; Rhamnus_p, *Rhamnus pumila*; Xerolekia_s, *Xerolekia speciosissima*; Potentilla_c, *Potentilla caulescens*; Kernera_s, *Kernera saxatilis*; Amelanchier_o, *Amelanchier ovalis*; Globularia_c, *Globularia cordifolia*; Ficus_c, *Ficus carica*; Parietaria_j, *Parietaria judaica*; Blackstonia_p, *Blackstonia perfoliata*; Centranthus_r, *Centranthus ruber*; Sedum_a, *Sedum album*; Euphorbia_c, *Euphorbia cyparissias*. Relevé codes in the dendrogram: O, original relevés (community of *C. elatinoides* on walls); Gi, relevés carried out by Giupponi (2020) (community of *C. elatinoides* on rocks/cliffs); PT, relevés of Sutter (1961, 1969) (*Potentillo caulescentis-Telekietum speciosissimae*).

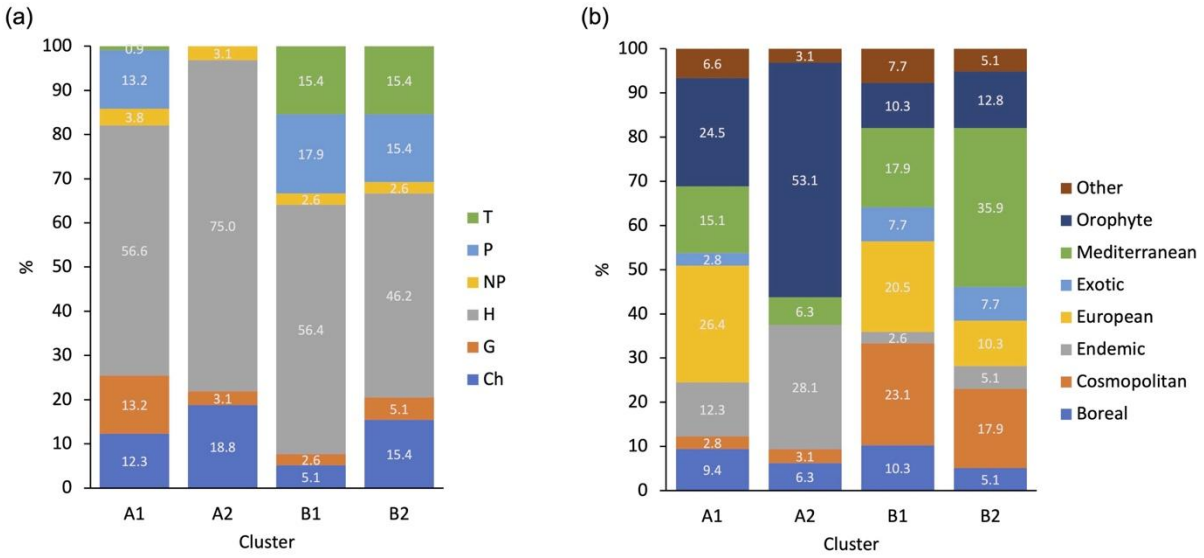


Fig. 3 Life-form (a) and chorological (b) spectra of the four vegetation clusters: A1, *Potentillo caulescentis-Campanuletum elatinoidis*; A2, *Potentillo caulescentis-Telekietum speciosissimae*; B1, *Cymbalaria muralis-Asplenium trichomanes* community; B2, *Parietaria judaica-Centranthus ruber* community. Key: T, therophytes; P, phanerophytes; NP, nanophanerophytes; H, hemicryptophytes; G, geophytes; Ch, chamaephytes.

