

Article

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

Marco Varricchione ¹, Maria Laura Carranza ^{1,*}, Valter Di Cecco ², Luciano Di Martino ²
and Angela Stanisci ¹

¹ EnvixLab, Department of Biosciences and Territory, University of Molise, C. da Fonte Lappone. 86090, Pesche and Via Duca degli Abruzzi 67, 86039 Termoli, Italy

² Maiella Seed Bank, Maiella National Park, Loc. Colle Madonna, 66010 Lama dei Peligni, Italy

* Correspondence: carranza@unimol.it

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



Citation: Varricchione, M.; Carranza, M.L.; Di Cecco, V.; Di Martino, L.; Stanisci, A. Warmer and Poorer: The Fate of Alpine Calcareous Grasslands in Central Apennines (Italy). *Diversity* **2022**, *14*, 695. <https://doi.org/10.3390/d14090695>

Academic Editor: Michael Wink

Received: 28 July 2022

Accepted: 19 August 2022

Published: 23 August 2022

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

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].

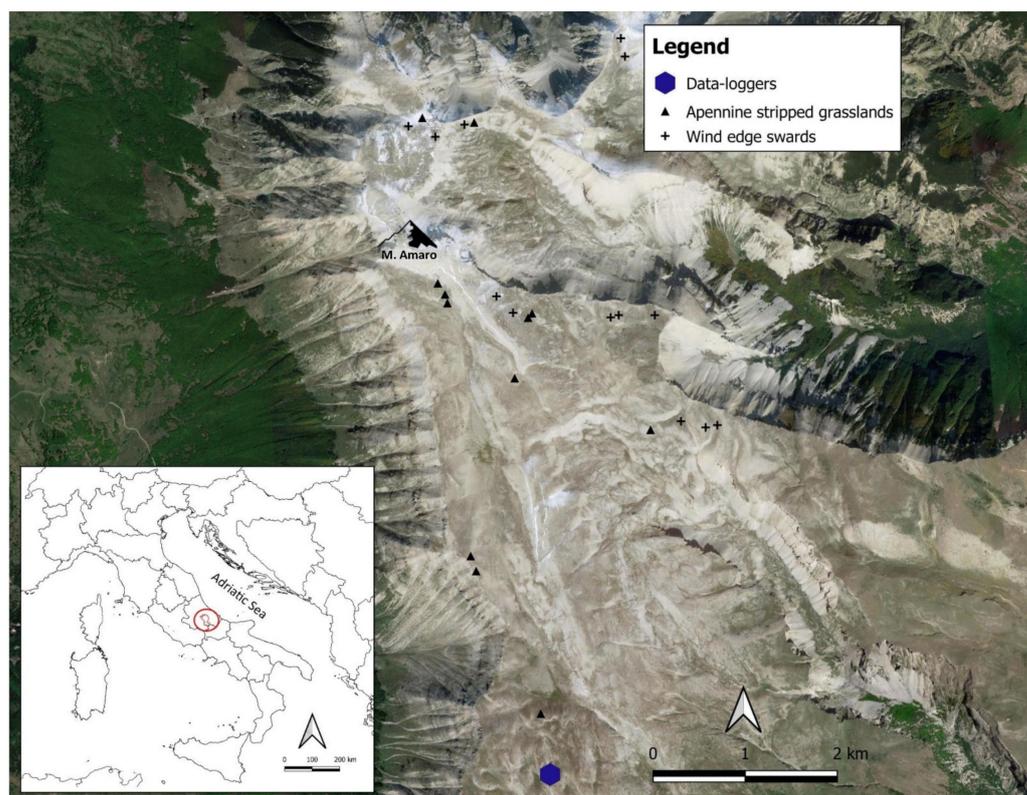


Figure 1. Study area (Maiella National Park) along with the distribution of vegetation plots on Apennine stripped grasslands (EUNIS code E4.436) and wind edge swards (EUNIS code E4.42) and of the GLORIA data-loggers measuring soil temperatures on Mt. Femmina Morta.

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).

