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RESEARCH

Characterization and distribution of the endemic flora in Northern Italy

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Abstract
Floristic mapping advances the biogeographical knowledge by revealing patterns of biodiversity through a standardized grid-based survey of species' occurrences. It consists of the systematic grid-based survey of species occurrence, aimed at producing distribution maps of vascular plants within a given territory. We compiled a dataset of 32,939 floristic records (field observations, herbarium specimens, and literature) referenced to the Central European Floristics Mapping standard, documenting the distribution of 447 endemic taxa across 3,612 grid cells (5' of longitude and 3' of latitude) in Northern Italy. This study aims to characterize the composition and distribution of Northern Italy's endemic flora—encompassing the Alps and the northern Apennines, including Alpine-restricted taxa whose range extends beyond the Italian border), highlighting major geographical patterns and their functional and ecological attributes. We quantified endemic species richness, life-form and habitat preferences, and Landolt's ecological indicator values. Endemism was spatially aggregated, with clear hotspots along the Alpine and Prealpine belts and species-poor, fragmented assemblages in the lowlands; regional floristic affinities mirrored shared substrates and elevation ranges. We also detected coherent ecological gradients, with a light/temperature axis opposing a moisture/nutrients axis, consistent with topographic and edaphic controls. Habitat use by endemics tended to be focused on open, primary substrates (e.g., rocky outcrops, grasslands, screes). Together, these results provide a complete overview of Northern Italy's endemic flora, identify priority areas for conservation, and offer a reproducible baseline for land-use planning and climate-change monitoring.

Keywords Endemic plants · Northern Italy · Floristic atlas · Spatial distribution · Floristic composition

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Introduction

By definition, a species' range represents the geographical area within which it is naturally distributed. This distribution is the result of its evolutionary history, origin, their biological dispersal capabilities, the geographic and climatic factors that influence its presence, its ecological requirements, the human disturbance and biotic interactions with other species. While most species exhibit broad or intermediate global ranges, a subset of plant and animal species displays a narrow or localized range of distribution. In biological sciences, and particularly in botany, De Candolle (1820) extended the original medical meaning of the term to describe those taxa that are restricted to a defined geographical region as endemic species. The distribution pattern of endemic species is particularly linked to historical factors (e.g., glacial refugia, climatic shifts) and ecological drivers (e.g., climate, altitude, geology, topography), and species distributions have been strongly influenced by past climatic events, particularly the Last Glacial Maximum (Médail & Diadema 2009). The Quaternary, with its alternating glacial and interglacial cycles, had profound consequences for the distribution, evolution, and composition of alpine European flora, promoting processes of migration, isolation, and speciation (G. Hewitt 2000).

An endemic vascular plant is generally the result of a new speciation event, either allopatric or sympatric, or of a range contraction. Climatic stability and geographic isolation are regarded as primary drivers of species evolution and the emergence of new taxa (G. M. Hewitt 1996; Tordoni et al. 2020). The longer the periods of environmental stability, the higher the likelihood of persistence of species pools and survival of specialized species with highly restricted ranges and low dispersal capacity (Cowling & Lombard 2002; Jansson 2003).

The richness of endemic species is widely used as an indicator of overall biodiversity and for the identification of global biodiversity hotspots (Myers et al. 2000). Endemic richness is an ecologically distinctive and crucial biodiversity indicator, which does not necessarily coincide with other metrics such as species richness or the concentration of threatened species (Orme et al. 2005). Various studies, both in alpine regions and beyond, further highlight how the presence of endemic plants is associated with greater biodiversity, with evident correlations between plant flora and other taxonomic groups such as insects and vertebrates, serving as indicators of overall biodiversity (Médail & Quézel 1999; Pauli et al. 2005). From a conservation perspective, the protection of endemic species is now recognized as one of the primary challenges in biodiversity conservation, involving governments, environmental organizations, and local communities. A small number of populations and a restricted range are two of the criteria used by the International Union for Conservation of Nature (IUCN) to classify the threat level faced by living organisms (IUCN 2025). These species, often characterized by limited distribution, small population size, and low genetic variability, are particularly vulnerable to climate change, habitat fragmentation, and the introduction of invasive alien species, and thus require targeted and integrated protection strategies (Coelho et al. 2020). To ensure their long-term conservation, it is essential to integrate ecological, genetic, and climatic data to identify areas of highest conservation priority and to predict the response of endemic species to future environmental change scenarios (Thuiller et al. 2005). In this framework, there is an urgent need for synthetic studies on the distribution of endemic flora in Europe to improve our understanding of its geographical and ecological patterns, which may have significant implications for conservation management, especially in the design and prioritization of protected areas. In this regard, floristic cartography and ongoing field data collection represent indispensable tools for monitoring the effectiveness of applied strategies and for responding promptly to emerging threats. The systematic and accurate collection of floristic data through floristic mapping is a fundamental prerequisite for understanding biodiversity and implementing sound conservation practices for species, especially endemics. It allows for informed territorial management, sustainable land use, and planning in the face of climate change and looming extinctions, which are disrupting biotic interactions in ways that are difficult to predict (Alexander et al. 2015). To achieve these goals, it is essential to rely on comprehensive knowledge of species distributions and the spatial patterns of endemic hotspots. Although a list of the endemic species of Italy (Peruzzi et al. 2014) has been compiled together with that of *the loci classici*, a detailed distributional framework of these entities is still lacking.