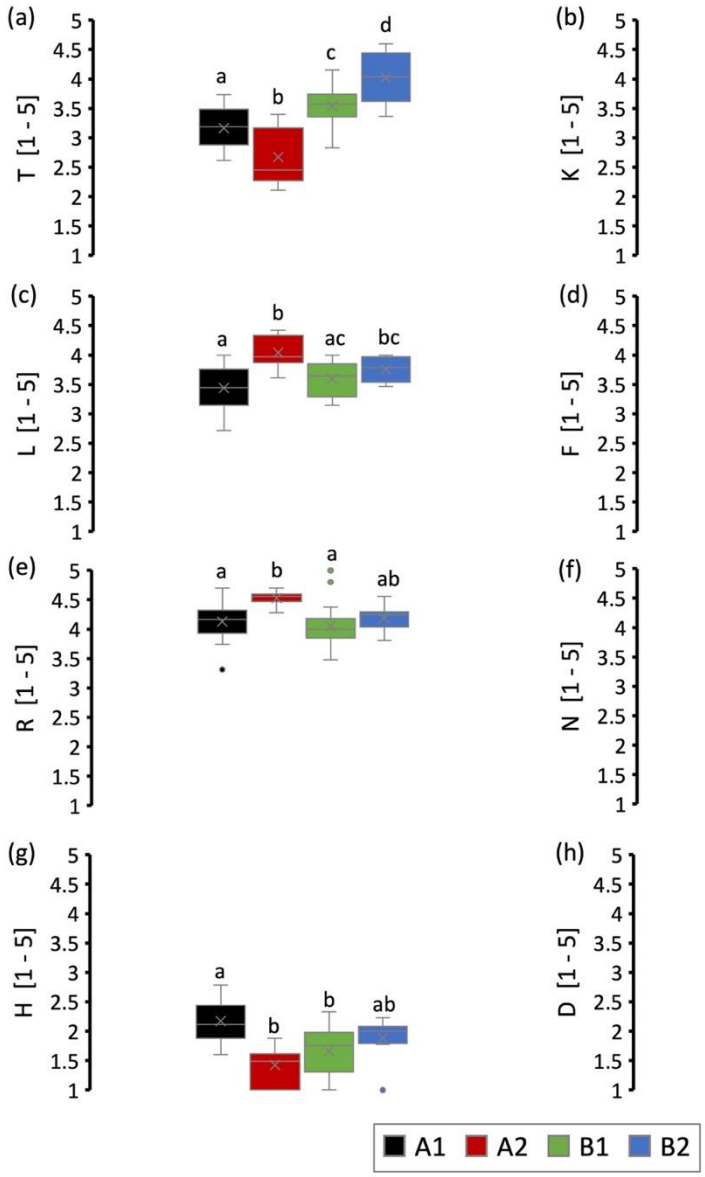


Fig. 4 Boxplots of ecological indices of Landolt et al. (2010): index of temperature – T (a); index of continentality – K (b); index of light intensity – L (c); soil moisture index – F (d); index of substrate reaction – R (e); index of nutrients – N (f); index of humus – H (g); aeration index – D (h). For each boxplot, mean (cross) and median (line) are highlighted. Different letters above the error bars indicate significant differences ($p < 0.05$) among plant communities obtained by the one-way ANOVA and the Tukey post-hoc test (ns, not significant). Plant communities/associations: A1, *Potentillo caulescentis-Campanuletum elatinoidis*; A2, *Potentillo caulescentis-Telekietum speciosissimae*; B1, *Cymbalaria muralis-Asplenium trichomanes* community; B2, *Parietaria judaica-Centranthus ruber* community.

