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Grassland Changes in the Eastern Alps Over Four Decades: Unveiling Patterns Along an Elevation Gradient

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ABSTRACT

Aims: Alpine valleys have faced escalating global changes in recent decades such as a decline of traditional management and rural expansion. Grasslands are likely the type of vegetation most affected by these transformations. This study investigates the multifaceted changes in plant diversity over the past four decades in a major valley of the Italian Eastern Alps and examines whether changes occurred uniformly across different elevations.

Location: Valsugana Valley, Eastern Alps, Italy.

Methods: In 2022, we resurveyed 115 vegetation plots (including vascular plants, mosses, and lichens) originally sampled in 1986–1988. Plots were collected in grasslands and span along an elevation gradient of 2000 m. At each time period, we automatically classified these plots using the EUNIS expert system of habitats. We analysed the variation over time in species richness, species diversity, beta diversity (turnover and nestedness), and relative proportion of life form, woodiness, and neophyte species along an elevation gradient, subdivided in low-, middle-, and high-elevation belts. Lastly, we quantified the number of gained, winning, stable, losing, and lost species.

Results: We found differences in the classification of EUNIS habitats and elevation-dependent changes in community diversity and composition. Many grassland types were transformed into other grassland types or into forests and man-made habitats. Species richness varied along the elevation gradient over time, being constant at lower elevations but markedly increasing at high elevations. Temporal turnover dominated across elevations, especially at lower sites, while nestedness components increased towards high elevations. Neophytes increased and hemicryptophytes decreased in the low-elevation belt, while therophytes and geophytes increased at low- and high-elevation belts. In the middle-elevation belt, many dry grassland species were replaced by nitrophilous and woody species. High-elevation witnessed species replacement with the loss of mountain species and the increase of therophyte and geophyte species.

Conclusions: Grasslands of Valsugana valley have undergone substantial changes over four decades. Different processes likely acted across the elevation gradient. Nonetheless the driver, impoverishment of semi-natural grassland species was observed over time across elevations. Understanding these changes in vegetation is essential for a comprehensive evaluation of ecological variations over time. Conservation management strategies should be tailored to address biodiversity changes at varying elevations to counteract the negative trends of plant diversity loss and the ongoing habitat transformation of grasslands in the Alps.

1 | Introduction

Global change of the last decades altered the structure of the landscape in many mountain areas of Europe. Low-elevation areas are more at risk than higher ones, due to the dramatic environmental consequences of land-use change (Hilpold et al. 2018). Bottom valleys have seen an intensification of agriculture and an expansion of urban settlements over formerly natural areas (Kindermann et al. 2024). Low-elevation natural areas support a high concentration of rare habitats and plant species, typical of previously extensively managed areas, meadows, humid areas and wetlands, and are also more vulnerable to neophyte invasion (Chytrý et al. 2005). Middle and high-mountain ecosystems are also experiencing a dramatic shift in grazing management, with extensive regimes gradually being replaced by more intensive ones, where grazers are concentrated in smaller areas (MacDonald et al. 2000). These changes led to two contrasting effects on vegetation: abandonment of land use triggered processes of natural recolonisation with the expansion of forests and shrublands (Tasser et al. 2007; Orlandi et al. 2016; Ferrara et al. 2021); and intensification of land use, including fertilisation and increasing stocking rates, led to a drop in plant diversity (Dengler et al. 2014). Despite these widespread phenomena in the Alps and other mountain ranges across Europe, environmental change studies in mountain ecosystems have largely focused on high elevations, neglecting a large part of the ecological transformations in progress at lower elevations (Pauli et al. 2012; Steinbauer et al. 2018). As different environmental changes may occur along the whole bottom valley-summit gradient (Bricca et al. 2022), monitoring vegetation is crucial to detect the temporal trajectory of plant communities across elevation.

Understanding how vegetation responds to environmental changes over time poses significant challenges (Staude, Weigelt, and Wirth 2023). A crucial aspect involves comprehending how shifts in environmental conditions affect the processes governing vegetation dynamics. Typically, studies on vegetation dynamics rely on indirect observations, where comparisons are made among sites simultaneously along ecological gradients (referred to as 'space-for-time substitution' or chronosequences; Laliberté et al. 2010). This approach extrapolates from spatially distinct sites that are assumed to represent various stages of temporal succession (Pickett 1989). While useful, chronosequences alone do not allow making accurate predictions of vegetation changes under novel environmental conditions (Sternberg et al. 2011). Long-term monitoring of vegetation, when available, provides a better alternative for assessing biodiversity changes (Schmidt 1988; Al Hajj et al. 2024), investigating underlying causes, and evaluating the conservation status of specific habitats (Finderup Nielsen et al. 2019; Klinkovská et al. 2023). Currently, in Europe, about 55 thousands of permanent vegetation plots are in place (Knollová et al. 2024). In the absence of long-term vegetation monitoring schemes, re-visitation of historical phytosociological plots has been suggested to be the best approach to assess vegetation changes (Chytrý et al. 2014; Hédl et al. 2017).

Several re-visitation studies in mountain ecosystems have found differences in plant diversity over time (Dullinger et al. 2003; Evangelista et al. 2016; Gillet et al. 2016; Giarrizzo et al. 2017). However, such long-term analyses of biodiversity data have often reported a 'biodiversity conservation paradox', meaning that biological communities show substantial species composition change accompanied by little changes in species richness (Jandt et al. 2022).

Here, we revisited 115 historical phytosociological grassland plots four decades after the first survey to monitor vegetation and flora variations in a major valley of the Alpine Arch (Valsugana Valley, Eastern Alps, Italy), representative of many other Alpine valleys. Using vascular plant, moss, and lichen data collected in a resurvey carried out by the original surveyor, we aimed to assess how vegetation changed over time along a 2000 m elevation gradient. Specifically, we asked (1) how has species diversity changed? (2) how has the species composition changed? (3) how has the relative proportion of life forms, woody species, and neophytes changed? and (4) are these variations different at different elevations?

2 | Materials and Methods

2.1 | Study Area

The Valsugana Valley is in the Trentino-Alto Adige region of northern Italy. It is positioned in the eastern segment of the Autonomous Province of Trento. This east–west-oriented valley is bounded by the Lagorai mountain range to the north and the Vicentine Alps to the south, with the Brenta River coursing through its expanse. The geological diversity of the region hosts the presence of Meso-Cenozoic limestones, Pre-Permian and Permian siliceous rocks, crystalline basement and effusive volcanic rocks.

