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**ANALYSIS OF HIGH MOUNTAIN VEGETATION CHANGES IN
CENTRAL APENNINES (ITALY) OVER THE LAST 20 YEARS**

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ABSTRACT

High mountain ecosystems host a high number of specialized, endemic and rare species and constitute important hotspots of biodiversity. Such high diversity came out from the interplay among peculiar environmental characteristics (e.g. complex mosaics of habitats on small areas) and bio-geographic and evolutionary history (e.g. dispersal barriers and isolation). At the same time, being the composition and distribution of the alpine plant communities particularly shaped by climatic and edaphic conditions (e.g. temperatures, summer and winter precipitations, cover and persistence of the snowpack, wind exposure and landscape position) they resulted among the most vulnerable ecosystems to global change.

In response to the ongoing biodiversity loss, several high mountain habitats are included in the European Habitat Directive 43/92/EEC (hereafter HD), a legal instrument to protect them that claim continuous monitoring and report activities.

In this context, the current PhD research focused on two main goals:

1) to analyze vegetation changes (e.g. floristic composition, ecological features and structure) occurred over the last 20 years on Mediterranean high mountain ecosystems in central Apennines (Italy), by implementing a re-visitation approach and to explore the potential of diagnostic species as ecological indicators for habitat monitoring over time;

2) to measure and analyze some important functional traits of vascular flora on central Apennines and to assess functional diversity and redundancy across different high mountain plant communities.

The research focused on four alpine plant communities, which are widespread in alpine and subalpine belts in central Apennines: I) *Galium magellense* community growing on screes; II) *Trifolium thalii* community of snowbeds; III) *Sesleria juncifolia* community growing on steep slopes; and IV) *Carex myosuroides* community growing on wind edge swards.

The comparison of data collected on historical and revisited georeferenced phytosociological relevés (re-visitation study) in high mountain ecosystems of central Apennines evidenced consistent changes on vegetation diversity, composition, structure and ecology and such changes varied across different communities and land units.

In particular, the *Galium magellense* community showed an increase in species richness and plant diversity values over time, while the *Trifolium thalii* community showed an opposite decreasing pattern. These changes could be due to both increasing land use pressure (e.g. new wildlife grazing pressure given by Apennine chamois) and climate change (e.g. increasing temperatures). Concerning the *Sesleria juncifolia* community growing on steep slopes and the *Carex myosuroides* community growing on wind edge swards, we registered a significant loss of biodiversity, given by a decrease in plant species cover and richness. These changes could be linked with the combined effect of rising temperatures, longer growing period and decreasing soil water content all triggered by climatic change and that, on carbonate substrates, are particularly stringent. Among the analyzed communities, *Sesleria juncifolia* grasslands growing on steep slopes, registered a high decline in cryophilous, rare and endemic species, and resulted the most vulnerable to global change.

Concerning diagnostic species, their variation on diversity values always coherent with the observed trends registered on the overall species pool, confirmed a great potential for ecosystem monitoring

on high mountain habitats and suggested the usefulness of diagnostics to support local management bodies on implementing monitoring and reporting campaigns (e.g. Habitats Directive).

The results on functional diversity and redundancy (based on field measured H: plant height, SLA: Specific Leaf Area and LDMC: Leaf Dry Matter Content), highlighted consistent differences among plant communities function (e.g. higher redundancy on harsher environmental conditions) suggesting a key role of environmental features (e.g. climate and soil moisture) in shaping mountain vegetation distribution. The analysis of functional diversity also contributed to better understanding the mechanisms ruling species coexistence (e.g. high functional diversity denoting competition and the differentiate utilization of resources) and offered scientific support to assess their resilience to environmental change. For instance the *Carex myosuroides* community is characterized by high redundancy and functional convergence for all the analyzed traits (H, SLA and LDMC) probably because the stringent environmental filtering mechanisms that occur in particularly cold environments of the highest altitudes. The *Sesleria juncifolia* community, instead, presented high values of FR_{SLA} and FR_{LDMC} and low values of $SES-FD_{SLA}$ and $SES-FD_{LDMC}$, related to the interaction of two environmental filtering factors, cold stress and soil drought, which are particularly severe in the Mediterranean limestone massifs. The absence of specific FD and FR pattern observed on screes, may be linked with random processes of colonization and extinction, and the absence of a mature and well-structured community.

A relevant contribution of the present PhD thesis is the creation of the first database of field measured plant FUNctional traits of VegetatION of centraL Apennines (FUN-VIOLA). It helps to fill the gap of knowledge about the functional ecology of Mediterranean high mountain taxa, containing records of 9 plant traits of 80 species and subspecies. Moreover, it represents a good starting point for a wide range of future ecological studies on functional strategies at local, regional and national/international level and to explore the intra- and inter-specific functional diversity on high mountain plants.

In conclusion, the present PhD thesis provided a scientific contribution to improve the current knowledge on the floristic changes that occurred over the last 20 years and on the morpho-functional characteristics of the alpine vegetation in central Apennines (Italy). Moreover, it offered a solid baseline to perform further comparisons of taxonomic and functional ecology with other Mediterranean and non-Mediterranean ecosystems.

The applied re-visitation approach together with the new information stored in FUN-VIOLA database conforms a sound basis for the assessment of alterations in functional diversity and resilience over time offering scientific information needed for monitoring and the preserving high mountain ecosystems in the context of global warming.

INTRODUCTION

High mountain ecosystems, distributed above the upper limit of forests (tree line), represent the 3% of the terrestrial environments (Heywood, 1995; Körner et al., 2011). They host approximately the 4% of Earth's flora (8000-10.000 plant species; Körner, 2003), conforming a real hotspot of biodiversity (Aeschimann et al., 2013, Winkler et al., 2016). In Europe, alpine ecosystems contain approximately the 20% of the native plants in the continent (Väre et al., 2003), with a large number of mountain endemics that increases following a gradient from boreal and temperate mountains to the richer Mediterranean summits (Faverger et al., 1972; Gils et al., 2012). During the ice age of Pleistocene, the Mediterranean-alpine ecosystems resulted glaciated only in part and remained isolated from the northern summits for very long periods (Hughes et al., 2008), assuring an important refuge for plant species, in particular for the cryophilous endemic ones (Catonica et al., 2002; Valle et al. 2022).

Mediterranean summits are biodiversity hotspots (Valavanidis and Vlachogianni, 2013; Rogora et al., 2018) characterized by a huge diversity of vascular plants and a large number of endemic and rare taxa (Pauli et al., 2003; Stanisci et al., 2011; Van Gils et al., 2012; Carlson et al., 2013, Bartolucci et al., 2018; Testolin et al., 2021). Such high concentration of plant species in small areas is most likely related with two main factors: the peculiar environmental characteristics (e.g. a complex mosaic of high mountain habitats with different soil characteristics and variable temperatures and water availability), and the biogeographic context (e.g. dispersal barriers between mountain ranges promoting speciation of cold-adapted slow-growing taxa and plant communities; Conti and Bartolucci, 2016). Indeed, the composition and distribution of alpine plant communities are particularly shaped by climate and local edaphic conditions (Körner, 2003) as temperatures, summer and winter precipitation (Fisk et al., 1998), cover and persistence of the snowpack (Green et al., 2009; Carlson et al., 2015), wind exposure and geomorphology (slope and aspect) regulating the duration of the vegetative period of the plants (Hua et al., 2022).

At the same time, high mountain habitats are among the most vulnerable ecosystems world-wide with a high risk of biodiversity loss (Pauli and Halloy, 2019). They are vulnerable to climate and land use changes (e.g., rising temperatures, changes in precipitation patterns, and grazing pressure) which affect biodiversity and ecosystem functioning (Thuiller et al., 2005; Gottfried et al., 2012; Frate et al., 2018).

The last Intergovernmental Panel on Climate Change (IPCC, 2022) highlighted that climate change impacts on mountain areas have increased in recent decades with observable and serious consequences for ecosystems and people. Specifically, IPCC-2022, evidenced that since 1850 each decade has registered higher increasing temperature values. During the last two decades (2001-2020), global surface temperature is raised by 0.99 °C with respect to the previous half century (1850-1900) (IPCC, 2022). On mountain areas, besides the increase of temperatures, the alteration of climatic seasonality and the reduction of snow cover (snow depth and duration) have been registered during the last half century, still an increase in atmospheric N deposition was observed (Gillet et al., 2016). Several ecological studies, based on short-term (Erschbamer et al., 2009; Pauli et al., 2012) and long-term (Cannone & Pignatti, 2014; Evangelista et al., 2016a) vegetation monitoring data, gave evidence of a variety of climate change effects on the distribution and abundance of alpine species and on the spatial pattern of high mountain vegetation (Stocker et al., 2013; Klein et al., 2018). With the rising temperatures registered during the last decades, plant species typical of mid and low elevations tended to shift upwards and to interact (e.g. competing) with high altitude species (Winkler et al., 2016;

Steinbauer et al., 2018; Payne et al., 2020). This phenomenon, so called “thermophilization process”, together with a “range-filling process” (e.g. species colonization and expansion from the neighboring communities of the same elevation belt mosaic, Calabrese et al., 2018), is leading to a general increase in species cover and richness on alpine plant communities (Myers-Smith et al., 2011; Pauli et al., 2012; Matteodo et al., 2016). Thermophilization of mountain plant communities is particularly evident in areas, as the Alps and the Mediterranean mountains, which are facing a steep increase of temperatures (Gottfried et al., 2012). During the last decades, also shrub expansion, local herbaceous species extinctions and alterations in the ecology and structure of high mountain vegetation were registered (Kullman, 2010; Gottfried et al., 2012; De Toma et al., 2022).

Among the taxa particularly vulnerable to climate change, endemic cryophilous plants, characterized by specialized habitat requirements, narrow distribution ranges, and geographic isolation (Erschbamer et al., 2009; Stanisci et al., 2011) are of high conservation concern. A decline in endemic and cryophilous plant species abundance and richness as a consequence of global change were recorded on Mediterranean summits (Jiménez-Alfaro et al., 2014; Evangelista et al. 2016a; Stanisci et al. 2016a). The high vulnerability of alpine endemics on south Europe is also related with the reduced size of the remaining populations and their low genetic diversity (Schwartz et al., 2006; Dirnbock et al., 2011; Fernández-Calzado et al., 2012; Kougioumoutzis et al., 2021).

Another aspect of climate change that is threatening high mountain ecosystems in the central and southern Mediterranean basin is the reduction of annual rainfalls (Nogués-Bravo et al., 2008; Cherif et al., 2021). In particular, the extension of the summer drought period (Nogués Bravo et al., 2008; Sillmann et al., 2013) combined with the increase of temperatures, are likely aiding important changes in alpine vegetation floristic diversity (Crimmins et al., 2011). Recent studies carried out on limestone massifs of the southern Mediterranean area (Kazakis et al., 2021; Lamprecht et al., 2021) and on the Alps (Nicklas et al., 2021), highlighted a particular trend of biodiversity loss in high altitude ecosystems. Such decrease on vegetation cover and richness over time was explained by the combined effect of temperatures increase and precipitations decrease, that on carbonate substrates gave rise to markedly stringent water stress conditions (Cutini et al., 2021).

For their great biodiversity value and high vulnerability to global change, several high mountain habitats are of conservation concern in Europe and are included in the European Habitat Directive 43/92/EEC (hereafter HD). HD, is a legal instrument that aids ecosystems conservation and protection throughout the European territory (Gaston et al., 2008; Louette et al., 2015). In order to assess the achievement of the HD goals, monitoring reports on high mountain ecosystems’ conservation status are needed. Monitoring activities on such remote and isolated ecosystems often implies important economic and time consuming commitments for field activities that needs to be improved and optimized (Janssen et al., 2016; Gigante et al., 2018).

For monitoring vegetation changes several approaches can be implemented. One of the soundest procedures requires data collection on permanent plots (Pauli et al., 2007; Păcurar et al., 2014; Winkler et al., 2016; Porro et al., 2019; Steinbauer et al., 2022) as another important approach is supported by data collected during the re-visitation of historical georeferenced vegetation plots (Matteodo et al., 2013; Jiménez-Alfaro et al., 2014; Evangelista et al., 2016a; Calabrese et al., 2018; Steinbauer et al., 2018). The monitoring approach based on permanent plots is very reliable and, as it covers the last decades, represents the most rigorous method to assess vegetation change occurred on medium-short time periods. An excellent example of permanent plots system for monitoring high mountain vegetation is represented by the network GLORIA (Global Observation Research Initiative

in Alpine Environments; Pauli et al., 2015) which assures rigorous collected data for the main mountain ranges across the world. GLORIA is world-wide network of permanent observation points covering alpine environments aimed at detecting temporal trends in species diversity, composition and abundance on vegetation in relation to global change (Bürli et al., 2021). Among the shortcomings of the permanent monitoring areas we can mention that periodical surveys on remote areas require a dedicated staff with costs and time not always easy to assure. Moreover, permanent plots can be installed only on safe geographical areas (Hoffmann et al., 2014) and unfortunately, the utilization of data is often restricted (Michener, 2015).

On the other hand, the re-visitation monitoring approach, based on re-sampling historical georeferenced vegetation plots surveyed by other authors, in the same area (Stöckli et al., 2011; Evangelista et al., 2016a; Calabrese et al., 2018; Steinbauer et al., 2018), often represents the only available tool for assessing long-term vegetation changes (e.g. from the 50s onwards; Schaminée et al., 2011; Chytrý et al., 2014; Franklin et al., 2017). One important support for implementing this monitoring approach is given by the vegetation geodatabases, in which historical vegetation samples are stored. One example of international global database of vegetation meta-data is the GIDV project (Global Index of Vegetation-Plot Database, <http://www.givd.info>; Dengler et al., 2011), which gathers over 300 databases with over 3 million vegetation plots distributed world-wide (Dengler et al., 2011). In Europe, EVA (European Vegetation Archive, <http://euroveg.org/eva-database>, Chytrý et al., 2016), is a centralized database of phytosociological relevés, that was developed and implemented in 2012 by the International Association for Vegetation Science (IAVS) and in particular by the Working Group: European Vegetation Survey (EVS). EVA contains over 100 databases with 2 million vegetation plots carried out in Europe and adjacent areas, providing a unique data source for large-scale analysis of European vegetation diversity for both: academic research and fundamental applications in nature conservation and ecological restoration (Chytrý et al., 2016).

In Italy, a collaborative long-term project, supported by the Italian Society of Vegetation Science (SISV) and the Italian Society of Botany (SBI) have developed a National Vegetation Database called VEGITALY (<http://www.vegitaly.it/>, GIVD ID EU-IT-001). VEGITALY is a vegetation database gathering vegetation data at national level, which contains historical and new data, both: published and unpublished (Gigante et al., 2012; Landucci et al., 2012; Venanzoni et al., 2012; Lucarini et al., 2015). Among the Italian vegetation databases, a valuable example is the Database of high mountain Vegetation Of Central Apennines (VIOLA; <http://www.givd.info/ID/EU-IT-019>). VIOLA database, created in 2016, contains over 1800 phytosociological relevés of high elevation habitats occurring in central Apennines collected from 1955 to our days (Stanisci et al., 2016b). VIOLA offers an excellent overview of Mediterranean high mountain plant species and community diversity in central Apennines and represents an important baseline for ecological monitoring studies, providing useful information on the ecological effects of climate and land use changes on alpine and subalpine ecosystems (Evangelista et al., 2016b).

In this context, the present PhD research aims to analyze vegetation changes (e.g. floristic composition, ecological features, structure, functional traits) occurred over the last 20 years on central Apennines (Italy) high mountain ecosystems, helping to increase knowledge on high elevation ecosystem vulnerability to global change in Mediterranean mountains. We explored some ecological hypotheses on the dynamics of such ecosystems using as a training ground four alpine plant communities sampled in the Maiella National Park (MNP; LTER_EU_IT_022, Central and Southern

Apennines: Majella-Matese; Capotondi et al., 2021), which are representative of alpine and subalpine ecosystems in central Apennines: I) *Galium magellense* community growing on screes; II) *Trifolium thalii* community of snowbeds; III) *Sesleria juncifolia* community growing on steep slopes; and IV) *Carex myosuroides* community growing on wind edge swards.

The *Galium magellense* community is characterized by sparse discontinuous vegetation intermingled with bare surfaces. This community grows on limestone screes with incoherent substrate, abundant debris and underdeveloped dry soils (Stanisci et al., 2011; Biondi et al., 2014).

The *Trifolium thalii* snowbeds community, is characterized by continuous vegetation cover dominated by perennial grasses and forbs and grows on small micro-dolines, where snow cover remains for long periods (at least 8 months). Dolines soils are humid, well-developed, and rich in organic matter (Blasi et al., 2003; Di Pietro et al., 2017).

The *Sesleria juncifolia* community is characterized by scraped and garland grasslands and grows on steep slopes with rendzina soils poor in organic matter and on prevalent E-SE aspects (Petriccione and Bricca, 2019).

The *Carex myosuroides* community is characterized by meso-xerophile and relatively continuous grasslands and grows on wind edge swards. Wind swards environmental units are characterized by evolved calcareous cryoturbated soils, rich in organic matter (brown rendzina), where the strong winds limit the presence of snow cover favoring high day-night temperature differentials (Di Pietro et al., 2017).

All four the analyzed plant communities are rich in endemic and sub-endemic taxa, and host a large array of Mediterranean-montane species, and Southern European orophytes (Van Gils et al., 2012; Ciaschetti et al., 2016; Conti et al., 2019). The considered communities are attributable to two Habitats of European conservation concern (*sensu* 92/43/EEC): 6170 EU Habitat “alpine and subalpine calcareous grasslands”, and 8120 EU Habitat “calcareous and calcshist screes of the montane to alpine levels-*Thlaspietea rotundifolii* (Biondi et al., 2009); and to 4 EUNIS (European Nature Information System) habitat types: Apennine stripped grasslands (code E4.436), Oro-Apennine closed grasslands (code E4.38), Temperate-montane calcareous and ultra-basic screes (code H2.4) and Windy edge swards (code E4.42) (Chytrý et al., 2020).

The present PhD research is organized in two main sections:

In the first section (**Chapter 1**), we analyzed floristic and ecological features of high mountains vegetation over time by implementing a re-visitation approach. Specifically, we extracted from the VIOLA Database (Evangelista et al., 2016b; Stanisci et al., 2016b), 55 georeferenced phytosociological relevés referable to four plant communities (15 on *Galium magellense* community, 15 on *Trifolium thalii* community, 12 on *Sesleria juncifolia* community and 13 on *Carex myosuroides* community), sampled in the year 2003 according with a random-stratified protocol (Pelino et al., 2005), and revisited them during summer 2020 – 2021 (Varricchione et al., 2021, 2022).

In **Chapter 1.1**, we analyzed temporal changes of two vegetation types (*Galium magellense* community growing on scree and *Trifolium thalii* community of snowbeds). Specifically, we: I) analyzed the variation of plant diversity pattern occurred over the last 20 years and II) explored the role of diagnostic species as ecological indicators for habitat monitoring over time (Varricchione et al., 2021).

In **Chapter 1.2**, we investigated community changes occurred on the *Sesleria juncifolia* grasslands of steep slopes and the *Carex myosuroides* community growing on wind edge swards. On this chapter we I) analyzed plant community changes in composition, structure and ecology and II) explored the changes in the pool of endemic species (Varricchione et al., 2022).

In the second section (**Chapter 2**), we dealt with measurements and analysis of important plant functional traits of vascular flora on central Apennines and with the assessment of functional diversity and redundancy across different environmental units. Functional traits are morpho-functional characteristics that affect the fitness of species, i.e. plant growth, reproduction, competition and survival, in a specific environmental context (Violle et al., 2007).

Despite the well-known value of plant traits as indicators of ecosystem functioning and of environmental change (Díaz et al., 2016; Boonman et al., 2021; Steinbauer et al., 2022), the knowledge on functional traits of plant species growing on the alpine belt on central Apennines was still partial and incomplete.

During this research, we implemented the first database of FUNctional traits of VegetatION of centraL Apennines (FUN-VIOLA; Varricchione et al., 2023) (**Chapter 2.1**). Specifically, we measured the data of 6 vegetative traits and 3 seed traits of 80 species and subspecies, following the standardized protocol of Pérez-Harguindeguy et al., (2016).

Then, (**Chapter 2.2**) we used the measured functional traits data to explore how the functional diversity and redundancy vary across the different high mountain plant communities in central Apennines (Bricca et al., 2021).

Chapter 1 – Exploring high mountain vegetation species composition over time

1.1 - *Diagnostic species diversity pattern can provide key information on vegetation change: an insight into high mountain habitats in central Apennines*



Article

Diagnostic Species Diversity Pattern Can Provide Key Information on Vegetation Change: An Insight into High Mountain Habitats in Central Apennines

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Abstract: High mountain ecosystems are hotspots of biodiversity that are highly vulnerable to climate warming and land use change. In Europe, high mountain habitats are included in the EC Directive 92/43/EEC (Habitats Directive) and the identification of practices facilitating effective monitoring is crucial for meeting HD goals. We analyzed the temporal changes in species composition and diversity on high mountain EU habitats and explored if the subgroup of diagnostic species was able to summarize the comprehensive information on plant community variations. We performed a re-visitation study, using a set of 30 georeferenced historical plots newly collected after 20 years on two EU habitats (*Galium magellense* community growing on screes (8120 EU) and *Trifolium thalii* community of snowbeds (6170 EU)) in the Maiella National Park (MNP), which is one of the most threatened Mediterranean mountains in Europe. The presence of several endangered species and the availability of a botanical garden, a seed bank, and a nursery, make the MNP an excellent training ground to explore in situ and ex situ conservation strategies. We compared overall and diagnostic species richness patterns over time by rarefaction curves and described the singular aspects of species diversity (e.g., richness, Shannon index, Simpson index, and Berger–Parker index), by R enyi’s diversity profiles. Diversity values consistently varied over time and across EU habitat types, with increasing values on scree communities and decreasing values on snowbeds. These changes could be associated with both land use change, through the increase of grazing pressure of Apennine chamois (*Rupicapra pyrenaica ornata*), which determined a rise of nitrophilous species in the scree community, and an increase of grasses at the expense of forbs in snowbeds, and to climate change, which promoted a general expansion of thermophilous species. Despite the two opposite, ongoing processes on the two plant communities studied, our results evidenced that diagnostic species and overall species followed the same trend of variation, demonstrating the potential of diagnostics for EU habitat monitoring. Our observations suggested that the re-visitation of historical plots and the implementation of frequent monitoring campaigns on diagnostic species can provide important data on species abundance and distribution patterns in these vulnerable ecosystems, supporting optimized in situ and ex situ conservation actions.

Keywords: ecological monitoring; EU Habitats Directive; rarefaction curves; R enyi’s diversity profiles; re-visitation study; vegetation database



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1. Introduction

High mountain ecosystems are hotspots of biodiversity [1,2], as they host a high number of plant species with a large number of endemic and rare taxa [3–7], most of

which are vulnerable to climate warming [8,9]. In Europe, they contain ca. 20% of all the native flora of the continent [10]. Due to their peculiar environmental characteristics, these ecosystems are very sensitive and threatened by direct and indirect human impacts, such as climate and land use change (e.g., rising temperatures, changes in precipitation patterns, and grazing pressure), which affect biodiversity and ecosystem functioning [11–13].

Encompassing global change, severe alterations in plant diversity have been observed based on short-term [14,15] and on long-term vegetation analysis [16–18]. For instance, a significant thermophilization of high mountain plant communities has been observed due to the immigration of thermophilous plants from lower altitudinal belts along with a decrease in the number of cryophilous species [1,4,13,19–25]. Shrubs expansion, local herbaceous species extinctions, and consistent changes in the ecology and structure of high mountain communities were also described [12,18,26].

In response to the ongoing biodiversity loss, several high mountain habitats are included in the European Habitat Directive 43/92/EEC (hereafter HD), a legal instrument to protect them and ensure their resilience to global changes [27–29]. According to the HD, the preservation, continuous monitoring, and reporting of high mountain ecosystems' status are a priority at both the national and European level [30,31]. In fact, the identification of practices facilitating effective monitoring is crucial for meeting HD goals [30].