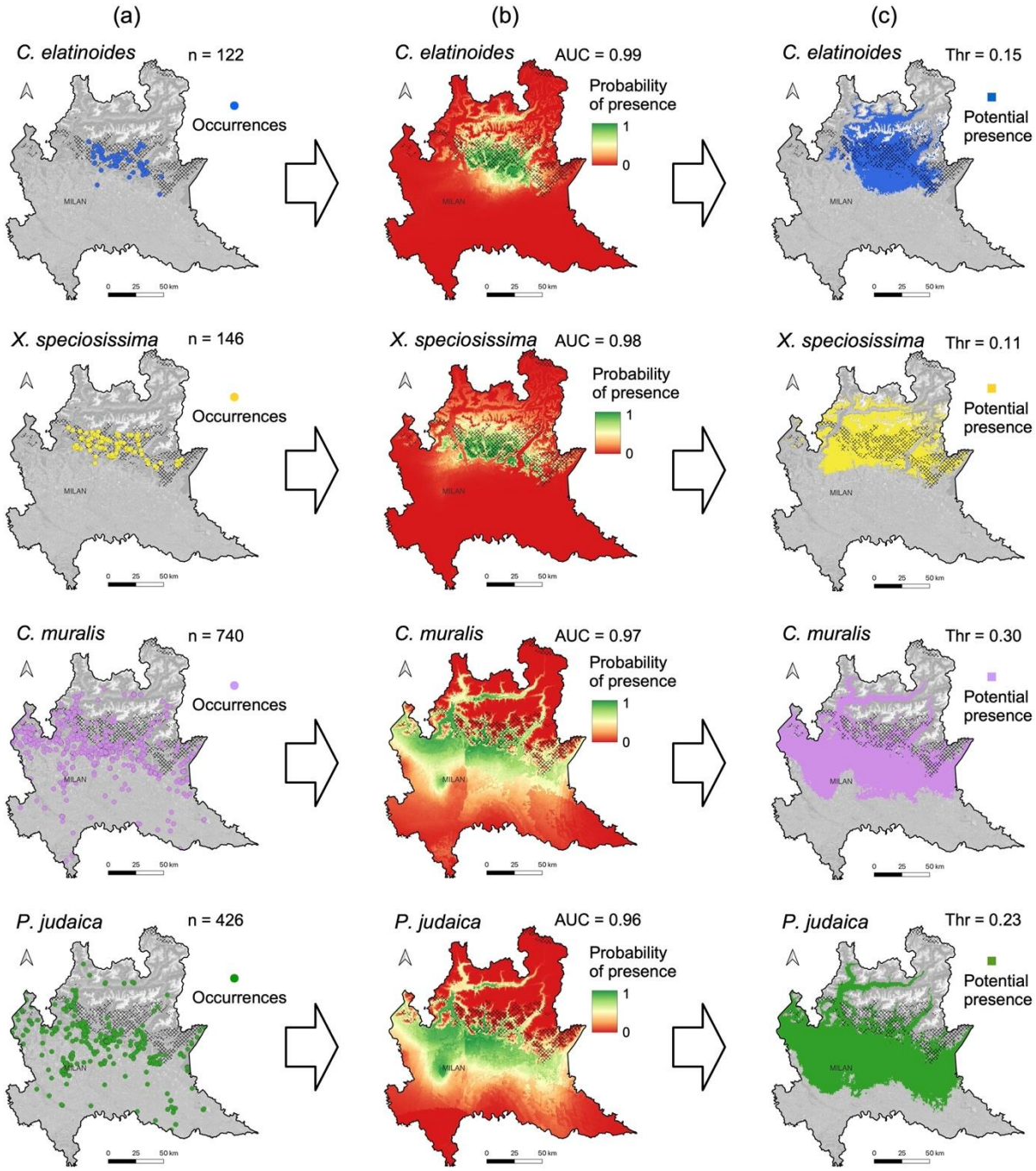


Fig. 5 Occurrence maps of *C. elatinoides*, *X. speciosissima*, *C. muralis*, and *P. judaica* in Lombardy (a), MaxEnt-predicted habitat suitability maps showing the probability of occurrence (b), and binary maps of potential species distribution based on climatic suitability (c). For each species, the number of occurrence records (n) used to build the model, the AUC value, and the threshold derived from the maximum sensitivity plus specificity criterion are reported. Areas with calcareous-dolomitic bedrock are highlighted on the maps using a diamond-hatched pattern.