Throughout the area, granitoids, conglomerates, and Quaternary deposits are scattered. The valley, spanning elevations from 430 (Borgo Valsugana) to 2408 (Mount Gronlait) m a.s.l., is characterised by a mesalpic climate. The mean annual temperature for the period 1980–2018 ranges from

1.2°C to 11.7°C, for higher and lower elevations, respectively. Precipitation exhibits two peaks, one in spring and another in autumn, along with two minima, one in summer and a more pronounced one in winter. Mean annual precipitation varies between 998 and 1197 mm, with higher-elevation sites experiencing greater precipitation and lower temperature values (Crespi et al. 2021).

The study area experienced strong environmental changes over the last 35 years, with differences along the elevation gradient (Figure 1). At lower elevations (bottom valley), semi-natural grasslands decreased at the expense of new vineyards, small fruit plantations (e.g., *Vaccinium corymbosum*), expansion of apple orchards, and rural settlements. In middle- and high-elevation belts, pastures were originally used mainly by transhumant flocks of sheep. Between the 1980s and 1990s, there was a marked abandonment of mountain pastures. This trend was reversed in the 1990s: in 1993, in the whole Trentino region, there were 221 mountain pastures grazed. Between 1999 and 2004, the number of alpine pastures increased from 283 to 321. The number of sheep has increased from 16,100 in 1995 to 46,688 in 2021 (ISPAT, APSS 2022). For a long time, sheep have inhabited the mountain ridges in the area, although in the past they were kept in small groups. They were released by small private farmers at the beginning of the season and retrieved at the end of the season. Today, also because of the return of the wolf in the area (Davoli et al. 2022), this traditional type of grazing has disappeared and has been replaced by large, guarded flocks, which have led to the transformation of the sward.

2.2 | Original Sampling

In 1986, 1987, and 1988, 134 vegetation plots were sampled to have a vegetation and cartographic representation of grasslands present in the Valsugana Valley (Prosser 1988; Appendix S1). These plots were conducted in grasslands, including both meadows and pastures, and a few plots of shrub communities, ranging in size from 50 to 100 m^2 depending on the community. Location of the plots was selected based on opportunistic phytosociological criteria but taking into account the whole elevation gradient of Valsugana Valley, meaning from the bottom valley to the mountaintop. Original data include vascular plants, mosses, and lichens. Data were collected by recording plant cover values using the percentage scale and related vegetation layer (tree, shrub, herb, juvenile, moss, and lichen layers).

2.3 | Resurvey

We aimed to resurvey the original plots of Valsugana Valley grassland vegetation along the entire elevation gradient. As in all temporal studies, we needed to 44deal with three common

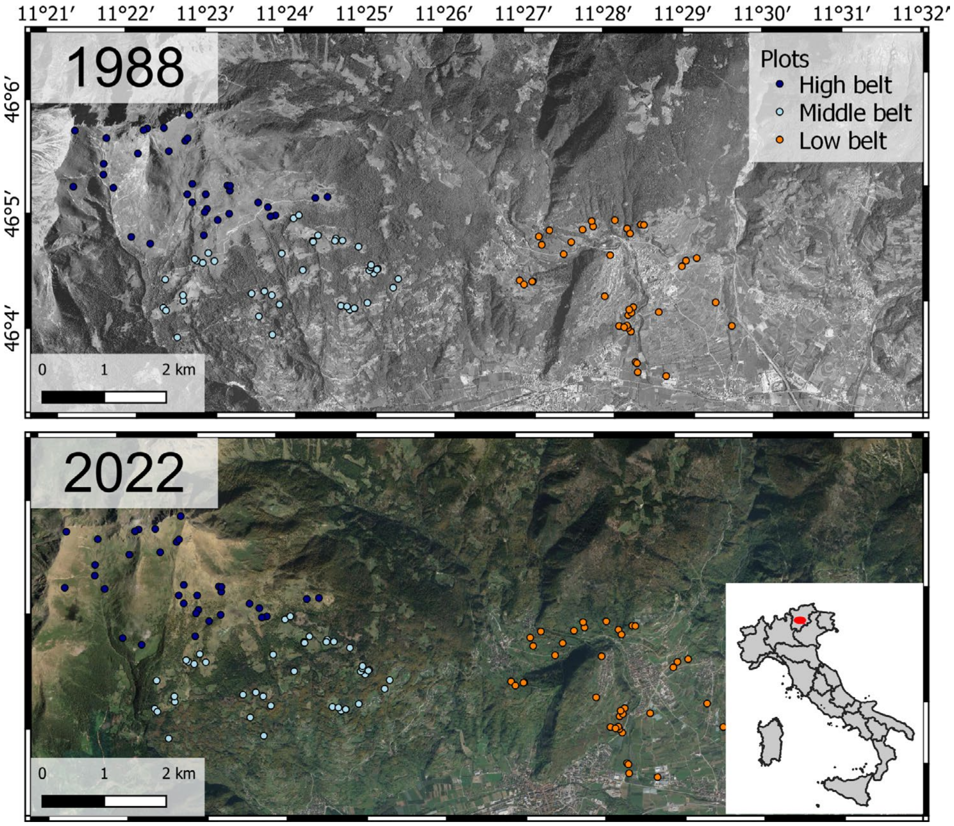

FIGURE 1 | Multitemporal orthophotos of the study area for the period 1988–2022 including 115 vegetation plots. Note the increase in rural settlements for the year 2022. The inset map shows the location of the study area inside Italy. Map data from: 1988—Ministero dell'Ambiente e della Sicurezza Energetica—Geoportale Nazionale https://gn.mase.gov.it/portale/en/consultation-service-wms; 2022—Google, CNES/Airbus Maxar Technologies Google Earth.

problems: plot relocation, observer bias, and seasonality bias (Kapfer et al. 2017). To reduce their effect and improve data quality, we adopted a series of precautions.