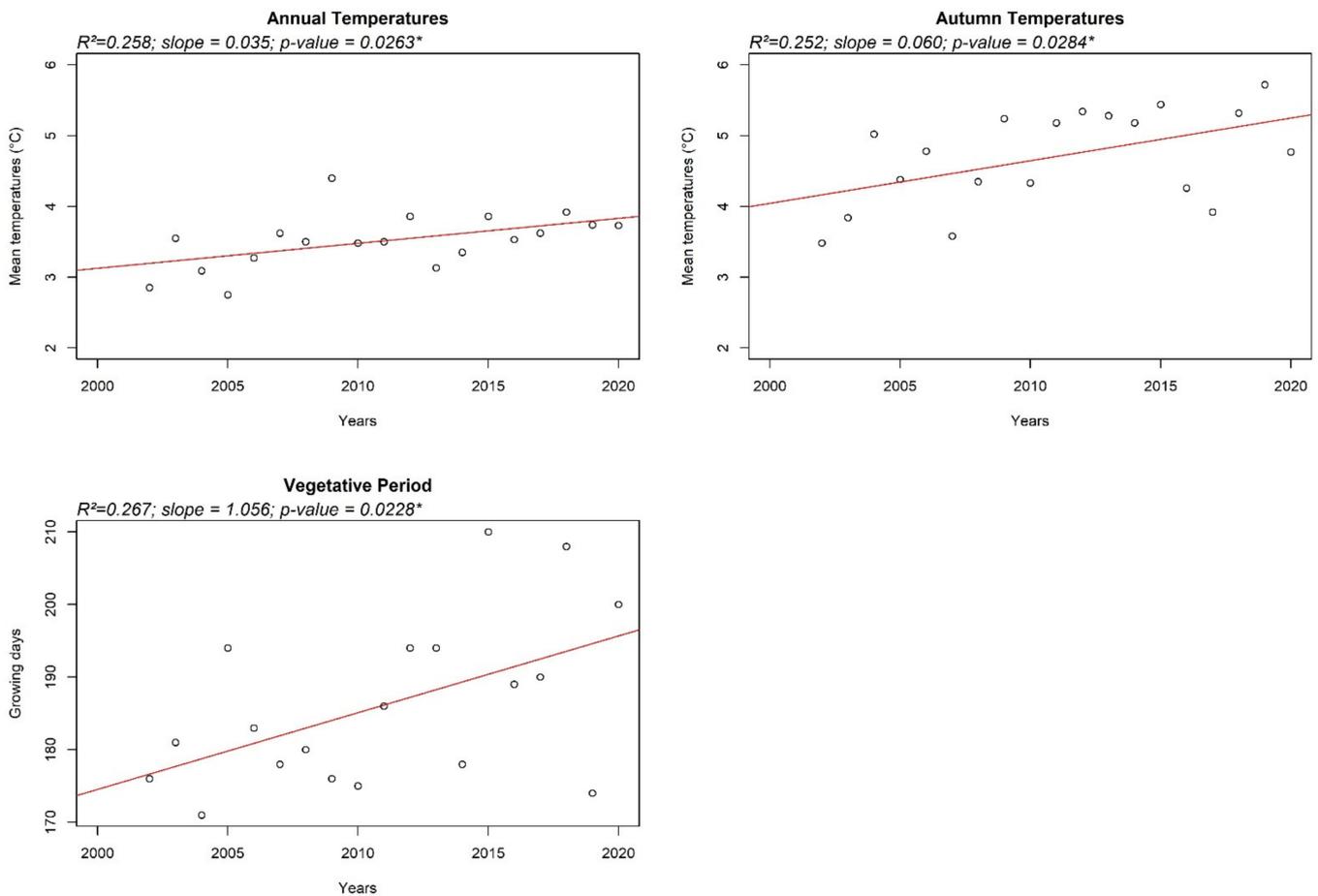


Figure 2. Annual and autumn (September–November) mean soil temperatures ($^{\circ}\text{C}$) and vegetative period (e.g., the number of days with temperatures above 2°C) for the period 2002 to 2020. Asterisks indicate significant trends. Data were retrieved from data-loggers of GLORIA monitoring network (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 salinca</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*).

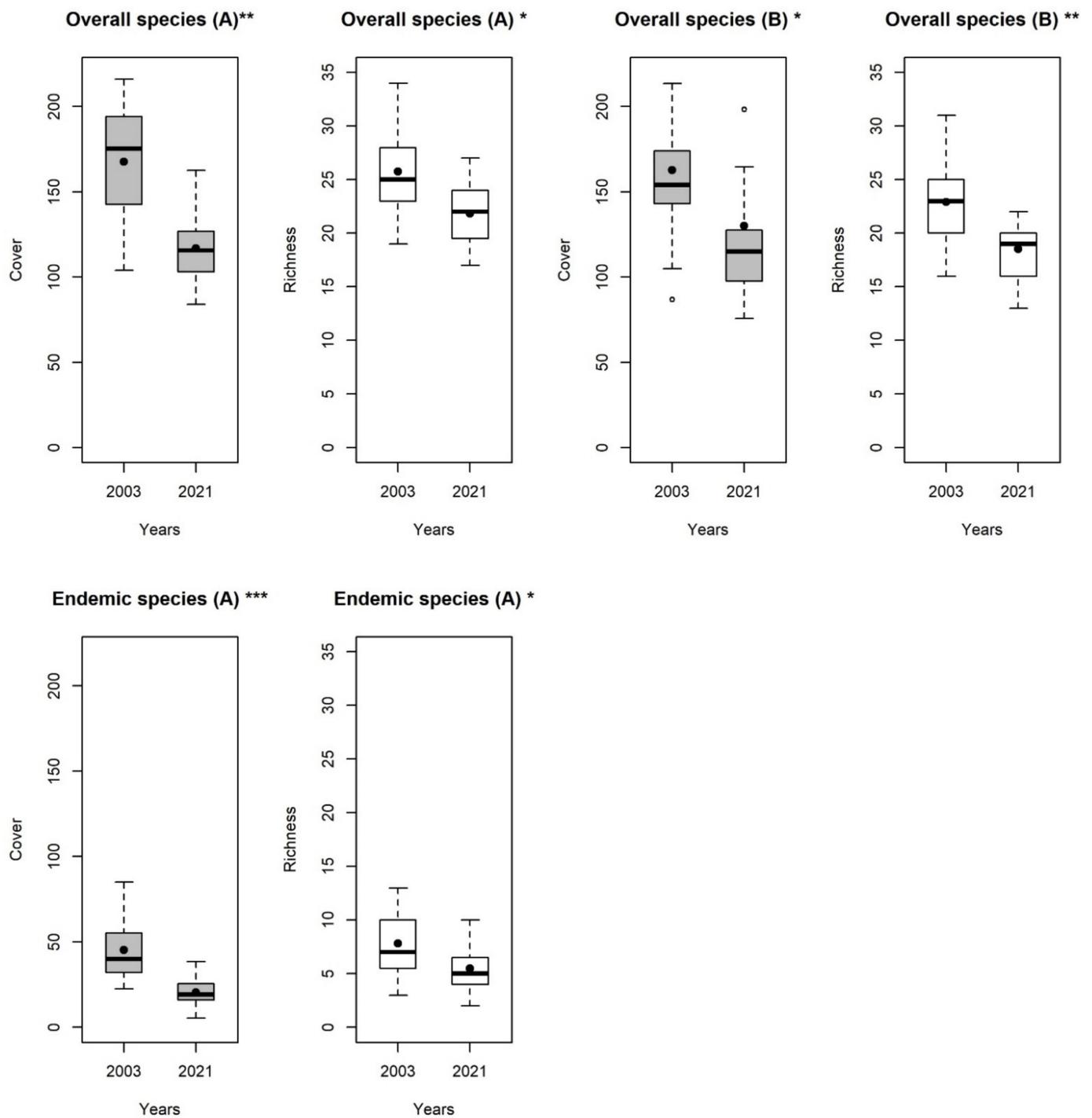


Figure 3. Boxplot comparing cover (grey) and species richness per 4×4 m plot (white) of overall and endemic species in two time steps (T1: 2003 and T2: 2021) in Apennine stripped grasslands (A) and wind edge swards (B). Only the significant results are reported. Asterisks indicate significant differences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

