

Article

# Long-Term Changes in the Composition, Ecology, and Structure of *Pinus mugo* Scrubs in the Apennines (Italy)

Valentina Calabrese <sup>1</sup>, Maria Laura Carranza <sup>1,\*</sup> , Alberto Evangelista <sup>1</sup>, Marco Marchetti <sup>2</sup> , Adriano Stinca <sup>3</sup>  and Angela Stanisci <sup>1</sup> 

<sup>1</sup> Envix-Lab, Dipartimento di Bioscienze e Territorio, Università degli Studi del Molise, Contrada Fonte Lappone, 86090 Pesche, Italy; valentinacalab90@gmail.com (V.C.); evangelistalberto@gmail.com (A.E.); stanisci@unimol.it (A.S.)

<sup>2</sup> Centro ArIA, Università degli Studi del Molise Via F. De Sanctis, 86100 Campobasso, Italy; marchettimarco@unimol.it

<sup>3</sup> Dipartimento di Scienze e Tecnologie Ambientali, Biologiche e Farmaceutiche, Università della Campania Luigi Vanvitelli, via Vivaldi 43, 81100 Caserta, Italy; adriano.stinca@unina.it

\* Correspondence: carranza@unimol.it; Tel.: +39-320-479-3882

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**Abstract:** Mountain ecosystems are vulnerable because of land-use and climate change. In this study, we performed a re-visitation study using historical and newly collected vegetation plots to explore the primary trends in the floristic, ecological, and structural features of Mediterranean *Pinus mugo* krummholz over past decades. The plant community composition over time (1992 vs. 2016–17) was analyzed by a detrended correspondence analysis followed by a statistical comparison of time steps and an analysis of the contribution of each species to temporal differences. Ecological and structural changes were analyzed by a permutational multivariate analysis of variance followed by a post hoc comparison. We observed relevant changes in the floristic composition, structure, and ecological characteristics of *Pinus mugo* scrub. Some subalpine and treeline species that characterize the early stages of *Pinus mugo* succession declined as several warm-adapted species increased. Furthermore, these changes were most likely due to the natural evolution of high-mountain krummholz combined with a thermophilization process occurring in alpine habitats. In contrast, a small group of cold-adapted species also increased, probably because the patchy spatial pattern of *Pinus mugo* scrubs gives rise to “mesic patches” in a matrix of arid grasslands. The re-visitation approach adopted for long-term analysis in this study can potentially be applied to other mountainous regions to better understand long-term ecological changes in high alpine vegetation.

**Keywords:** Ellenberg indicator values; global change; life forms; long-term analysis; Mediterranean mountains; re-visitation study

## 1. Introduction

High mountain habitats are vulnerable because of human impacts, such as global change (e.g., rising temperatures, changes in precipitation patterns, and nitrogen deposition) and land abandonment, which influence biodiversity and ecosystem functioning [1–4]. Consistent changes in biodiversity have been observed in numerous central European mountains using short-term [5–7] and long-term vegetation analyses [8–16], and upward migration of alpine species toward mountain summits, shrub displacement, changes in community composition, and local extinctions have also been documented [17–22]. However, the responses within each community may be idiosyncratic [23],

and upward migration is often difficult to recognize as the vegetation may “lean” upslope within existing ranges [24–26].

Regarding *Pinus mugo* scrubs, a widespread expansion has been recorded across European mountains since the 1950s, mainly at the expense of secondary grasslands, whose extent have been reduced [25–31]. These changes have been related to the abandonment of traditional grazing and agroforestry activities that began after the 1950s [2,28], as well as global warming [32,33]. In contrast, Dullinger et al. [27] and Wild et al. [34] showed that despite the favorable climatic conditions of European subalpine regions, *Pinus mugo* colonizes high-mountain abandoned pastures at low rates.

In the Italian Apennines, as in other European mountains [27,30], land use over the past decades has greatly changed the prior landscape above the beech forest line, which was characterized by stands of *Pinus mugo* scattered over a matrix of secondary grasslands and stands of dwarf juniper [35–38]. Currently, the landscape above the beech forest line consists of a patchwork of dense *Pinus mugo* shrublands and open grassland stands with different degrees of vegetation cover [28,33], but changes occurring after land abandonment and scrubland recovery are generally accompanied by the simplification and homogenization of these landscapes [39–41], which should result in a decrease in the biodiversity that is typically sheltered by historical landscape mosaics [42]. Despite the peculiarities of shrubland and grassland dynamics that characterize Mediterranean high mountains and their sensitivity to landscape change, few studies have described the composition and ecological changes in such plant communities, and these studies have mainly addressed a relatively short time period [43,44]. Therefore, additional research efforts aimed at better understanding the long-term effects of the shrub encroachment process on plant community composition and structure are still necessary [45–47]. One of the few possibilities for carrying out long-term ecological studies in areas where permanent plot data are unavailable is the utilization of historical vegetation data [16,48,49]. In this context, new long-term re-visitation studies of historical plots have recently been carried out in Mediterranean high-mountain vegetation (e.g., [16,45,50]). The initial results of these long-term studies have shown a decrease in grassland specialist species in Spanish mountains as a consequence of shrub expansion and climate change [45], as well as a significant increase in warm-adapted species in the alpine belt of the Italian Apennines [16,50]. Such early results confirm the effectiveness of the re-visitation approach and have spurred us to explore long-term changes in the high-mountain krummholz vegetation, which has become denser in the last decades.