To make a preliminary assessment of the plots in the past, we prepared and photo-interpreted orthophotos from 1988, 1997, 2000, 2006, 2012, and 2015 for each plot. The dataset of the orthophotos is available in Appendix S2. This step allowed us to visually assess the changes and determine the feasibility of the resurvey. Our strategy to relocate our plots encompassed the use of high-quality original sketches made by the original surveyor who conducted the first sampling (i.e., Filippo Prosser, hereafter 'original surveyor') and a map (1:10,000) present in Prosser (1988). These sketches contained elements to relocate the plots almost precisely, including the cardinal direction from a plot corner. Elements used were rocks, trees in the grassland, stone walls, or any other detail in the landscape that could help the relocalisation. We estimated the relocation error of vegetation plots to vary between 0 m, when the references on the ground were completely secure, up to 200 m (one case only), when landmarks were missing. More than half of the plots have an estimated relocation error between 10 and 20 m. The estimated discrepancy in the position of historical and resurveyed plots is very limited. Thus, we consider our data as quasi-permanent plots and reliable for further analyses (Kapfer et al. 2017).

To reduce observer bias (Boch et al. 2022), the operator who repeated the survey was the same as in the original sampling. As in the original sampling, the resurveyed plots included the recording of vascular plants, mosses, and lichens in percentage values. The original plot size was consistently maintained in the resurveyed plots to avoid the influence of plot dimension on community composition and diversity. In addition, to ensure comparable vegetation development and minimize seasonal bias, we conducted the survey during the same season as the original.

To summarise, in 2022, we resurveyed 115 grassland plots (50 m^2 $N = 7$; 100 m^2 $N = 108$). These plots cover an elevation gradient in grasslands and are distributed as follows: 38 low-elevation plots (383 min–794 max m a.s.l.; mean 588 m a.s.l.), 43 middle-elevation plots (982–1608 m a.s.l.; 1293 m a.s.l.), and 34 high-elevation plots (1629–2356 m a.s.l.; 1917 m a.s.l.). From here on, we refer to the vegetation-plot record from the initial survey as 'original plots' and as 'resurveyed plots' for the revisited ones.

2.4 | Analyses

Species were treated at the specific taxonomic level or grouped into aggregates (e.g., *Galium mollugo* agg., *Festuca rubra* agg.) following the taxonomic concepts and nomenclature of Ehrendorfer (1973), largely used in the region. We retrieved biological forms from the Italian Flora (Pignatti 2017–2019), while neophyte species of Trentino were obtained from Prosser et al. (2019). Also, we distinguished species into woody and non-woody to calculate the proportion of woodiness. Lastly, we used ecological indicator values (EIVs) adapted for the Italian Flora for vascular plants from Pignatti (2017–2019) and EIVs for mosses and lichens from Ellenberg et al. (2001). To have a better understanding of vegetation processes and according to other recent resurvey studies (Sperandii et al. 2019; Jandt et al. 2022), in the following analyses we considered metrics based on species presence/absence and species cover.

Since in both sampling periods, mosses and lichens were also identified in the plots by the same operator, we included them in the analyses. All data manipulation and statistical analyses were performed with R software v. 4.3.1 (R Core Team 2023).

2.5 | Changes in EUNIS Habitats

To highlight possible changes in habitat classification between the original and resurveyed plots, we used the classification of European habitats of the European Nature Information System (EUNIS) (Chytrý et al. 2020). The application of this tool broadens its use in the context of temporal vegetation studies.

We ran the EUNIS expert system v. 2021-06-01 based on logical formulas (assignment rules) to classify the original and the resurveyed plots using JUICE program v. 7.1 (Tichý 2002). We applied the expert system to both the original and resurveyed data. This approach helped us determine whether the plots were still assigned to the same EUNIS habitat and to the same level of hierarchical habitat classification. We then calculated the number of plots belonging to each habitat type for the two periods of 1986–1988 and 2022. The classification changes for the two periods were visualised using a Sankey diagram.

2.6 | Changes in Ecological indicator Values

Preliminarily, we investigated if the ecological features changed over time in the study area using the EIVs. We calculated the community mean values of each EIV (CM_{EIV}), including mosses and lichens, for the two sampling periods. Aware that using observed EIVs with standard statistical tests can produce false positives due to the link between species attributes (EIVs) and community composition, we integrated the ANOVA model with a permutation procedure named 'column-permutation approach' (Zelený 2018). This permutation tests whether community composition is linked to species attributes (EIVs), revealing if the results of standard tests are false positives or not (Zelený and Schaffers 2012; Zelený 2018). Specifically, we calculated the observed R^2 of the ANOVA model, and 999 expected R^2 after shuffling EIVs across the species before calculating CM_{EIV}. Finally, we compared the observed R^2 with the distribution of 999 expected R^2 values to calculate a new *p*-value expressed as the proportion of the expected R^2 values that are greater than the observed R^2 (Zelený and Schaffers 2012).

Moreover, we investigated whether EIVs changed at different rates along the elevation gradient. For this purpose, we expressed the temporal variation for each plot as the difference of the EIVs between two sampling periods as: $\Delta CM_{EIV} = CM_{EIV}$ of 2022—CM_{EIV} of 1986–1988. Then, we ran a linear model (integrated with 'column-permutation approach') with ΔCM_{EIV} as response variable and elevation included as a quadratic term as predictor. To calculate the CM of EIVs, we used the *cwm* function, while to run ANOVA models we used the *test_cwm* function in the weimea package (Zelený 2020). Linear models were run with the *lm* function in the stats package.

2.7 | Changes in Species Diversity and Composition

We considered species richness and Simpson diversity as indicators of alpha-taxonomic diversity and we tested their variation over time using a *t*-test. Also, since we were interested in the rate of temporal variation along elevation, we calculated the delta (Δ) of species richness and Simpson diversity as the difference between the resurveyed and original values of the paired plot. We run regression analysis with elevation as a predictor. Recognising that plant diversity can change unimodally with elevation, we incorporated a quadratic term for elevation in all models (Rahbek 1995; Bricca et al. 2022). We checked model assumptions (normality, homoscedasticity, and independence of the residuals) by visual inspection of the pattern of residuals.

We then investigated how species composition changed over time using constrained distance-based redundancy analysis (dbRDA; Legendre and Anderson 1999), in which plot identity (i.e., each plot including the old and corresponding new record) was used as a covariate together with the elevation and its interaction with time. For the dbRDA, we used Bray–Curtis distance to calculate the dissimilarity matrix of species composition after applying a square-root transformation to have Euclidean property.

Further, we calculated a temporal beta diversity based on presence/absence species data for each pair of original and resurveyed plots using Jaccard dissimilarity. In addition, to obtain finer details on the beta diversity trend, we partitioned the overall beta diversity values into their turnover and nestedness components (Baselga 2010; Bonari et al. 2021) using the *beta.temp* function in the betapart package (Baselga et al. 2023).