The plethora of approaches proposed for monitoring high mountain vegetation can be schematically organized in two main categories: the first one is based on data collected on permanent plots (e.g., [25,32,33]), and the second one is supported by the re-visitation of historical vegetation plots (e.g., [20,21,34–36]). The most reliable monitoring method is based on multi-temporal data collection on a fixed set of permanent plots [4,32]. An excellent example of a sound protocol for monitoring high mountain ecosystem is offered by the GLORIA project (Global Observation Research Initiative in Alpine Environments; [37]), which operates a world-wide observation network with standardized permanent plot sites aimed at assessing climate change impacts on alpine vegetation and biodiversity [38]. The International Long Term Ecological Network [39] includes several mountain sites for which long time-series ecological data are available. However, permanent observation areas are not easy to implement and a staff dedicated to periodical surveys is hardly assured. Accordingly, this approach can be carried out over a limited set of geographical areas [40]. Furthermore, data on permanent observation areas are not always open access [41], with the temporal coverage mostly including short-term periods over the last decades [42].

Another increasingly used approach for describing vegetation changes over time is given by re-visitation studies, which entails re-sampling historical vegetation plots surveyed by other authors, in the same area [13,17,18,34,36]. A considerable number of historical plots are stored in vegetation geodatabases (e.g., European Vegetation Archive; <http://euroveg.org/eva-database>; accessed date 7 April 2021 [43]), which make them easy to share and use. In some cases, the re-survey approach represents the only available tool for monitoring vegetation changes [44,45].

Although the need for ecosystem monitoring is clear, the regular assessment of biodiversity in high mountain ecosystems is difficult to undertake [46], especially if the overall species richness for each habitat must be recorded [47]. The economic restrictions in many countries hinder the implementation of monitoring plans supported by large-scale field-work [48]. Furthermore, collecting extensive data on the overall species pool could be hampered by the time and the effort required to reach some remote monitoring areas [48,49]. As a result, such sampling limitations restrict the implementation of sound monitoring schemes that are essential for the better understanding and modelling of high mountain biodiversity over time [50].

Some research, carried out to identify cost-effective indicators of the conservation status and function of natural and semi-natural habitats, has suggested the usefulness of diagnostic species for describing different ecosystems, such as forests (e.g., [51,52]), grasslands [53], and coastal dunes [54,55]. Diagnostic species (as defined by HD) are those taxa with a major role in determining plant community structure, function, and

conditions [54,56]. Diagnostic species can be considered “focal taxa”, which help to assure the functionality of the entire habitat and are particularly sensitive to environmental changes [13,57]. For instance, diagnostic species indicated in the HD for high mountain habitats may play a major role in determining the structure and functioning of these systems as they could regulate the supply of resources for other species [58–60]. Moreover, their alteration may promote significant changes in the local environment, driving a spatial shift, modification, or subsistence of the surrounding habitats [16,18].

Although the response of high mountain plant species or habitats of European interest to environmental threats have been repeatedly documented (e.g., [1,4,25,38]), the analysis of diagnostic species diversity patterns with respect to the entire pool of species still requires further attention.

The present work set out to explore the temporal changes in species composition and diversity of two high mountain vegetation types that are representative and widespread in the Italian Apennine’s alpine belt (e.g., *Galium magellense* community growing on screes (8120 EU Habitat) and *Trifolium thalii* community of snowbeds (6170 EU Habitat)). We explored whether diagnostic species were able to summarize the comprehensive information on plant community changes by comparing the diversity patterns of diagnostic species assemblages with those of overall species on vegetation plots revisited after 20 years. We specifically analyzed these two habitats of conservation concern (sensu 92/43/EEC) in the Maiella National Park to address the following questions: (i) how have the plant diversity patterns changed during the last 20 years? (ii) does the diversity pattern of diagnostic species and of the overall species pool vary in a similar way?

By adopting the widely used EU Habitat standard system of vegetation classification, we were able to supply specific habitat insights that were useful for supporting monitoring strategies at the European scale and for contributing to the definition of conservation and management priorities.

2. Materials and Methods

2.1. Study Area

The study area included the highest sector of the Maiella National Park (about 24.5 km² over 2300 m a.s.l.), which is one of the most important limestone mountain groups in the Central Apennines (Figure 1). The Park consists mainly of carbonate mountains, separated by valleys and karst high plateaus, with a broad altitudinal range (130–2793 m a.s.l.). The Maiella massif has more than 60 peaks, with half of them rising above 2000 m, and includes the second highest peak in the Apennines, i.e., Mount Amaro (2793 m a.s.l.). The mountain chain, which developed with a north-south alignment for about 30 km [61,62], is formed by peaks with gentle summit profiles and extensive summit areas, bordered by steep slopes and crossed by deep valleys of glacial origin [63].

The Park territories are part of the Natura 2000 network. The boundaries coincide with a Special Protection Area (SPA) for the conservation of wild birds (established by the Birds Directive 79/409/EEC). Furthermore, four Special Areas of Conservation (SAC) established by Habitat Directive 92/43/EEC [64] occur within the Park.

The Park is an example where ex situ and in situ conservation strategies (e.g., endemic, rare, and endangered species) are implemented in a complementary way. It is extremely rich in plant vascular species, with its flora listing a high number of specific and subspecific taxa, for a total of 2286 [65], and a sizeable group of southern European orophytes and Mediterranean montane species [5], thus representing a true biodiversity hotspot [66]. The natural biodiversity is supported by shelters offered by geography and the natural environment, and the park authority assures a set of facilities required to implement ex situ conservation strategies, such as a botanical garden, a seed bank, a nursery, and a network of “guardian farmers” [64].

From a bioclimatic point of view, the study area is included in the alpine biogeographical region [67] and the climate corresponds to the subalpine-alpine humid type as far as the lower summit is concerned, whereas the other summits belong to the alpine

humid type [68]. The analysis of temporal climate series in the higher Apennine massifs showed a significant increase in the last 50 years in terms of annual temperatures ($+1.7\text{ }^{\circ}\text{C}$), amounting to $0.26\text{ }^{\circ}\text{C}$ per decade [17]. Moreover, during the last century, the spring and winter minimum temperatures increased by $2.87\text{ }^{\circ}\text{C}$ and $4.38\text{ }^{\circ}\text{C}$, respectively [69]. Summer minimum temperatures have increased ($3.17\text{ }^{\circ}\text{C}$), while summer maximum temperatures have decreased ($-2.69\text{ }^{\circ}\text{C}$) [18]. Furthermore, the summer (June–August) mean soil temperatures of the Maiella summits have increased by $1\text{ }^{\circ}\text{C}$ in the last 20 years (see details on general trends on [37]; for local soil temperatures, see Appendix A).

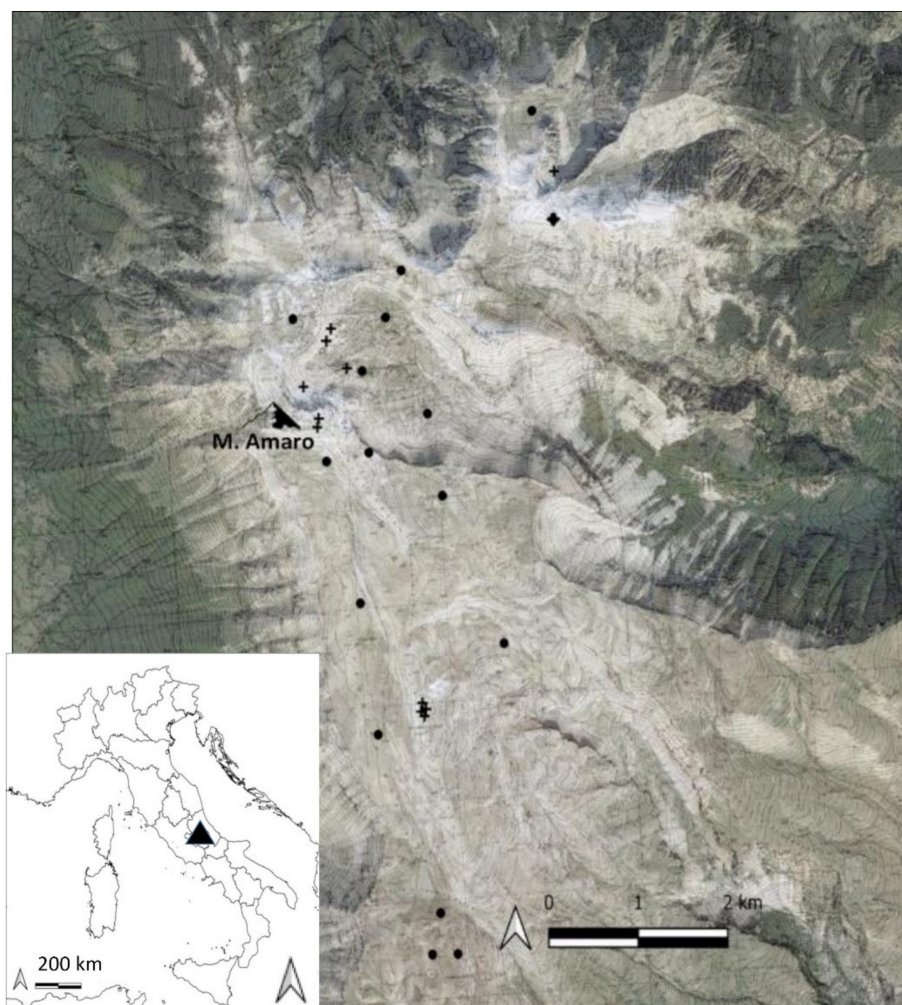


Figure 1. Study area (Maiella National Park in Central Italy) along with the distribution of plots relative to screes plant communities (+) and snowbed plant communities (●).

Traditional land use in the Maiella National Park was shaped by human practices, such as pastoralism, and has gradually changed over the last half century. Natural sub-alpine and alpine communities are changing due to the abandonment of traditional land use and the tree-line rise towards upper grasslands [13,70], as well as to the recent re-introduction of the Apennine chamois (*Rupicapra pyrenaica ornata* Neumann, 1899; [71,72]). The population of the Apennine chamois were reintroduced in the years 1991–1992 and 2000, and has expanded [73], reaching 1300 individuals by the year 2019 (<http://www.camoscioappenninico.it/>; (accessed on 7 April 2021).

We focused on the *Galium magellense* community, growing on screes, and the *Trifolium thalii* community of snowbeds. The former is included in the 8120 EU Habitat (calcareous and calcshist screes of the montane to alpine levels—*Thlaspietea rotundifolii*) and occupies the steep slopes with incoherent substrate and abundant limestone debris, occur-

ring at mean altitudes of 2660 m a.s.l. Vegetation in such limiting environmental conditions, where soils are undeveloped, dry, and poor in organic matter, is sparsely distributed and intermingled with bare surfaces [5].

The snowbed plant community is included in the 6170 EU Habitat (alpine and sub-alpine calcareous grasslands; [74,75]) and grows on small micro-dolines occurring at a mean altitude of 2450 m a.s.l., where the snow cover remains for long periods (at least 8 months). Snowbed soils are wet, well-developed, and rich in organic matter, and vegetation is characterized by close formations dominated by perennial grass and forb species [5].

2.2. Vegetation Data

For this study, we extracted, from the VIOLA database [76,77], a set of 30 georeferenced vegetation plots (15 for the scree plant community and 15 the for snowbed plant community) sampled in the years 2001 and 2003 (hereafter T1) in Maiella National Park and we resampled them in the years 2015 and 2020 (here after T2). In detail, these data include eight permanent plots from the GLORIA project (Global Observation Research Initiative in Alpine Environments; [37]) collected during 2001 and re-sampled in 2015, and 22 phytosociological relevés sampled in 2003 [78] and resampled in 2020.

For each georeferenced vegetation plot of 16 m² (4 × 4 m), all plant species and their cover/abundance along the Braun-Blanquet scale [79,80] were registered.

The nomenclature follows the updated checklists of the vascular flora native to Italy [81]. For each taxon, the accepted name and the Italian endemic status are reported. Diagnostic species of the analyzed high mountain plant communities (Table 1) were identified following the “Vegetation Prodrome” [82], which conforms to the Interpretation Manual of European Union Habitats [75] and the Italian Interpretation Manual of the 92/43/EEC Directive Habitats [74]. These diagnostic plant species are locally common, but highly specialized to live on mountain summits and, therefore, are restricted to this environment [74,83]. In order to depict the main plant strategies of the analyzed communities, we also considered the life growth for each species [84,85] (Table 1).

Table 1. Diagnostic species of the compared high mountain plant communities (conforming the Vegetation Prodrome of Italy [82] and the Italian Interpretation Manual of the 92/43/EEC Directive Habitats [74]) along with their relative life growth (LGr: sensu [85]). CH pulv: pulvinate chamaephytes; CH suffr: suffruticose chamaephytes; G rhiz: rhizomatose geophyte; H caesp: caespitose cemicryptophytes; H ros: hemicryptophytes with rosette; H scap: scapose hemicryptophytes; and T scap: scapose therophytes.

Galium magellense Community (Screes)		Trifolium thalii Community (Snowbeds)	
TAXON	LGr	TAXON	LGr
* <i>Achillea barrelieri</i> subsp. <i>barrelieri</i>	H scap	<i>Crepis aurea</i> subsp. <i>glabrescens</i>	H ros
* <i>Arenaria bertolonii</i>	CH suffr	<i>Draba aizoides</i> subsp. <i>aizoides</i>	H ros
<i>Campanula cochleariifolia</i>	H scap	<i>Helianthemum oelandicum</i> subsp. <i>alpestre</i>	CH suffr
<i>Carduus chrysacanthus</i>	H scap	<i>Luzula spicata</i> subsp. <i>bulgarica</i>	H caesp
* <i>Cerastium tomentosum</i>	CH suffr	<i>Phyteuma orbiculare</i>	H scap
<i>Crepis pygmaea</i>	G rhiz	<i>Plantago atrata</i> subsp. <i>atrata</i>	H ros
* <i>Cymbalaria pallida</i>	H scap	* <i>Polygala alpestris</i> subsp. <i>angelisii</i>	H scap
<i>Doronicum columnae</i>	G rhiz	<i>Pulsatilla alpina</i> subsp. <i>millefoliata</i>	H scap
* <i>Galium magellense</i>	H scap	* <i>Ranunculus pollinensis</i>	H scap
<i>Isatis apennina</i>	G rhiz	<i>Sagina glabra</i>	H caesp
<i>Leucopoa dimorpha</i>	H caesp	* <i>Taraxacum apenninum</i>	H ros
* <i>Linaria purpurea</i>	H scap		
* <i>Noccaea stylosa</i>	CH suffr		
<i>Papaver alpinum</i> subsp. <i>alpinum</i>	H scap		
<i>Ranunculus brevifolius</i>	G rhiz		
* <i>Saxifraga oppositifolia</i> subsp. <i>speciosa</i>	CH pulv		
* <i>Scorzoneroides montana</i> subsp. <i>breviscapa</i>	H ros		
<i>Sedum atratum</i>	T scap		
* <i>Viola magellensis</i>	H scap		

* Endemic taxon.

2.3. Data Analysis

For each community, we compared the β -diversity (i.e., diversity between plots) of the 30 plots hosting the comprehensive sampled pool with the β -diversity of the same plots after having set non-diagnostic species as absent in the site-species matrix. The β -diversity values of these two groups of plots were expressed as multivariate variances computed as the distance between each group's items (i.e., plots) and each group's centroid by reducing the original Bray-Curtis distances to principal coordinates [86]. Differences in multivariate variances were assessed through the multivariate analogue to Levene's test of the equality of variances, evaluating their significance with a permutation test with 999 repetitions [87].

Subsequently, we described overall and diagnostic species diversity patterns over time using rarefaction curves, a widely used method for estimating standardized species richness [88], which proved efficient to describe high mountain vegetation patterns [5]. We compared patterns of overall species richness and diagnostic species richness for the considered time steps (T1 and T2), calculating plot-based rarefaction curves [88,89]. In order to explore the singular aspects of species diversity (e.g., richness, equitability, and dominance) of all species and of the subgroup of diagnostic species, we realized Rényi's diversity profiles for cover values on both dataset time steps (T1 and T2) [90,91] and calculated Shannon and Simpson diversity indices.

All analyses were performed in R [92], using *vegan* [87], *Rarefy* [93] and *BiodiversityR* [94] packages, and PAST (paleontological statistics software for education and data analysis [95]).

Based on the observation that traditional diversity indices measure different aspects of the partition of abundance between species, [90] proposed a unifying formulation of diversity, according to Rényi's generalized entropy measure, which represents the starting point for a continuum of possible diversity measures. In fact, for a distribution function characterized by its proportional abundance $p_i = (p_1, p_2, \dots, p_N)$, [96] extended the concept of Shannon's information (entropy) defining a generalized entropy of order α as:

$$H_\alpha = \frac{1}{1-\alpha} \log \sum_{i=1}^N p_i^\alpha$$

where $0 \leq \alpha \leq 1$ and p_i denote the relative abundance of the i th element in a system ($i = 1, 2, \dots, N$), such that $0 \leq p_i \leq 1$ and $\sum_{i=1}^N p_i = 1$.

Rényi's formula summarizes a sequence of diversity indices that become increasingly dependent on the commonest element types for increasing values of the parameter α . The parameter α represents a sort of complex nonlinear measure of the weight that the index H_α attributes to species richness and dominance concentration for a specific community. Notice that several popular diversity indices consist of particular cases of H_α [90]. For example, for $\alpha = 0$, $H_0 = \log N$, where N is the total number of species; for $\alpha = 1$, $H_1 = \exp H$, where H is Shannon's index $\sum_{i=1}^N p_i \log p_i$ [97]; for $\alpha = 2$, $H_2 = \log 1/D$, where D is Simpson's index $\sum_{i=1}^N p_i^2$ [98], and for $\alpha = \infty$, $H_\infty = \log 1/d = \log 1/p_{\max}$, where d is the Berger-Parker index [99] and p_{\max} is the proportional abundance of the most abundant species in the community.

For a given community, H_α is a decreasing function of α . Thus, changing α allows for vector representation of community structure that can be plotted by a diversity profile of H_α versus α [100].

3. Results

The recorded species list included 145 vascular plant species and subspecies, 70 for the *Galium magellense* community (screes) and 75 for the *Trifolium thalii* community (snowbeds). Thirty of the total species registered are diagnostic (about 21%), specifically 19 for screes (27%) and 11 for snowbeds (15%) (Table 2).

Table 2. Basic floristic data for both plant communities in the two time intervals (T1: 2001–2003; T2: 2015–2020). M: number of sampled plots; $S_{\text{all species}}$: number of all species recorded; and $S_{\text{diagnostics}}$: number of diagnostic species recorded.

	<i>Galium magellense</i> Community		<i>Trifolium thalii</i> Community	
	T1	T2	T1	T2
M	15	15	15	15
$S_{\text{all species}}$	51	67	70	60
$S_{\text{diagnostics}}$	15	19	11	9

For both communities, multivariate Levene’s test for homogeneity of a group’s variances did not report significant differences between β -Diversity values of plots with the overall species pool and those with only diagnostic species (e.g., *screens* p value = 0.960; and *dolines* p value = 0.126; Figure 2).

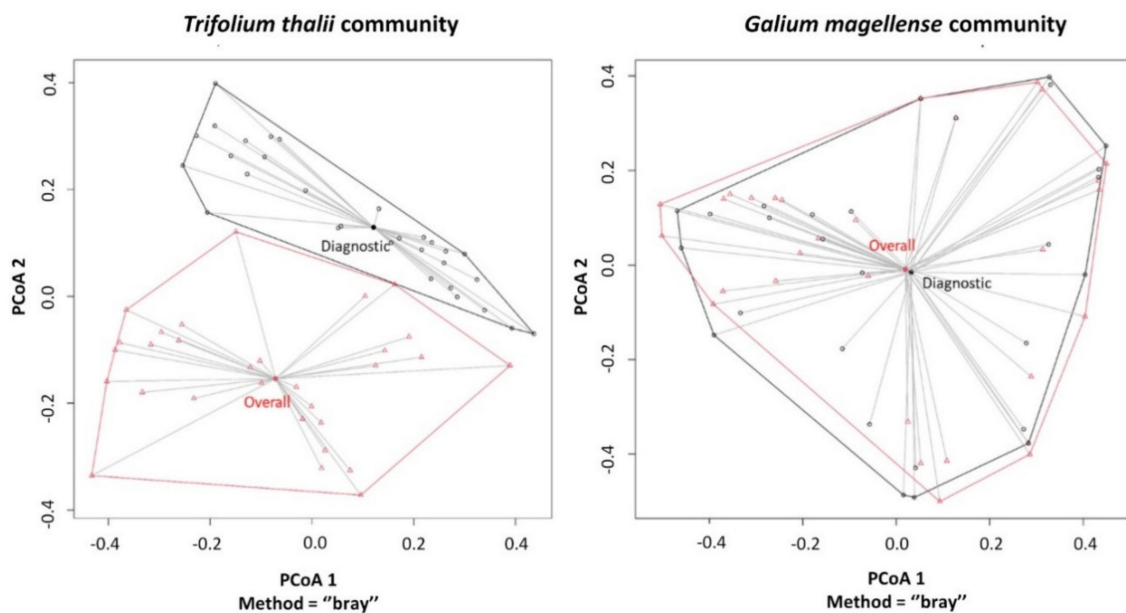


Figure 2. β -Diversity analysis for *Trifolium thalii* community and *Galium magellense* community performed on cover values for overall and diagnostic species. Principal coordinate plots report the two groups of sites within the minimum convex polygons, along with their multivariate centroids. Multivariate Levene’s test showed no significant differences between multivariate variances of the two groups of plots in both plant communities.

Rarefaction curves and the Rényi profiles in T1 and T2 for the overall species pool and for the diagnostic species showed different temporal changes in the two studied plant communities (Figures 3 and 4). Rarefaction curves on the *Galium magellense* community showed a temporal increase in the overall species richness, growing from 51 to 67 (Table 3) as well as on the diagnostic species, which increased from 15 to 19. Similarly, the Rényi’s diversity profiles showed consistent increases of diversity values over time for both overall and diagnostic species. Shannon and Simpson total values increased from 3.649 to 3.916 and from 0.9676 to 0.9743 respectively (Table 3), while Shannon and Simpson diagnostic values increased from 2.404 to 2.709 and from 0.8885 to 0.9187, respectively. Rarefaction curves on the *Trifolium thalii* community revealed a temporal decrease in the overall species richness, which declined from 70 to 61 (Table 3), as well as on the diagnostic species, which decreased from 11 to 9. Likewise, the Rényi’s diversity profiles showed consistent decreases over time of diversity values for both overall and diagnostic species. Shannon and Simpson total values decreased from 3.932 to 3.814 and from 0.976 to 0.9739, respectively (Table 3), while Shannon and Simpson diagnostic values decreased from 2.109 to 1.921 and from 0.8567 to 0.826 respectively.