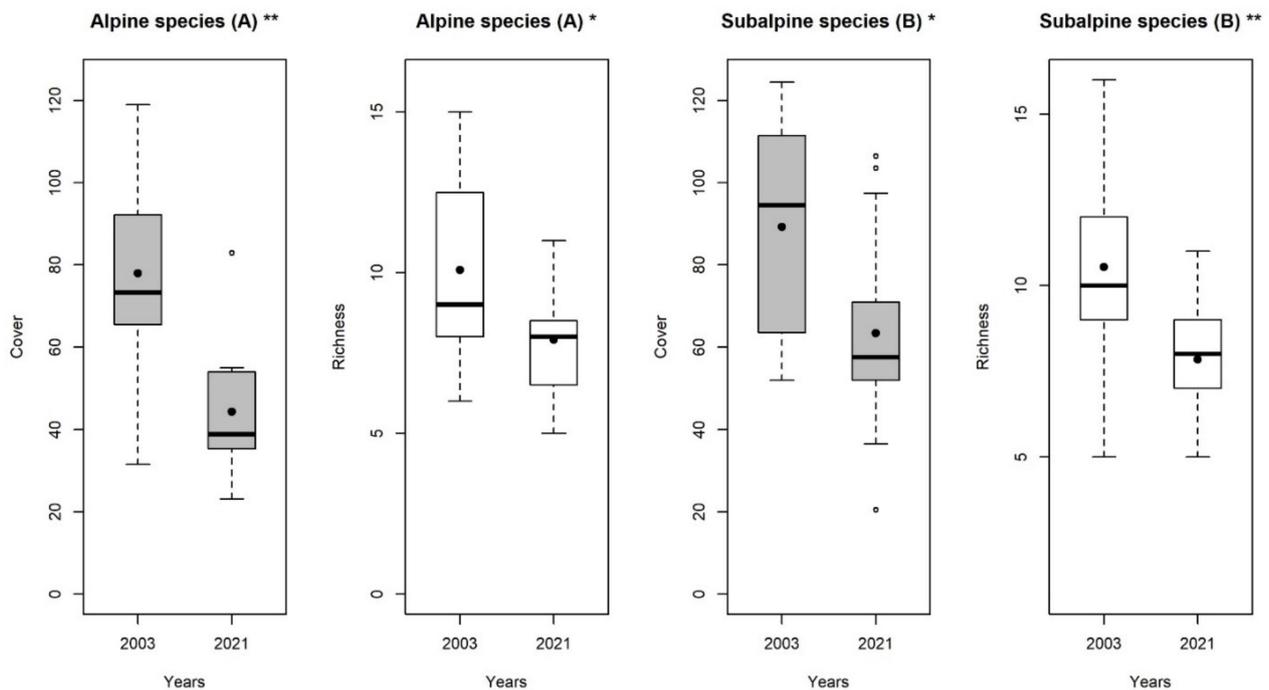


Figure 4. Boxplot comparing cover (grey) and richness per 4×4 m plot (white) of alpine species (T: 1–1.5) and subalpine species (T: 2–2.5) in two time steps (T1: 2003 and T2: 2021) in Apennine stripped grassland (A) and wind edge swards (B). Only the significant results are reported. Asterisks indicate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

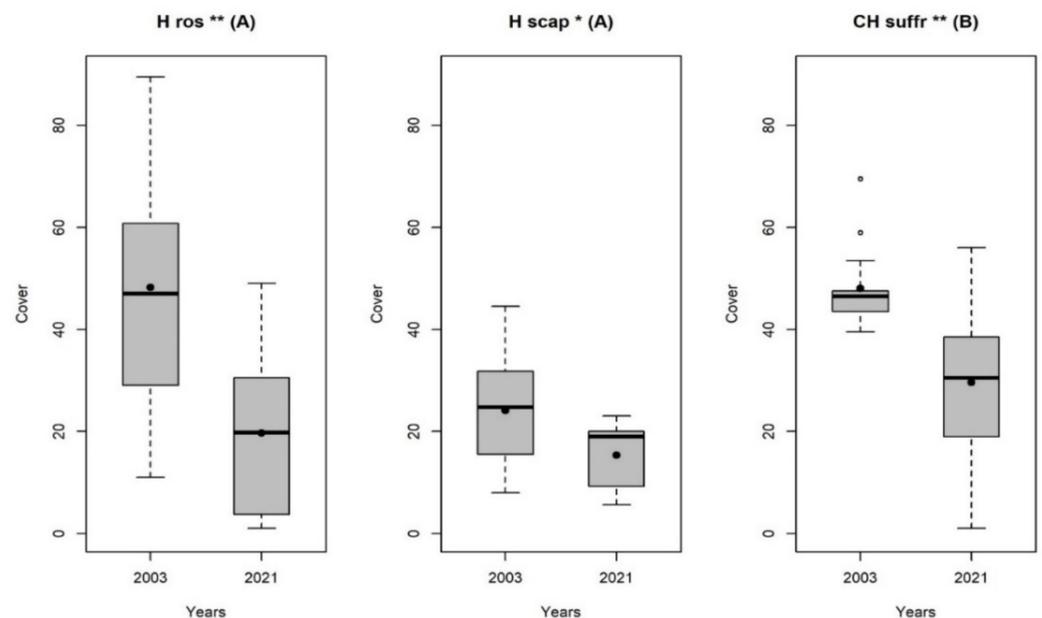


Figure 5. Boxplot comparing cover of growth forms (*sensu* Pignatti et al. [74]) in two time steps (T1: 2003 and T2: 2021) in Apennine stripped grasslands (A) and wind edge swards (B). H ros: hemicryptophytes with rosette; H scap: scapose hemicryptophytes; CH suffr: suffruticose chamaephytes. Asterisks 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.

Author Contributions: Conceptualization, M.V., A.S. and M.L.C.; methodology, M.V., A.S. and M.L.C.; formal analysis, M.V. and M.L.C.; data curation, M.V. and V.D.C.; writing—original draft preparation, M.V., A.S. and M.L.C.; writing—review and editing, M.V., V.D.C., A.S., 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.

Funding: The research was partially funded, as a subcontractor of the University of Vienna, by European Research Council Executive Agency Grant Agreement Number 883669, project MICROCLIM “A microscale perspective on alpine floras under climate change”.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study are available upon request from the corresponding author.

Acknowledgments: The research took advantage of facilities of the LTER network, as it was carried out in LTER IT01-001-T Appennino centro-meridionale: Majella-Matese <https://deims.org/c85fc568-df0c-4cbc-bd1e-02606a36c2bb> (accessed on 1 February 2022). We are grateful to the reviewers and the editors for their valuable comments, which help us to improve the manuscript.