In the study area (see below), comprising the Italian Alps and part of the Northern Apennines, research on the endemic flora has mainly appeared in broad syntheses on Alpine endemism (Pampanini 1903; Pawlowski 1970; Ozenda 1995; Aeschimann et al. 2011a, 2011b), or on specific Alpine sectors (Ozenda 1950; Martini 1984; Reisigl 1996; Tribsch 2004; Casazza et al. 2016), or accounts limited to individual administrative regions (Martini 1985, Friuli—Venezia Giulia; Montacchini and Forneris 1997, Piemonte; Prosser 2000 Trentino). Saccani and Salvoni (2015), referring to the Northern Apennines, discussed endemics as well as rare and protected species.

The aim of this study is to provide an accurate analysis of the diversity of vascular endemic species in Northern Italy, as presented in the maps of the Atlas by Bertolli et al. (2024), offering an in-depth examination. In particular, we focused on the characterization of the composition and distribution of the endemic flora, highlighting the main geographical patterns and their functional (i.e., life form) and ecological features (i.e., habitat, indicator values).

Material and methods

Study area

The study area encompasses eight administrative regions of Northern Italy (Liguria, Piemonte, Valle d'Aosta, Lombardia, Trentino-Alto Adige, Veneto, Friuli Venezia Giulia, Emilia-Romagna), including their respective 47 provinces, and covers 120,260 km^2.

Northern Italy is a highly heterogeneous region, characterized by several major geophysical features, among which the Alps, the Veneto-Po Valley, and the Northern Apennines are particularly prominent. The Northern Apennines branch off from the Alps at the Bocchetta di Altare (or Cadibona Pass). In the context of this study, the Alps are defined according to the SOIUSA (Suddivisione Orografica Internazionale del Sistema Alpino) classification system (Marazzi 2005), while the Northern Apennines, excluding the Apuan Alps, are considered to extend southward as far as Bocca Serriola. Approximately 46% of the study area falls within the Alpine domain, 34% within the Po Plain, and the remaining 20% corresponds to the Northern Apennines (Fig. 1).

From a geological perspective, the Alps are primarily composed of crystalline and metamorphic rocks, interspersed with sedimentary sequences (Schmid et al. 1996). The Po Plain, in contrast, consists mainly of alluvial deposits, with extensive fluvial terraces shaped by the Po and Adige rivers and their tributaries. Geomorphologically, the region

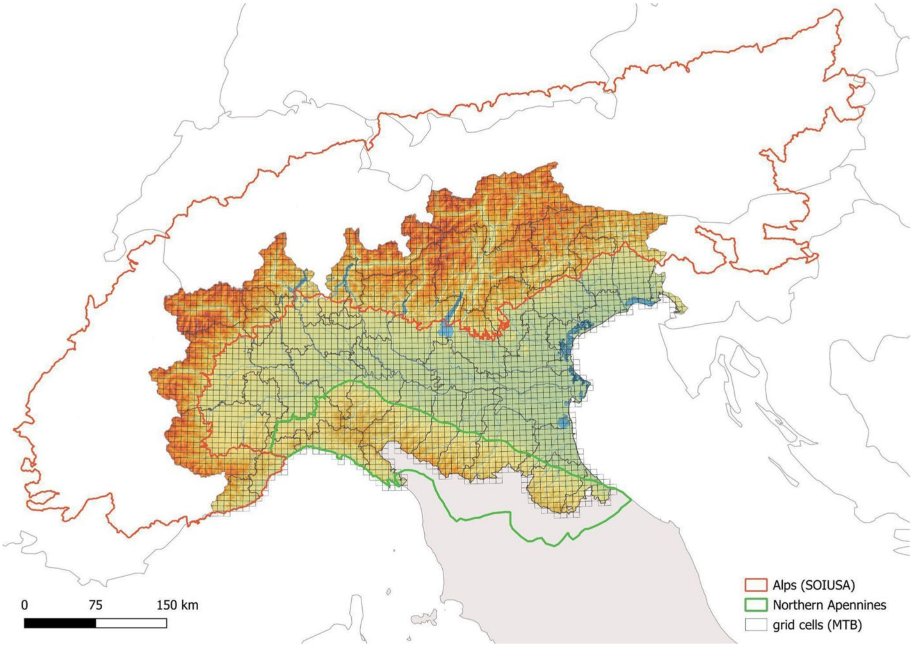

Fig. 1 Map of the study area (Northern Italy), showing the boundaries of the Alpine and Northern Apennine regions and grid of cells covering Northern Italy, used for mapping and analysis. The cartographic base is derived from a colorized Digital Terrain Model (DTM). The mapped area is bounded by provincial and national borders of Italy (in grey), and includes major rivers and lakes (in blue)

exhibits sharp reliefs in the mountainous areas, with glacial valleys and karst features in the Alps, and a gently undulating landscape in the Po Plain (Ravazzi et al. 2012).