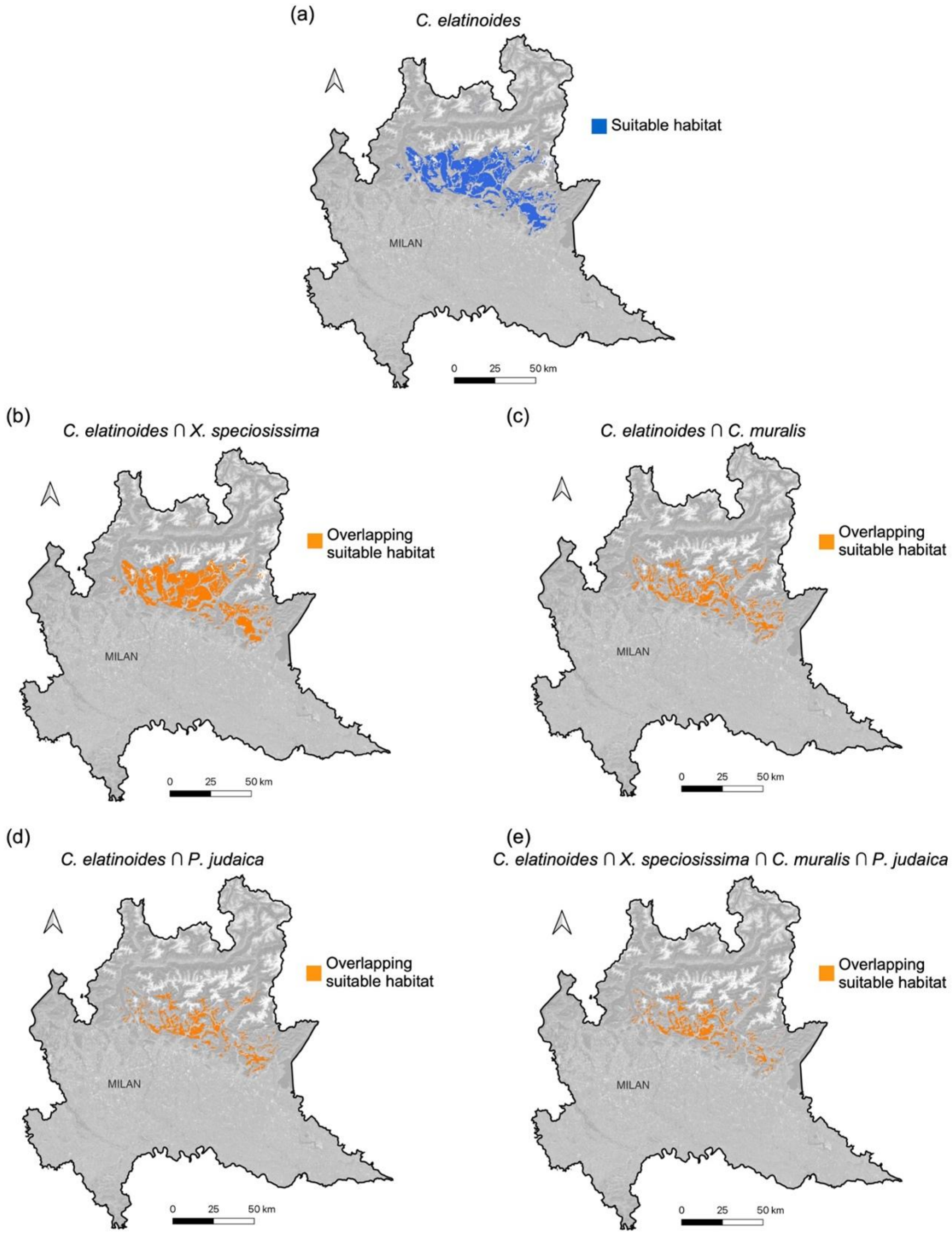


Fig. 6 Suitable habitat of *C. elatinoides* based on climatic conditions and geological substrate (a), and overlap between the suitable habitat of *C. elatinoides* and the suitable habitats of *X. speciosissima* (b), *C. muralis* (c), *P. judaica* (d), and all species considered combined (e).