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

References

- Chelli, S.; Wellstein, C.; Campetella, G.; Canullo, R.; Tonin, R.; Zerbe, S.; Gerdol, R. Climate change response of vegetation across climatic zones in Italy. *Clim. Res.* **2017**, *71*, 249–262. [\[CrossRef\]](#)
- Rogora, M.; Buzzi, F.; Dresti, C.; Leoni, B.; Lepori, F.; Mosello, R.; Patelli, M.; Salmasso, N. Climatic effects on vertical mixing and deep-water oxygen content in the subalpine lakes in Italy. *Hydrobiologia* **2018**, *824*, 33–50. [\[CrossRef\]](#)
- Verrall, B.; Pickering, C.M. Alpine vegetation in the context of climate change: A global review of past research and future directions. *Sci. Total Environ.* **2020**, *748*, 141344. [\[CrossRef\]](#)
- Körner, C. *Alpine Plant Life*, 2nd ed.; Springer: Berlin, Germany, 2003.
- Carlson, B.Z.; Choler, P.; Renaud, J.; Dedieu, J.P.; Thuiller, W. Modelling snow cover duration improves predictions of functional and taxonomic diversity for alpine plant communities. *Ann. Bot.* **2015**, *116*, 1023–1034. [\[CrossRef\]](#) [\[PubMed\]](#)
- Green, K.; Pickering, C. Vegetation, microclimate and soils associated with the latestlying snowpatches in Australia. *Plant Ecol. Divers.* **2009**, *2*, 289–300. [\[CrossRef\]](#)
- Fisk, M.C.; Schmidt, S.K.; Seastedt, T.R. Topographic patterns of above-and belowground production and nitrogen cycling in alpine tundra. *Ecology* **1998**, *79*, 2253–2266. [\[CrossRef\]](#)
- Hua, X.; Ohlemüller, R.; Sirguy, P. Differential effects of topography on the timing of the growing season in mountainous grassland ecosystems. *Environ. Adv.* **2022**, *8*, 100234. [\[CrossRef\]](#)
- Heywood, V.H. *Global Biodiversity Assessment*; Cambridge Press: Cambridge, UK, 1995.
- Körner, C. The grand challenges in functional plant ecology. *Front. Plant Sci.* **2011**, *2*, 1–3. [\[CrossRef\]](#)
- Médail, F.; Quézel, P. Biodiversity hotspots in the Mediterranean Basin: Setting global conservation priorities. *Conserv. Biol.* **1999**, *13*, 1510–1514. [\[CrossRef\]](#)

12. Väre, H.; Lampinen, R.; Humphries, C.; Williams, P. Taxonomic diversity of vascular plants in the European alpine areas. In *Alpine Biodiversity in Europe*; Nagy, L., Grabherr, G., Körner, C., Thompson, D.B.A., Eds.; Springer: Berlin, Germany, 2003; pp. 133–148.
13. Aeschimann, D.; Rasolofoa, N.; Theurillat, J.-P. Analyse de la flore des Alpes. 5: Milieux et phytosociologie. *Candollea* **2013**, *68*, 5–27. [[CrossRef](#)]
14. Myers, N.; Mittermeier, R.A.; Mittermeier, C.G.; da Fonseca, G.A.B.; Kent, J. Biodiversity hotspots for conservation priorities. *Nature* **2000**, *403*, 853–858. [[CrossRef](#)] [[PubMed](#)]
15. Körner, C. Impact of atmospheric changes on alpine vegetation: The ecophysiological perspective. In *Potential Ecological Impacts of Climate Change in the Alps and Fennoscandian Mountains*; Guisan, A., Holten, J.I., Spichiger, R., Tessler, L., Eds.; Conservatoire et Jardin Botaniques de Genève: Geneva, Switzerland, 1995; pp. 113–120.
16. Testolin, R.; Attorre, F.; Borchardt, P.; Brand, R.F.; Bruelheide, H.; Chytrý, M.; De Sanctis, M.; Dolezal, J.; Finckh, M.; Haider, S.; et al. Global patterns and drivers of alpine plant species richness. *Global Ecol. Biogeogr.* **2021**, *30*, 1218–1231. [[CrossRef](#)]
17. Favarger, C. Endemism in the Montane Floras of Europe. In *Taxonomy Phytogeography and Evolution*; Valentine, D.H., Ed.; Academic Press: London, UK; New York, NY, USA, 1972; pp. 191–204.
18. Gils, H.V.; Conti, F.; Ciaschetti, G.; Westinga, E. Fine resolution distribution modelling of endemics in Majella National Park, Central Italy. *Plant Biosyst.* **2012**, *146*, 276–287. [[CrossRef](#)]
19. Hughes, P.D.; Woodward, J.C. Timing of glaciation in the Mediterranean mountains during the last cold stage. *J. Quat. Sci.* **2008**, *23*, 575–588. [[CrossRef](#)]