Similarly to the Δ of species richness and Simpson diversity, the temporal beta diversity (total and its two components) was modelled by running a linear quadratic term, when significant. The dbRDA was run using the *capscale* function in the vegan package (Oksanen et al. 2024).

2.8 | Changes in the Proportion of Life Forms, Woodiness, and Neophytes

To indicate the functional composition of plant communities, we calculated the relative proportion of life forms for vascular plants (i.e., therophytes, chamaephytes, hemicryptophytes, geophytes, nanophanerophytes, and phanerophytes; Raunkiær 1934), mosses, woodiness (i.e., proportion of woody species), and neophytes, for each plot for both sampling periods. While woodiness can be an indicator of vegetation successional trends following land abandonment, neophyte species can be informative about the effect of anthropogenic pressure over time (Malavasi et al. 2018; Schwaiger, Lenzer, and Essl 2022; Kindermann et al. 2024).

We tested if woodiness and neophytes increased over time by running a *t*-test. Then, as for other taxonomic indicators, we calculated the delta (Δ) of the relative proportion of life forms, mosses, woodiness, and neophytes for each paired plot. We did not account for the variation in the relative proportion of lichens because there were too few species ($N = 4$).

2.9 | Changes in Species Occurrence and Cover

We relied on the definition of *gained* and *lost* species provided by Kitchel and Pinsky (2023). Gains were identified as species observed in at least one resurvey of the site but not in any original survey of the same site from the preceding sampling period. Thus, *gained* species were also classified as newly recorded species. Lost species were defined as species absent in all the resurveyed plots after being present in at least one original survey from the preceding sampling period. Thus, *lost* species could also be classified as species locally extinct. However, this dichotomy did not consider whether species present in both periods are benefiting from environmental changes over time (Schwaiger, Lenzer, and Essl 2022). Therefore, we also classified species into *winning*, *losing*, and *stable* categories based on whether they increased, decreased, or maintained an equal number of occurrences over time. For each of these classes, we quantified the number and the relative contribution of the total species for the study area and for each elevation belt separately.

Lastly, we investigated if each species increased or decreased its cover over time by running a *t*-test (Harásek, Klinkovská, and Chytrý 2023). These calculations were performed using the *t-test* function in the stat package.

3 | Results

3.1 | Changes in EUNIS Habitats

The results of EUNIS classification of the original and resurveyed plots are shown in Figure 2. For clarity, we report the classification of plots at the first and second hierarchical levels of the EUNIS classification. The table detailing their classification is presented in Appendix S3, Table S1. We observed a partial shift in the proportions of habitats within the study area. Overall, dry grasslands (R1) decreased, with some being replaced by mesic grasslands (R2), forests (T), and, to a lesser extent, by heathlands (S) and wet grasslands (R3). Mesic grasslands (R2) partially experienced a loss of specialist species, as some plots previously classified at the second hierarchical level (R2) were classified to the first hierarchical level R in the resurvey, while others were assigned to different habitats and a higher hierarchical level (e.g., R3, R5, S, V). Approximately half of the wet grasslands remained stable, while the rest transitioned into mesic grasslands (R2) or forests (T). Alpine and subalpine grasslands (R4) largely remained stable, though some plots were converted into mesic grasslands (R2), accompanied by a loss of specialist species (R).

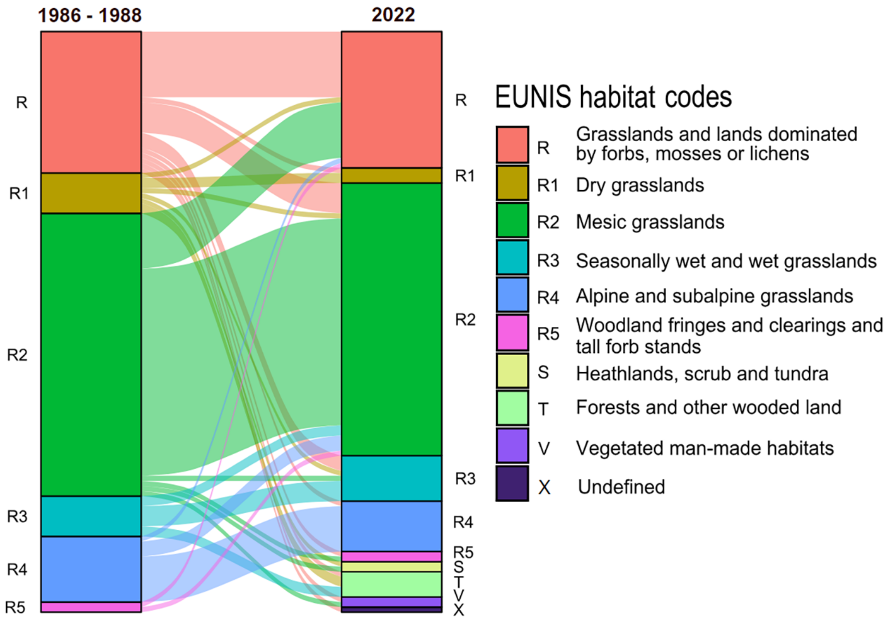

FIGURE 2 | Sankey diagram summarising the changes in the number of plots belonging to EUNIS habitat types for the periods 1986–1988 and 2022. We report the classification of plots at the first and second levels of EUNIS classification illustrating the transition of habitat types over time. The third level, when present, is reported in Appendix S3, Table S1.

3.2 | Changes in Ecological Indicator Values

The analysis of EIVs detected overall changes in ecological conditions between the two sampling periods for light and soil nutrients (Appendix S3, Table S2). Specifically, we found a significant decrease in light-demanding species (from 7.2 ± 0.3 to 7.0 ± 0.4) and a significant increase in eutrophic species (from 4.0 ± 0.9 to 4.5 ± 1.0). Nonetheless, we found no significant variation in the $\Delta \mathrm{CM}_{\mathrm{EIV}}$ along the elevation gradient (Appendix S3, Figure S2).

3.3 | Changes in Species Diversity and Composition

Species richness did not change significantly over time with an average ranging from 46 (original plots) to 45 (resurveyed plots) ($t = 0.86$; $p > 0.05$), while Simpson diversity increased over time from 0.78 (original plots) to 0.83 (resurveyed plots) ($t = 2.6$; $p < 0.05$).