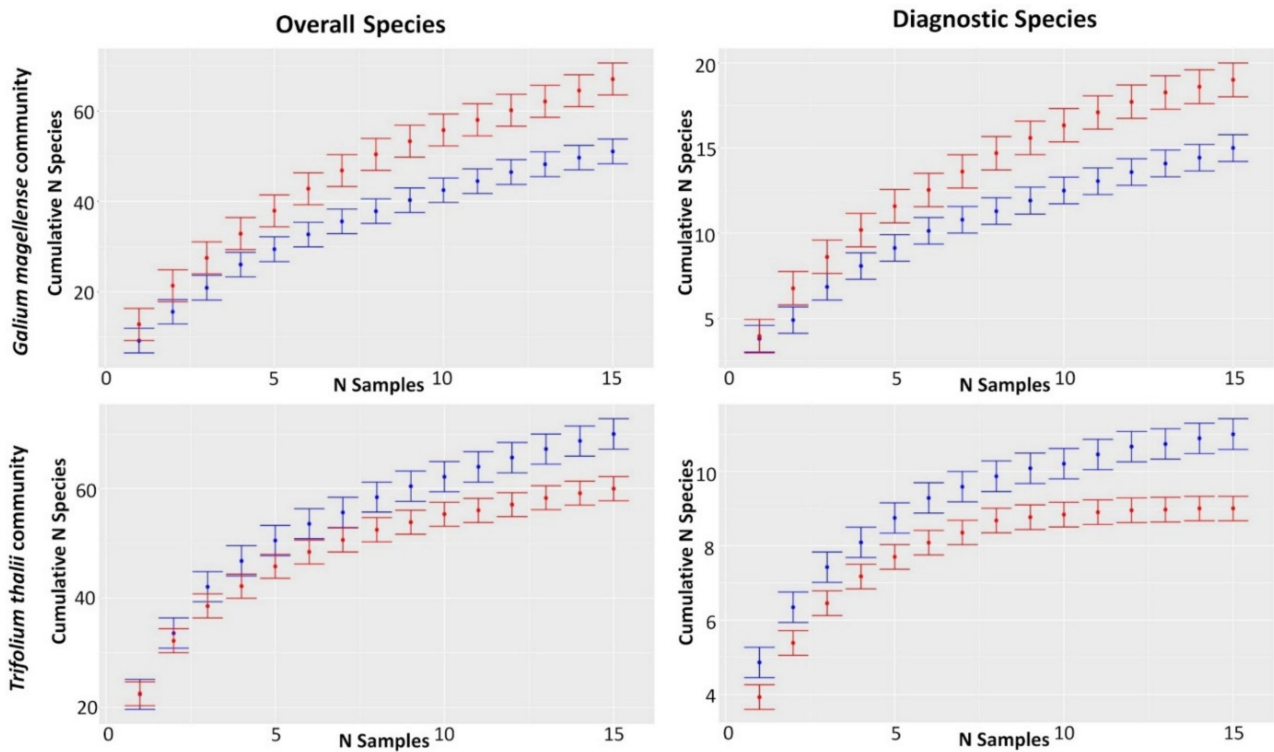


Figure 3. Plot-based rarefaction curves of the two studied plant communities, *Trifolium thalii* community and *Galium magellense* community, performed in the two time steps (blue: T1: 2001 and 2003; and red: T2: 2015 and 2020).

Table 3. Comparison of diversity parameters of overall species and diagnostic species between two time steps (T1 = 2001 and 2003; and T2 = 2015 and 2020) in *Galium magellense* community (scree) and *Trifolium thalii* community (snowbeds) R_{MaoTao} : Richness_{MaoTao}; H_{MaoTao} : Shannon_{MaoTao}; S_{MaoTao} : Simpson_{MaoTao}; and BP_{MaoTao} : Berger-Parker_{MaoTao}.

	<i>Galium magellense</i> Community (Scree)						<i>Trifolium thalii</i> Community (Snowbeds)					
	T1	Lower	Upper	T2	Lower	Upper	T1	Lower	Upper	T2	Lower	Upper
	Overall Species						Overall Species					
R_{MaoTao}	51	50.28	50.72	67	66.22	67.78	70	69.03	70.97	60	59.12	60.88
H_{MaoTao}	3.649	3.574	3.668	3.916	3.845	3.931	3.932	3.888	3.946	3.814	3.772	3.828
S_{MaoTao}	0.9676	0.9641	0.9689	0.9743	0.9714	0.9753	0.976	0.9745	0.9766	0.9739	0.9724	0.9745
BP_{MaoTao}	0.0655	0.0568	0.08188	0.05565	0.05233	0.07143	0.04312	0.04226	0.05304	0.04458	0.04325	0.05484
	Diagnostic Species						Diagnostic Species					
R_{MaoTao}	15	14.59	15.41	19	18.6	19.4	11	10.62	11.38	9	8.75	9.25
H_{MaoTao}	2.404	2.292	2.46	2.709	2.615	2.75	2.109	2.033	2.157	1.921	1.841	1.975
S_{MaoTao}	0.8885	0.8714	0.8979	0.9187	0.9059	0.9251	0.8567	0.8417	0.8663	0.826	0.8067	0.8392
BP_{MaoTao}	0.1797	0.1559	0.2237	0.1701	0.1345	0.2081	0.2169	0.1952	0.256	0.2584	0.2274	0.3023

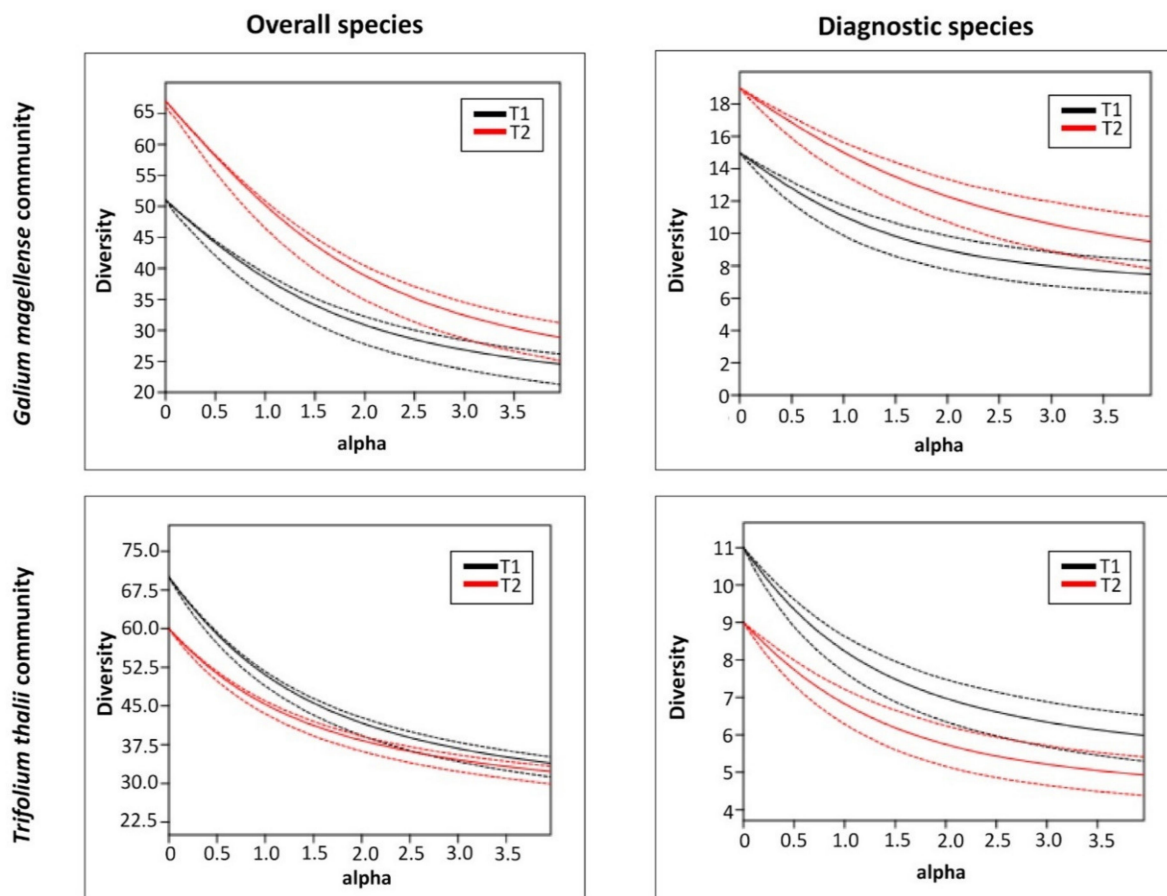


Figure 4. Renyi's diversity profiles of the two studied plant communities, *Trifolium thalii* community and *Galium magellense* community, performed on cover values for overall species and for diagnostic species in two time steps (T1: 2001 and 2003, and T2: 2015 and 2020).

4. Discussion

The diversity pattern on the analyzed high mountain ecosystems significantly changed over the last 20 years, with such temporal trends varying across plant communities. As shown by β -Diversity analyses, the variability of the diagnostic and the overall species pool are comparable. Furthermore, the temporal change on diversity values of the diagnostic species results were consistent with the alterations registered for the entire species pool.

Specifically, the *Galium magellense* community registered a sizeable gain of species richness and diversity, which could be related to an ongoing scree stabilization process caused by the increase of consolidating species, such as *Androsace villosa* subsp. *villosa*, *Salix retusa*, *Iberis saxatilis* subsp. *saxatilis*, and *Leucopoa dimorpha* (Appendix B: rank-abundance curves; and Appendix D, Table A1: complete list of recorded species and relative cover). Similar trends were observed on other European summits [101,102] and were associated with the development of incipient soils expanding inward on the scree from its base and fringes. Moreover, we also registered an increase of nitrophilous species, such as *Carduus chrysacanthus*, and *Poa alpina* subs. *alpina*, which is most likely related to the growing presence of the Apennine chamois (*Rupicapra pyrenaica ornata* Neumann, 1899). This ungulate spends the summer months on screes, providing available nitrogen in the soil with its feces [72]. However, the gain in nitrophilous species could also be due to the combined effect of faster organic matter decomposition rates due to rising temperatures [19,103,104], a prolonged growing season [105], and an increased atmospheric nitrogen deposition, which become particularly severe on mountain summits [106].

On the other hand, the *Trifolium thalii* community registered a reduction of diversity values, with a moderate decline of species richness and an increase of the dominance index values. Concerning richness reduction, most of the species present in the past and registered in the recent re-survey (e.g., the diagnostic species as *Phyteuma orbiculare*, along with other taxa as *Arabis alpina* subsp. *caucasica*, *Cerastium cerastoides*, *Hypericum richeri* subsp. *richeri*, *Oxytropis campestris*, and *Thesium parnassi*) are scapose hemicryptophytes (H Scap). Among the forbs, the scapose hemicryptophytes are slightly less performing towards grazing pressure [107], and their decrease could be ascribed to the increasing grazing pressure exerted by the Apennine chamois. It is noteworthy that during summer, the Apennine chamois females and juveniles preferentially feed on snowbed grasslands [108] occupied by dense herbaceous communities [5].

The increase of dominance values in the snowbed community is supported by a cover gain of species already present in the year 2001. We also recorded an expansion of thermophilic herbaceous species well adapted to live on grasslands at lower elevation, such as *Trifolium pratense* subsp. *semipurpureum*, *Carex kitaibeliana*, and *Taraxacum apenninum* [17,18,109] (Appendix C: rank-abundance curves; and Appendix D: complete list of recorded species and relative cover). Similar greening processes were observed in other alpine ecosystems and were interpreted as a climate change effect [110] and, in particular, to a winter cold stress reduction [111]. Other species expanding their cover (e.g., the diagnostic *Luzula spicata* subsp. *bulgarica*, and other species such as *Trifolium thalii*, *Phleum rhaeticum*, and *Festuca violacea* subsp. *italica*) are caespitose hemicryptophytes (H Caesp). The plants belonging to this life form, being capable of vegetative reproduction and spread, are well adapted to moderate-high grazing pressure [112–114], here exerted by the Apennine chamois. This wild ungulate preferentially feed on snowbed grassland with clover (e.g., *Trifolium* sp.) during late spring and early summer, which supplies a protein-rich diet optimal for weaning [13,72,77,108].

The diversity pattern over time varied among plant communities of screes (e.g., increasing values) and snowbeds (e.g., decreasing richness and Shannon values), and the behavior of diagnostic species in both communities was consistent with the overall species pool. Our results suggest the potential of diagnostic species as a cost-effective approach for monitoring high mountain plant communities. With existing evidence supporting the role of diagnostic species for describing different ecosystems, such as forests (e.g., [51,52]), grasslands [53], and coastal dunes [54,55], these results demonstrate it can extend its field of application to include monitoring high mountain EU habitats. Such findings contribute to meet the requirement for ecosystem monitoring of regions (as high mountains) where logistic or economic restrictions make the overall periodic recording of species very difficult and time-consuming to undertake.

The re-visitation of historical vegetation plots, and the possibility of frequent monitoring based on diagnostic species, can provide updated species abundance and distribution patterns and support optimized conservation actions. Monitoring research could help to prioritize in situ measures for protecting and assuring natural environmental conditions, as well as to indicate the taxa in need of immediate ex situ conservation actions (e.g., germination test of the seeds stored in the MPP bank and species bedding and planting on alpine botanical gardens).

5. Conclusions

The present study, implemented by a re-visitation approach, revealed a significant change in diversity of the high mountain vegetation of the Maiella National Park over the last 20 years. In particular, it showed two opposite trends of variation in the two plant communities analyzed. Regarding the *Galium magellense* community growing on screes, the diversity values and species richness have grown. While, in the *Trifolium thalii* community of snowbeds, we found a reduction of diversity values with a moderate decline of species richness.

These changes could be associated with two important factors: firstly, land use change, due to increase of grazing pressure of Apennine chamois introduced at the beginning of 1991 in the Park, which determined a rise of nitrophilous species in scree community and an increase of grasses (H Caesp) at the expense of forbs (H Scap) in snowbeds; and secondly, climate change, which encouraged a general expansion of thermophilous species.

Moreover, our study highlighted the role of diagnostic species in the monitoring of high mountain vegetation over time. In fact, despite the two opposite processes ongoing on the two plant communities studied, the pool of diagnostic species followed the same trend of variation of overall species pools in both communities.

Our results could support the implementation of monitoring protocols under the HD. The Habitats Directive obligates European countries to a six year reporting period and recommends an estimation of short-term trends over two reporting cycles (i.e., 12 years) and long-term trends over four reporting cycles (i.e., 24 years). Our results could help to optimize monitoring efforts by, for instance, alternating two different field collection campaigns: a) exhaustive measurements registering overall species (every 12 years) and b) partial measurements registering only diagnostics species (every 12 years). In the case of permanent plots or re-visitation sampling design, we could divide the plots into two groups and, in the first six years, register the entire pool of species in one group and the diagnostics in the second group, and then rotate, over the subsequent data collection cycles, the groups in which overall species and diagnostics are measured. Further studies conducted to better investigate the role of diagnostic species on long-term ecological monitoring over time would be beneficial.

Our study responds to the need for further monitoring studies that are able to depict vegetation dynamics occurring in remote and low-accessibility areas. The adopted re-visitation approach, based on historical plots stored in a georeferenced database, could help to reduce the gap on ecological data time series, and the results can be collated with those derived from existing permanent observation networks (e.g., LTER and GLORIA). Considering that historical vegetation plots and vegetation databases are widely available in many European countries, this adopted re-visitation study has the potential for application to other remote areas and EU habitat types in Italy and Europe at scales ranging from local to regional. The proposed monitoring approach, using historical vegetation data, can provide data over long periods of time on the abundance and distribution of species of conservation interest to be cultivated *ex situ* and conserved in seed banks.

Author Contributions: Conceptualization, M.V., A.S., and M.L.C.; methodology, M.V., M.D.F., A.S., and M.L.C.; software, M.V., M.D.F., and M.L.C.; validation, M.V., M.D.F., A.S., and M.L.C.; formal analysis M.V., M.D.F., and M.L.C.; investigation M.V., V.D.C., L.A.S., A.S., M.D.F., L.D.M., and M.L.C.; resources, A.S., L.D.M., and M.L.C.; data curation, M.V., V.D.C., and L.A.S.; writing—original draft preparation, M.V., M.D.F., A.S., and M.L.C.; writing—review and editing, M.V., V.D.C., L.A.S., A.S., M.D.F., L.D.M., and M.L.C.; supervision, A.S., and M.L.C. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

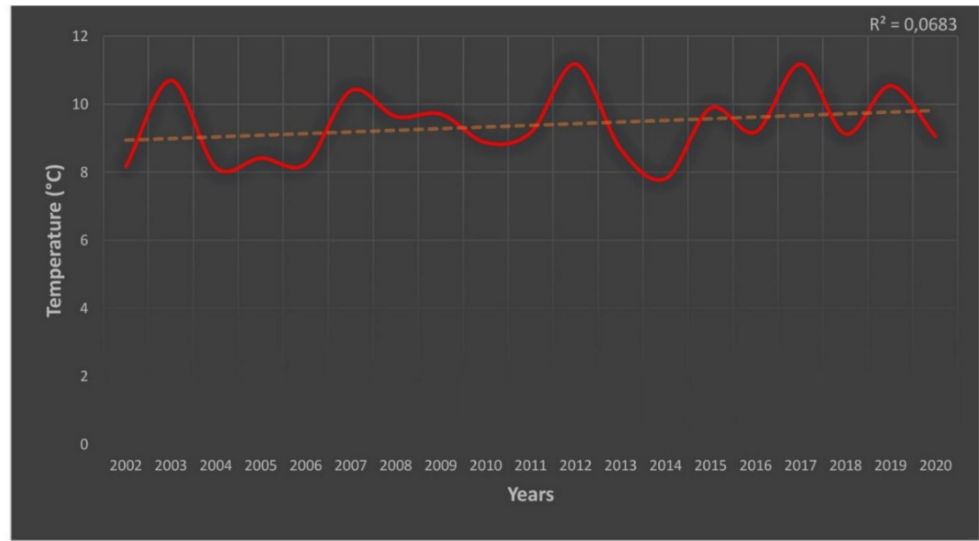


Figure A1. Mean summer (June–August) soil temperatures (°C) of the Maiella summits for the period 2002–2020. Performed by temperature data recorded by data-logger in the three GLORIA summits of Maiella massif (Femmina Morta Mount, 2405 m a.s.l; Macellaro Mount, 2635 m a.s.l; and Mammoccio Mount, 2727 m a.s.l).

Appendix B

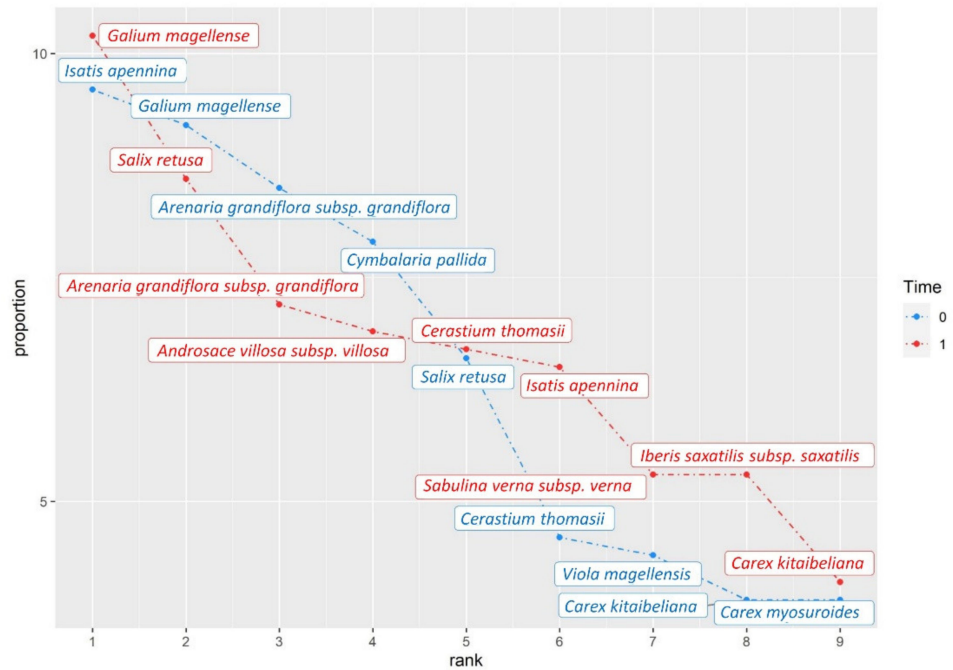


Figure A2. Rank-abundance graphics of the two plant communities analyzed, performed for overall species pool on *Galium magellense* community.

Appendix C

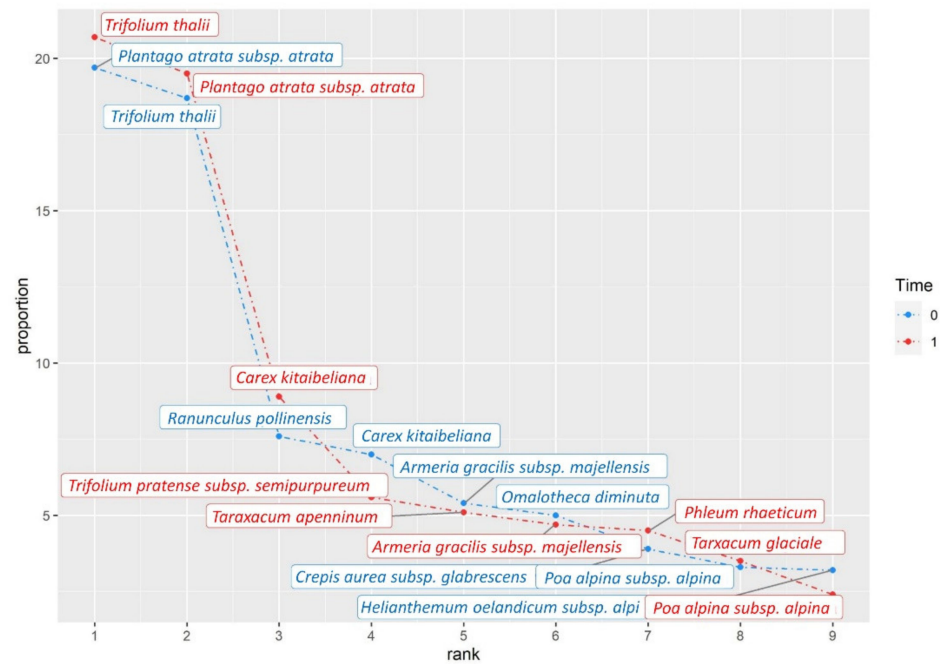


Figure A3. Rank-abundance graphics of the two plant communities analyzed, performed for overall species pool on *Trifolium thalii* community.

Appendix D

Table A1. List of the recorded species in the analyzed plant communities. For each species the life growth form (LGr), the taxonomic family (Family), and the mean cover in the compared time steps (T1: 2003–2005; T2: 2015–2020) are reported.

TAXON	LGr	Family	% Cover T1	% Cover T2
<i>Galium magellense</i> Community(Screens)				
* ^d <i>Achillea barrelieri</i> subsp. <i>barrelieri</i>	H scap	Asteraceae	0	0.13
* <i>Alyssum cuneifolium</i>	CH suffr	Brassicaceae	2.03	0.93
<i>Androsace villosa</i> subsp. <i>villosa</i>	CH rept	Primulaceae	2.23	4.2
* <i>Androsace vitaliana</i> subsp. <i>praetutiana</i>	CH suffr	Primulaceae	1.4	0.23
<i>Anthemis cretica</i>	H scap	Asteraceae	0	0.23
<i>Anthyllis vulneraria</i> subsp. <i>pulchella</i>	H caesp	Fabaceae	2	1.2
<i>Arabis alpina</i> subsp. <i>caucasica</i>	H scap	Brassicaceae	0.63	0.1
* ^d <i>Arenaria bertolonii</i>	CH suffr	Caryophyllaceae	0.2	0.07
<i>Arenaria grandiflora</i> subsp. <i>grandiflora</i>	CH suffr	Caryophyllaceae	5.4	4.37
* <i>Armeria gracilis</i> subsp. <i>majellensis</i>	H ros	Plumbaginaceae	0	0.2
<i>Aster alpinus</i> subsp. <i>alpinus</i>	H scap	Asteraceae	0.2	0.2
<i>Bistorta vivipara</i>	G rhiz	Polygonaceae	0.03	0.2
^d <i>Campanula cochleariifolia</i>	H scap	Campanulaceae	0.2	1.04
<i>Campanula scheuchzeri</i> subsp. <i>scheuchzeri</i>	H scap	Campanulaceae	1	0
^d <i>Carduus chrysacanthus</i>	H scap	Asteraceae	0	1
<i>Carex kitaibeliana</i>	H caesp	Cyperaceae	2.5	2.5
<i>Carex myosuroides</i>	H caesp	Cyperaceae	2.5	2.5
* <i>Cerastium thomasii</i>	CH suffr	Caryophyllaceae	2.9	4.07
* ^d <i>Cerastium tomentosum</i>	CH suffr	Caryophyllaceae	0.03	0.2
* <i>Crepis magellensis</i>	H ros	Asteraceae	0	0.2
^d <i>Crepis pygmaea</i>	G rhiz	Asteraceae	0.23	0.23
* ^d <i>Cymbalaria pallida</i>	H scap	Plantaginaceae	5	1.2
* <i>Cynoglossum magellense</i>	CH suffr	Boraginaceae	0	0.2
^d <i>Doronicum columnae</i>	G rhiz	Asteraceae	1	0.2

Table A1. Cont.