20. Catonica, C.; Manzi, A. L'influenza della storia climatica e geologica recente sulla Flora d'alta quota dei gruppi montuosi del Gran Sasso e della Majella (Appennino Centrale). *Riv. Piemont. Stor. Nat.* **2002**, *23*, 19–29.
21. Stocker, T.F.; Qin, D.; Plattner, G.-K.; Alexander, L.V.; Allen, S.K.; Bindoff, N.L.; Bréon, F.-M.; Church, J.A.; Cubasch, U.; Xie, S.-P. Technical Summary. In *Climate Change 2013: The Physical Science Basis*; Contribution of working group to the fifth assessment report of the intergovernmental panel on climate change; Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M., Eds.; Cambridge University Press: Cambridge, UK; New York, NY, USA, 2013; pp. 33–109.
22. Klein, G.; Rebetz, M.; Rixen, C.; Vitasse, Y. Unchanged risk of frost exposure for subalpine and alpine plants after snowmelt in Switzerland despite climate warming. *Int. J. Biometeorol.* **2018**, *62*, 1755–1762. [[CrossRef](#)]
23. Pauli, H.; Gottfried, M.; Dullinger, S.; Abdaladze, O.; Akhalkatsi, M.; Alonso, J.L.B.; Coldea, G.; Dick, J.; Erschbamer, B.; Calzado, R.F.; et al. Recent plant diversity changes on Europe's mountain summits. *Science* **2012**, *336*, 353–355. [[CrossRef](#)]
24. Matteodo, M.; Ammann, K.; Verrecchia, E.P.; Vittoz, P. Snowbeds are more affected than other subalpine–alpine plant communities by climate change in the Swiss Alps. *Ecol. Evol.* **2016**, *6*, 6969–6982. [[CrossRef](#)]
25. Steinbauer, M.J.; Grytnes, J.-A.; Jurasinski, G.; Kulonen, A.; Lenoir, J.; Pauli, H.; Rixen, C.; Winkler, M.; Bardy-Durchhalter, M.; Barni, E.; et al. Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature* **2018**, *556*, 231–234. [[CrossRef](#)]
26. Cannone, N.; Sgorbati, S.; Guglielmin, M. Unexpected impacts of climate change on alpine vegetation. *Front. Ecol. Environ.* **2007**, *5*, 360–364. [[CrossRef](#)]
27. Holzinger, B.; Hulber, K.; Camenisch, M.; Grabherr, G. Changes in plant species richness over the last century in the eastern Swiss Alps: Elevational gradient, bedrock effects and migration rates. *Plant Ecol.* **2008**, *195*, 179–196. [[CrossRef](#)]
28. Parolo, G.; Rossi, G. Upward migration of vascular plants following a climate warming trend in the Alps. *Basic Appl. Ecol.* **2008**, *9*, 100–107. [[CrossRef](#)]
29. Britton, A.J.; Beale, C.M.; Towers, W.; Hewison, R.L. Biodiversity gains and losses: Evidence for homogenisation of Scottish alpine vegetation. *Biol. Conserv.* **2009**, *142*, 1728–1739. [[CrossRef](#)]
30. Engler, R.; Randin, C.F.; Thuiller, W.; Dullinger, S.; Zimmermann, N.E.; Araújo, M.B.; Pearman, P.B.; Le Lay, G.; Piedallu, C.; Albert, C.H.; et al. 21st Century Climate Change Threatens Mountain Flora Unequally Across Europe. *Glob. Change Biol.* **2011**, *17*, 2330–2341. [[CrossRef](#)]
31. Palombo, C.; Chirici, G.; Marchetti, M.; Tognetti, R. Is land abandonment affecting forest dynamics at high elevation in Mediterranean mountains more than climate change? *Plant Biosyst.* **2013**, *147*, 1–11. [[CrossRef](#)]
32. Erschbamer, B.; Unterluggauer, P.; Winkler, E.; Mallaun, M. Changes in plant species diversity revealed by long-term monitoring on mountain summits in the Dolomites (northern Italy). *Preslia* **2011**, *83*, 387–401.
33. Gottfried, M.; Pauli, H.; Futschik, A.; Akhalkatsi, M.; Barančok, P.; Benito Alonso, J.L.; Coldea, G.; Dick, J.; Erschbamer, B.; Fernández Calzado, M.R.; et al. Continent-wide response of mountain vegetation to climate change. *Nat. Clim. Chang.* **2012**, *2*, 111–115. [[CrossRef](#)]
34. Stanisci, A.; Frate, L.; Di Cella, M.U.; Pelino, G.; Petey, M.; Siniscalco, C.; Carranza, M.L. Short-Term Signals of Climate Change in Italian Summit Vegetation: Observations at Two GLORIA Sites. *Plant Biosyst. Int. J. Deal. All Asp. Plant Biol.* **2014**, *150*, 227–235. [[CrossRef](#)]
35. Evangelista, A.; Frate, L.; Carranza, M.L.; Attorre, F.; Pelino, G.; Stanisci, A. Changes in composition, ecology and structure of high-mountain vegetation: A re-visitation study over 42 years. *AoB Plants* **2016**, *8*, 1–11. [[CrossRef](#)]