Simpson diversity did not change differently along the elevation gradient over time, in contrast to species richness (Appendix S3, Table S3). Specifically, for species richness, we found unimodal variation with respect to elevation with an increasing trend of species ($\Delta > 0$) at the two ends of the gradient (with a higher rate for high elevations) and constant values for middle elevations (Figure 3a).

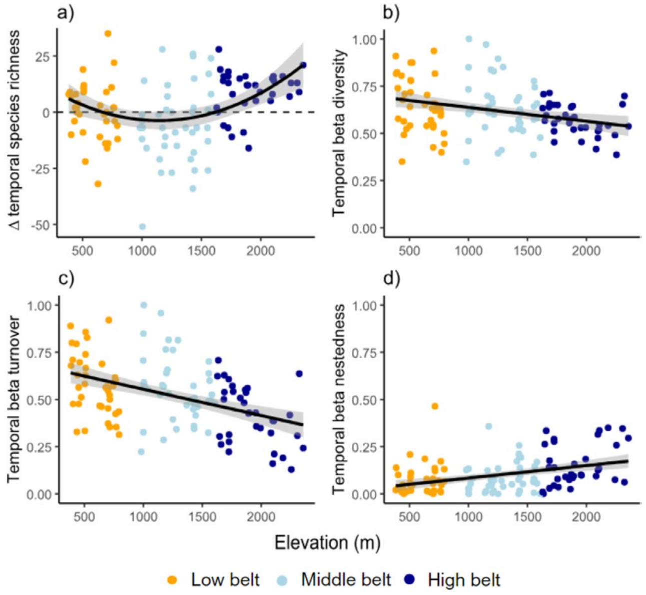

FIGURE 3 | Taxonomic temporal variation of (a) alpha-diversity (expressed as species richness), (b) temporal beta diversity, (c) temporal beta turnover, and (d) temporal beta nestedness along the elevation gradient. Lower/higher values indicate lower/higher compositional changes over time.

Regarding species composition, we found significant changes in beta diversity overall, as indicated by a permutation test on the constrained dbRDA (999 permutations, $F = 4.755$, $p = 0.001$) where time ($F = 2.86$, $p = 0.001$), elevation ($F = 12.79$, $p = 0.001$), their interaction ($F = 1.45$, $p = 0.001$), and plot_ID ($F = 2.69$, $p = 0.001$) had a significant effect (Appendix S3, Figure S3). Also, we found a significant variation of the temporal total beta diversity (based on presence/absence data) and its two components, namely turnover and nestedness. Specifically, we found a significant decrease in total beta diversity in the communities with increasing elevation (Figure 3b). This pattern was mainly driven by the turnover component (Figure 3c). Regarding variation of nestedness, this component increased along elevation (Figure 3d), although it contributed very little to the total beta diversity. Detailed information about models is reported in Appendix S3, Table S4.

3.4 | Changes in the Proportion of Life Forms, Woodiness, and Neophytes

Regarding the analysis of life forms, we found significant temporal changes only for therophytes, geophytes, and hemicryptophytes (Appendix S3, Table S3). Specifically, we found an increase in therophytes over time for plant communities of low elevations (Figure 4a). Geophytes showed a unimodal trend with relative occurrence increasing at low and high elevations (Figure 4b). Hemicryptophytes showed a strong reduction of their occurrence over time in the low and middle elevations, remaining overall constant at high elevations (Figure 4c).

We found a total of 40 woody species for the entire study area considering the first and second sampling periods. Among these 40 woody species, 38 species increased their occurrence over time and only two species decreased their occurrence (Appendix S3, Table S5). Overall, the relative proportion of woodiness increased between the first (0.5%) and second (2.9%) sampling periods for the entire study area according to the *t*-test ($t = 4$, $p < 0.01$; Appendix S3, Figure S4). Particularly, this increase occurred at higher rates in the middle elevation (Figure 4d).

We found a total of 32 neophyte species for the entire study area considering both sampling periods, 27 of which increased in occurrence over time, while five species decreased (Appendix S3, Table S6). Similarly to woodiness, the relative proportion of neophytes increased between the first (0.7%) and second (2.3%) sampling periods for the entire study area according to the *t*-test ($t = 4.4$, $p < 0.01$; Appendix S3, Figure S4). However, in this case, we detected a stronger increase over time for lower elevations, with a decreasing trend along the elevation gradient (Figure 4e).

3.5 | Changes in Species Occurrence and Cover

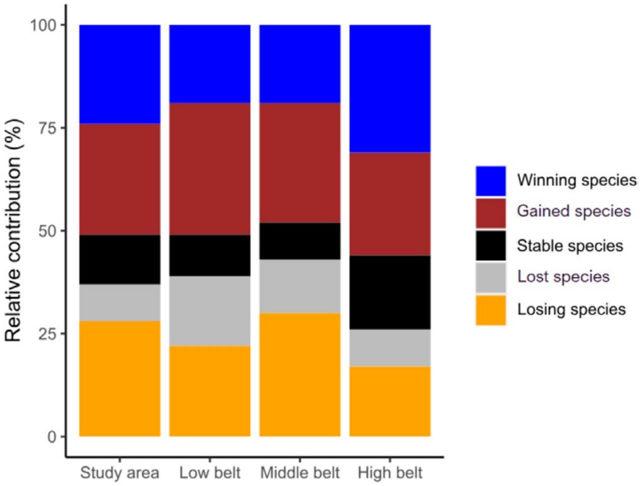

FIGURE 5 | Relative contribution of gained, lost, winning, losing, and stable species for the entire study area and each elevation belt. Gained species were identified as newly recorded species. Lost species were defined as species that are locally extinct. Winning, losing, and stable species were classified based on whether they increased, decreased, or maintained an equal number of occurrences over time.

The relative contribution of gained species to the total number of species decreased consistently along the elevation gradient from 32% (low-elevation belt) to 25% (high-elevation belt; Figure 5). We observed similar trends for lost species, which declined from 17% to 9% along the elevation gradient. Regarding species present in both sampling periods, the high-elevation belt, compared to the other two elevation belts, was characterised by a higher contribution of winning species (i.e., increasing their occurrence; 31%) and stable species (i.e., maintained their occurrence; 18%) but by a lower contribution of losing species (i.e., decreasing their occurrence; 17%). When considering the whole study area, we found a higher contribution of winning species compared to losing ones. Detailed information is reported in Appendix S3, Table S7.