Moreover, the climate in the area is highly heterogeneous. The Alpine areas experience cold winters with significant snowfall and mild summers, with peculiar zones characterized by high precipitation (e.g., Insubric region, Carnic and Julian Alps, Northern Apennines) or very dry valleys (e.g., Aosta Valley, Venosta Valley in South Tyrol, Valtellina valley in Lombardy, and all the valley with exposition E-W). The Apennine region shows a temperate climate with marked altitudinal gradients, ranging from humid and snowy conditions in the higher elevations to milder and drier ones in the foothills and intermontane valleys. In contrast, the Po Plain has a humid subtropical climate, with hot summers, foggy winters, and moderate precipitation (Gobiet et al. 2014). Land use in the study area reflects both natural and anthropogenic influences. The Alpine region is largely covered by forests and alpine pastures (some abandoned), with scattered settlements in valleys. The Apennine areas are characterized by extensive forests, mixed agro-silvo-pastoral systems, and areas of land abandonment, while the Po Plain is intensively cultivated, dominated by cereals, maize, and other arable crops, fragmented with urban and industrial areas (Pijl & Tarolli 2022) and intensive farming.

This remarkable territorial heterogeneity results in the presence of three biogeographical regions, Alpine, Continental, and Mediterranean, and contributes to a high floristic biodiversity: more than 6,000 native taxa are recorded according to the latest checklist of the Italian flora (Bartolucci et al. 2024), as well as more than 1400 alien taxa (Galasso et al. 2024).

Sampling design and data collection

The data were collected within the framework of 19 local floristic mapping projects (Alessandrini et al. 2022; Andreatta et al. 2022; Bona 2022; Bovio and Mainetti 2022; Peccenini 2022; Selvaggi et al. 2022; Wilhalm et al. 2022; Martini et al. 2023) which aims to produce distribution maps of all vascular plants in Northern Italy (Adorni et al. 2022) using the standardized grid for floristic mapping adopted by the Central European Floristics Mapping Project (Ehrendorfer and Hamann 1965; Niklfeld 2021). The grid cells have an extension of 5’ of longitude and 3’ of latitude and are called MTB quadrants (from “Messtischblatt”, the sheet of the German topographic map) with an average area of approximately 36 km^2 in Northern Italy. The grid cells have a fixed longitudinal extension of 5.55 km, while their latitudinal dimension varies depending on longitude. Starting from the comprehensive floristic data collected in these territories at the MTB grid scale, a dedicated effort in research and data validation was focused on the endemic species occurring therein, with the aim to produce the “Atlas of the endemic Flora in Northern Italy” (Bertolli et al. 2024). This method avoids focusing on specific taxa or areas of presumed interest, thereby enabling a general and unbiased estimation of biodiversity within each surveyed territory (Scoppola and Blasi 2005). For the purpose of this study, all 3,612 grid cells that intersect, at least partially, the Northern Italian territory were considered (Fig. 1). We compiled a dataset of 32,939 records from herbarium, literature or field observations sources; all records were georeferenced at the grid-cell resolution.

The oldest data refer to bibliographic records or herbarium specimens dating back to 1750. The field data have been collected from 1990 onwards. A bar chart, reporting the number of data collected before 1990 and from 1990 onwards is reported in Supplementary materials (Fig. S1). These data are considered sufficiently robust and accurate, as data collection for the various mapping projects was carried out in strict compliance with grid boundaries and specifically aimed to record species that were still missing in the individual cells.

Inventory of the taxa evaluated

In accordance with the interpretation adopted by Bertolli et al. (2024), this study considers all the taxa endemics of the study area (i.e., Alps, the Northern Apennines, and the Po plain) and those species not restricted only to the study area range but with a limited distribution outside the selected border. The geographic frame used in this study corresponds to the delimitation proposed by Bertolli et al. (2024) for Northern Italy (Alps, Northern Apennines, and Po Plain/Veneto–Friulian lowlands), and is adopted here without modifications. Therefore, taxa are included even if their range partially extends beyond Northern Italy into surrounding countries or regions. Taxa with very limited populations ($<10\%$ of their range) occurring outside the boundary of the Alpine chain or the Northern Apennines were also taken into account (southern limit at Bocca Serriola). For the species whose range extends beyond the borders of Northern Italy, only the portion of the range within Northern Italy was considered in this analysis. The study also includes taxa that inhabit the Po valley and Veneto-Friuli plains and hilly areas within Northern Italy, such as the karstic region, thus encompassing not only strictly montane but also lowland species. The taxa, mostly apomictic, belonging to the genera *Alchemilla, Hieracium, Pilosella, Rubus* and *Taraxacum*, as well as the *Ranunculus auricomus* L. group, were excluded.

A more detailed discussion of the criteria for the inclusion and exclusion in the list of considered taxa is provided in Bertolli et al. (2024). The inventory of the taxa evaluated is available in Supplementals (Table S1). Nomenclature and taxonomy follow Bartolucci et al. (2024).

Ecological traits

Species biological life form (sensu Raunkiaer 1934), the habitat optimum and the Landolt's ecological indicator values (light, nutrients, pH, temperature and soil moisture with the exception of soil salinity and climatic continentality indicators) were derived from Landolt et al. (2010). Focusing on the ecological preferences of the species, nine simplified habitat types were considered, namely coastal environments, rocky habitats, forests and hedgerows, shrublands, subalpine areas, streambeds and screes, primary grasslands, secondary grasslands, snowbed communities, and wetlands. Each taxon was then assigned to one of these categories based on the primary ecological preference reported in the species accounts by Bertolli et al. (2024). For each grid cell, the mean indicator value was calculated across all endemic taxa present (i.e., when the alpha diversity (α-diversity) was > 2), allowing for the identification of spatial patterns in ecological conditions across the study area. For missing values concerning species that do not appear in the reference used, a panel of experts assigned values based on their experience (see Table S2).