TAXON	LGr	Family	% Cover T1	% Cover T2
<i>Galium magellense</i> Community(Screens)				
<i>Draba aizoides</i> subsp. <i>aizoides</i>	H ros	Brassicaceae	1	1
<i>Edraianthus graminifolius</i> subsp. <i>graminifolius</i>	CH suffr	Campanulaceae	1	1.03
<i>Erigeron epiroticus</i>	H scap	Asteraceae	0	0.03
<i>Euphrasia liburnica</i>	T scap	Orobanchaceae	0	0.2
<i>Festuca alfrediana</i>	H caesp	Poaceae	0	0.03
* <i>Festuca violacea</i> subsp. <i>italica</i>	H caesp	Poaceae	0	1.03
* ^d <i>Galium magellense</i>	H scap	Rubiaceae	5.8	6.2
<i>Getiana orbicularis</i>	H ros	Gentianaceae	0.03	0.03
<i>Helianthemum oelandicum</i> subsp. <i>alpestre</i>	CH suffr	Cistaceae	0	0.2
* <i>Helictochloa praetutiana</i> subsp. <i>praetutiana</i>	H caesp	Poaceae	0	0.07
<i>Iberis saxatilis</i> subsp. <i>saxatilis</i>	CH suffr	Brassicaceae	2.4	3.2
^d <i>Isatis apennina</i>	G rhiz	Brassicaceae	6.1	3.93
<i>Leontopodium nivale</i>	H scap	Asteraceae	1.03	0.23
^d <i>Leucopoa dimorpha</i>	H caesp	Poaceae	0.2	1.03
<i>Linaria alpina</i>	H scap	Plantaginaceae	0.07	0.31
* <i>Linaria purpurea</i>	H scap	Plantaginaceae	0	0.03
<i>Sabulina verna</i> subsp. <i>verna</i>	CH suffr	Caryophyllaceae	1.43	3.23
* <i>Myosotis graui</i>	H scap	Boraginaceae	0.23	0.5
* ^d <i>Noccaea stylosa</i>	CH suffr	Brassicaceae	0.2	0.07
^d <i>Papaver alpinum</i> subsp. <i>alpinum</i>	H scap	Papaveraceae	0.53	0.37
* <i>Pedicularis elegans</i>	H ros	Orobanchaceae	0.03	0.2
<i>Phyteuma orbiculare</i>	H scap	Campanulaceae	0.2	0.03
<i>Poa alpina</i> subsp. <i>alpina</i>	H caesp	Poaceae	0.7	1.5
<i>Poa molinerii</i>	H caesp	Poaceae	0.03	0.2
<i>Potentilla crantzii</i>	H scap	Rosaceae	0.2	0.03
<i>Pulsatilla alpina</i> subsp. <i>millefoliata</i>	H scap	Ranunculaceae	0	0.23
^d <i>Ranunculus brevifolius</i>	G rhiz	Ranunculaceae	0	0.03
<i>Ranunculus seguieri</i> subsp. <i>seguieri</i>	H scap	Ranunculaceae	0.03	0.03
<i>Rumex nebroides</i>	H scap	Polygonaceae	0.2	0.03
<i>Salix retusa</i>	CH frut	Salicaceae	4.17	5.2
* <i>Saxifraga exarata</i> subsp. <i>ampullacea</i>	H scap	Saxifragaceae	0.03	0.07
<i>Saxifraga glabella</i>	CH pulv	Saxifragaceae	0.2	0
* ^d <i>Saxifraga oppositifolia</i> subsp. <i>speciosa</i>	CH pulv	Saxifragaceae	0.43	0.63
* ^d <i>Scorzoneroides montana</i> subsp. <i>breviscapa</i>	H ros	Asteraceae	0.43	0.17
^d <i>Sedum atratum</i>	T scap	Crassulaceae	0.03	0.07
<i>Senecio squalidus</i> subsp. <i>rupestris</i>	H bienn	Asteraceae	0.8	0.6
<i>Silene acaulis</i> subsp. <i>bryoides</i>	CH pulv	Caryophyllaceae	0.4	1.2
* <i>Taraxacum apenninum</i>	H ros	Asteraceae	0	0.2
<i>Thymus praecox</i> subsp. <i>polytrichus</i>	CH rept	Lamiaceae	0	0.23
* <i>Trifolium pratense</i> subsp. <i>semipurpureum</i>	H scap	Fabaceae	0	0.2
<i>Trinia dalechampii</i>	H scap	Apiaceae	1.23	0.23
<i>Valeriana montana</i>	H scap	Caprifoliaceae	1	0.23
<i>Valeriana saliuunca</i>	H scap	Caprifoliaceae	0.6	0.63
* <i>Viola eugeniae</i> subsp. <i>eugeniae</i>	H scap	Violaceae	0.3	0
* ^d <i>Viola magellensis</i>	H scap	Violaceae	2.8	0.47
<i>Ziziphora granatensis</i> subsp. <i>alpina</i>	CH suffr	Lamiaceae	0	0.03
<i>Trifolium thalii</i> community (Snowbeds)				
* <i>Achillea barrelieri</i> subsp. <i>barrelieri</i>	H scap	Asteraceae	0.33	0.1
<i>Anthyllis vulneraria</i> subsp. <i>pulchella</i>	H caesp	Fabaceae	0.6	2.97
<i>Arabis alpina</i> subsp. <i>caucasica</i>	H scap	Brassicaceae	0.03	0
<i>Arabis surculosa</i>	H scap	Brassicaceae	0.87	0.5
<i>Arenaria grandiflora</i> subsp. <i>grandiflora</i>	CH suffr	Caryophyllaceae	0.03	0.03
* <i>Armeria gracilis</i> subsp. <i>majellensis</i>	H ros	Plumbaginaceae	8.57	8.2
<i>Astragalus depressus</i> subsp. <i>depressus</i>	H ros	Fabaceae	0.47	2.8
<i>Bellidiastrum michelii</i>	H ros	Asteraceae	0	0.03
<i>Bellis perennis</i>	H Ros	Asteraceae	0.1	0

Table A1. Cont.

TAXON	LGr	Family	% Cover T1	% Cover T2
<i>Trifolium thalii</i> community (Snowbeds)				
<i>Bistorta vivipara</i>	G rhiz	Polygonaceae	0.2	0.03
<i>Botrychium lunaria</i>	G rhiz	Ophioglossaceae	0.33	0.2
<i>Campanula scheuchzeri</i> subsp. <i>scheuchzeri</i>	H scap	Campanulaceae	0.9	0.1
<i>Carduus chrysacanthus</i>	H scap	Asteraceae	1.47	1
<i>Carex kitaibeliana</i>	H caesp	Cyperaceae	11.23	15.6
<i>Cerastium arvense</i> subsp. <i>suffruticosum</i>	H scap	Caryophyllaceae	0.7	0.23
<i>Cerastium cerastoides</i>	H scap	Caryophyllaceae	0.03	0
* <i>Cerastium thomasii</i>	CH suffr	Caryophyllaceae	0.7	0.3
* <i>Cerastium tomentosum</i>	CH suffr	Caryophyllaceae	0	1
^d <i>Crepis aurea</i> subsp. <i>glabrescens</i>	H ros	Asteraceae	6.2	1.47
<i>Crepis pygmaea</i>	G rhiz	Asteraceae	0.2	0
^d <i>Draba aizoides</i> subsp. <i>aizoides</i>	H ros	Brassicaceae	0.47	0.1
* <i>Edraianthus graminifolius</i> subsp. <i>graminifolius</i>	CH suffr	Campanulaceae	0.23	0
<i>Erigeron epiroticus</i>	H scap	Asteraceae	0.1	0.17
<i>Euphrasia liburnica</i>	T scap	Orobanchaceae	2.5	2.83
<i>Euphrasia salisburgensis</i>	T scap	Orobanchaceae	0.07	0.2
* <i>Festuca violacea</i> subsp. <i>italica</i>	H caesp	Poaceae	0.5	1.6
* <i>Galium magellense</i>	H scap	Rubiaceae	0.3	0.07
<i>Gentiana orbicularis</i>	H ros	Gentianaceae	0	0.03
<i>Gentiana verna</i> subsp. <i>verna</i>	H ros	Gentianaceae	0.3	0.6
* <i>Gentianella columnae</i>	H bienn	Gentianaceae	0	0.03
^d <i>Helianthemum oelandicum</i> subsp. <i>alpestre</i>	CH suffr	Cistaceae	5.07	1.24
* <i>Helictochloa praetutiana</i> subsp. <i>praetutiana</i>	H caesp	Poaceae	0.23	1.3
<i>Herniaria glabra</i> subsp. <i>nebrodensis</i>	T scap	Caryophyllaceae	1.27	0
<i>Hypericum richeri</i> subsp. <i>richeri</i>	H scap	Hypericaceae	0.2	0
* <i>Leucopoa dimorpha</i>	H caesp	Poaceae	0.2	0
^d <i>Luzula spicata</i> subsp. <i>bulgarica</i>	H caesp	Juncaceae	0.43	1.07
<i>Sabulina verna</i> subsp. <i>verna</i>	CH suffr	Caryophyllaceae	2.07	1.23
* <i>Myosotis graui</i>	H scap	Boraginaceae	0.13	0.07
* <i>Noccaea stylosa</i>	CH suffr	Brassicaceae	0.27	0.01
<i>Omalotheca diminuta</i>	H scap	Asteraceae	7.97	2.7
<i>Oreojuncus monanthos</i>	G rhiz	Juncaceae	0.03	0.2
<i>Oxytropis campestris</i>	H scap	Fabaceae	0.03	0
* <i>Pedicularis elegans</i>	H ros	Orobanchaceae	0.03	0.1
<i>Phleum rhaeticum</i>	H caesp	Poaceae	3.37	7.93
^d <i>Phyteuma orbiculare</i>	H scap	Campanulaceae	0.23	0
<i>Pilosella lactucella</i> subsp. <i>nana</i>	H ros	Asteraceae	1.23	0.5
^d <i>Plantago atrata</i> subsp. <i>atrata</i>	H ros	Plantaginaceae	31.57	34.03
<i>Poa alpina</i> subsp. <i>alpina</i>	H caesp	Poaceae	5.33	4.23
^d <i>Polygala alpestris</i> subsp. <i>angelisii</i>	H scap	Polygonaceae	0.03	0.07
<i>Potentilla crantzii</i>	H scap	Rosaceae	0.73	3.93
^d <i>Pulsatilla alpina</i> subsp. <i>millefoliata</i>	H scap	Ranunculaceae	0.2	0.07
<i>Ranunculus brevifolius</i>	G rhiz	Ranunculaceae	0.23	0.03
* ^d <i>Ranunculus pollinensis</i>	H scap	Ranunculaceae	12.1	3.63
<i>Rumex nebroides</i>	H scap	Polygonaceae	0.43	0.2
^d <i>Sagina glabra</i>	H caesp	Caryophyllaceae	0.7	0
<i>Salix retusa</i>	CH frut	Salicaceae	0.2	3.53
<i>Saxifraga adscendens</i> subsp. <i>adscendens</i>	H bienn	Saxifragaceae	0	0.07
<i>Saxifraga paniculata</i>	H ros	Saxifragaceae	0.03	0
* <i>Scorzoneroides montana</i> subsp. <i>breviscapa</i>	H ros	Asteraceae	0.83	0.4
<i>Sedum acre</i>	CH succ	Crassulaceae	0.47	0.6
<i>Sedum atratum</i>	T scap	Crassulaceae	0.17	0.15
<i>Senecio squalidus</i> subsp. <i>rupestris</i>	H bienn	Asteraceae	0.03	1.07
<i>Sibbaldia procumbens</i>	H scap	Rosaceae	0.03	0
<i>Silene acaulis</i> subsp. <i>bryoides</i>	CH pulv	Caryophyllaceae	0.63	1.5
* ^d <i>Taraxacum apenninum</i>	H ros	Asteraceae	1.93	8.9
* <i>Taraxacum glaciale</i>	H ros	Asteraceae	4	6.13

Table A1. Cont.

TAXON	LGr	Family	% Cover T1	% Cover T2
<i>Trifolium thalii</i> community (Snowbeds)				
<i>Thesium parnassi</i>	H scap	Thesiaceae	0.23	0
<i>Thymus praecox</i> subsp. <i>polytrichus</i>	CH rept	Lamiaceae	2.7	0.43
<i>Trifolium noricum</i> subsp. <i>praetutianum</i>	H caesp	Fabaceae	0.2	1
* <i>Trifolium pratense</i> subsp. <i>semipurpureum</i>	H scap	Fabaceae	4.47	9.7
<i>Trifolium thalii</i>	H caesp	Fabaceae	29.97	36.07
<i>Trinia dalechampii</i>	H scap	Apiaceae	0.27	0.07
* <i>Viola eugeniae</i> subsp. <i>eugeniae</i>	H scap	Violaceae	1.33	0.27
<i>Ziziphora granatensis</i> subsp. <i>alpina</i>	CH suffr	Lamiaceae	0.9	1.9

* Endemic taxa; ^d: diagnostic taxa.

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




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1.2 - *Warmer and poorer: the fate of alpine calcareous grasslands in central Apennines (Italy)*

Article

Warmer and Poorer: The Fate of Alpine Calcareous Grasslands in Central Apennines (Italy)

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Abstract: Global change threatens alpine biodiversity and its effects vary across habitat types and biogeographic regions. We explored vegetation changes over the last 20 years on two Mediterranean alpine calcareous grasslands in central Apennines (Italy): stripped grasslands (EUNIS code E4.436) with *Sesleria juncifolia* growing on steep slopes, and wind edge swards (EUNIS code E4.42) with *Carex myosuroides*. Based on a re-visitation of 25 vegetation plots of 4 × 4 m, we assessed changes in overall and endemic plant species cover and richness by nonparametric Kruskal–Wallis test. We explored changes in structure and ecology using growth forms and Landolt indicators for temperatures. We identified species' contribution to temporal changes using the similarity percentage procedure (SIMPER). The results evidenced a significant decline in all species cover and richness on both plant communities with a significant decline in alpine and endemic species and in hemicryptophytes with rosette and scapose ones on stripped grasslands, as well as a decline in subalpine and suffruticose chamaephytes species on wind edge swards. Such biodiversity loss, so far observed only in the warmest and Southern Mediterranean summits of Europe, is likely attributable to the combined effect of higher temperatures; the increase in the vegetative period; and the decrease in water availability, which is particularly severe in calcareous regions. Our study suggested the vulnerability of the analyzed alpine ecosystems to global change and the importance of monitoring activities to better understand vegetation trends and adaptation strategies in subalpine, alpine, and nival ecosystems.

Keywords: climate change; endemic species; Landolt ecological indicator; life forms; plant diversity loss; re-visitation study; stripped grasslands; wind edge swards



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1. Introduction

Alpine ecosystems, distributed over the limit of forests and beyond to the snow line, are among the ecosystems most sensitive to and threatened by climate change (e.g., raising temperatures and change in precipitation patterns) [1–3]. Alpine plant communities are mainly shaped by temperatures and hydrologic features, which in turn derive from the interaction of winter precipitation, wind exposure, landscape position [4], snowpack accumulation [5], snowmelt patterns [6], and summer soil moisture [7], overall influencing the duration of the vegetative period [8].

The alpine life zone encompasses low stature vegetation above the climatic tree line worldwide and accounts for approximately 3% of the vegetated land area on Earth [9,10] and, due to their environmental and biogeographic peculiarities, they contain 4% of the Earth's flora (8000–10,000 species of plants) [4]. Alpine ecosystems in Europe host 20% of the native plants, conforming a hotspot of biodiversity [11–13]. Moreover, the complex mosaic of mountain habitats and the presence of dispersal barriers have promoted the presence of highly specialized communities [14], particularly rich in endemic and rare vascular plants [15,16]. Mediterranean summits in Europe deserve particular attention

because of the presence of a high amount of endemism [17,18]. Mediterranean alpine ecosystems, having been only partially glaciated during the ice age of Pleistocene [19] and remaining isolated for very long periods, constitute a major refuge of plant species, several of which are cryophilic endemic [20].

Climate change shapes alpine vegetation and plant diversity in different ways. For instance, the increase in temperatures recorded in the last decades [21,22] has consistently altered alpine and nival species' distribution. In several European alpine plant communities, a general increase in species richness [23–25] was registered and it was explained as a “thermophilization process”, which consists of the upward shifting of thermophilic plants towards higher altitudes [23,26–35], or as a “range-filling process”, performed by species dispersing from existing neighbor communities within the same elevation belt [36,37].

Climate warming may likewise lead to a decline in cryophilic endemic taxa, which become particularly vulnerable because of their specialized habitat requirements, narrow distribution ranges, and low capacity to modify their geographic distribution [38]. Alpine endemics on south Europe, being distributed in small populations with low genetic diversity, are even more vulnerable to global warming [39–41].

In addition to the ongoing increase in temperatures, a reduction in winter rainfalls over the central and southern Mediterranean basin, including Italian Apennines, has been registered during the second half of the 20th century [42,43]. The combination of rising temperatures and decreasing precipitation is most likely related to a steep biodiversity decline documented by recent studies on some Mediterranean summits [23,44–46] and on some calcareous grasslands of the Alps [47].

Considering the consistent and heterogeneous changes ongoing on alpine ecosystems, likely related with both the increase in temperatures [21,22] and the reduction in annual rainfalls [1,42,48–51], the present work sets out to explore vegetation dynamics on alpine Mediterranean calcareous grasslands and swards in central Apennines (Italy). Through a re-visitation vegetation study (after 18 years), we explored the temporal changes in two alpine communities in the Maiella National Park (MNP) that are representative of the central Apennine's alpine belt: Apennine stripped grasslands, growing on steep slopes, and wind edge swards, both included in the 6170 EU Habitat “alpine and subalpine calcareous grasslands” [52,53].

We addressed the following questions: (i) what happened during the last 18 years on Apennine stripped grasslands and wind edge swards in terms of species composition, structure (growth forms), and ecology (Landolt indicator values)? (ii) Do the endemic species cover and richness changed over time?

2. Materials and Methods

2.1. Study Area

The study area, located in central Italy, includes the higher sectors (from ~2400 up to 2793 m a.s.l.) of the Maiella National Park (Figure 1), characterized by a large limestone summit plateau covered by a thick (1–3 m) mantle of debris, modelled by periglacial processes in which tectonic-karst depressions are surrounded by steep slopes [54,55]. The most prominent soils on the plateau are those with a patterned ground surface of either micro-sorted circles or micro-sorted stripes [56]. The presence of the second highest peak in the Apennines (Mount Amaro, 2793 m a.s.l.) and the great extension of the alpine ecosystems above 2000 m of elevation (59 km²) [55] ensure that alpine vegetation is well expressed in terms of its typical flora [57,58].

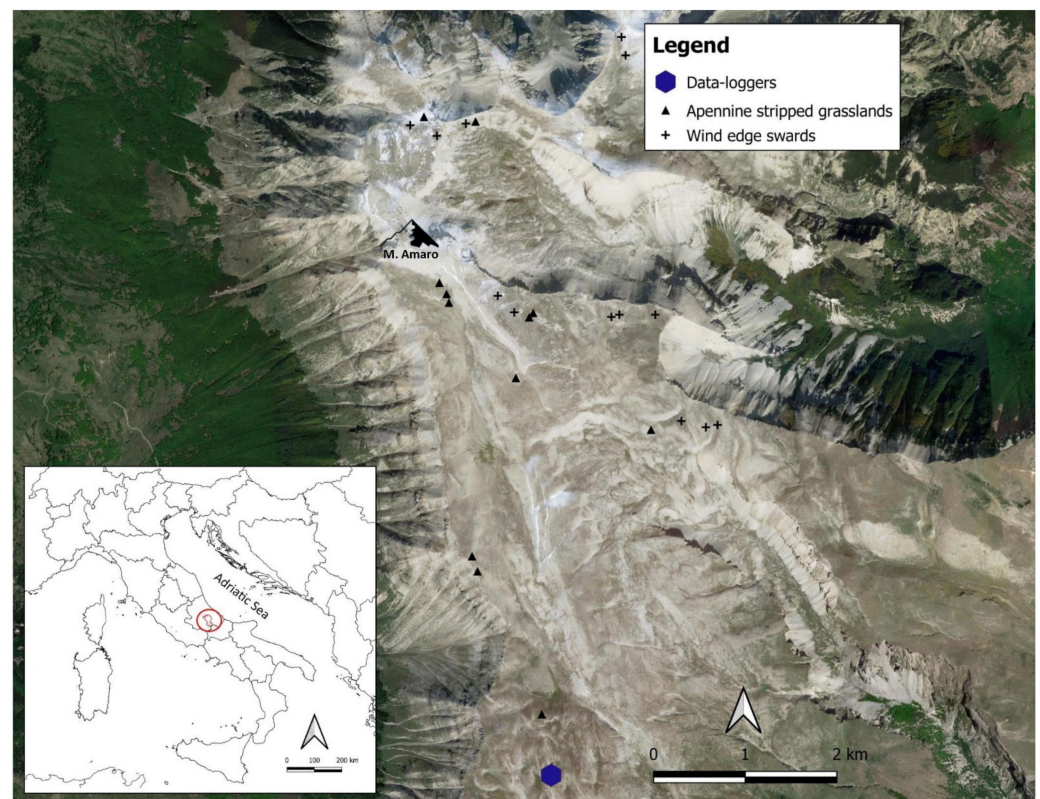


Figure 1. Study area (Maiella National Park) along with the distribution of vegetation plots on Apennine stripped grasslands (EUNIS code E4.436) and wind edge swards (EUNIS code E4.42) and of the GLORIA data-loggers measuring soil temperatures on Mt. Femmina Morta.

For these reasons, it is considered an adequate site for investigating climate change effects on Mediterranean alpine vegetation [31,59,60].

2.2. Climate Features

From a bioclimatic point of view, the analyzed summits are included in the alpine biogeographical region [61] and the climate corresponds to the subalpine–alpine humid type. As in other alpine ecosystems, the climate in central Apennines has consistently changed during the last 60 years, with a significant increase in mean annual temperatures (+1.7 °C, amounting to 0.26 °C per decade) [35,62], spring and winter minimum temperatures, and summer mean temperatures [37]. At the same time, a decrease in annual precipitations (−30 mm) and an increase in the number of very dry years per decade were also recorded [62]. Steinbauer et al. [63] in a recent paper evidenced an increase in the in situ mean soil temperatures, for central Apennines summits, of 0.5 °C per decade (since 2001), values that are above the global average warming [64].

The analysis of local time series of soil temperatures registered by data-loggers in the Majella summits in the context of GLORIA monitoring network (Global Observation Research Initiative in Alpine Environments; “IT CAM FEM”: 2405 m a.s.l.) [65] evidenced a similar increase in temperatures. Specifically, we have registered a significant increase during the last two decades in the mean annual and mean autumn soil temperatures (from 2.85 °C to 3.73 °C and from 3.48 °C to 4.77 °C, respectively; Figure 2) and an increase in the vegetative period (e.g., the number of days with temperatures above 2 °C), which, during in the last twenty years, have raised from 176 to 200 days per year (Figure 2).