Moreover, we found a significant effect of time on cover for 54 species. Specifically, 17 species increased their cover over time, while 37 species decreased their cover over time (Table 1).

4 | Discussion

In this study, we documented marked plant community changes over time at different rates and trajectories along an elevation gradient of a major valley in the Eastern Alps. Our main finding shows a strong replacement of original vegetation—especially at particular elevations—driven by a notable decrease in species of dry and wet semi-natural grasslands, which were outcompeted by neophytes, woody species, and nitrophilic species.

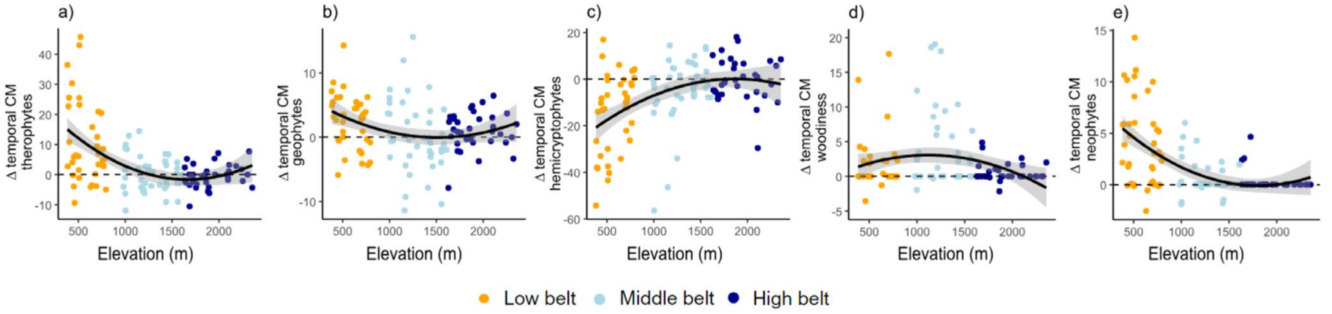

FIGURE 4 | Temporal variation of the relative occurrence (CM) of (a) therophytes, (b) geophytes, (c) hemicryptophytes, d) woodiness, and (e) neophytes along the elevation gradient. Delta > 0—increasing over time, Delta = 0—stable relative occurrence over time, and Delta < 0—decreasing over time.

TABLE 1 | List of vascular plant species and moss species with increased ($N = 17$) and decreased ($N = 37$) mean cover between original (1986–1988) and resurveyed (2022) grassland vegetation plots. *t*-statistic and *p*-values are reported.

Species	Before (% mean)	After (% mean)	*t*-statistic	*p*-value	Cover trend
Achillea millefolium agg.	0.850	1.678	2.420	0.016	Increasing
Agropyron repens	0.002	1.039	2.277	0.025	Increasing
Carex pallescens	0.017	0.078	2.160	0.033	Increasing
Centaurea nigrescens	0.264	1.324	3.495	0.001	Increasing
Echinochloa crus-galli	0.026	0.191	2.290	0.023	Increasing
Fragaria vesca	0.004	0.073	2.028	0.045	Increasing
Holcus lanatus	0.632	1.296	2.104	0.037	Increasing
Knautia arvensis	0.074	0.232	2.616	0.010	Increasing
Lysimachia vulgaris	0.003	0.150	2.142	0.034	Increasing
Ptychostomum imbricatulum	0.000	0.000	2.276	0.025	Increasing
Ranunculus nemorosus	0.011	0.152	2.915	0.004	Increasing
Rubus idaeus	0.001	0.227	2.615	0.010	Increasing
Rumex obtusifolius	0.028	0.673	3.136	0.002	Increasing
Setaria glauca	0.004	0.272	2.296	0.023	Increasing
Silene alba	0.005	0.302	2.478	0.015	Increasing
Silene vulgaris	0.128	0.306	2.614	0.010	Increasing
Stellaria graminea	0.073	0.190	2.067	0.040	Increasing
Agrostis tenuis	5.874	2.750	−2.632	0.009	Decreasing
Allium carinatum	0.012	0.005	−2.097	0.037	Decreasing
Anthyllis vulneraria	0.012	0.001	−3.522	0.001	Decreasing
Arabidopsis thaliana	0.006	0.000	−2.677	0.009	Decreasing
Arabis ciliata	0.011	0.001	−3.167	0.002	Decreasing
Arabis hirsuta	0.015	0.000	−4.419	0.000	Decreasing
Bellis perennis	0.140	0.004	−2.266	0.025	Decreasing
Botrychium lunaria	0.005	0.000	−2.417	0.017	Decreasing
Bromus erectus	0.743	0.202	−2.026	0.045	Decreasing
Campanula barbata	0.010	0.001	−2.917	0.004	Decreasing
Carex sempervirens	1.822	0.710	−2.106	0.037	Decreasing
Dactylorhiza sambucina	0.004	0.000	−2.181	0.031	Decreasing
Danthonia decumbens	0.519	0.100	−2.175	0.031	Decreasing
Dianthus carthusianorum	0.015	0.003	−3.341	0.001	Decreasing
Festuca rubra	1.595	0.535	−2.290	0.024	Decreasing
Gentiana verna	0.005	0.000	−2.505	0.014	Decreasing
Gymnadenia conopsea	0.011	0.003	−2.425	0.016	Decreasing
Hieracium piloselloides	0.006	0.001	−2.135	0.034	Decreasing
Lilium bulbiferum	0.021	0.005	−3.872	0.000	Decreasing

(Continues)

TABLE 1 | (Continued)

Linum catharticum	0.012	0.001	−3.494	0.001	Decreasing
Lychnis flos-cuculi	0.016	0.001	−4.080	0.000	Decreasing
Melampyrum pratense	0.004	0.000	−2.027	0.045	Decreasing
Myosotis alpestris	0.009	0.003	−1.978	0.049	Decreasing
Orchis tridentata	0.004	0.000	−2.229	0.028	Decreasing
Paradisea liliastrum	0.022	0.007	−3.390	0.001	Decreasing
Parnassia palustris	0.006	0.000	−2.677	0.009	Decreasing
Poa pratensis	2.883	1.378	−2.251	0.026	Decreasing
Polytrichum commune	0.008	0.002	−2.081	0.039	Decreasing
Silene rupestris	0.012	0.002	−2.948	0.004	Decreasing
Soldanella alpina	0.004	0.000	−2.274	0.025	Decreasing
Thlaspi alpestre	0.019	0.001	−4.681	0.000	Decreasing
Thymus praecox	0.405	0.071	−2.157	0.033	Decreasing
Thymus pulegioides	0.194	0.047	−2.540	0.012	Decreasing
Trifolium montanum	0.289	0.075	−2.128	0.035	Decreasing
Trifolium repens	3.534	1.331	−2.632	0.010	Decreasing
Trisetum flavescens	3.330	1.737	−2.476	0.014	Decreasing
Viola tricolor	0.024	0.008	−3.612	0.000	Decreasing

4.1 | What Drives the Change?