Statistical analyses

All maps and geospatial analyses were realized using open-source software tools, including QGIS (QGIS Development Team 2025), PostgreSQL 15, and its management interface pgAdmin 4.

All variables were first compiled and processed in Microsoft Excel to generate a dataset of endemic plant species including their life-form classification, habitat preferences, and Landolt indicator values. These variables (including α-diversity) were then aggregated at the level of individual grid cells. Subsequent analyses and visualizations were carried out in R (R Core Team 2024). Pie charts were produced using ggplot2 (Wickham 2016) to summarize the relative proportions of family, life forms, habitat types, and ecological indicator values across grid cells. In addition, violin plots were generated to illustrate the distribution of these variables (expressed as percentages) within each grid cell.

Results

This study considers 447 endemic taxa grouped into 44 families (Table S1). The most represented families were Asteraceae, Brassicaceae, Caryophyllaceae, Poaceae, Primulaceae, and Campanulaceae, which together accounted for 50% of the total endemic species (Fig. 2). At the genus level, the highest number of endemic taxa were found in *Festuca, Saxifraga, Phyteuma, Pedicularis, Carduus, Laserpitium, Erysimum, Achillea* and *Gentiana* with at least 2.5% (Fig. S2). The families and genera hosting a high number of endemic taxa highlighted here largely coincide with those identified across the entire Alpine arc by Aeschimann et al. (2011b).

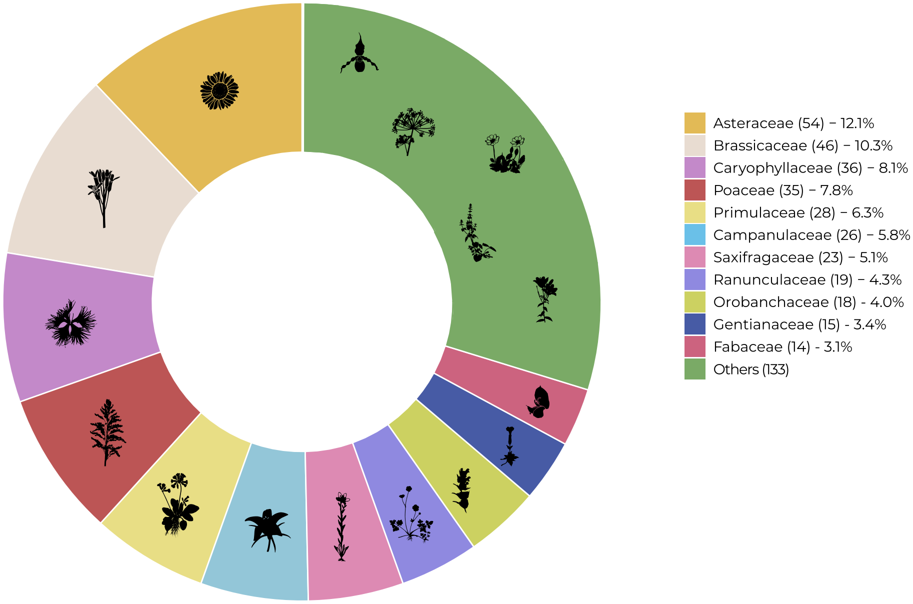

Fig.2 Doughnut chart of families showing both the absolute numbers and the percentage share of the most common families

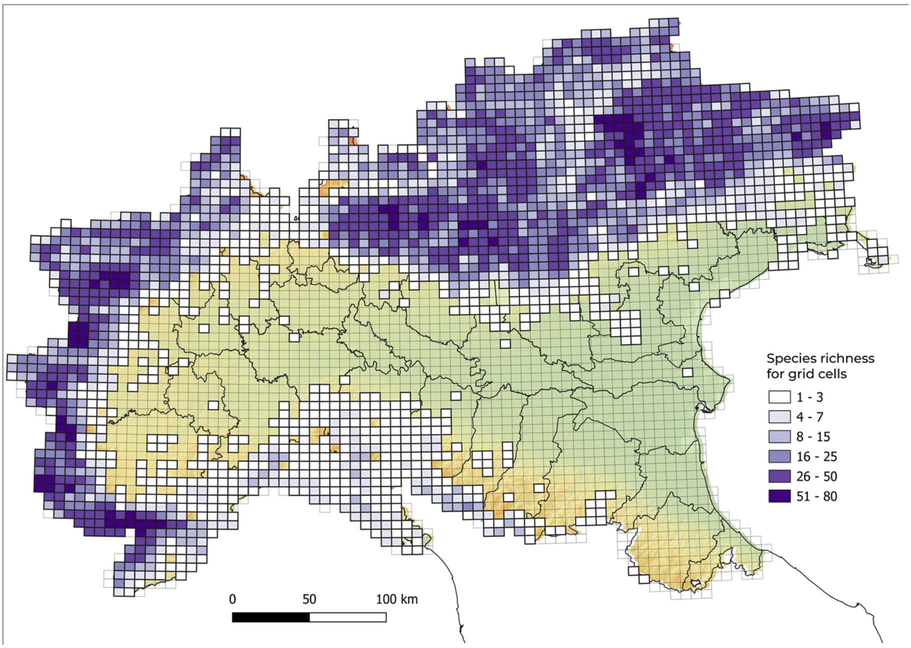

Fig. 3 Spatial distribution of the endemic species richness

Figure 3 shows the species richness across the considered grid cells, expressed as the total number of endemic taxa, based on all types of data (literature, herbarium, and field records), excluding casual or naturalized introduced occurrences. The mean number of species per grid cell was 9.1 ± 13.8 (SD).