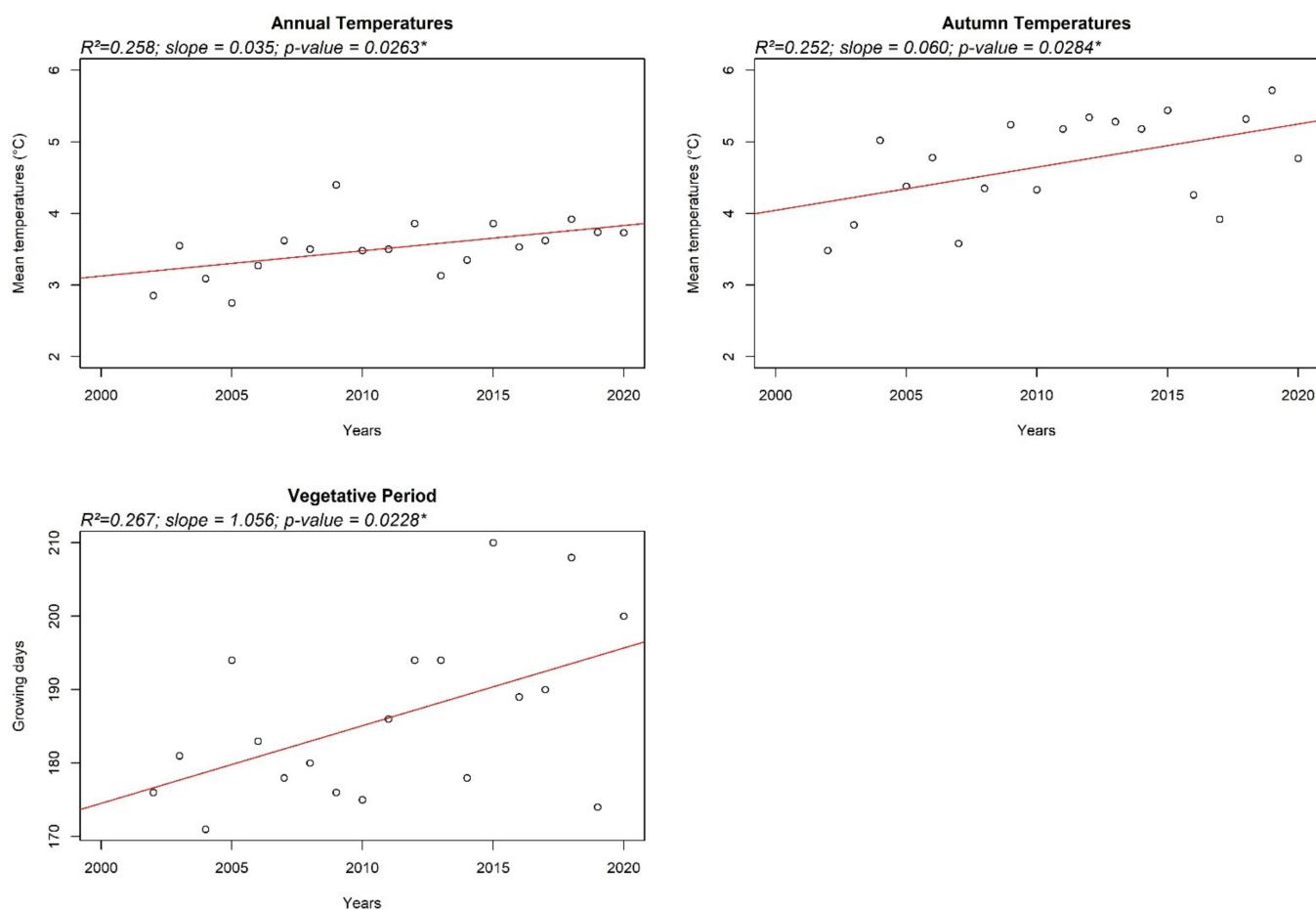


Figure 2. Annual and autumn (September–November) mean soil temperatures ($^{\circ}\text{C}$) and vegetative period (e.g., the number of days with temperatures above 2°C) for the period 2002 to 2020. Asterisks indicate significant trends. Data were retrieved from data-loggers of GLORIA monitoring network (Global Observation Research Initiative in Alpine Environments) IT CAM FEM (2405 m a.s.l.).

2.3. Plant Communities

We analyzed two alpine plant communities: (a) the Apennine stripped grasslands (EUNIS code E4.436) [66], represented by *Sesleria juncifolia* scraped and garland grasslands, and (b) the wind edge swards (EUNIS code E4.42) [66], characterized by meso-xerophile and relatively continuous *Carex myosuroides* grasslands. Both communities are quite widespread in central Apennine summit areas and are of conservation concern in Europe (Habitat 6170 EU: “alpine and subalpine calcareous grasslands”) [52,53]. Apennine stripped grasslands with *Sesleria juncifolia* grow on steep slopes with rendzina soils poor in organic matter and on prevalent E-SE aspects [67]. The wind edge swards with *Carex myosuroides* grow on more evolved calcareous cryoturbated soils rich in organic matter (brown rendzina) [67]. Both communities are characterized by the abundance of endemic, sub-endemic taxa, Mediterranean-montane species, and southern European orophytes [67].

Apennine stripped grasslands and wind edge swards grasslands in the study area have a very low anthropo-zoogenic pressure as they are in the core area of the Majella national park, where the livestock has been strictly regulated since more than 50 years ago [18]. The alpine zone of the park hosts the chamois (*Rupicapra pyrenaica ornata*), which, however, occurs preferentially on other environmental units as cliffs, screes, and snowbeds.

2.4. Vegetation Data

We re-visited, in the year 2021 (hereafter T2), 25 georeferenced phytosociological relevés previously sampled with a random-stratified sampling protocol in the year 2003 (hereafter T1). Re-visited vegetation plots are stored in VIOLA Database [60,68] and are distributed as follows: 12 on Apennine stripped grasslands and 13 on wind edge swards. Detailed local information of each revisited plot is reported in Appendix A.

Re-visitation of relevés were conducted in the same season (July–August) in order to remove the effects of phenological variability [69] and following the same sampling protocol (e.g., plot size; previous species lists; and plot headers' information: geographic coordinates, slope, altitude, and aspect) [70]. For each georeferenced vegetation plot of 16 m² (4 × 4 m), all plant species and their cover/abundance in compliance with the Braun–Blanquet scale [71,72] were registered. Vegetation plots were permanent and marked by metal pegs. The nomenclature follows the updated checklists of the vascular flora native to Italy [73]. Growth forms and chorotypes (e.g., endemic species) conform the “Flora d'Italia” [74]. We assigned to each taxa the species' ecological indicator value for temperature (T) according to Landolt [75], which ranges from 1 to 5 according to the elevation distribution of the species, which is related to the average air temperature during the growing season. We adopted Landolt T values because of their demonstrated usefulness in depicting the response of vegetation to local topographic micro-thermal heterogeneity [74]. We classified species into three groups according to the average altitudinal distribution of the species *sensu* Landolt [73]: alpine (T: 1–1.5), subalpine (T: 2–2.5), and montane (T: 3–3.5). For the endemic Mediterranean flora, without Landolt indicators, values were assigned by the authors after checking the requirements of the species in the literature [58,76]. For further quantitative analysis, we rescaled the original Braun–Blanquet cover values for each species on the percentage cover scale [77].

2.5. Statistical Analysis

After a brief inspection of the species list on T1 and T2, we compared for both of the analyzed communities the number and cover of overall and endemic species over time by the nonparametric Kruskal–Wallis test for equal medians on ranked data (cover and richness).

Furthermore, we explored the changes in vegetation structure and ecology using the growth forms [78] and Landolt indicators values for temperatures.

We also identified the species that contribute most consistently to differences between the two temporal steps (T1 and T2) using a similarity percentage procedure (SIMPER) [79].

All analyses were performed in R statistical computing program [80] using the Vegan package [81] and PAST (paleontological statistics software for education and data analysis) [82].

3. Results

The recorded species list included 91 vascular plant species and subspecies mainly belonging to *Asteraceae*, *Fabaceae* and *Poaceae* families—72 on the Apennine stripped grasslands and 76 on the wind edge swards. A total of 23 of the total species were endemic (about 25%), with 21 occurring on stripped grasslands (29%) and 17 on wind edge swards (22%) (Table 1). Most of the endemic species were scapose hemicryptophytes (48%) and suffruticose chamaephytes (22%; Table 1).

Table 1. Endemic species present in the analyzed alpine plant communities along with their relative growth form (*sensu* Pignatti et al. [74]), average altitudinal distribution of the species, and species' ecological indicator value for temperature (EIVs T) *sensu* Landolt [75]. CH pulv: pulvinate chamaephytes; CH suffr: suffruticose chamaephytes; H caesp: caespitose hemicryptophytes; H ros: hemicryptophytes with rosette; H scap: scapose hemicryptophytes; and T scap: scapose therophytes.

Species	Growth Form	Average Altitudinal Distribution	EIVs T
<i>Achillea barrelieri</i> subsp. <i>barrelieri</i>	H scap	Alpine	1.5
<i>Alyssum diffusum</i> subsp. <i>diffusum</i>	CH suffr	Montane	3
<i>Androsace vitaliana</i> subsp. <i>praetutiana</i>	CH suffr	Alpine	1.5
<i>Armeria gracilis</i> subsp. <i>majellensis</i>	H ros	Subalpine	2
<i>Carduus chrysacanthus</i>	H scap	Subalpine	2.5
<i>Cerastium thomasii</i>	CH suffr	Alpine	1.5
<i>Erysimum majellense</i>	H scap	Subalpine	2.5
<i>Festuca violacea</i> subsp. <i>italica</i>	H caesp	Alpine	1.5
<i>Galium magellense</i>	H scap	Alpine	1.5
<i>Helictochloa praetutiana</i> subsp. <i>praetutiana</i>	H caesp	Subalpine	2.5
<i>Leontopodium nivale</i>	H scap	Alpine	1.5
<i>Myosotis graui</i>	H scap	Subalpine	2.5
<i>Noccaea stylosa</i>	CH suffr	Subalpine	2
<i>Pedicularis elegans</i>	H ros	Subalpine	2.5
<i>Phyllolepidum rupestre</i>	CH suffr	Alpine	1.5
<i>Ranunculus pollinensis</i>	H scap	Subalpine	2.5
<i>Rhinanthus wettsteinii</i>	T scap	Subalpine	2
<i>Saxifraga italica</i>	CH pulv	Alpine	1
<i>Scorzoneroides montana</i> subsp. <i>breviscapa</i>	H ros	Alpine	1.5
<i>Trifolium pratense</i> subsp. <i>semipurpureum</i>	H scap	Montane	3.5
<i>Valeriana saliunca</i>	H scap	Alpine	1
<i>Viola eugeniae</i> subsp. <i>eugeniae</i>	H scap	Subalpine	2.5
<i>Viola magellensis</i>	H scap	Alpine	1

The temporal comparison (T1 vs. T2) of species richness and cover per plot for the entire pool by Kruskal–Wallis test evidenced similar temporal trends on both of the studied plant communities. We registered a significant decrease in overall species cover and richness per plot on stripped grassland ($P_{\text{same}} < 0.01$ and $P_{\text{same}} = 0.03$, respectively) and on wind edge swards ($P_{\text{same}} = 0.04$ and $P_{\text{same}} < 0.01$, respectively) (Figure 3).

Similarly, we registered a significant decline in endemic species on stripped grassland (cover $P_{\text{same}} < 0.001$; richness $P_{\text{same}} = 0.04$) (Figure 3).

Concerning the average altitudinal distribution of the species, we detected on stripped grassland a significant decrease in alpine species per plot (cover $P_{\text{same}} < 0.01$ and richness $P_{\text{same}} = 0.03$) and, on wind edge swards, a decline in subalpine species (cover $P_{\text{same}} = 0.02$ and richness $P_{\text{same}} < 0.01$) (Figure 4).

We also observed some changes in vegetation structure, with stripped grasslands registering a significant decrease in cover for the hemicryptophytes, in particular for the hemicryptophytes with rosette (H ros) and scapose hemicryptophytes (H scap) ($P_{\text{same}} < 0.01$ and $P_{\text{same}} = 0.04$, respectively), and the wind edge swards showing a significant reduction in cover for the suffruticose chamaephytes (CH suffr) species over time ($P_{\text{same}} < 0.01$) (Figure 5).

According to the similarity percentage analysis (SIMPER) (Table 2), 8 of the 72 species for Apennine stripped grasslands and 7 of the 76 species for wind edge swards contributed to 50% of the observed temporal differences (T1 vs. T2) in vegetation composition. Two of these declining species are endemics (*Armeria gracilis* subsp. *majellensis* and *Festuca violacea* subsp. *italica*).

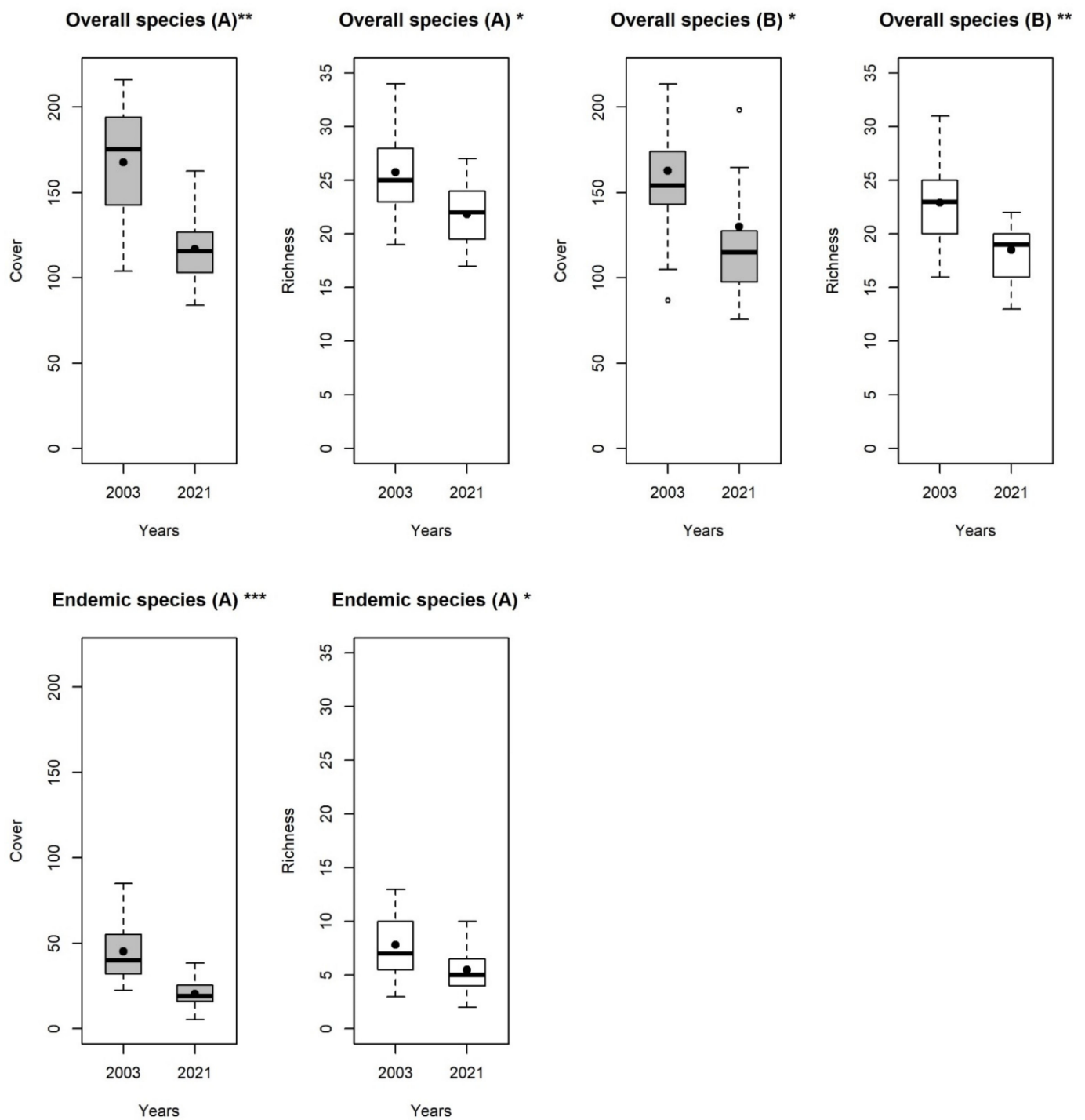


Figure 3. Boxplot comparing cover (grey) and species richness per 4×4 m plot (white) of overall and endemic species in two time steps (T1: 2003 and T2: 2021) in Apennine stripped grasslands (A) and wind edge swards (B). Only the significant results are reported. Asterisks indicate significant differences according to the Kruskal–Wallis test for equal medians (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

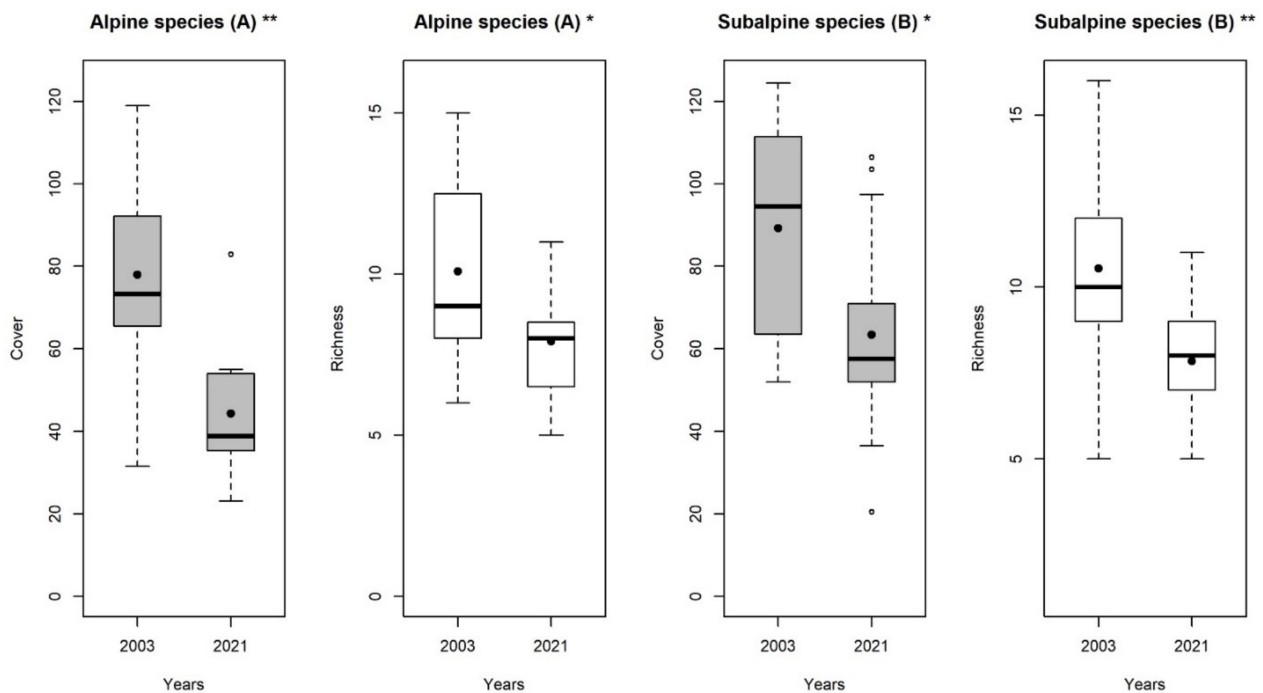


Figure 4. Boxplot comparing cover (grey) and richness per 4×4 m plot (white) of alpine species (T: 1–1.5) and subalpine species (T: 2–2.5) in two time steps (T1: 2003 and T2: 2021) in Apennine stripped grassland (A) and wind edge swards (B). Only the significant results are reported. Asterisks indicate significant differences according to the Kruskal–Wallis test for equal medians (* $p < 0.05$, ** $p < 0.01$).

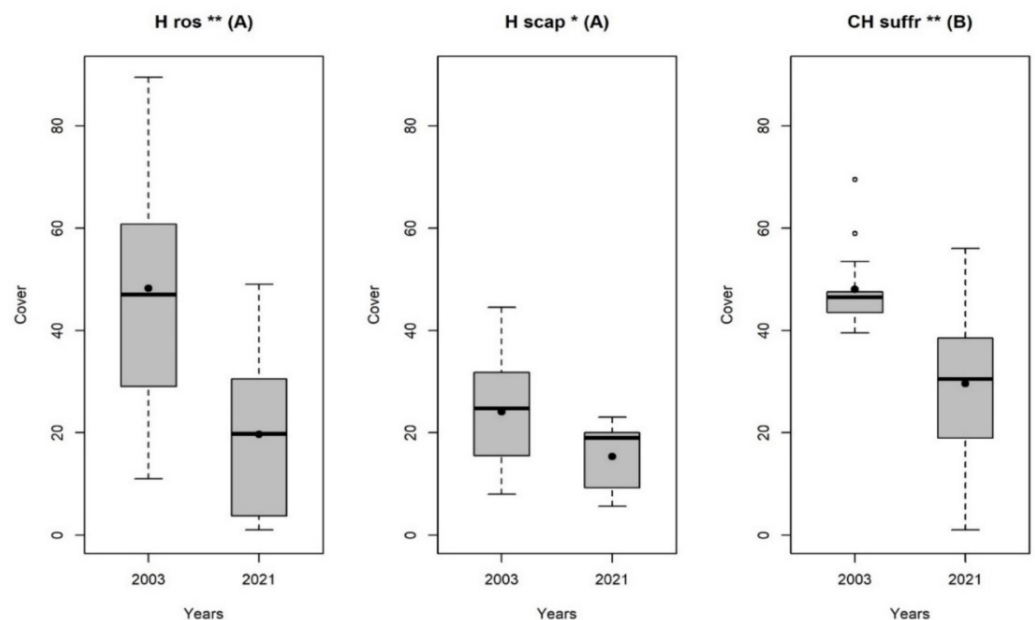


Figure 5. Boxplot comparing cover of growth forms (*sensu* Pignatti et al. [74]) in two time steps (T1: 2003 and T2: 2021) in Apennine stripped grasslands (A) and wind edge swards (B). H ros: hemicryptophytes with rosette; H scap: scapose hemicryptophytes; CH suffr: suffruticose chamaephytes. Asterisks indicate significant differences according to the Kruskal–Wallis test for equal medians (* $p < 0.05$, ** $p < 0.01$).

Table 2. Plant species that contribute up to the 50% to floristic changes over time (T1: 2003 and T2: 2021) assessed by the similarity percentage procedure (SIMPER) [79]. For each taxon, the growth form, the average altitudinal distribution of the species (Range), and species' ecological indicator value for temperature (EIVs T) *sensu* Landolt [75], as well as the specific and cumulative contribution and the mean cover on T1 and T2, are also reported.

Plant Community	Species	Growth Form	Range	EIVs	Species Contribution (%)	Cumulative Contribution (%)	Mean Cover	
				T			T1	T2
Apennine stripped grasslands	<i>Plantago atrata</i> subsp. <i>atrata</i>	H ros	Alpine	1.5	10	10	20.5	8.8
	<i>Anthyllis vulneraria</i> subsp. <i>pulchella</i>	H scap	Montane	3	7.9	17.9	11.7	15.4
	<i>Carex kitaibeliana</i>	H caesp	Subalpine	2	7	25	18.5	20.6
	◦ <i>Armeria gracilis</i> subsp. <i>majellensis</i>	H ros	Subalpine	2	6.7	31.7	14.8	3.1
	◦ <i>Festuca violacea</i> subsp. <i>italica</i>	H caesp	Alpine	1.5	6.4	38	13.9	7.3
	<i>Poa alpina</i> subsp. <i>alpina</i>	H caesp	Alpine	1.5	5.6	43.6	12	2.6
	<i>Helianthemum oelandicum</i> subsp. <i>alpestre</i>	CH suffr	Subalpine	2.5	5	48.6	7	4.5
	<i>Silene acaulis</i> subsp. <i>bryoides</i>	CH pulv	Alpine	1	4.1	52.7	5.9	5.6
Wind edge swards	<i>Carex kitaibeliana</i>	H caesp	Subalpine	2	12.4	12.4	25.1	20.3
	<i>Helianthemum oelandicum</i> subsp. <i>alpestre</i>	CH suffr	Subalpine	2.5	11.1	23.5	39.4	23.3
	<i>Salix retusa</i>	CH frut	Alpine	1.5	7.9	31.4	5.9	13.3
	◦ <i>Festuca violacea</i> subsp. <i>italica</i>	H caesp	Alpine	1.5	5.7	37.1	10.7	4.9
	<i>Carex myosuroides</i>	H caesp	Alpine	1.5	5.4	42.5	4.3	8.5
	<i>Oxytropis campestris</i>	H scap	Alpine	1.5	4.2	46.7	5.9	2.6
	<i>Anthyllis vulneraria</i> subsp. <i>pulchella</i>	H scap	Montane	3	4.2	50.9	14	14

◦ Endemic species.