36. Cannone, N.; Pignatti, S. Ecological responses of plant species and communities to climate warming: Upward shift or range filling processes? *Clim. Chang.* **2014**, *123*, 201–214. [[CrossRef](#)]
37. Calabrese, V.; Carranza, M.L.; Evangelista, A.; Marchetti, M.; Stinca, A.; Stanisci, A. Long-term changes in the composition, ecology, and structure of *Pinus mugo* scrubs in the Apennines (Italy). *Diversity* **2018**, *10*, 70. [[CrossRef](#)]
38. Erschbamer, B.; Kiebach, T.; Mallaun, M.; Unterluggauer, P. Short-term signals of climate change along an altitudinal gradient in the South Alps. *Plant Ecol.* **2009**, *202*, 79–89. [[CrossRef](#)]
39. Schwartz, M.W.; Iverson, L.R.; Prasad, A.M.; Matthews, S.N.; O'Connor, R.J. Predicting extinctions as a result of climate change. *Ecology* **2006**, *87*, 1611–1615. [[CrossRef](#)]
40. Dirnbock, T.; Essl, F.; Rabitsch, W. Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Glob. Chang. Biol.* **2011**, *17*, 990–996. [[CrossRef](#)]
41. Fernández-Calzado, R.; Molero, M.J.; Merzouki, A.; Casares, P. Vascular plant diversity and climate change in the upper zone of Sierra Nevada, Spain. *Plant Biosyst.* **2012**, *146*, 1044–1053. [[CrossRef](#)]
42. Nogués-Bravo, D.; Araújo, M.B.; Lasanta, T.; Moreno, J.I.L. Climate Change in Mediterranean Mountains during the 21st Century. *Ambio* **2008**, *37*, 280–285. [[CrossRef](#)]
43. Cherif, S.; Doblas-Miranda, E.; Lionello, P.; Borrego, C.; Giorgi, F.; Iglesias, A.; Jebari, S.; Mahmoudi, E.; Moriondo, M.; Pringault, O.; et al. Climate and Environmental Change in the Mediterranean Basin—Current Situation and Risks for the Future. In *Drivers of Change*; Cramer, W., Guiot, J., Marini, K., Eds.; Union for the Mediterranean, Plan Bleu, UNEP/MAP: Marseille, France, 2021; pp. 59–180.
44. Lamprecht, A.; Pauli, H.; Fernández Calzado, M.R.; Lorite, J.; Molero, M.J.; Steinbauer, K.; Winkler, M. Changes in plant diversity in a water-limited and isolated high-mountain range (Sierra Nevada, Spain). *Alp. Bot.* **2021**, *131*, 17–39. [[CrossRef](#)]
45. Kazakis, G.; Ghosn, D.; Remoundou, I.; Nyktas, P.; Talias, M.A.; Vogiatzakis, I.N. Altitudinal Vascular Plant Richness and Climate Change in the Alpine Zone of the Lefka Ori, Crete. *Diversity* **2021**, *13*, 22. [[CrossRef](#)]
46. Porro, F.; Tomaselli, M.; Abeli, T.; Gandini, M.; Gualmini, M.; Orsenigo, S.; Petraglia, A.; Rossi, G.; Carbognani, M. Could plant diversity metrics explain climate-driven vegetation changes on mountain summits of the GLORIA network? *Biodivers. Conserv.* **2019**, *28*, 3575–3596. [[CrossRef](#)]
47. Nicklas, L.; Walde, J.; Wipf, S.; Lamprecht, A.; Mallaun, M.; Rixen, C.; Steinbauer, K.; Theurillat, J.-P.; Unterluggauer, P.; Vittoz, P.; et al. Climate Change Affects Vegetation Differently on Siliceous and Calcareous Summits of the European Alps. *Front. Ecol. Evol.* **2021**, *9*, 642309. [[CrossRef](#)]
48. Turco, M.; Vezzoli, R.; De Ronco, P.; Mercogliano, P. *Variation in Discharge, Precipitation and Temperature in Po River and Tributaries Basins*; no. 185; Centro Euro-Mediterraneo sui Cambiamenti Climatici (CMCC): Lecce, Italy, 2013.
49. Sillmann, J.; Kharin, V.V.; Zwiers, F.W.; Zhang, X.; Bronaugh, D. Climate extremes indices in the CMIP5 multimodel ensemble: Part 2. Future climate projections. *J. Geophys. Res. Atmos.* **2013**, *118*, 2473–2493. [[CrossRef](#)]
50. Barredo, J.I.; Mauri, A.; Caudullo, G.; Dosio, A. Assessing Shifts of Mediterranean and arid climates under RCP4.5 and RCP8.5 climate projections in Europe. *Pure Appl. Geophys.* **2018**, *175*, 3955–3971. [[CrossRef](#)]
51. Di Nuzzo, L.; Vallese, C.; Benesperi, R.; Giordani, P.; Chiarucci, A.; Di Cecco, V.; Di Martino, L.; Di Musciano, M.; Gheza, G.; Lelli, C.; et al. Contrasting multitaxon responses to climate change in Mediterranean mountains. *Sci. Rep.* **2021**, *11*, 4438. [[CrossRef](#)]
52. Biondi, E.; Blasi, C.; Burrascano, S.; Casavecchia, S.; Copiz, R.; Del Vico, E.; Galdenzi, D.; Gigante, D.; Lasen, C.; Spampinato, G.; et al. *Manuale Italiano di Interpretazione Degli Habitat Della Direttiva 92/43/CEE*; Ministero dell'Ambiente e della Tutela del Territorio e del Mare, Direzione per la Protezione della Natura: Rome, Italy, 2009; pp. 1–16.
53. European Commission DG Environment. Interpretation Manual of European Union Habitats. [Eur 28. Nature ENV B.3]. 2013. Available online: http://ec.europa.eu/environment/nature/legislation/habitatsdirective/docs/Int_Manual_EU28.pdf (accessed on 26 June 2019).
54. Jaurand, E. Les Heritages Glaciaire de l'Apennin. Ph.D. Thesis, Éditions de la Sorbonne Paris, Paris, France, 1994.
55. Giraudi, C. Nuovi dati sul glacialismo della montagna della Majella (Abruzzo, Italia centrale). *Ital. J. Quat. Sci.* **1998**, *11*, 265–271.
56. Romeo, R.; Vita, A.; Manuelli, S.; Zanini, E.; Freppaz, M.; Stanchi, S. *Understanding Mountain Soils: A contribution from Mountain Areas to the International Year of Soils 2015*; FAO: Rome, Italy, 2015.
57. Blasi, C.; Di Pietro, R.; Fortini, P.; Catonica, C. The main Plant community types of the alpine belt of the Apennine chain. *Plant Biosyst.* **2003**, *137*, 83–110. [[CrossRef](#)]
58. Stanisci, A.; Carranza, M.L.; Pelino, G.; Chiarucci, A. Assessing the diversity pattern of cryophilous plant species in high elevation habitats. *Plant Ecol.* **2010**, *212*, 595–600. [[CrossRef](#)]
59. Stanisci, A.; Pelino, G.; Blasi, C. Vascular plant diversity and climate change in the alpine belt of the central Apennines (Italy). *Biodivers. Conserv.* **2005**, *14*, 1301–1318. [[CrossRef](#)]
60. Stanisci, A.; Evangelista, A.; Frate, L.; Stinca, A.; Carranza, M.L. VIOLA—Database of high mountain vegetation of central Apennines. *Phytocoenologia* **2016**, *46*, 231–232. [[CrossRef](#)]
61. Cervellini, M.; Zannini, P.; Di Musciano, M.; Fattorini, S.; Jiménez-Alfaro, B.; Rocchini, D.; Field, R.; Vetaas, O.R.; Severin, D.H.I.; Beierkuhnlein, C.; et al. A grid-based map for the Biogeographical Regions of Europe. *Biodivers. Data J.* **2020**, *8*, e53720. [[CrossRef](#)] [[PubMed](#)]
62. Petriccione, B.; Bricca, A. Thirty years of ecological research at the Gran Sasso d'Italia LTER site: Climate change in action. *Nat. Cons.* **2019**, *34*, 9–39. [[CrossRef](#)]