The grid cells with the highest number of endemic species were located in the Western Alps, corresponding to important portions of the Ligurian and Maritime Alps and Nice Prealps, with a peak of 80 taxa per grid cell in the Monte Saccarello range, as well as the Cottian Alps, and Graian Alps. In the Eastern Alps important hotspots occur in the Orobic Alps and Prealps, Southern Rhaetian Alps, Brescia and Garda Lake Prealps, Dolomites, and Julian Alps and Prealps. In the Eastern Alps the Presolana-Arera group stands out with 70 endemic taxa per grid cell. The lowlands showed no or a very low and fragmented endemic species richness.

The most frequent species were *Phyteuma betonicifolium* Vill. (1135 grid cells) and *Cirsium spinosissimum* (L.) Scop. (825 grid cells) while singletons were 16 species amongst which we report as an example *Centaurea kartschiana* Scop. subsp. *kartschiana* (1) and *Epipactis zaupolensis* (Barbaro & Kreutz) Bongiorni, De Vivo & Fori (1). The complete frequency is reported in Table S1.

In terms of the biological spectrum the endemic flora of Northern Italy is characterized by a dominance of hemicryptophytes (H), (> 65.0%), followed by chamaephytes (Ch = 21.5%) and geophytes (G = 8.3%), while the frequency sum of the life forms with lower frequencies, namely nanophanerophytes (NP), phanerophytes (P), therophytes (T), and hydrophytes (I), amount to approximately 5% (Fig. 4a). Also reported is the distribution of the value for the 3 main life forms (i.e., H, Ch, and G) within the grid cells (Fig. 4b). In line with the overall endemic flora, it was found that H was the most common life form in all cells, with an average value of 67.0%, followed by Ch and G with averages of 14.1% and 14.7%, respectively. Hemicryptophytes are the primary contributors to the endemic flora of the Central and Western Alps while their percentage was relatively low in the Apennine range and in the Eastern Alps (Fig. 4c). The proportion of Ch was high in the eastern areas, while G species had two distribution hotspots, one in the Apennines and Ligurian mountains and one in the Insubric region (Figs. 4d-e).

Most of the endemic flora finds an optimal habitat in open primary habitats (Fig. 5a). In fact, cliff and rocky environments, primary grasslands, gravel beds, and screes account for 75.9%. Forests and woody habitats (woodland and hedgerows) as well as secondary grasslands were also important. The most common habitats in all cells were cliffs and rocky environments, with an average species proportion per grid cell of 27.2%, followed by primary grasslands and gravel beds and scree slopes, with averages of 23.2% and 12.4%, respectively (Fig. 5b).

Species of cliff and rocky environments were most represented in the Prealps and foothills across the whole alpine range (Fig. 5c), whereas species of primary grasslands were concentrated mainly in the inner range of the central Alps (Fig. 5d). The Eastern Alps were mainly characterized by endemic species found in gravel beds and screes (Fig. 5e).

The results illustrated in maps (Fig. 6 a-e), each representing one of the five Landolt ecological gradients, clearly show the heterogeneity of the endemic flora of Northern Italy. The mean value of Landolt's light indicator values was 3.77 (± 1.26), for the reaction 2.92 (± 1.34), for the temperature 2.40 (± 1.23), for the moisture 2.05 (± 0.87), and for the nutrients 1.89 (± 0.71).

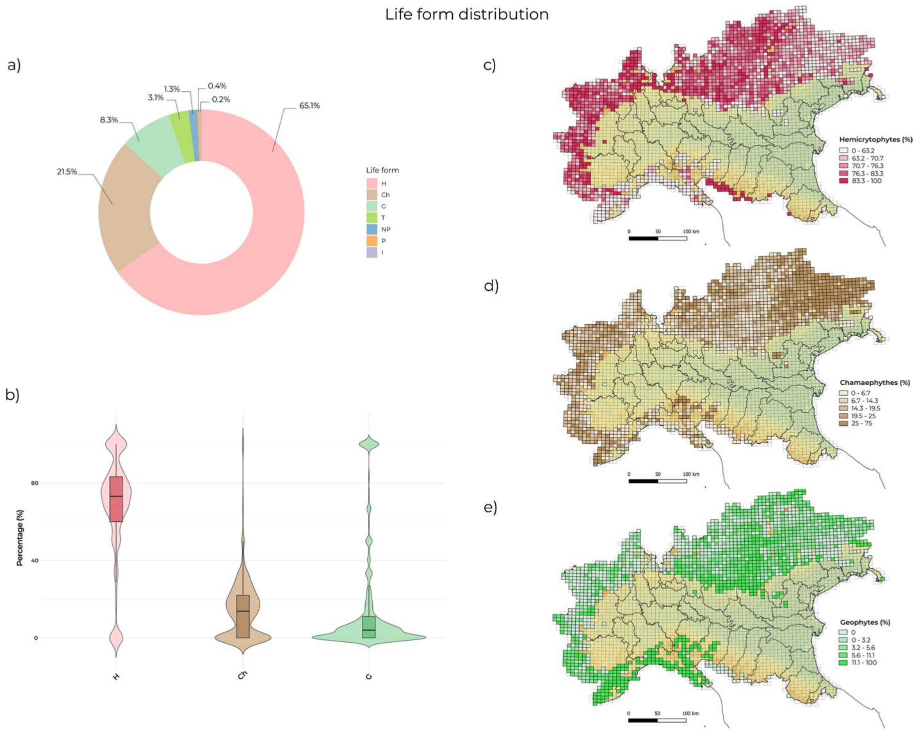

Fig.4 **a**) Doughnut chart of the biological life form spectrum with percentage values. Hemicryptophytes (H), chamaephytes (Ch), geophytes (G), therophytes (T), nanophanerophytes (NP), phanerophytes (P), hydrophytes (I). **b**) Violin plot of the most represented life forms' distribution across the grid cells (H, Ch, G). **c**), **d**), **e**) Maps of life forms distribution pattern across the study area are also shown