Our study reveals significant habitat changes in the area, where many historical dry and wet grasslands have been replaced by mesic grasslands and forests. The classification of many resurveyed plots to a higher hierarchical level of habitat classification compared to the original plots suggests a change of species composition with a loss of original species. This pattern has also been found for grasslands outside the Alps (Klinkovská et al. 2024).

We are aware of the fact that this is not an attribution study and the effect of the drivers was not tested directly. Although our patterns can be most likely largely ascribed to land-use changes, there may also be contributions from different drivers like climate change; for example, in the upward expansion of neophyte species along the elevation gradient (Dainese et al. 2017) or in the increase of species richness in mountain summits (Steinbauer et al. 2018). The community mean values of ecological indicators of temperature do not seem to support this interpretation, but it cannot be definitively ruled out. Despite the contribution of climate change in affecting plant diversity is likely to increase in the future compared to that of land-use change—as suggested by a recent global-scale study (Di Marco et al. 2019)—we attempt to discuss our results in the light of land-use changes following the Second World War since our patterns are aligned with those widely found throughout Europe, especially land abandonment and land-use intensification (Harásek, Klinkovská, and Chytrý 2023; De Pauw et al. 2024; Vild et al. 2024) (Figure 6).

4.2 | Low-Elevation Belt

Lower elevations have seen the development of new urban areas. Most semi-natural grasslands have been lost due to the establishment of new vineyards, small fruit plantations, and apple orchards. In areas where semi-natural grasslands persist, we have observed a shift in grassland management practices from extensive to intensive grazing. The concomitance of these processes leads to an intense temporal variation of species composition. Notably, the variation of species composition over time is primarily driven by the turnover between original vascular plant species, which are mainly hemicryptophytes typical of semi-natural grasslands (e.g., *Leucanthemum vulgare*, *Lychnis flos-cuculi*, *Agrostis tenuis*, *Dianthus carthusianorum*), and new species—mainly therophytes—adapted to disturbed conditions (McIntyre, Lavorel, and Tremont 1995; Midolo et al. 2024). Additionally, the spread of neophytes (e.g., *Oxalis fontana* and *Galinsoga ciliata*), which are typically associated with disturbed conditions (Chytrý et al. 2005), represents another indicator of the temporal impoverishment of the original flora.

4.3 | Middle-Elevation Belt

Extensive grazing practices previously common in the middle-elevation belt have been replaced by intensive grazing, dramatically impacting vegetation. This transition has led to the abandonment of many semi-natural grassland parcels. Post-abandonment succession is a well-documented phenomenon