In the stripped grasslands, we observed the reduction in cover on six of these eight species and four of them are alpine (T = 1–1.5). Only two species, the montane *Anthyllis vulneraria* subsp. *pulchella* and the subalpine *Carex kitaibeliana*, increased in cover over time.

In the wind edge swards, the species that contributed most to the decreasing plant cover value over time were the subalpine (T = 2–2.5) *Carex kitaibeliana* and *Helianthemum oelandicum* subsp. *alpestre*. Only two species, the alpine *Salix retusa* and *Carex myosuroides*, increased their cover and the montane *Anthyllis vulneraria* subsp. *pulchella* remained stable over time.

4. Discussion

The re-visitation after 18 years of stripped grasslands and wind edge swards vegetation plots in central Apennines evidenced an important decline in plant diversity with a significant decrease in species richness and cover and the loss of some endemic species. It also evidenced significant alterations in plant communities' structure and ecology with a reduction in alpine and hemicryptophytes in stripped grasslands with *Sesleria juncifolia* and in subalpine and suffruticose chamaephytes in wind edge swards with *Carex myosuroides*.

Similar decreasing trends in species richness and cover over time were observed in other Mediterranean and alpine summits in Europe. For instance, a decrease in alpine plants was observed in Mediterranean summits of Corsica [23], Sierra Nevada [44], and Crete [45], and those changes were attributed by the authors to biological effects of climate warming and the consequent decrease in water availability [44].

Similarly, Porro et al. [46] have observed a decline in plant diversity in northern Apennines and Nicklas et al. [47] described a slow and progressive loss of species richness in the calcareous grasslands of the Alps. Such biodiversity decline registered on some mountain summits is most likely a result of a combination of rising temperatures and decreasing summer precipitations occurring in southern Europe during the last decades [41,83–85]. Indeed, during the last five decades, a general increase in annual mean temperatures [86–88] with a decrease in annual precipitations and an extension of the dry summer season [43,89,90] across the Italian peninsula and Europe were recorded.

In this light, the increase in soil temperatures registered in the study area (by the GLORIA network data loggers), in particular in autumn, as well as the prolongation of the growing season (e.g., later accumulation of snow and earlier meltdown), should be related with the decline in species' diversity registered in both stripped grasslands and wind edge swards. For instance, the warmer conditions registered in autumn could stimulate the

premature germination of seeds [91] and the production of early seedlings that are not able to survive to the following harsh winter conditions (e.g., steep diurnal temperature range and the alternation of warm and very cold days) [92,93].

Notice that the decline in species richness registered during the last 18 years in the stripped grasslands is a result of the drop in alpine (e.g., *Plantago atrata* subsp. *atrata* and *Poa alpina* subsp. *alpina*) and endemic plants (e.g., *Festuca violacea* subsp. *italica*). Alpine species are cryophilous taxa, which are vulnerable to the increase in temperatures and the decrease in soil water availability [29,30,33,35,85]. Concerning the observed decline in endemic plants, similar results were reported in recent studies carried out in the southern Mediterranean summits of Europe such as Sierra Nevada [44] and Crete [45], and those changes were interpreted by the authors as a reaction of vegetation to climate change. We also observed in stripped grasslands a decline in hemicryptophytes with rosette (H ros) and scapose hemicryptophytes (H scap) (e.g., *Plantago atrata* subsp. *atrata*, *Armeria gracilis* subsp. *majellensis*, *Ranunculus pollinensis*, *Scorzoneroides montana* subsp. *Breviscarpa* and *Viola eugeniae* subsp. *eugeniae*), which are common in continuous grasslands [35,94] and are weakly adapted to cope with the new climatic conditions (e.g., higher temperatures, the prolongation of the growing season, and the consequent increased water stress) [63].

The decline in diversity values observed in the wind edge swards is due to the decrease in subalpine species (e.g., *Carex kitaibeliana*, *Helianthemum oelandicum* subsp. *alpestre*), which may be attributable to the harsher environmental conditions registered during the last decades [2]. Indeed, the prolongation of the growing season (e.g., later accumulation of snow and earlier meltdown) likely promoted in wind edge swards steeper diurnal temperature ranges and higher winter frost stress, limiting both the development and survival of several subalpine species [62,95]. On the other hand, the stability of the stress-tolerant and cold-adapted alpine species, in which wind edge swards in central Apennines are rich [96], is likely due to their ability to cope, at least so far, with such effects of climate change. The observed species cover changes in the wind edge swards vegetation structure are due to the decrease in suffruticose chamaephytes (CH suffr; e.g., *Helianthemum oelandicum* subsp. *alpestre*, *Iberis saxatilis* subsp. *saxatilis*, *Noccaea stylosa*). As observed by Steinbauer et al. [63] on alpine ridges across southern European summits, in our case too, climate warming seems to induce a decrease in cushion plants cover.

The observed decline in plant species richness and cover registered on central Apennines stripped grasslands and wind edge formations is most likely related to the rise in temperatures, the increased vegetative period, and the reduction in soil water content, which are impinging European summits and are particularly severe in calcareous regions [47]. The temperature rise registered in the study area in combination with a series of exceptionally dry summers (2003, 2015, 2021) [97], frequent summer storms with high runoff particularly detrimental on a karstic bedrock [98], and the convention winds promoting high evapotranspiration, likely all contribute to the observed change in plant diversity values.

Our study evidenced a particular process of diversity loss ongoing on alpine stripped and wind edge grasslands, which had not been observed so far on other plant communities in central Apennines. In fact, previous studies on the Mediterranean Apennines registered a stability of species richness and an increase in plant cover on *Pinus mugo* scrubs [37,76] on scree and snowbeds vegetation [35,94]. Such a temporal increases in plant cover and richness have been attributed to range filling processes (e.g., greening) and to the upward shift of montane/subalpine species towards the alpine and nival belts (e.g., thermophilization process), both promoted by climatic warming [33,76,99]. Southern mountains of the northern hemisphere (such as those in the Mediterranean area) host several species' range-edge populations [41,47,100], which are more vulnerable to climatic changes than core populations [51,101–104].

The observed decline in plant species diversity is particularly worrying if accounting for the most updated climate change models that, for mountain areas in south Europe, have predicted increasing temperatures, decreasing precipitations, and a lengthening summer

season [43,64,89,90]. Similarly, recent climatic projections for the next 50 years on Mediterranean mountains have predicted an increase in temperatures (+1.4 °C) and a reduction in precipitation (−4.8%) [42]. Altered climatic conditions that are shrinking the European mountain flora [23] are even more dangerous on Mediterranean areas, like the analyzed alpine stripped and wind edge grasslands, which, being rich in endemics [23,105–107], should have permanent damage on biodiversity.

These endemic alpine plant populations already placed at maximum local elevational gradients could face “mountaintop extinction” [104] and survive only in “warm-stage microrefugia”, geomorphologic niches that constantly maintain cold-air pooling and temperature inversions [108], with implications for the conservation of regional biodiversity.

Our results evidenced the urgent need for identifying “warm-stage microrefugia” in alpine protected areas able to support “climate-smart” in situ conservation planning for the Mediterranean mountains [106,109]. Such microrefugia could form a network of conservation sites of taxonomic and genetic diversity (e.g., alpine endemics), which should be strictly protected [108,110]. Those measures should be integrated with ex situ conservation practices, such as those locally implemented in the Majella Seed Bank [111], both complementary cost-effective actions [112].

5. Conclusions

The present re-visitation study evidenced significant changes over the last 18 years in the stripped grassland and wind edge swards plant communities in central Apennines.

Both plant communities showed a significant decrease in plant species cover and richness. As on Apennine stripped grassland, we observed a loss in alpine and endemic species, on wind edge swards, a reduction in subalpine species was registered. These changes are likely attributable to the combined effect of higher temperatures, the increase in the growing period (e.g., later accumulation of snow and earlier meltdown), and the decrease in soil water availability triggered by global change.

This study evidenced an ongoing biodiversity loss on calcareous alpine grasslands of mountaintops in central Apennines, which had so far been observed until now only in the warmest and Southern Mediterranean summits of Europe. Furthermore, in our study area, the stripped and garland calcareous grasslands (especially those dominated by *Sesleria juncifolia*) have been revealed to be the most sensitive to this effect.

The current re-visitation study contributed to increasing our knowledge about vegetation changes in central Mediterranean mountain top plant communities and underlined the need for monitoring activities on these sentinel ecosystems, which are increasingly threatened by global change.

Analogous monitoring research should be carried in other Mediterranean high mountains, where consistent effects of climate change are forecasted in order to better understand local vegetation trends and adaptation strategies in subalpine, alpine, and nival ecosystems.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Headers information of each re-sampled plot in both the studied plant communities.

Plant Community	Relevé Number	Relevé Area (m ²)	Altitude (m a.s.l.)	Aspect	Slope (Degree)
Apennine stripped grasslands	1	16	2555	E	15
	2	16	2563	E	18
	3	16	2601	NW	15
	4	16	2483	S	13
	5	16	2558	SW	5
	6	16	2614	S	20
	7	16	2539	S	15
	8	16	2572	S	22
	9	16	2501	S	34
	10	16	2400	N	6
	11	16	2554	NE	7
	12	16	2567	E	7
Wind edge swards	1	16	2658		7
	2	16	2524	NW	10
	3	16	2529	SW	10
	4	16	2525	NW	7
	5	16	2479	S	5
	6	16	2481	S	7
	7	16	2481	E	4
	8	16	2610	SW	22
	9	16	2617	E	10
	10	16	2665	SE	16
	11	16	2597	NE	18
	12	16	2598	E	12
	13	16	2536	SE	20

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Chapter 2 – Measurement and analysis of plant functional traits on high mountain vegetation

2.1 - FUN-VIOLA: FUNctional traits of VegetatION of centraL Apennines

FUN-VIOLA: FUNctional traits of VegetatIOn of centraL Apennines

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Running head: Plant Functional traits on central Apennines

Abstract: FUN-VIOLA (FUNctional traits of VegetatIOn of centraL Apennines) is a database of field measured plant functional traits for species of Mediterranean high mountain habitats in central Italy. It includes records of 9 plant traits (Leaf Area, Specific Leaf Area, Leaf Dry Matter Content, Plant Height Vegetative, Plant Height Generative, Leaf Thickness, Seed Mass, Seed Length and Seed Width) of 80 species and subspecies widespread in alpine and subalpine grasslands of central Apennines. The species were retrieved from the most abundant ones of 139 relevés occurring in the VIOLA Database (<http://www.givd.info/ID/EU-IT-019>) and sampled in 5 EUNIS habitats type (code E4.436, code E1.54, code E4.38, code H2.4 and code E4.42). Species traits were measured by dedicated field measurements in the years 2017, 2020 and 2021. FUN-VIOLA provides unique information depicting plant functional ecology of alpine and subalpine vegetation in Mediterranean limestone mountains. FUN-VIOLA is included in TRY Plant Traits Database (www.try-db.org/TryWeb/Home.php).

Keywords: Alpine and subalpine species; Endemics; EUNIS habitats; Limestone Mountains; Mediterranean; Plant functional traits

Abbreviations: EUNIS = European Nature Information System

FUN-VIOLA (FUNctional traits of VegetatIOn of centraL Apennines) is a database of field measured plant functional traits depicting high mountain vegetation on central Italy (Gran Sasso, Maiella, Mainarde, Matese, Velino summits). It includes 80 plant species and subspecies, 29 of which endemics, distributed in 25 taxonomic families for which more of 500 records of 9 plant traits were collected on the alpine and sub-alpine grasslands of central Apennines. The taxonomic attribution and nomenclatural updates of vascular plant taxa follow Bartolucci et al. (2018). The measured traits are: Leaf Area (LA, mm²), Specific Leaf Area (SLA, mm²/mg), Leaf Dry Matter Content (LDMC, mg/g), Plant Height Vegetative (PHV, cm), Plant Height Generative (PHG, cm), Leaf Thickness (LT, g/mm²), Seed Mass (g), Seed Length (mm) and Seed Width (mm).

The measured species were selected as the most abundant ones (summing up 80% of total vegetation cover) on 139 relevés stored on the VIOLA (high mountain VegetatIOn of centraL Apennines) Database (<http://www.givd.info/ID/EU-IT-019>) (Stanisci et al. 2016b), which are representative of 5 EUNIS (European Nature Information System) habitat types: Apennine stripped grasslands (code E4.436), Central and southern Apennine dry grasslands (code E1.54), Oro-Apennine closed

grasslands (code E4.38), Temperate-montane calcareous and ultra-basic screes (code H2.4) and Windy edge swards (code E4.42).

Species traits were measured in a representative number of replicates and conforming a standardized protocol (Pérez-Harguindeguy et al. 2016). During field campaigns carried out on summer of the years 2017, 2020 and 2021 we measured for at least 10 individuals of each species: plant height (PHV and PHG), leaf traits (LA, SLA and LDMC of at least 20 healthy fully expanded leaves) and seed characteristics (Seed Mass, Seed Length and Seed Width of at least 100 seeds). Leaf and seed measurements were carried out in the “Majella Seed Bank” structure of the Maiella National park (Di Cecco et al. 2020).

FUN-VIOLA provides unique information depicting plant functional ecology of alpine and subalpine vegetation in Mediterranean limestone mountains. The database has a great potential for supporting ecological studies at different scales ranging from the analysis of functional strategies on alpine and subalpine habitats or the comparative study of high mountain vegetation worldwide to the comparison of ecological strategies on different ecosystems and biomes. Moreover, it may help to better explore the intra- and inter-specific functional diversity on high mountain plants. FUN-VIOLA is included in TRY Plant Traits Database (www.try-db.org/TryWeb/Home.php).

Author contributions: A.S. planned the research, A.S., M.V., L.D.M. and V.D.C. conducted the field sampling, A.S., M.V. and M.L.C. performed the statistical analyses and led the writing, while all authors critically revised the manuscript.

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2.2 - *Exploring plant functional diversity and redundancy of Mediterranean high-mountain habitats in the Apennines*

Article

Exploring Plant Functional Diversity and Redundancy of Mediterranean High-Mountain Habitats in the Apennines

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Abstract: We analyzed plant functional diversity (FD) and redundancy (FR) in Mediterranean high-mountain communities to explore plant functional patterns and assembly rules. We focused on three above-ground plant traits: plant height (H), a good surrogate of competition for light strategies, and specific leaf area (SLA) and leaf dry matter content (LDMC), useful indicators of resource exploitation functional schemes. We used the georeferenced vegetation plots and field-measured plant functional traits of four widely spread vegetation types growing on screes, steep slopes, snowbeds and ridges, respectively. We calculated Rao's FD and FR followed by analysis of standardized effect size, and compared FD and FR community values using ANOVA and the Tukey post hoc test. Assemblage rules varied across plant communities and traits. The High FR_H registered on snowbeds and ridges is probably linked to climatic filtering processes, while the high FD_H and low FD_{SLA} and FD_{LDMC} on steep slopes could be related with underlying competition mechanisms. The absence of FD patterns in scree vegetation pinpoint random assembly processes which are typical of highly unstable or disturbed ecosystems. Improved knowledge about the deterministic/stochastic processes shaping species coexistence on high mountain ecosystems should help researchers to understand and predict vegetation vulnerability to environmental changes.

Keywords: functional traits; plant height (H); specific leaf area (SLA); leaf dry matter content (LDMC); alpine vegetation; environmental heterogeneity; habitat filtering; assembly rules; competition



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1. Introduction

During the last few decades, there has been considerable interest in ecological research to analyze the distribution and fitness of natural communities across environmental gradients [1] to understand community assembly rules, a key factor in assessing the effects of global change on biodiversity [2–4]. Previous studies explored the processes behind species assemblages by analyzing taxonomic diversity [5–8], with the assumption that all species are equally dissimilar and contribute in a comparable way to ecosystem functioning [9,10]. However, there is great functional variability among plant species and different taxa likely play different roles in ecosystem functioning [11,12].

Functional traits are morpho-physio-phenological characteristics that affect the fitness of species, i.e., their growth, reproduction, competition and survival, in a specific environmental context [13]. Given their importance in providing early signals of environmental change and depicting the relationships between species and ecosystem functioning, there has been an increasing number of plant community studies based on the analysis of functional traits [10,14–17].

The coexistence of species in a community is determined by the interplay of deterministic processes (abiotic and biotic drivers) and stochastic processes (random drivers) [1]. Thus, functional diversity values (e.g., the variability of functional traits) of plant communities assembled by deterministic processes tend to depart from the diversity values that would be expected by chance [1,18]. In plant communities with high functional diversity values, species coexistence is ruled by biotic interactions such as competition. These interactions promote niche partitioning mechanisms (“limiting similarities”) [19] and prevent the occurrence of species with similar traits, or, in other words, a species assemblage with low functional redundancy. In the short term, such plant communities marked by specialized and low-redundance taxa could be particularly vulnerable to environmental alterations, as the extinction of a single species and the attendant loss of its ecological role could alter the ecosystem’s functioning [3,20]. Moreover, in the long term, high functional diversity values could support the ability of the altered plant community to adapt to environmental changes [11,21,22]. On the other hand, in a community with lower functional diversity than expected by chance, species coexistence may be ruled by harsh environmental factors that promote species convergence towards a few well-adapted and redundant functional traits in a process called “habitat filtering” [23]. Plant communities marked by species that share similar traits are quite resistant, because the loss of one species can be buffered by the presence of other functionally similar species, and thus the functioning of the ecosystem would not undergo alterations. However, in the long term, this low range of functional strategies would limit the altered plant community’s ability to adapt to and survive further changes [9].

While species assemblage patterns such as niche overlap or partition and their relation to ecosystem functioning have been analyzed in grassland and forest ecosystems [15,24,25], there is a need for the analysis of ecosystems particularly affected by and sensitive to global change, such as the arctic tundra and high mountains [17,26]. There has been some research dealing with single aspects of plant diversity in high-mountain communities, such as taxonomic diversity [27,28] and functional diversity [29–31], but functional redundancy issues have yet to be explored sufficiently [32].

High-mountain ecosystems are hotspots of plant diversity [33–35] expressing a unique interplay of biogeographic, biotic and abiotic factors. Unfortunately, high mountains are threatened by direct and indirect human pressures that alter biodiversity and ecosystem functioning. In particular, Mediterranean summits can be considered prominent “hotspots” of climate change [35,36], where biodiversity erosion is highly concerning [37]. There is evidence that, on these summits, the rapid increase in temperatures and drought stress is altering the composition and function of plant communities [32,38,39]. As on other summits around the world, mountain ecosystems in the central Apennines are being altered by global climate change [35,38], and there is an urgent need for more in-depth research on functional strategies that cope with the ongoing changes. Understanding functional assemblage mechanisms as well as functional redundancy issues at the species and community level is crucial for modelling and forecasting how biodiversity will change and how the functioning of ecosystems will alter in response to these global changes [40].

Given these considerations, the present work sought to analyze species assembly and functional redundancy across high-mountain Mediterranean plant communities. To explore the underlying mechanisms of plant species’ local coexistence, we analyzed functional diversity and redundancy based on a set of traits commonly used for depicting processes of competition (plant height: H) and resource exploitation (specific leaf area: SLA, leaf dry matter content: LDMC) that are involved in specific ecosystem services such as soil fertility and climate mitigation [41]. We specifically analyzed the ecosystem mosaic in the calcareous central Apennines, formed by four main vegetation types: the *Leucopoa dimorpha* community growing on screes, the *Sesleria juncifolia* community on steep slopes, the *Plantago atrata* community on snowbeds and the *Silene acaulis* community on ridges. In particular, we focused on the following questions: (1) How do functional diversity and

redundancy vary among plant traits? (2) Do functional diversity and redundancy vary across the different plant communities?

2. Materials and Methods

2.1. Study Area

We analyzed four plant community types representative of the high elevation zone of the Apennines limestone chain (Appendix A) and referable to the specific land units of screes, steep slopes, snowbeds and ridges [42]. Specifically, we considered: (a) the *Sesleria juncifolia* community, which consists of calciphilous stepped and garland grasslands, common on rendzina soils, sampled on steep slopes; (b) the *Leucopoa dimorpha* community that grows on limestone screes characterized by discontinuous vegetation growing on steep slopes with dry and debris-rich soils; (c) the *Silene acaulis* community represented by discontinuous vegetation in wind-scoured ridges growing on shallow soils, rich in debris; and (d) the *Plantago atrata* community, which consists of Oro–Apennine continuous grasslands growing on small snowbeds where there is a long period with long snow cover, a short vegetative period and humid soils [31,42–46]. Table 1 reports information on taxonomy (species richness and number of species), environmental conditions (elevation and slope) and ecological conditions, quantified with Ellenberg indicator values (ordinal classification of plants according to the position of their realized ecological niche along an environmental gradient) [47].

All the selected plant communities are habitats of conservation concern in Europe (EUcode 6170: Alpine and subalpine calcareous grasslands, EUcode 8120: Calcareous and calcshist screes of the montane to alpine levels) [48]) and are particularly rich in endemics, Southern European orophytes and Mediterranean montane species [42,49,50].

The climate in the central Apennines shows a typical Mediterranean pattern with low summer precipitation, negligible summer aridity and a wetter period in autumn. Summer precipitation increases towards higher elevations, which have a humid/hyperhumid water regime [51–53]. According to the Köppen–Geiger classification, the climate ranges from temperate–oceanic (Cfb) in the lower sector to subarctic (Dfc) at the summits [54].

Table 1. Brief description of the analyzed plant communities (A: *Leucopoa dimorpha* community, B: *Sesleria juncifolia* community, C: *Plantago atrata* community, D: *Silene acaulis* community) occurring in the different land units (according to Stanisci et al. [42]) in terms of taxonomic diversity (species diversity reported as 1-Simpson), community mean for Ellenberg indicator values (CM_{EIVS}) for Italian flora [55] calculated with presence/absence species data (L, light; T, temperature; U, soil moisture; R, soil reaction; N, soil nutrients) and local environmental features registered at plot level. Mean plot values along with standard deviation (in brackets) are reported.

		A— <i>Leucopoa dimorpha</i> Community	B— <i>Sesleria juncifolia</i> Community	C— <i>Plantago atrata</i> Community	D— <i>Silene acaulis</i> Community
Land unit		Screes	Steep slopes	Snowbeds	Ridges
Taxonomic diversity	Species richness	11 (6)	20 (5)	18 (6)	17 (7)
	Species diversity	0.61 (0.25)	0.8 (0.07)	0.77 (0.09)	0.77 (0.17)
Community Mean Ellenberg indicator values (CM_{EIVS})	CM_L	8.7 (0.9)	9.0 (0.3)	8.4 (0.3)	9.1 (0.3)
	CM_T	4.0 (0.9)	4.2 (0.8)	3.2 (0.3)	3.2 (0.3)
	CM_U	3.5 (0.5)	3.2 (0.2)	3.9 (0.3)	3.5 (0.3)
	CM_R	6.9 (0.5)	6.8 (0.4)	6.5 (0.4)	6.9 (0.4)
	CM_N	2.3 (0.6)	2.3 (0.2)	2.5 (0.4)	2.1 (0.3)
Environmental variables	Elevation (m a.s.l)	2266 (307)	2085 (264)	2392 (158)	2547 (165)
	Slope (°)	32.5 (10)	20.4 (10)	9.9 (12)	17.9 (16)

2.2. Data Collection

We extracted vegetation data from the VIOLA database (high mountain Vegetation of central Apennines [45,56]; European Vegetation Archive code—EU-IT-019 [57]). Plots carried out during the last few decades describing the four target plant communities were extracted and selected according to: (a) the presence of the pool of the diagnostic species, as reported in the Italian vegetation prodrome and EUcode manual for habitat identification [58,59], (b) maximized inter-plot spatial distance (plots separated by at least 200 m) and (c) comparable vegetation cover among plots. In total, 164 plots were selected, with an average size of 45 m², distributed as follows: 23 of the *Leucopoa dimorpha* community, growing on calcareous screes; 55 of the *Sesleria juncifolia* community, occurring on steep slopes; 49 of the *Plantago atrata* community, growing in snowbeds, and 37 of the *Silene acaulis* community, growing on mountain ridges. Taxa nomenclature follows that of Pignatti [60].