Discussion

The Alps are well recognized as a hotspot of vascular flora diversity (Myers et al. 2000; Sabatini et al. 2022). This work aims at enforcing the knowledge on the distribution pattern and characterization of the endemic flora of Northern Italy. In particular, the results provide valuable insights into the spatial patterns of species richness, life forms, habitat preferences, and ecological characteristics of endemic plant taxa in Northern Italy. These findings will have important implications for better understanding regional plant diversity and guiding conservation priorities.

The pattern of species richness revealed the occurrence of distinct hotspots of endemism in the Alpine region, particularly in the Ligurian and Maritime Alps (Western Alps), including Mount Saccarello, in the Bergamasque Prealps (Central Alps), with Mount Presolana, and in the Eastern Alps, encompassing the Dolomites and the Julian Prealps. Moreover, the peaks of endemic species richness (80 species) recorded in the MTB grid cells of our study area (80 species) were approximately three times higher than the maxima reported in previous surveys conducted north of the Alps, where no more than 25 endemic vascular plant species were recorded per equivalent spatial unit (Essl et al. 2009). In the south-eastern Alpine sector, particularly along the foothills, endemic species are often confined to specific geomorphological contexts such as major river valleys, where

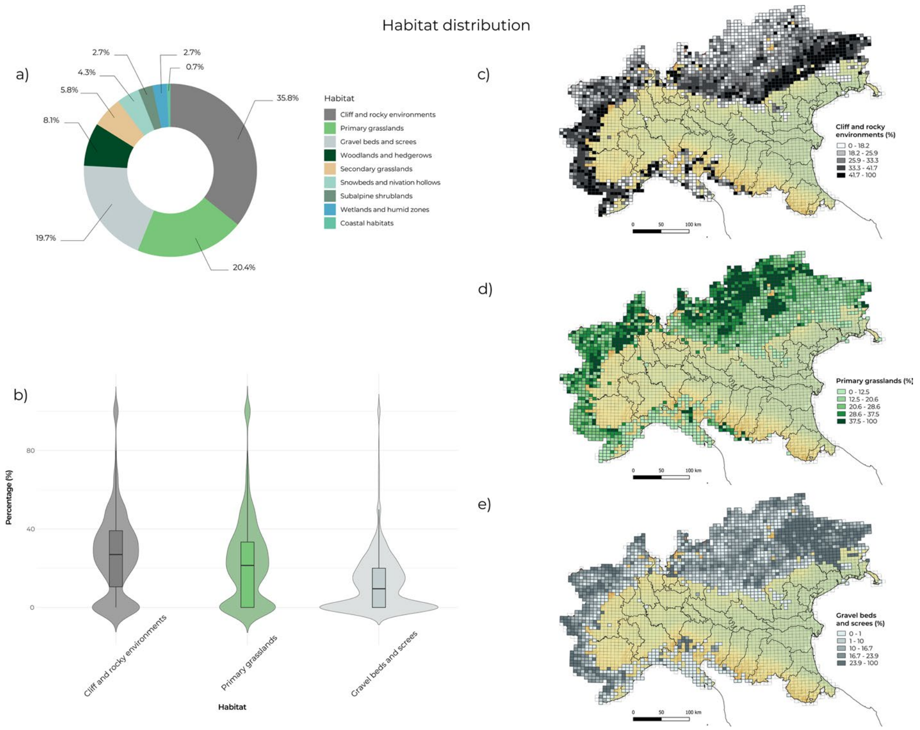

Fig.5 **a**) Doughnut chart of the habitat spectrum with percentage values. **b**) Violin plot of the most represented habitat (cliff and rocky environments, primary grasslands and gravel beds and screes). Map of percentage distribution along the grid cells of the most represented biological life forms in cliff and rocky environments (**c**), primary grasslands (**d**) and gravel beds and screes (**e**) respectively

conglomerate cliffs and rocky outcrops offer suitable refugia for taxa whose main distribution lies in the northern and eastern Alps, reflecting more recent, high-elevation centers of endemism associated with post-glacial isolation processes (Smyčka et al. 2017). In the south-western Alps (Maritime–Ligurian Alps), where numerous range-restricted taxa occur within a complex mosaic of calcareous and ophiolitic substrates, the area stands out as a major refugial hotspot for more ancient endemic taxa (Casazza et al. 2016; Harrison & Noss 2017). The Po plain harbors only a few narrowly distributed steno-endemics, restricted to extra- or azonal habitats such as, clean running water, halophilous grasslands, fens, and relict dry grasslands. In the Northern Apennines, the interplay between calcareous, serpentinite and siliceous, combined with marked topographic heterogeneity, sustains localized endemism. These areas, previously identified as endemism hotspots, likely represent historical refugia and centers of diversification (Schönswetter et al. 2005; Tordoni et al. 2020), consistent with previous studies that identified them as areas of high floristic uniqueness and ecological heterogeneity (Scheepens et al. 2015; Schönswetter et al. 2005; Smyčka et al. 2017).