63. Steinbauer, K.; Lamprecht, A.; Winkler, M.; Di Cecco, V.; Fasching, V.; Ghosn, D.; Maringer, A.; Remoundou, I.; Suen, M.; Stanisci, A.; et al. Recent changes in high-mountain plant community functional composition in contrasting climate regimes. *Sci. Total Environ.* **2022**, *829*, 154541. [CrossRef] [PubMed]
64. Intergovernmental Panel on Climate Change. *Sixth Assessment Report. Climate Change 2022: Impacts, Adaptation and Vulnerability*; Cambridge University Press: Cambridge, UK, 2022.
65. Pauli, H.; Gottfried, M.; Lamprecht, A.; Niessner, S.; Rumpf, S.; Winkler, M.; Steinbauer, K.; Grabherr, G. *The GLORIA Field Manual*; Global Observation Research Initiative in Alpine Environments: Vienna, Austria, 2015.
66. Chytrý, M.; Tichý, L.; Hennekens, S.M.; Knollová, I.; Janssen, J.A.M.; Rodwell, J.S.; Peterka, T.; Marcenò, C.; Landucci, F.; Danihelka, J.; et al. EUNIS Habitat Classification: Expert system, characteristic species combinations and distribution maps of European habitats. *Appl. Veg. Sci.* **2020**, *23*, 648–675. [CrossRef]
67. Biondi, E.; Blasi, C.; Allegrezza, M.; Anzellotti, I.; Azzella, M.M.; Carli, E.; Casavecchia, S.; Copiz, R.; Del Vico, E.; Facioni, L.; et al. Plant communities of Italy: The Vegetation Prodrôme. *Plant Biosyst.* **2014**, *148*, 728–814. [CrossRef]
68. Evangelista, A.; Frate, L.; Stinca, A.; Carranza, M.L.; Stanisci, A. VIOLA-The vegetation database of the central Apennines: Structure, current status and usefulness for monitoring Annex I EU habitats (92/43/EEC). *Plant Sociol.* **2016**, *53*, 47–58. [CrossRef]
69. Vymazalová, M.; Axmanová, I.; Tichý, L. Effect of intra-seasonal variability on vegetation data. *J. Veg. Sci.* **2012**, *23*, 978–984. [CrossRef]
70. Chytrý, M.; Tichý, L.; Hennekens, S.M.; Schaminée, J.H.J. Assessing vegetation change using vegetation-plot databases: A risky business. *Appl. Veg. Sci.* **2014**, *17*, 32–41. [CrossRef]
71. Braun-Blanquet, J. *Pflanzensoziologie: Grundzüge der Vegetationskunde*; Springer: Berlin, Germany, 1964; ISBN 3709140781.
72. Westhoff, V.; Van Der Maarel, E. The braun-blanquet approach. In *Classification of Plant Communities*; Springer: Berlin/Heidelberg, Germany, 1978; pp. 287–399.
73. Bartolucci, F.; Peruzzi, L.; Galasso, G.; Albano, A.; Alessandrini, A.; Ardenghi, N.M.G.; Astuti, G.; Bacchetta, G.; Ballelli, S.; Banfi, E.; et al. An updated checklist of the vascular flora native to Italy. *Plant Biosyst.* **2018**, *152*, 179–303. [CrossRef]
74. Pignatti, S.; Guarino, R.; La Rosa, M. *Flora d'Italia*; Edagricole: Rome, Italy, 2017; Volume 1, ISBN 8850652429.
75. Landolt, E.; Bäumlér, B.; Erhardt, A.H.O.; Klötzli, F.; Lämmli, W.; Nobis, M.; Rudmann-Maurer, K.; Schweingruber, F.H.; Theurillat, J.-P.; Urmi, E.; et al. *Flora Indicativa. Ecological Indicator Values and Biological Attributes of the Flora of Switzerland and the Alps*, 2nd ed.; Haupt Verlag: Berna, Switzerland, 2010.
76. Frate, L.; Carranza, M.L.; Evangelista, A.; Stinca, A.; Schaminée, J.H.J.; Stanisci, A. Climate and land use change impacts on Mediterranean high-mountain vegetation in the Apennines since the 1950s. *Plant Ecol. Divers.* **2018**, *11*, 85–96. [CrossRef]
77. Tichý, L.; Hennekens, S.M.; Novák, P.; Rodwell, J.S.; Schaminée, J.H.J.; Chytrý, M. Optimal transformation of species cover for vegetation classification. *Appl. Veg. Sci.* **2020**, *23*, 710–717. [CrossRef]
78. Raunkjær, C.C. *The Life Forms of Plants and Statistical Plant Geography*; Oxford University Press: Oxford, UK, 1934.
79. Clarke, K.R. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* **1993**, *18*, 117–143. [CrossRef]
80. R Core Team. *A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2020; Available online: <http://www.r-project.org/index.html> (accessed on 7 February 2021).
81. Oksanen, A.J.; Blanchet, F.G.; Friendly, M.; Kindt, R.; Legendre, P.; McGinn, D.; Minchin, P.R.; Hara, R.B.O.; Simpson, G.L.; Solymos, P.; et al. *Vegan Package 2020*. Available online: <https://github.com/vegandevs/vegan> (accessed on 7 February 2021).
82. Hammer, Ø.; Harper, D.A.T.; Ryan, P.D. *Past Palaeontological Statistics, Ver. 1.79*. 2001, pp. 1–88. Available online: [https://palaeo-electronica.org/2001_1/past/issue1_01.htm#:~:text=The%20program%2C%20called%20PAST%20\(PALeontological,plotting%2C%20and%20simple%20phylogenetic%20analysis](https://palaeo-electronica.org/2001_1/past/issue1_01.htm#:~:text=The%20program%2C%20called%20PAST%20(PALeontological,plotting%2C%20and%20simple%20phylogenetic%20analysis) (accessed on 10 June 2021).
83. Mariotti, A.; Zeng, N.; Yoon, J.-H.; Artale, V.; Navarra, A.; Alpert, P.; Li, L.Z.X. Mediterranean water cycle changes: Transition to drier 21st century conditions in observations and CMIP3 simulations. *Environ. Res. Lett.* **2008**, *3*, 044001. [CrossRef]
84. Toreti, A.; Fioravanti, G.; Percontia, W.; Desiato, F. Annual and seasonal precipitation over Italy from 1961 to 2006. *Int. J. Climatol.* **2009**, *29*, 1976–1987. [CrossRef]
85. Fernández Calzado, M.R.; Molero, J. Changes in the summit flora of a Mediterranean mountain (Sierra Nevada, Spain) as a possible effect of climate change. *Lazaroa* **2013**, *34*, 65–75. [CrossRef]
86. Brunetti, M.; Buffoni, L.; Mangianti, F.; Maugeri, M.; Nanni, T. Temperature, precipitation and extreme events during the last century in Italy. *Glob. Planet Chang.* **2004**, *40*, 141–149. [CrossRef]
87. Elguindi, N.; Rauscher, S.A.; Giorgi, F. Historical and future changes in maximum and minimum temperature records over Europe. *Clim. Chang.* **2013**, *117*, 415–431. [CrossRef]
88. Simolo, C.; Brunetti, M.; Maugeri, M.; Nanni, T. Increasingly warm summers in the Euro-Mediterranean zone: Mean temperatures and extremes. *Reg. Environ. Chang.* **2014**, *14*, 1825–1832. [CrossRef]
89. Christensen, J.H.; Hewitson, B.; Busuioic, A.; Chen, A.; Gao, X.; Held, I.; Jones, R.; Kolli, R.K.; Kwon, W.T.; Laprise, R.; et al. *AR4 Climate Change 2007: The Physical Science Basis*; Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change; Cambridge Univ. Press: Cambridge, UK, 2007; pp. 847–940.
90. Benito, B.; Lorite, J.; Penas, J. Simulating potential effects of climatic warming on altitudinal patterns of key species in Mediterranean-alpine ecosystems. *Clim. Chang.* **2011**, *108*, 471–483. [CrossRef]
91. Mondoni, A.; Rossi, G.; Orsenigo, S.; Probert, R.J. Climate warming could shift the timing of seed germination in alpine plants. *Ann. Bot.* **2012**, *110*, 155–164. [CrossRef]