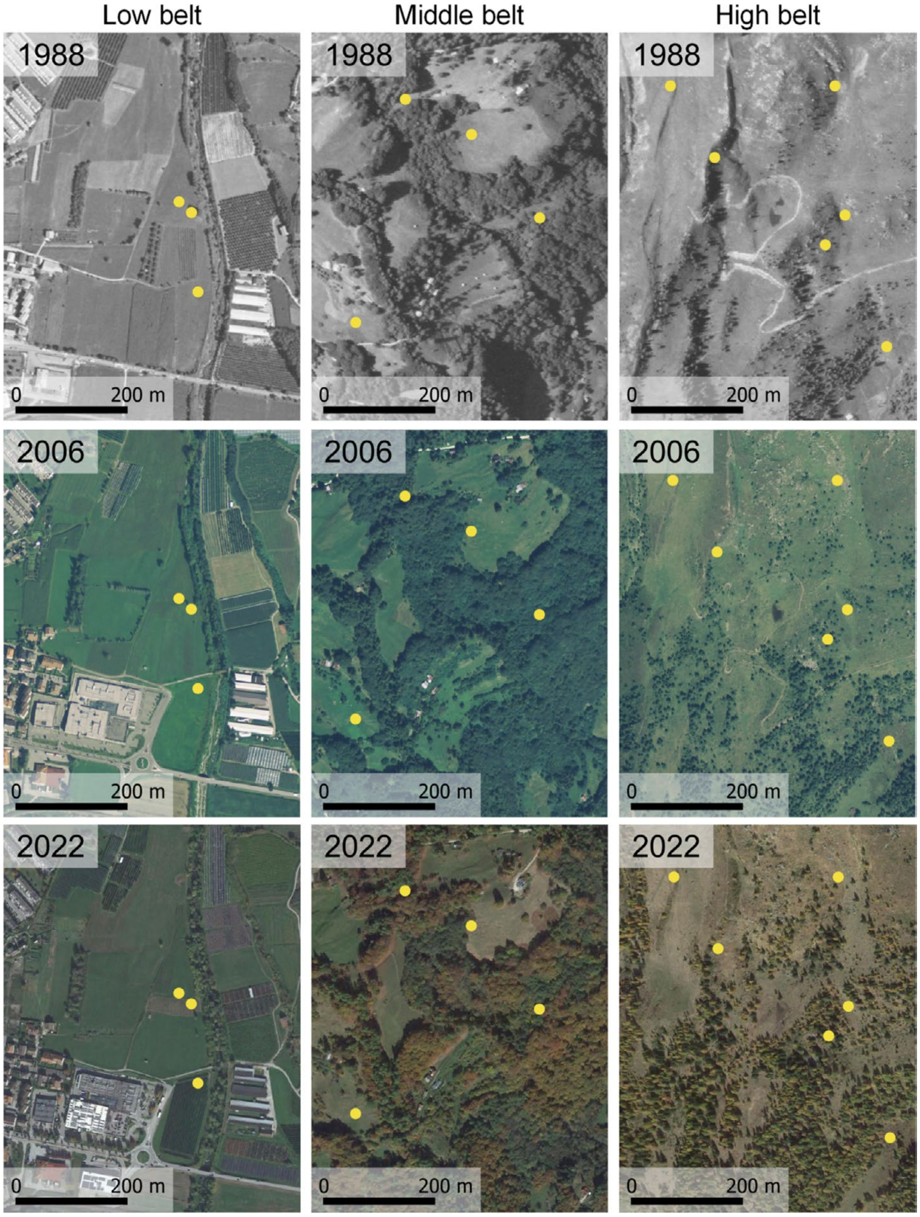

FIGURE 6 | Multitemporal orthophotos exemplifying habitat changes occurring at different elevations from 1988 to 2022. Circles represent the original grassland sampling points of 1988 resurveyed in 2022. Map data were retrieved from: 1988 and 2006—Ministero dell'Ambiente e della Sicurezza Energetica—Geoportale Nazionale; 2022—Google, CNES/Airbus Maxar Technologies Google Earth. For a list of source URLs, see Appendix S2, Table S2.

in the Alps and other European mountain ranges (Dullinger et al. 2003; Orlandi et al. 2016). The reduction in the grazing intensity by cattle has led to varying vegetation responses, ranging from encroachment to complete reforestation (Malavasi et al. 2018; Scotton and Crestani 2019; Calvia et al. 2022; Kindermann et al. 2024). In our study area, this trend is well evidenced by a concurrent decline of semi-natural grassland species and light-demanding species (e.g., *Rhinanthus alectorolophus*, *Paradisea liliastrum*), partly due to encroachment by shrub species such as *Rubus fruticosus* agg., *Rosa canina* agg., and tree species (e.g., *Sorbus aucuparia*, *Fagus sylvatica*) (Orlandi et al. 2016). Moreover, we documented an increase of expansive species like *Arrhenaterum elatius* and *Agropyron repens*. Expansive species are native plants that exhibit similar ecological behaviour to neophytes (Axmanová et al. 2024). Their increase after land abandonment is another concurrent driver of plant diversity decline (Tardella et al. 2020; Múgica et al. 2021; Ferrara and Bricca 2023; Harásek, Klinkovská, and Chytrý 2023). Encroachment and increase of expansive species may also have contributed to the decline of Orchidaceae species (e.g., *Orchis morio*), which were found in only 19 resurveyed plots compared to 38 original plots, aligning with a general decrease in Orchidaceae presence in Trentino (Geppert et al. 2020). The increase in moss species over time occurs mainly in the high-elevation belt and, to a lesser extent, in the middle-elevation belt. In this respect, we report the increase of the generalist moss species *Hypnum cupressiforme*. By contrast, the decrease of the moss species *Climacium dendroides* is ecologically significant, as it is often linked to wet grasslands and tends to disappear with abandonment and eutrophication.

4.4 | High-Elevation Belt

High elevations experienced an overall increase in species richness despite species composition remained more stable compared to lower elevations. Such a pattern can be linked to the upward shift of intensive grazing that can have led to over-fertilisation (Scotton and Crestani 2019). This phenomenon is likely contributing to the floristic impoverishment of eutrophic zones, as observed in resurvey studies of semi-natural grasslands (Schwaiger, Lenzer, and Essl 2022, and references therein) and the large formations now dominated by *Deschampsia cespitosa* (Krahulec et al. 2001). Moreover, this upward shift of grazing management may be driving the contrasting trends in hemicryptophyte abundance across elevations. Grazers may have acted as dispersal agents, facilitating the spread and establishment of hemicryptophytes from middle- to the high-elevation belt (de Bello, Lepš, and Sebastià 2005). Accordingly, plant species indicators of intensive grazing and eutrophication (e.g., *Heracleum sphondylium*) are increasing at the expense of mountain species (e.g., *Soldanella alpina*). However, we should note that grazing was patchily distributed in the mountain summit where intensive and free-to-graze areas coexist. These areas can explain the increase in the proportion of woodiness for some plots, with the gain of shrub species like *Rosa canina* agg. and *Vaccinium myrtillus* and tree species like *Larix decidua* and *Populus tremula*. Such increase of woody species in some plots, alongside an overall increase of species richness, might also be concurrently attributed to increasing temperatures (Steinbauer et al. 2018; De Toma et al. 2024).

5 | Conclusions

The Valsugana grasslands have undergone significant alterations in their habitats, vegetation, and flora over the last four decades, most likely as the consequence of changes in land use and intensification. Our observations do not reveal a notable variation in species richness, but rather a strong phenomenon of species replacement. However, we speculate these transformations can be attributed to distinct phenomena at varying elevations. In the low-elevation belt, shifts in agricultural practices and urban sprawl have led to a decline in dry grassland species coupled with an increase of neophytes, while the middle-elevation belt experienced natural reforestation accompanied by an augmented presence of nitrophilic species due to coexisting trends of land abandonment. The high-elevation belt exhibited more stable vegetation characterised by a marked nestedness and a limited loss of high-mountain species.

These results can be transferred with caution to many other Alpine valleys where similar processes of land-use change are taking place. To comprehensively understand diversity changes, we advocate for the implementation of a multifaceted approach when monitoring vegetation; recognising that each level of ecosystem complexity (e.g., habitat, vegetation, and flora) provides distinct insights and that their simultaneous consideration may avoid misleading ecological inference (Blowes et al. 2024). In addition, we emphasise the invaluable importance of qualitative ecological information that individual species contribute when properly considered in resurvey studies. Conservation management efforts should be tailored to address specific changes at different elevations, aiming to counteract negative trends in plant diversity and prevent the biotic impoverishment of native species as well as the ongoing habitat transformation of grasslands in the Alps.

Author Contributions

G.B. and F.P. conceived the study. F.P. and G.T. relocated the original vegetation plots. F.P. led both surveys and identified the species. G.B., G.T., and L.D. participated in the resurvey campaign. A.Br analysed the data and prepared the graphs. D.A. prepared the multitemporal orthophoto images. G.B. and A.Br wrote the text. A.Be secured funds for field surveys. All authors revised the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data used in this study are stored in CircumMed Resurvey database (Database custodian Gianmaria Bonari: gianmaria.bonari@unisi.it) and are also available in ReSurveyEurope database (dataset IT_0011d; https://euroveg.org/resurvey/database).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.