For functional analyses, given that it was not feasible to measure the trait values for all species in each plot [61], we selected the most abundant species limited to those taxa whose relative cumulative cover was 70% of vegetation cover on at least one of the considered plots [61]. Thus, for each plot, we ordered the species by decreasing relative cover values and, beginning from the most abundant one, we summed them up to 70% of the total plot vegetation cover. Following this procedure, we identified a set of 62 species for which we measured vegetative plant height (H, cm), specific leaf area (SLA, mm²/mg) and leaf dry matter content (LDMC, mg/g), which are good surrogates of the ecological functions of competitive ability and resource exploitation [62]. Species trait values were partially retrieved from recent measurements performed in the analyzed area (2016–2017) [31] and by dedicated field measurements carried out following the standardized protocol (2019) [62], in line with Zanzottera et al. [63]. Trait research based on data specifically measured in the analyzed area ensures more accurate information about plant strategies than that obtained from databases [64].

2.3. Indicator Species Analysis and Species-Level Redundancy

First, we explored the distribution pattern of the 62 most abundant species and their measured traits (H, SLA and LDMC) across the four analyzed plant communities by implementing indicator species analysis (ISA) [65] followed by species redundancy analysis [66]. The “species x plot” matrix was analyzed using plant community types as a grouping factor, with 999 permutations [65]. We identified the species discriminating each plant community (hereafter “community indicator species”), as those with ISA relative abundance over 0.6 and relative frequency higher than 0.25 [67].

Next, for each of the community indicator species identified, we measured their individual trait redundancy value (r_H , r_{SLA} , r_{LDMC}) with respect to the other species of the plant community as follows [66]:

$$r_i = 1 - \sum_{j \neq i} \frac{p_j}{1 - p_i} \delta_{ij} \quad (1)$$

where r_i is the redundancy value of species i with respect to the other species in the community, and δ is the functional dissimilarity for a given trait between species i and j . Functional dissimilarity (δ_{ij}), calculated with Gower distance [68], is = 0 when two species assume exactly the same trait values and 1 when two species have exactly the opposite trait values. Species redundancy values are expressed in a range from 0 to 1. The ISA was performed in the R environment (R Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org>, accessed on 1 April 2021) using the *mutipatt* function in the *indicspecies* package, while the species functional redundancy was calculated with R function *uniqueness*, provided by Ricotta et al. [66].

2.4. Community-Level Functional Diversity and Redundancy

The next step was to calculate the community-level functional diversity (FD) and redundancy (FR) using Rao's Quadratic Entropy (Q) [69]. We selected Rao's Q because it is able to summarize the abundance of the species and the functional distance of their traits and offers a sound framework for the simultaneous analysis of a variety of facets, such as taxonomic and functional parameters [70]. Rao's Quadratic Entropy expresses the expected dissimilarity between two individuals of a given assemblage selected at random with replacement:

$$Q = \sum_{i,j}^S \delta_{ij} p_i p_j \quad (2)$$

where S is the number of species, δ_{ij} is the dissimilarity between the i -th and j -th species, and p_i and p_j are the proportion of abundance of the i -th and j -th species in the vegetation plot.

When Q is implemented for measuring FD, the dissimilarity (δ_{ij}) between the i -th and j -th species may vary from 0 (two species have the same trait values) to 1 (two species have completely different trait values).

Rao's Q was also used for calculating the functional redundancy (FR), as follows [66]:

$$FR = 1 - \frac{FD}{TD} \quad (3)$$

where FD is functional diversity and TD is the Simpson index of dominance (1-Simpson) calculated with Rao's Q . TD represents the maximum value that FD may achieve, since the distance between each pair of species is fixed as $\delta_{ij} = 1$ for all $i \neq j$. Thus, FD may vary from 0 (all species present the same trait values) to TD (all species are completely functionally different) [63]. FR can assume values ranging from 1 (a highly redundant community in which all species are functionally identical) to 0 (no redundant communities with all the species functionally dissimilar). It should be noted that since FR is a fraction of FD and TD, it is independent of species richness [66].

For each community (the *Leucopoa dimorpha*, *Sesleria juncifolia*, *Plantago atrata* and *Silene acaulis* communities), we calculated FR and FD for each trait (FR_H , FR_{SLA} , FR_{LDMC} , FD_H , FD_{SLA} , FD_{LDMC}), using the Gower measure (δ_{ij}) because it standardizes the distance values (from 0 to 1) [68], allowing a comparison between TD and FD [70], which is necessary to calculate FR. Continuous trait values were log-transformed before calculation of the indices [61]. We calculated functional redundancy (FR) and functional diversity (FD) using the R function *uniqueness* [66].

To detect community assembly processes, we generated the distribution of expected random values of FD by shuffling the trait values across species 999 times and by calculating the standardized effect size [18] of FD for each trait (SES: observed FD values—mean 999 expected FD values/standard deviation of 999 expected FD values). Then, we assessed whether the distribution of SES values for each FD trait per plant community was significantly different from zero using a two-tailed t -test. Distribution of SES values significantly lower than 0 denotes "functional convergence", while that of values significantly higher than 0 indicates "functional divergence".

Variations in the standardized effect size of functional diversity (SES-FD) and in functional redundancy (FR) for each trait (i.e., H, SLA, LDMC) across the considered plant communities were quantified with distinct one-way analysis of variance (ANOVA) type I models, followed by Tukey post hoc tests [71]. For each significant model, the normality, homogeneity and independence of residuals were checked by the visual inspection of the residuals [72].

The *aov*, *TukeyHSD* and *t.test* functions in the stats package served to perform the ANOVAs, the Tukey post hoc test and the t -test, respectively.

3. Results

3.1. Indicator Species Analysis and Species-Level Redundancy

The results of ISA on the 62 most abundant taxa highlighted an elevated number of indicator species for each plant community, with 10 species for the *Silene acaulis* community (indicator values min = 0.49—max = 0.79); 9 for the *Plantago atrata* community (indicator values min = 0.65—max = 0.98); and 6 for both the *Leucopoa dimorpha* community (indicator values min = 0.42—max = 0.69) and the *Sesleria juncifolia* community (indicator values min = 0.44—max = 0.94).

The mean values of species-level functional redundancy for plant height (r_H) were lower for the *Sesleria juncifolia* community (mean = 0.74) and the *Leucopoa dimorpha* community (mean = 0.75), due to the co-occurrence of different strategies, namely those of tall graminoids (*Leucopoa dimorpha*) and short forbs (*Doronicum columnae*). On the other hand, the mean value of species-level height redundancy (r_H) was higher in the *Silene acaulis* community (mean = 0.81; *Pedicularis elegans* and *Galium magellense*) and the *Plantago atrata* community (mean = 0.84, *Poa alpina* subsp. *alpina*, *Ranunculus pollinensis* and *Trifolium thalii*) (Table 2).

Table 2. List of community indicator species for each plant community derived from ISA analysis. For each taxon, we report the indicator value (IndVal) and the species-level redundancy value for each trait (r_H : plant height; r_{SLA} : specific leaf area; r_{LDMC} : leaf dry matter content). Statistical significance of indicator values is also reported (n.s. $p > 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

Plant Community	IndVal	r_H	r_{SLA}	r_{LDMC}
A. <i>Leucopoa dimorpha</i> community				
<i>Achillea barrelieri</i> subsp. <i>barrelieri</i>	0.43 ***	0.86	0.79	0.64
<i>Arabis caucasica</i>	0.51 ***	0.86	0.90	0.76
+ <i>Cymbalaria pallida</i>	0.63 ***	0.63	0.81	0.67
<i>Doronicum columnae</i>	0.58 ***	0.74	0.79	0.66
+ <i>Isatis apennina</i>	0.69 ***	0.74	0.87	0.64
+ <i>Leucopoa dimorpha</i>	0.69 ***	0.68	0.73	0.52
B. <i>Sesleria juncifolia</i> community				
<i>Anthyllis montana</i>	0.80 ***	0.80	0.92	0.86
<i>Aster alpinus</i> subsp. <i>alpinus</i>	0.44 *	0.83	0.87	0.84
<i>Bromopsis erecta</i>	0.54 ***	0.65	0.91	0.79
<i>Carex humilis</i>	0.76 ***	0.82	0.92	0.88
<i>Globularia meridionalis</i>	0.79 ***	0.65	0.88	0.86
<i>Sesleria juncifolia</i> subsp. <i>juncifolia</i>	0.95 ***	0.73	0.92	0.83
C. <i>Plantago atrata</i> community				
<i>Crepis aurea</i> subsp. <i>glabrescens</i>	0.71 ***	0.87	0.65	0.65
<i>Gnaphalium diminutum</i>	0.94 ***	0.81	0.82	0.79
<i>Plantago atrata</i> subsp. <i>atrata</i>	0.96 ***	0.85	0.75	0.78
<i>Poa alpina</i> subsp. <i>alpina</i>	0.96 ***	0.88	0.80	0.67
+ <i>Ranunculus pollinensis</i>	0.92 ***	0.87	0.79	0.79
+ <i>Taraxacum apenninum</i>	0.70 ***	0.81	0.72	0.70
+ <i>Taraxacum glaciale</i>	0.66 ***	0.87	0.58	0.64
+ <i>Trifolium pratense</i> subsp. <i>semipurpureum</i>	0.76 ***	0.88	0.72	0.82
<i>Trifolium thalii</i>	0.98 ***	0.76	0.82	0.75
D. <i>Silene acaulis</i> community				
+ <i>Androsace villosa</i> subsp. <i>villosa</i>	0.55 **	0.80	0.87	0.85
<i>Anthyllis vulneraria</i> subsp. <i>pulchella</i>	0.68 ***	0.84	0.92	0.68
<i>Arenaria grandiflora</i> subsp. <i>grandiflora</i>	0.57 ***	0.83	0.90	0.84
+ <i>Armeria gracilis</i> subsp. <i>majellensis</i>	0.67 ***	0.76	0.76	0.76
+ <i>Festuca violacea</i> subsp. <i>italica</i>	0.50 *	0.82	0.92	0.83
+ <i>Galium magellense</i>	0.57 **	0.87	0.69	0.78
<i>Kobresia myosuroides</i>	0.52 ***	0.78	0.91	0.75
+ <i>Pedicularis elegans</i>	0.54 **	0.86	0.84	0.84
<i>Salix retusa</i>	0.80 ***	0.83	0.88	0.82
<i>Silene acaulis</i> subsp. <i>bryoides</i>	0.76 ***	0.69	0.92	0.84

+ Endemic taxon.

The mean value of species-level leaf area redundancy (r_{SLA}) was low in the *Plantago atrata* community (mean = 0.73, *Crepis aurea* subsp. *glabrescens* and *Taraxacum glaciale*)

and high in the *Sesleria juncifolia* community (mean = 0.90; *Sesleria juncifolia* and *Carex humilis*). Intermediate values of r_{SLA} were observed in the *Leucopoa dimorpha* community (mean = 0.82; with *Achillea barrelieri* subsp. *barrelieri* and *Isatis apennina*) and in the *Silene acaulis* community (mean = 0.86; *Anthyllis vulneraria* subsp. *pulchella* and *Arenaria grandiflora* subsp. *grandiflora*) (Table 2).

The mean value of species-level redundancy for LDMC (r_{LDMC}) assumed lower values in the *Leucopoa dimorpha* community (mean = 0.65 with *Leucopoa dimorpha* and *Isatis apennina*) and higher values in the *Sesleria juncifolia* community (mean = 0.84; *Carex humilis* and *Globularia meridionalis*). Intermediate r_{LDMC} values were observed in the species of the *Plantago atrata* community (mean = 0.73; *Ranunculus pollinensis* and *Trifolium thalii*) and of the *Silene acaulis* community (mean = 0.80; *Androsace villosa* subsp. *villosa* and *Arenaria grandiflora* subsp. *grandiflora*) (Table 2).

3.2. Community-Level Functional Diversity

The standardized effect size of functional diversity (SES-FD) for all the considered traits (H, SLA and LDMC) significantly varied among plant communities (Figure 1; Appendix B). Regarding plant height strategies, the *Sesleria juncifolia* and *Leucopoa dimorpha* communities showed significantly higher SES-FD_H values than the *Plantago atrata* and *Silene acaulis* communities (Figure 1a). The analysis of community leaf trait strategies (SES-FD_{SLA} and SES-FD_{LDMC}) evidenced higher SES-FD_{SLA} and SES-FD_{LDMC} values for the *Leucopoa dimorpha* and *Plantago atrata* communities (Figure 1b,c) than for the *Sesleria juncifolia* and *Silene acaulis* ones (Figure 1b,c).

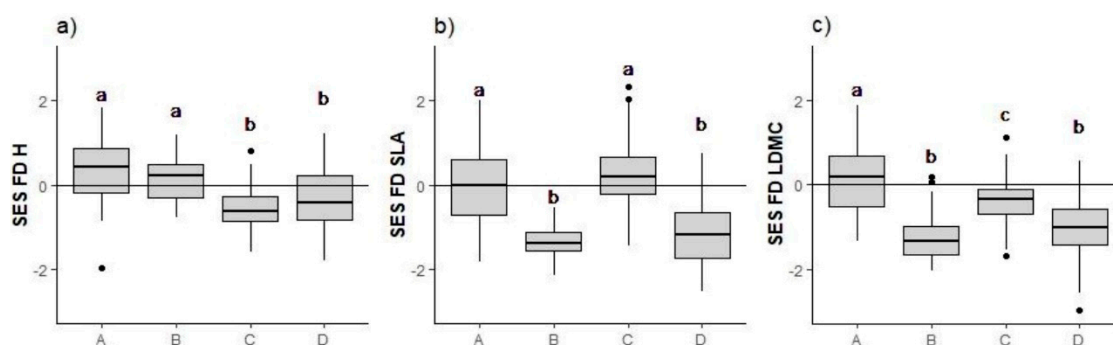


Figure 1. Boxplots comparing the analyzed plant communities in terms of standardized effect size functional diversity (SES-FD) for: (a) plant height (SES-FD_H), (b) specific leaf area (SES-FD_{SLA}) and (c) leaf dry matter content (SES-FD_{LDMC}) (A: *Leucopoa dimorpha* community, B: *Sesleria juncifolia* community, C: *Plantago atrata* community, D: *Silene acaulis* community). Boxplot letters indicate statistically significant differences among communities after Tukey's post hoc test ($p < 0.05$).

Significant departures of SES-FD_H from random expectation were observed for the *Sesleria juncifolia* community (functional divergence; Table 3) as well as for the *Plantago atrata* and *Silene acaulis* communities (functional convergence; Table 3). Conversely, the *Leucopoa dimorpha* community plant height assemblage did not differ from a random pattern (Table 3). Concerning leaf traits, the *Sesleria juncifolia* and *Silene acaulis* communities showed a convergent pattern (negative departure from random expectation) for both SLA and LDMC (Table 3). Conversely, the *Plantago atrata* community presented a divergent pattern for SLA and a convergent one for LDMC (Table 3), while the *Leucopoa dimorpha* community distribution pattern of SLA and LDMC did not differ from a random expectation (Table 3).

Table 3. Results of the two-tailed *t*-test assessing the standardized effect size of functional diversity per trait (SES-FD_H: plant height; SES-FD_{SLA}: specific leaf area; SES-FD_{LDMC}: leaf dry matter content) and plant community (A: *Leucopoa dimorpha* community, B: *Sesleria juncifolia* community, C: *Plantago atrata* community, D: *Silene acaulis* community). Statistical significance of *t*-test is also reported (n.s. $p > 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

Traits	A	B	C	D
SES-FD _H	0.35 n.s.	0.25 **	−0.49 ***	−0.3 *
SES-FD _{SLA}	−0.08 n.s.	−1.35 ***	0.29 *	−1.1 ***
SES-FD _{LDMC}	0.17 n.s.	−1.2 ***	−0.41 ***	−1 ***

3.3. Community-Level Functional Redundancy

Functional redundancy (FR) significantly varied across the analyzed plant communities and presented complementary behavior with respect to FD (Figure 2; Appendix B).

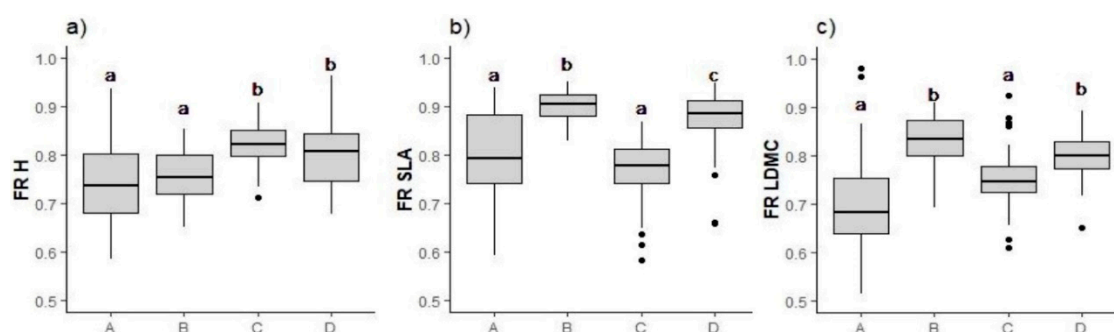


Figure 2. Boxplots comparing functional redundancy values (FR) of the analyzed plant communities (A: *Leucopoa dimorpha* community, B: *Sesleria juncifolia* community, C: *Plantago atrata* community, D: *Silene acaulis* community) for: (a) plant height (FR_H), (b) specific leaf area (FR_{SLA}) and (c) leaf dry matter content (FR_{LDMC}). Boxplots with different letters indicate statistically significant differences (Tukey’s post hoc test; $p < 0.05$).

We observed higher redundancy values for vegetative plant height (FR_H) in the *Plantago atrata* and *Silene acaulis* communities (Figure 2a). Concerning leaf traits, the *Sesleria juncifolia* community showed a higher redundancy value for both SLA (FR_{SLA}; Figure 2b) and LDMC (FR_{LDMC}; Figure 2c). On the other hand, we registered lower redundancy values for SLA in the *Plantago atrata* community (FR_{SLA}; Figure 2b) and for LDMC in the *Leucopoa dimorpha* community (FR_{LDMC}; Figure 2b).

4. Discussion

The distribution pattern of the 62 most abundant species varied across the different vegetation types. The relatively high number of indicator species for all the plant communities (higher number of species in the *Silene acaulis* community and lower number in *Sesleria juncifolia* communities) is most likely related to the high abiotic differences among the local environmental conditions of the plant communities forming the Apennine high-elevation vegetation mosaic [43]. Such high floristic variability between plant communities on high-mountain landscapes depicts the biodiversity response to topography, which plays a consistent role in modulating local climatic and soil conditions [73]. In the central Apennines, the interplay of climatic and edaphic factors across the altitudinal gradient has given rise to a complex mosaic of different vegetation types with distinct physiognomies and species composition [42] (see also Table 2). Accordingly, species coexistence patterns depicted by functional diversity (SES-FD_H, SES-FD_{SLA} and SES-FD_{LDMC}) and functional redundancy (FR_H, FR_{SLA} and FR_{LDMC}) varied across the analyzed vegetation mosaic. Functional redundancy varied but with a mirrored behavior with respect to functional diversity, confirming the “complementarity” of the information supplied by the two indices [74].

4.1. Vegetative Plant Height

The plant communities growing in particularly cold environments, such as the *Plantago atrata* vegetation of snowbeds and the *Silene acaulis* vegetation of ridges, presented significantly low functional diversity and high redundancy for plant height (low SES-FD_H and high FR_H). We observed a convergence in plant height, which could be related to the stringent climatic filtering mechanisms of upper elevations [23,30,75–77], which positively select short species able to benefit from a soil temperature that is higher than the air temperature [73,78]. Indeed, the climate of the Apennine summits and ridges is cold, with marked winter frosts [52] and long snow cover periods on snowbeds, all conditions that select functional strategies adapted to cold stress [29,31,76,77,79]—for example, those of specialist cryophilous species [42,78]. Here, the vegetation on snowbeds and ridges is dominated by short forbs (*Trifolium semipurpureum*: 3.1 cm; *Ranunculus pollinensis*: 2.7 cm; *Anthyllis pulchella*: 3.5 cm; *Galium magellense*: 2.46 cm; *Pedicularis elegans*: 4 cm) and short graminoids (*Kobresia myosuroides*: 8.5 cm; *Festuca italica*: 6.89 cm). The observed high redundancy for plant height (high FR_H) may enable plant communities to deal with environmental changes successfully in the short term, as the loss of one species could be buffered by the presence of other, functionally similar ones [9]. However, low plant height variability and high trait redundancy denote a reduced set of plant strategies, which indicates weak potential for reacting successfully to changing environmental conditions in the long term [11].

Conversely, mountain slopes with the *Sesleria juncifolia* community disclosed high values of plant height functional diversity (SES-FD_H) and low values of functional redundancy (FR_H). Given that vegetative plant height captures the functional dimension of competition for light [62], the high SES-FD_H is probably related to niche partitioning processes (limiting similarities) [19] that regulate species coexistence in the high mountain stands, where the growing season is longer. Indicator species in the *Sesleria juncifolia* community showed great variability in plant sizes, ranging from tall graminoids (*Sesleria juncifolia*: 16.8 cm; *Bromopsis erecta*: 32.7 cm) to short forbs (*Globularia meridionalis*: 2 cm; *Anthyllis montana*: 5.46 cm). Here, the higher diversity may suggest that the vegetation has a good ability to adapt to climate change in the long term, since the presence of functionally dissimilar species should indicate the potential of the vegetation to adapt to new environmental conditions [9,11]. In addition, the good cover of tall species should contribute to climate regulation processes and local soil fertility services (Appendix C).

The random behavior of SES-FD in the *Leucopoa dimorpha* community growing in screes suggests an underlying stochastic assemblage mechanism. Indeed, screes are characterized by sparse vegetation, with a small number of glareicole species coexisting with species coming from the neighboring communities, which randomly migrate and temporally survive on such extremely unstable substrates [80]. As such, this may preclude the establishment of a predictable plant community functionally modelled by such non-random assembly rules as habitat filtering and biotic interaction [1].

4.2. Leaf Traits

For the *Plantago atrata* snowbed community, we recorded high SES-FD_{SLA} values and low FR_{SLA}, which, as observed in other mountain ecosystems [81], could be interpreted as a community response to locally milder soil conditions [64]. Indeed, snowbeds are morphological units distributed at different altitudes and characterized by relatively rich and humid soils (CM_{EIV} for N; Table 1) [42], which may enhance local resource competition mechanisms and character shift strategies (Appendix C). Specifically, the high leaf diversity in snowbed vegetation is attributable to the co-occurrence of species having a broad spectrum of leaf functional performance ranging from fast-growing species (*Taraxacum glaciale*, SLA mean: 29.6 mm²mg⁻¹) to slow-growing species (*Plantago atrata*, SLA mean: 10 mm²mg⁻¹). Higher specific redundancy (functional similarity with coexistent species) was found for species having intermediate SLA values, such as *Gnaphalium diminutum* (SLA mean: 16.2 mm²mg⁻¹) and *Poa alpina* (SLA mean: 18.4 mm²mg⁻¹). Global warming and the consequent reduction in snow cover are expected to negatively affect snowbed

ecosystems, with results such as alterations in biogeochemical cycles, reduced forage for chamois kids and the filtering of water that feeds springs of potable water [82,83]. Snowbed ecosystem changes may also cause short-term alterations in leaf functions, but the presence of functionally dissimilar plants might support good mid/long-term potential to cope with climatic and land use alterations.