The large differences in endemic species richness between the northern and southern part of Eastern Alps are not solely the result of the distribution of refugia, since glacial refugia also existed in the northern Alps, but rather of the divergent climatic histories across the range. These climatic differences influenced the spatial structure and extent of refugia,

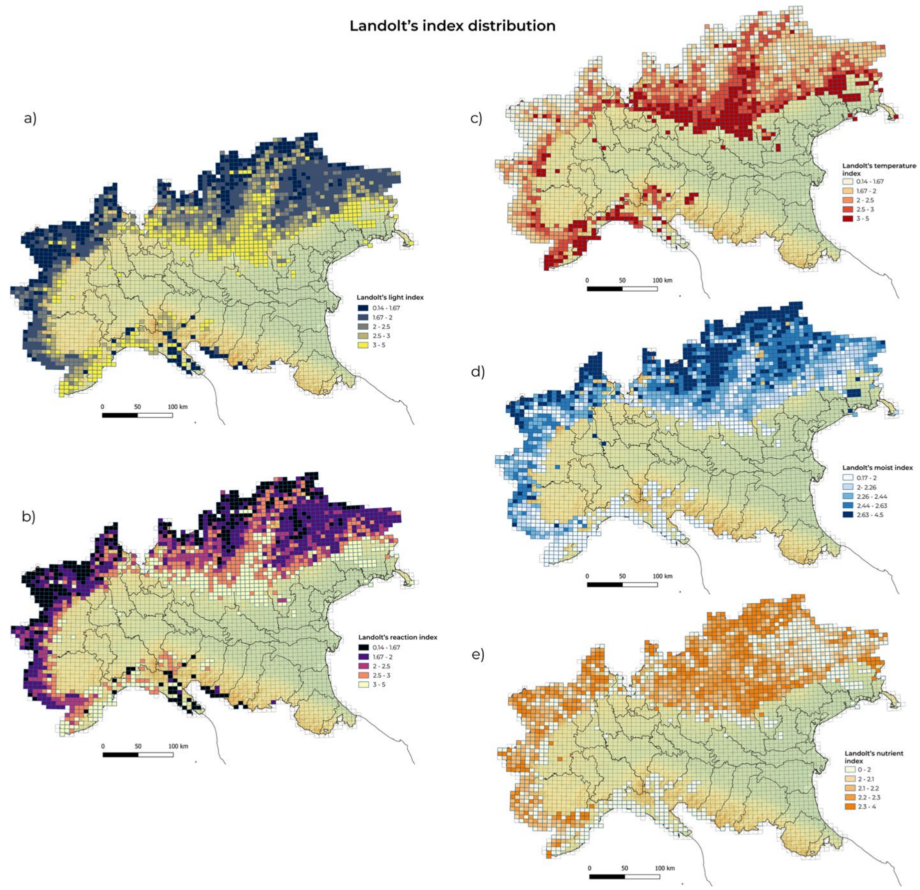

Fig. 6 Map showing the percentage distribution of the mean indicator values for the most relevant ecological variables according to Landolt in the grid cells: light (**a**), soil reaction/pH (**b**), temperature (**c**), moisture (**d**), and nutrients (**e**)

the duration of isolation of refugial populations, and the selective conditions within them (Kadereit 2024).

Analyses of the distribution of life forms have revealed some interesting patterns. The dominance of hemicryptophytes (H, over 65%) aligns with expectations for high-altitude and temperate environments already observed for the overall flora (Di Musciano et al. 2021), where perennial herbs with buds close to the soil surface are well adapted to cold and seasonal climates (Lubbe et al. 2021). In fact, the dominance of hemicryptophyte endemic flora likely reflects their morphological and physiological adaptations to the harsh climatic conditions and disturbance regimes (e.g., grazing), combined with their broad tolerance to temperature and moisture variability, which allows them to persist and diversify across a wide range of microhabitats (Amich et al. 2004; Vashistha et al. 2011). The high percentage of chamaephytes and geophytes further reflects the adaptation of these life forms to rocky, grassland, and alpine environments (Schnablová et al. 2024). These assumptions are consistent with the spatial distribution pattern of H and Ch, with the percentage being higher in the western and eastern Alps, respectively. This trend can apparently be explained by the distribution of the habitat preferences of the plants, which is related to the significant differences in the geomorphological characteristics of the two Alpine regions. In fact, the high occurrence of chamaephytes follows the distribution pattern of cliffs and rocky environments as well as gravel and river beds, as has already been studied (Maria & Anna 2017; Reczyńska & Świerkosz 2024). Chamaephytes appear to dominate in carbonate-rich regions where limestone and dolomite substrates generate steep slopes, high drainage, and nutrient-poor soils (Frisch et al. 2000). Instead, hemicryptophytes and geophytes align with the primary grassland habitats distribution, where they contribute significantly to the vegetation structure and biodiversity (Brullo et al. 2020), often related to high elevation ranges in the central and western Alps.

To confirm, the optimal habitats for most of the endemic plants considered are cliffs and rocky environments, primary grasslands, gravel beds, and scree slopes. Although the median values of the grid cell are relatively similar among the three habitats, the spatial distribution differs notably.