92. Giménez-Benavides, L.; Escudero, A.; Pérez-García, F. Seed germination of high mountain Mediterranean species: Altitudinal, interpopulation and interannual variability. *Ecol. Res.* **2005**, *20*, 433–444. [[CrossRef](#)]
93. Orsenigo, S.; Abeli, T.; Rossi, G.; Bonasoni, P.; Pasquaretta, C.; Gandini, M.; Mondoni, A. Effects of autumn and spring heat waves on seed germination of high mountain plants. *PLoS ONE* **2015**, *10*, e0133626. [[CrossRef](#)]
94. Varricchione, M.; Di Cecco, V.; Santoianni, L.A.; Stanisci, A.; Di Febbraro, M.; Di Martino, L.; Carranza, M.L. Diagnostic Species Diversity Pattern Can Provide Key Information on Vegetation Change: An Insight into High Mountain Habitats in Central Apennines. *J. Zool. Bot. Gard.* **2021**, *2*, 453–472. [[CrossRef](#)]
95. Edwards, A.C.; Scalenghe, R.; Freppaz, M. Changes in the seasonal snow cover of alpine regions and its effect on soil processes: A review. *Quat. Int.* **2007**, *162–163*, 172–181. [[CrossRef](#)]
96. Stanisci, A.; Bricca, A.; Calabrese, V.; Cutini, M.; Pauli, H.; Steinbauer, K.; Carranza, M.L. Functional composition and diversity of leaf traits in subalpine versus alpine vegetation in the Apennines. *AoB Plants* **2020**, *12*, 1–11. [[CrossRef](#)]
97. Haslinger, K.; Schöner, W.; Anders, I. Future drought probabilities in the Greater Alpine Region based on COSMO-CLM experiments—Spatial patterns and driving forces. *Meteorol. Z.* **2016**, *25*, 137–148. [[CrossRef](#)]
98. Cutini, M.; Marzialetti, F.; Giuliana, B.; Rianna, G.; Theurillat, J.-P. Bioclimatic pattern in a Mediterranean mountain area: Assessment from a classification approach on a regional scale. *Int. J. Biometeorol.* **2021**, *65*, 1085–1097. [[CrossRef](#)]
99. Chen, I.-C.; Hill, J.K.; Ohlemüller, R.; Roy, D.B.; Thomas, C.D. Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science* **2011**, *333*, 1024–1026. [[CrossRef](#)]
100. Rehm, E.M.; Olivás, P.; Stroud, J.; Feeley, K.J. Losing your edge: Climate change and the conservation value of range-edge populations. *Ecol. Evol.* **2015**, *5*, 4315–4326. [[CrossRef](#)]
101. Jump, A.S.; Peñuelas, J. Running to stand still: Adaptation and the response of plants to rapid climate change. *Ecol. Lett.* **2005**, *8*, 1010–1020. [[CrossRef](#)]
102. Hoffmann, S.; Irl, S.D.H.; Beierkuhnlein, C. Predicted climate shifts within terrestrial protected areas worldwide. *Nat. Commun.* **2019**, *10*, 1–10. [[CrossRef](#)]
103. Manes, S.; Costello, M.J.; Beckett, H.; Debnath, A.; Devenish-Nelson, E.; Grey, K.-A.; Jenkins, R.; Ming Khan, T.; Kiessling, W.; Krause, C.; et al. Endemism increases species' climate change risk in areas of global biodiversity importance. *Biol. Conserv.* **2021**, *25*, 109270. [[CrossRef](#)]
104. Watts, S.H.; Mardon, D.K.; Mercer, C.; Watson, D.; Cole, H.; Shaw, R.F.; Jump, A.S. Riding the elevator to extinction: Disjunct arctic-alpine plants of open habitats decline as their more competitive neighbors expand. *Biol. Conserv.* **2022**, *272*, 109620. [[CrossRef](#)]
105. Nagy, L.; Grabherr, G.; Körner, C.; Thompson, D.B.A. *Alpine Biodiversity in Europe*; Springer: Berlin, Germany, 2003.
106. Kougioumoutzis, K.; Kokkoris, I.P.; Panitsa, M.; Trigas, P.; Strid, A.; Dimopoulos, P. Plant Diversity Patterns and Conservation Implications under Climate-Change Scenarios in the Mediterranean: The Case of Crete (Aegean, Greece). *Diversity* **2020**, *12*, 270. [[CrossRef](#)]
107. Di Biase, L.; Pace, L.; Mantoni, C.; Fattorini, S. Variations in Plant Richness, Biogeographical Composition, and Life Forms along an Elevational Gradient in a Mediterranean Mountain. *Plants* **2021**, *10*, 2090. [[CrossRef](#)] [[PubMed](#)]
108. Gentili, R.; Baroni, C.; Caccianiga, M.; Armiraglio, S.; Ghiani, A.; Citterio, S. Potential warm-stage microrefugia for alpine plants: Feedback between geomorphological and biological processes. *Ecol. Complex.* **2015**, *21*, 87–99. [[CrossRef](#)]
109. Veron, S.; Faith, D.P.; Pellens, R.; Pavoine, S. Priority areas for phylogenetic diversity: Maximising gains in the mediterranean basin. In *Phylogenetic Diversity: Applications and Challenges in Biodiversity Science*; Springer International Publishing: Cham, Switzerland, 2018; pp. 145–166.
110. Haight, J.; Hammill, E. Protected areas as potential refugia for biodiversity under climatic change. *Biol. Conserv.* **2020**, *241*, 108258. [[CrossRef](#)]
111. Di Cecco, V.; Di Santo, M.; Di Musciano, M.; Manzi, A.; Di Cecco, M.; Ciaschetti, G.; Marcantonio, G.; Di Martino, L. The Majella National Park: A case study for the conservation of plant biodiversity in the Italian Apennines. *Ital. Bot.* **2020**, *10*, 1–24. [[CrossRef](#)]
112. Hawkes, J.G.; Maxted, N.; Ford-Lloyd, B.V. *The Ex Situ Conservation of Plant Genetic Resources*; Springer Science and Business Media: Berlin, Germany, 2012.