In the *Silene acaulis* community growing on ridges, we noted the functional convergence of leaf strategies (low $SES-FD_{SLA; LDMC}$ and high $FR_{SLA; LDMC}$), which, like observations for plant height, could be related to a cold filtering effect. The higher redundancy of slow-growing species suggests the ability to hold the position in an extreme environment and to keep ecosystem functions after species loss (high resistance) [82]. However, the SLA values on criophilous indicator species are very variable and range from relatively high values for *Galium magellense* (SLA mean: $23.2 \text{ mm}^2\text{mg}^{-1}$) and *Armeria majellensis* (SLA mean: $19.42 \text{ mm}^2\text{mg}^{-1}$) to relatively low values for *Anthyllis pulchella* (SLA mean: $13.44 \text{ mm}^2\text{mg}^{-1}$), *Silene acaulis* (SLA mean: $12.68 \text{ mm}^2\text{mg}^{-1}$) and *Festuca italica* (SLA mean: $11.4 \text{ mm}^2\text{mg}^{-1}$). This high variability in species leaf performance is attributable to the co-occurrence of different growth rate strategies that range from acquisitive resource use (high SLA values), which optimizes rapid carbon gain during the short growing season [31,77], to conservative resource use (low SLA values), in which the adoption of a slow-growth strategy assures the ability to survive environmental hazards [73,79].

The convergent pattern registered for leaf traits (low $SES-FD_{SLA; LDMC}$ and high $FR_{SLA; LDMC}$) in the *Sesleria juncifolia* community growing on calcareous slopes could be related to the interplay of two filtering environmental factors, winter frost stress and soil drought [31], which are particularly severe in Mediterranean limestone massifs [30,52,84]. In particular, the slow growth of perennial species (grasses and sedges) represents a good adaptation for both freezing and aridity [29,85] (see also CM_{EIV} for N in Table 1). This convergence towards similar leaf functional strategies well-adapted to climatic stress is seen in very similar indicator species (*Aster alpinus* mean SLA: $12.12 \text{ mm}^2\text{mg}^{-1}$, and *Sesleria juncifolia* mean SLA: $9.50 \text{ mm}^2\text{mg}^{-1}$). The high functional redundancy of the *Sesleria juncifolia* community should support good immediate ecosystem resistance to environmental alterations [86] but, at the same time, the limited range of leaf strategies makes these grasslands poorly adapted to further long-term environmental alterations.

The leaf trait diversity of the *Leucopoa dimorpha* community of screes ($SES-FD_{SLA; LDMC}$) did not differ from values generated by chance (Table 3), indicating the occurrence of casual processes of local colonization and extinction, and the absence of a mature, well-structured plant community. It should be noted that on high-mountain screes in the Central Apennines, soils are highly erodible due to the steepness of slopes, the incoherent substrate and the trampling pressure exerted by the endemic chamois [83]. The interplay of such dynamic abiotic and abiotic factors may enhance the stochastic colonization of plant species coming from neighboring habitats, as well as their local extinction.

In short, as observed in the temperate region [64], plant trait diversity in the central Apennine limestones seems to be related to local environmental variability.

5. Conclusions

The present research on high-mountain vegetation communities explored vegetation assembly rules from a functional perspective, as well as the degree of functional redundancy, and contributes to knowledge about the relations between plant species distribution patterns and the physical environment (snowbeds, ridges, steep slopes and screes) of Mediterranean landscapes. The interpretation of our results in light of previous research suggests the primary role of environmental features such as climate and soil moisture in community assembly, as we observed distinct selective effects (abiotic filters and biotic interaction) on all the measured above-ground plant traits and each considered plant community. Our findings gave further evidence of the essential contribution of trait-based analysis for understanding how ecosystems respond to environmental change. The varia-

tion in functional diversity was coupled with a converse variation in functional redundancy, revealing that both indices capture complementary information—namely, the degree of species unicity vs. similarity.

In addition, the analysis of species co-occurrence and the assessment of species-level redundancy sheds light on the functional role of indicator species, which should be of particular concern for endemic taxa. The species-level analysis made it possible to identify those functionally similar taxa that better express the species coexistence at community level. Even so, further studies are needed to explore the effects of climate variation on these functional strategies both at species and community level.

The measured above-ground plant traits captured different aspects of the ecological niches of species [16], but further investigation using other sets of traits, such as below-ground and reproductive traits, and incorporating intraspecific trait variability is needed to achieve a deeper understanding of the underlying mechanisms of species coexistence [77].

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Appendix A. Location of the Study Area

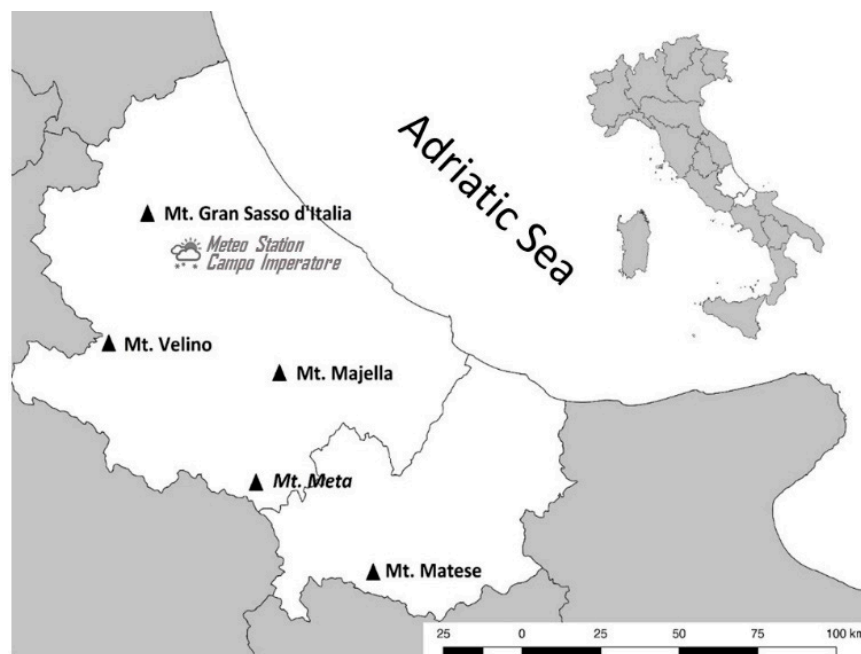


Figure A1. Location of the study area and the mountain massifs of the Central Apennines (Abruzzo and Molise Regions in white).

Appendix B. Detailed Results of ANOVA Models for Standardized Effect Size of Plant Height (H), Specific Leaf Area (SLA) and Leaf Dry Matter Content (LDMC)

Table A1. Results of the ANOVA tests for standardized effect size of functional diversity (SES-FD) and functional redundancy (FR) considering the traits of (H) plant height, (SLA) specific leaf area and (LDMC) leaf dry matter content. Plant community type was the grouping factor (df = 3).

Index	F	p	R ²
SES-FD _H	16	<0.001	0.23
FR _H	16	<0.001	0.23
SES-FD _{SLA}	56.48	<0.001	0.52
FR _{SLA}	48.4	<0.001	0.48
SES-FD _{LDMC}	32.57	<0.001	0.38
FR _{LDMC}	21	<0.001	0.28

Appendix C. Functional Composition (Community Weighted Mean: CWMs) of the Analyzed Plant Communities for Plant Height (H), Specific Leaf Area (SLA) and Leaf Dry Matter Content (LDMC)

To better describe the functional characteristics of the compared communities, we used the community-weighted mean values for each single trait (CWM_H; CWM_{SLA}; CWM_{LDMC}), which summarize the mean values of traits at plot level [87]. This was computed by multiplying the “species x plot” matrix with the “species x traits” matrix as follows:

$$CWM = \sum_{i=1}^s p_i x_i$$

where CWM is the community-weighted mean, x_i is the trait value of a given species and p_i is the relative frequency of the i -th species, based on cover data. We compared plant community CWM values using ANOVA followed by Tukey’s post hoc test. In order to reduce inflated type I error rates [88], we integrated ANOVA analysis with the “Max Test” procedure [84]. We ran the ANOVAs integrated with the Max Test with the *test.cwm* function (method “aov”, test “max”) in the *weimea* package [89].

As reported in Figure A2, *Plantago atrata* is characterized by higher CWM_{SLA} values (Figure A2b) and lower CWM_{LDMC}, which reflects its fast-growing strategies (higher cover of perennial forbs with competitive strategies), supported here by the fertile and humid soils of the snowbeds. The *Sesleria juncifolia* community presented lower values of SLA and higher values of LDMC, indicating the dominance of slow-growing strategies (higher presence of tall perennial grass species with competitive stress-tolerant strategies) able to grow and keep its position on high-mountain steep slopes. As previously reported [31], the *Silene acaulis* ridge community is characterized by low plants and high leaf dry matter content, denoting stress-tolerant mechanisms that increase their acquisitive strategies during the short growing season of the summer to maximize resource exploitation. Finally, the traits of the *Leucopoa dimorpha* community, growing on calcareous calcshit screes, depict random processes due to the dynamic substrate (see also the Discussion).

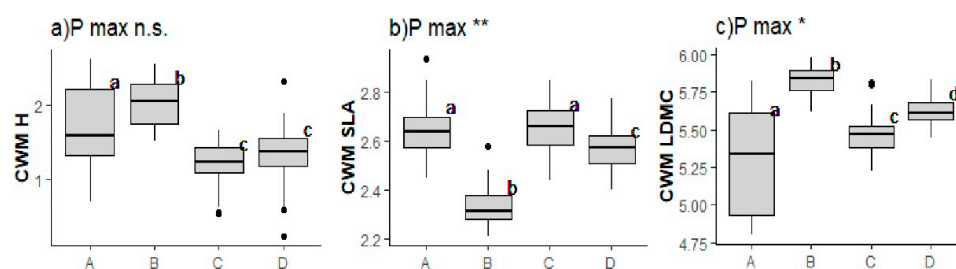


Figure A2. Boxplots comparing the functional characteristics of the analyzed plant communities (A: *Leucopoa dimorpha* scree community, B: *Sesleria juncifolia* steep slope community, C: *Plantago atrata* snowbed community, D: *Silene acaulis* ridge community) in terms of community-weighted mean (CWM) for the functional strategies related to plant height (a), SLA (b) and LDMC (c). Boxplots with different letters indicate statistically significant differences among them after Tukey's post hoc test ($p < 0.05$). Statistical significance of ANOVA analysis is also reported (n.s. $p > 0.05$; * $p < 0.05$; ** $p < 0.01$).

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CONCLUSION

The present PhD thesis contributes to increase and update the ecological knowledge concerning mid-term vegetation changes occurring in Mediterranean high mountain ecosystems. It provides new scientific information on floristic-structural and ecological changes occurred on alpine vegetation in central Apennines (Italy) over the last 20 years and on the morpho-functional characteristics of high mountain plant species.

The comparison of data collected on historical and revisited actual georeferenced phytosociological relevés (Re-visitation study) in high mountain ecosystems of central Apennines evidenced consistent changes on vegetation diversity, composition, structure and ecology and that such changes varied across different communities occurring on different land units.

The *Galium magellense* community, growing on screes, and the *Trifolium thalii* community on snowbeds, showed opposite trends of variation in species richness and diversity values (**Chapter 1.1**; Varricchione et al., 2021). As on screes we have registered an increase on species diversity, on snowbeds and dolines we observed a decrease. The obtained results are most likely related with two important drivers insisting in central Apennines summits: a) land use change, here related with increasing grazing pressure of Apennine chamois (*Rupicapra pyrenaica ornata* Neumann, 1899); and b) rising temperatures and climate change.

The Apennine chamois was reintroduced in the Maiella National Park at the beginning of 1991 and increased its population thereafter with reproduction rates of 20% per year (Antonucci et al., 2010), counting in 2021 over 1500 individuals. It is noteworthy that the Apennine chamois spends the summer months on screes, while during late spring and early summer, the females and juveniles preferentially feed on snowbed grasslands occupied by dense herbaceous communities (Stanisci et al., 2011), which supplies a protein-rich diet optimal for weaning (Frate et al., 2018; Lovari et al., 2020). On screes, the growing pressure of this wild ungulate, providing available nitrogen in the soil with its feces (Lovari et al., 2020), determined a gain in nitrophilous species (e.g. *Carduus chrysacanthus*, *Poa alpina* subsp. *alpina*). On snowbeds vegetation instead, the increased wildlife grazing pressure promoted a decrease of some scapose hemicryptophytes (H scap) species (e.g. *Phyteuma orbiculare*, *Arabis alpina* subsp. *caucasica*, *Cerastium cerastoides*) along with a low increase in cover of any caespitose hemicryptophytes (H caesp) species (e.g. *Trifolium thalii*, *Phleum rhaeticum*, *Festuca violacea* subsp. *italica*). In fact, among the forbs, the scapose hemicryptophytes are slightly less performant towards grazing pressure (López-i-Gelats et al., 2015), while the grasses (H caesp), being capable of vegetative reproduction and spread, are well adapted to moderate-high grazing pressure (Evju et al., 2009; Catorci et al., 2011; Mayer et al., 2017).

The rising temperatures also altered screes and snowbed plant communities on specific ways. On screes we registered an increase of nitrophilous species probably because the combination of milder temperatures promoting faster organic matter decomposition rates (of plant dead matter and wildlife feces) and a raise in atmospheric nitrogen deposition particularly severe on mountain summits (Gillet et al., 2016). Moreover, the increase in species richness and diversity values over time in the *Galium magellense* scree community is also linked with higher cover of consolidating species (e.g. *Androsace villosa* subsp. *villosa*, *Salix retusa*), which participate to scree stabilization processes. As observed in other European summits (Patil et al., 1982; Cannone et al., 2003), this process is due to the development of incipient soils expanding inward on the scree from its base and fringes. On snowbeds community we registered a general expansion and cover increase of some thermophilic herbaceous

species (e.g. *Trifolium pratense* subsp. *semipurpureum*, *Taraxacum apenninum*). Similar trends so called “greening process” were observed in other alpine ecosystems, where, due to increasing temperatures, some species typical of lower vegetation belts (mountain) expand their distribution towards upper mountain sectors, and other species living on environmental units with mild environmental conditions shift and expand their distribution to the neighboring communities (Carlson et al., 2017; Bolton et al., 2018).

Concerning, the *Sesleria juncifolia* community growing on steep slopes and the *Carex myosuroides* community growing on wind edge swards, we registered a significant loss of biodiversity, given by a the decrease in plant species cover and richness (**Chapter 1.2**; Varricchione et al., 2022). These changes could be linked with the combined effect of rising temperatures, longer growing period and decreasing soil water content all triggered by climatic change and that on carbonate substrates are particularly stringent. The climatic analysis of the study area using soil temperatures registered by the International Project GLORIA (Global Observation Research Initiative in Alpine Environments) during the last decades gave evidence of a rise in the mean annual and mean autumn soil temperatures and a prolongation of the vegetative period (e.g., the number of days with temperatures above 2 °C). These factors might determine on the *Carex myosuroides* community a decline in subalpine (e.g., *Carex kitaibeliana*, *Helianthemum oelandicum* subsp. *alpestre*) and suffruticose chamaephytes (CH suffr; e.g., *Iberis saxatilis* subsp. *saxatilis*, *Noccaea stylosa*) species; and, on the *Sesleria juncifolia* community, a decrease in some alpine (e.g., *Plantago atrata* subsp. *atrata* and *Poa alpina* subsp. *alpina*) and endemic (e.g., *Festuca violacea* subsp. *italica*) species, along with a decline in the hemicryptophytes with rosette (H ros) and scapose hemicryptophytes (H scap) (e.g., *Armeria gracilis* subsp. *majellensis*, *Ranunculus pollinensis*, *Scorzoneroides montana* subsp. *breviscarpa* and *Viola eugeniae* subsp. *eugeniae*) species. The late accumulation of snow and the early meltdown in the windy edge, allowed an increase of the daily temperature range and a higher winter frost stress, both conditions which limit the development and survival of several subalpine species (Edwards et al., 2007; Petriccione and Bricca, 2019). Moreover, as observed on other Mediterranean alpine ridges (Steinbauer et al., 2022), the harsher climatic conditions in the windy edges of central Apennines seem to induce a decrease in cushion plants cover (CH suffr).

In steep slope grasslands, in concomitance with the increase in temperatures and drought stress, we observed a decline on cryophilous alpine and endemic species, as well as of small hemicryptophytes (H ros; H scap) species, which seem more vulnerable and weakly adapted to cope with these new climatic conditions (Gottfried et al., 2012; Evangelista et al., 2016a; Steinbauer et al., 2022). Among the analyzed communities, *Sesleria juncifolia* grasslands growing on steep slopes, registered a high decline in cryophilous, rare and endemic species, and resulted the most vulnerable to global change. Our research evidenced a particular process of biodiversity loss on calcareous alpine grasslands of central Apennines, as recently observed in the warmest and Southern Mediterranean summits of Europe (Kazakis et al., 2021; Lamprecht et al., 2021). Such results confirm the great importance of adequate protection strategies for Mediterranean alpine-nival communities as well as ecological monitoring as claimed by the European Habitat Directive (43/92/EEC).

Another interesting output of our research concerns the usefulness of diagnostic species for monitoring purposes. On the analyzed plant communities the diagnostic species (identified according with the European Habitat Directive- 43/92/EEC), presented the same trends of variation over time of the overall species pool, suggesting their great potential for ecosystem monitoring on high mountain habitats. Our results gave evidence of the usefulness of diagnostic species to implement

monitoring campaigns and to support local management bodies on the achievement of the European community reporting exigencies and monitoring commitments.

The strength of our results depends also on the adopted re-visitation approach. Re-visitation, here implemented by extracting and re-sampling historical georeferenced plots stored in a database (VIOLA), represented a sound and cost-effective monitoring procedure that matches the need of periodical reporting requested by the European HD. Considering that historical vegetation plots and vegetation databases are widely available in many European countries (EVA, European Vegetation Archive; <http://euroveg.org/eva-database>, Chytrý et al., 2016), the adopted re-visitation study has the potential for application on other areas and EU habitat types in Italy and Europe at different scales (e.g. local, regional). Furthermore, the re-visitation of historical relevés, assures consistent data for long periods of time. In particular the knowledge of the abundance and distribution of species over time contributes to increase the understanding of vegetation dynamics of high mountain habitats and offers new support to planners for identifying effective strategies to protect and manage such fragile ecosystems. For example, our results suggested the need to improve ex situ conservation actions for cryophilous and endemic species, which are more threatened by the ongoing climate change, assuring a set of facilities such as a botanical gardens, seed banks, and nurseries that can assure the seed storage and the plant propagation. In addition, it is essential to investigate on micro-refugia where the endangered plant species may find suitable habitats to overcome the current warming period and implement plans for preserving these important conservative sites.

The contribution of the present research in the field of functional ecology is also relevant. This PhD thesis (**Chapter 2**) contributed to gain knowledge on plant traits (e.g. H: plant height, SLA: Specific Leaf Area and LDMC: Leaf Dry Matter Content) of high mountain species and their variation across community types and land units on high mountain landscapes in central Apennines. Concerning functional diversity and redundancy, we observed consistent plant traits differences across land units and plant communities encompassing environmental variability determined by factors shaping biodiversity at different scales (Bricca et al., 2021).

For instance, snowbeds community is characterized by high redundancy of plant height (FR_H : Functional Redundancy of height) and a convergence for functional diversity (low $SES-FD_H$), both functional strategies that may be assure species survival on habitats with very long periods of snow cover. Indeed, in this environment, plant species are well adapted to cold stress and tend to be very small and with low heights (Dainese et al., 2012). Concerning the specific leaf area (SLA) snowbeds present low functional redundancy values (FR_{SLA}) and a divergence for SLA diversity (e.g. high $SES-FD_{SLA}$) and such functional behavior may be linked with the presence of soils rich in organic matter and moisture that favor the coexistence of species with different leaf strategies (Stanisci et al., 2011). On the other hand, the windy edges community, is characterized by high redundancy and functional convergence values for all the analyzed traits (H, SLA and LDMC). This convergence of plant traits is most likely related with the stringent environmental filtering mechanisms which are particularly pronounced on very cold environments as high mountains (Pontes et al 2015, Petriccione and Bricca, 2019, Di Biase et al., 2021). On steep slopes we registered a functional convergence pattern of leaf traits (high values of FR_{SLA} and FR_{LDMC} and low values of $SES-FD_{SLA}$ and $SES-FD_{LDMC}$), that could be related with the interaction of two environmental filtering factors, cold stress and soil drought (Stanisci et al., 2020), which are particularly severe in the Mediterranean limestone massifs (Bricca et al., 2019). In contrast, on scree communities we registered the absence of significant patterns of FD and FR which could be due to random processes of colonization and extinction, and to the absence

of a mature and well-structured community. Screes indeed, in the central Apennines, are particularly dynamic environments, consisting of highly erodible soils due to the presence of inconsistent substrate and the pressure exerted by the Apennine chamois (Lovari et al., 2020).

Our results highlighted the great variability of plant species distribution pattern on high mountain landscapes and the occurrence of specific biodiversity changes on each vegetation type and land unit over the last 20 years. Furthermore, they increased the knowledge on species coexistence aiding to better understand high mountain vegetation vulnerability to environmental changes.

Another relevant new contribution of the present thesis is the creation of the first database of field measured plant functional traits for species of Mediterranean high mountain habitats in central Apennines (FUN-VIOLA; Varricchione et al., 2023). FUN-VIOLA stores plant traits measurements of 9 morphological variables (e.g. Leaf Area, Specific Leaf Area, Leaf Dry Matter Content, Plant Height Vegetative, Plant Height Generative, Leaf Thickness, Seed Mass, Seed Length and Seed Width) registered for 80 species and subspecies, providing unique information about high altitude vegetation of Mediterranean limestone mountains. FUN-VIOLA data was uploaded on the global database of plant traits (TRY: www.try-db.org/TRYWeb/Home.php), it is periodically updated, and can support a wide range of ecological studies on functional strategies on alpine and subalpine habitats at local, regional and national/international level. Furthermore, FUN-VIOLA represents a good starting point to explore the intra- and inter-specific functional diversity on high mountain plants.

The results of the present PhD thesis offer a sound baseline for further studies on vegetation dynamics and functional morphological characteristics on Mediterranean and non-Mediterranean ecosystems. Moreover, the applied re-visitation approach together with the new information stored in FUN-VIOLA database could aid to the analysis of functional and taxonomic diversity over time in high mountain ecosystems and carrying out an ecological monitoring of this ecosystem over time.

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SUPPLEMENTARY MATERIAL

Table S1 - Correspondence among the different analyzed vegetation types and the relative Habitat code according to the Annex I of the Habitats Directive (92/43/CEE) and the EUNIS classification (Chytrý et al., 2020).

Vegetation type	EU Habitat Code (92/43/CEE Directive)	EUNIS Code
<i>Trifolium thalii</i> community	6170 EU Habitat – alpine and sub- alpine calcareous grasslands	Code E4.38 - Oro-Apennine closed grasslands
<i>Plantago atrata</i> community	6170 EU Habitat – alpine and sub- alpine calcareous grasslands	Code E4.38 - Oro-Apennine closed grasslands
<i>Galium magellense</i> community	8120 EU Habitat- calcareous and calcshist screes of the montane to alpine levels - <i>Thlaspietea rotundifolii</i>	Code H2.4 - Temperate-montane calcareous and ultra-basic screes
<i>Leucopoa dimorpha</i> community	8120 EU Habitat- calcareous and calcshist screes of the montane to alpine levels - <i>Thlaspietea rotundifolii</i>	Code H2.4 - Temperate-montane calcareous and ultra-basic screes
<i>Sesleria juncifolia</i> community	6170 EU Habitat – alpine and sub- alpine calcareous grasslands	Code E4.436 - Apennine stripped grasslands
<i>Carex myosuroides</i> community	6170 EU Habitat – alpine and sub- alpine calcareous grasslands	Code E4.42 - Windy edge swards
<i>Silene acaulis</i> community	6170 EU Habitat – alpine and sub- alpine calcareous grasslands	Code E4.42 - Windy edge swards

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