Other studies showed that most of the ice-free nunatak areas of the Eastern Alps were located on exposed ridges and southern slopes (Schönswetter et al. 2002). Our analyses suggest that endemic species richness on slopes may derive from the legacy of ancient refugia, coupled with the ecological preferences of certain groups, particularly those confined to open habitats. At the landscape scale, rocky outcrops and alpine grasslands emerged as key environments for endemics, which is consistent with previous findings (Essl et al. 2009; Hobohm 2014). Due to the complex alpine topography, these habitats occur in a discontinuous pattern, and this spatial heterogeneity, intensified during successive glacial and interglacial phases, likely contributed to the long-term persistence and diversification of endemic taxa (Hobohm 2014; Smyčka et al. 2017; Vetaas & Grytnes 2002).

In particular, our maps suggest that species associated with screes and rocky habitats show an extra-alpine distribution, with a tendency towards the south-eastern sectors, possibly in line with the pattern observed for chamaephytes. By contrast, the endo-alpine (inner Alpine) sector appears to host mainly species of primary grasslands, typically occurring at higher elevations. This differentiation highlights how open habitats are geographically structured across the Alps. Moreover, the Eastern Alps are geologically young, highly dynamic, and strongly affected by fluvial and glacial processes, resulting in widespread screes and extensive gravel deposits (Frisch et al. 2000). This geomorphological context may help explain why species associated with rocky debris and unstable substrates show an extra-alpine distribution, particularly towards the south-eastern sectors. Such habitats appear to support only moderately diverse sets of endemic species, while gravel beds and screes show a more constrained pattern, with most taxa exhibiting relatively low percentages of occurrence, likely reflecting harsher or more unstable environmental conditions that allow only a few specialized taxa to survive (Panitsa et al. 2021).

Different habitat preferences are usually also associated with different ecological needs, which is evident from the spatial distribution of the Landolt indicator values. Notably, a strong correlation emerges between the light and temperature indices. This suggests that plant species demanding high light levels are also associated with warmer conditions, likely reflecting a preference for open, sun-exposed habitats at lower altitudes (Körner 2007; Scherrer & Körner 2011).

In contrast, the temperature and moisture indices display largely opposite spatial patterns. Areas with higher moisture values, particularly in the northwestern and central Alpine regions, correspond to lower temperature values. This is consistent with the general altitudinal gradient and the orographic precipitation patterns in the Alps (Körner 2007; Scherrer & Körner 2011; Wastl & Zängl 2008). Interestingly, a localized decline in the moisture index was observed in the Friuli, Belluno and Trentino areas, which coincides with carbonate (limestone and dolomite) outcrops (Wang et al. 2016). These substrates are highly permeable, resulting in rapid drainage (Lawless et al. 2006), and creating a steeper and rougher environment, which reduces water retention in the soil and nutrient availability (Larson et al. 2000; Mota et al. 2021). This interpretation is supported by the reaction index map, which shows more basic (alkaline) values in the same areas, consistent with the underlying dolomitic and, in general, carbonate rocks.

Indeed, when cross-referenced with geological maps of the Alps (Oxburgh 1968; Pfiffner 2014), this suggests that plant species closely follow pH gradients dictated by the bedrock composition, with more calcicolous species occurring over alkaline substrates.

Furthermore, it seems that the spatial distribution of habitats with high moisture values tend to be associated with primary grassland species, at least up to certain elevations (Acosta et al. 2008). Beyond that threshold, other ecological filters are likely to dominate (i.e., slope and temperature), possibly due to a shift toward more discontinuous scree habitats or other alpine terrain types (Kaňa et al. 2023; Liang et al. 2025).

Beyond the general spatial trends, an interesting aspect emerging from the maps is the fine-scale environmental heterogeneity, which is particularly evident in the moisture and nutrient indices. These maps reveal sharp variations in indicator values even between neighboring grid cells, suggesting the presence of localized environmental discontinuities or microhabitat variation (Espinosa del Alba et al. 2025). Such heterogeneity may arise from small-scale differences in topography, bedrock composition, past climate or recent climatic trends, or land use history, and highlights the complexity of Alpine landscapes (Kulonen et al. 2018; Pistón et al. 2018). This patchiness can have important ecological implications, as it may support a high diversity of plant species with varying ecological requirements within relatively short distances.

Accounting for this spatial variability is crucial for understanding species distributions and for guiding conservation strategies, especially in topographically and geologically complex regions like the Alps.

Conclusion

The endemic flora of Northern Italy reflects the complex interplay between long-term geological stability, substrate heterogeneity, and contrasting postglacial histories across the Alpine arc and the Northern Apennines.

Our results showed that the endemic flora in Northern Italy is not randomly distributed, but exhibits specific patterns: at the regional scale these are probably linked to biogeographical constraints, while at the local scale they are likely related to ecological gradients, particularly to those associated with pH, moisture, nutrient availability, and temperature, largely driven by bedrock geology and altitudinal variation.

We observed that carbonate outcrops and alkaline soils, as found in the Dolomites and parts of Friuli and Trentino, tend to host particular assemblages of endemic species. Moreover, small-scale environmental heterogeneity, especially in relation to moisture and nutrient availability, appears to foster localized biodiversity patterns and reflects the ecological complexity of the Alpine landscape. These observations suggest that geodiversity plays a role in shaping biodiversity and that the conservation of diverse geological substrates and habitat types may help sustain endemic species richness.

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Declarations

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