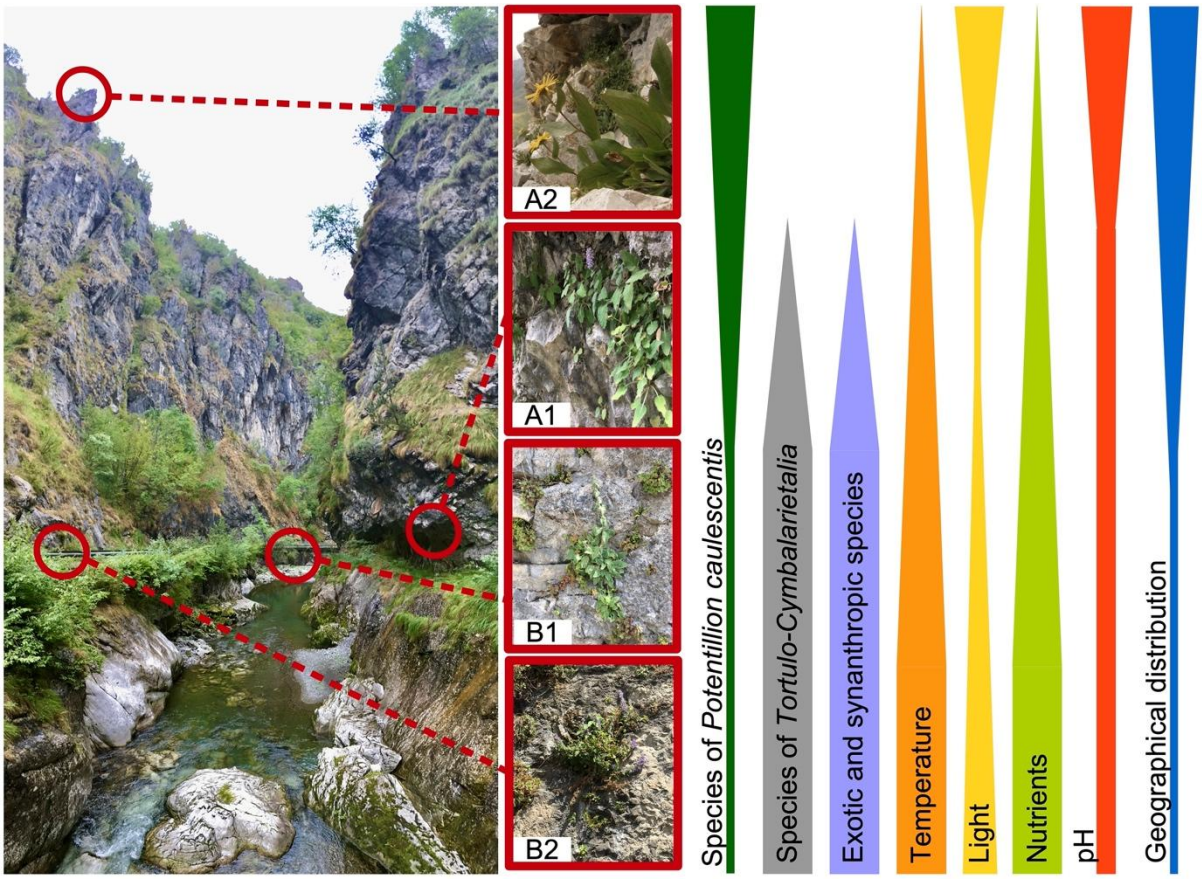


Fig. 7 Possible location in a gorge (Taleggio Valley) and summary of the characteristics of the four plant communities examined: A1, *Potentillo caulescentis-Campanuletum elatinoidis*; A2, *Potentillo caulescentis-Telekietum speciosissimae*; B1, *Cymbalaria muralis-Asplenium trichomanes* community; B2, *Parietaria judaica-Centranthus ruber* community. The variation of each characteristic/ecological factor is schematically illustrated.

Supplementary Files

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- TableS1.xlsx
- TableS2.xlsx
- TableS3.xlsx
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