Considering this context, the present work analyzes the plant species composition, ecology, and structure of *Pinus mugo* scrub above the beech forest line over time by comparing vegetation samples collected in the 1990s with those resurveyed in 2016–17. Specifically, our re-visitation study addressed the following questions: (i) Have the abundance and distribution of vascular plant species in *Pinus mugo* stands changed during the past decades; (ii) what is the trend in life-form abundance patterns over time; and (iii) does the ecology of the community change or remain stable over time?

Vegetation structure was analyzed using life forms based on Raunkiaer form frequencies [51,52], and changes in the ecology of the analyzed dwarf pine scrub were assessed using ecological plant indicator values [53].

As a consequence of land abandonment coupled with climate change in the central Apennines over the last half century [16,27,33,50], we should expect an increase in warm-adapted species from lower vegetation belts and a decrease in grass and forb species in the undergrowth of *Pinus mugo* stands, which have become denser.

## 2. Materials and Methods

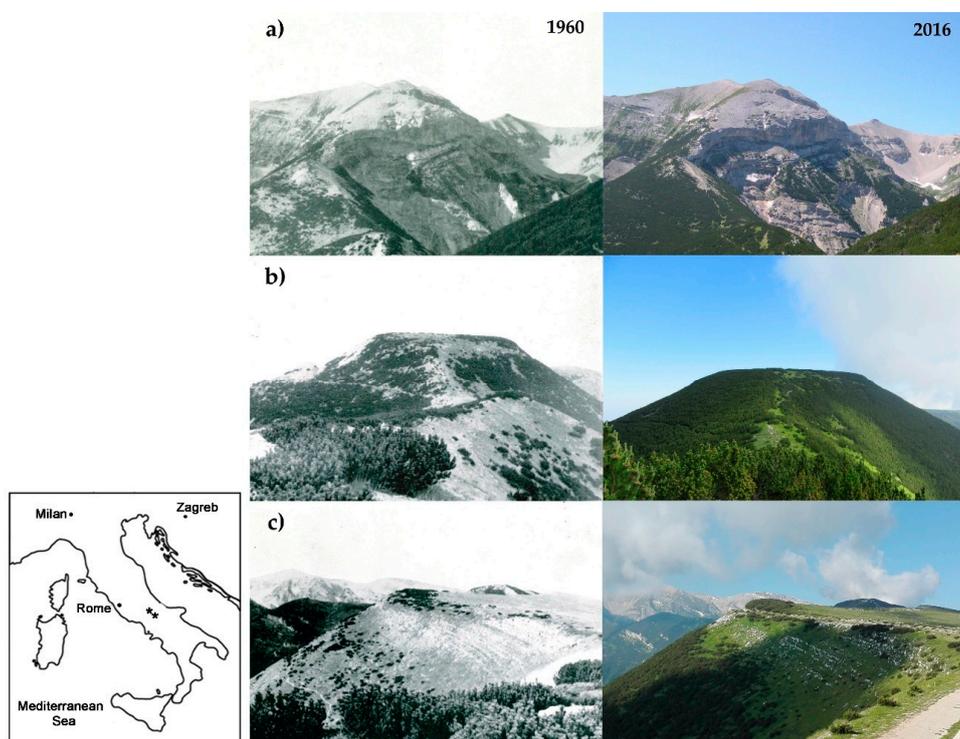
### 2.1. Study Area

The study area includes the high-mountain zone (1750–2420 m a.s.l.) of the central Apennines and is part of two national parks (Abruzzo, Lazio and Molise National Park and Majella National Park, Figure 1). These mountains are the only ones in the Apennines in which *Pinus mugo* krummholz occurs above the beech forest line. Furthermore, the study area is of high biogeographical and conservation

concern because it includes the southern distribution limit of *Pinus mugo* in the central Mediterranean basin [54].

*Pinus mugo* thickets are habitats of conservation concern in Europe (Habitat Directive 92/43/CEE EC: habitat 4070\*: bushes with *Pinus mugo* and *Rhododendron*) and are referable to the syntaxonomical alliance *Epipactido atropurpureae-Pinion mugo* [36]. In the study area, dense krummholz occurs between 1500 and 2300 m a.s.l., whereas small shrub patches reach 2500 m a.s.l. [28].

Land use in the investigated area has historically been characterized by grazing activities [28], but grazing pressure decreased after the Second World War due to the abandonment of transhumance practices and continued to decrease in more recent decades following the institution of the national parks [55]. This area, which is characterized by prairies and shrublands up to an elevation of 2400 m a.s.l., is considered an adequate site for investigating changes in the vegetation of Mediterranean mountains [28,56] (Figure 1).



**Figure 1.** Locations of the study areas in Central Italy along with a photographic comparison of *Pinus mugo* formations in the years 1960 [57] and 2016 in three localities of the Majella massif: (a) Mt. Cavallo and Mt. Focalone, (b) Blockhaus, and (c) Maielletta. The main changes in the landscape are related to an increase in krummholz density across the treeline ecotone.

The climate in the study area has changed during the last 50 years, with a significant increase in mean annual temperature of 1.7 °C (amounting to 0.26 °C per decade, see [16]). Moreover, the minimum temperatures in spring and winter have increased by 2.87 °C and 4.38 °C, respectively, during the last century [33]. Furthermore, summer minimum temperatures have increased (3.17 °C), and summer maximum temperatures have decreased (−2.69 °C).

## 2.2. Vegetation Data

From the VIOLA database [49,57], we extracted a set of 37 phytosociological relevés of *Pinus mugo* thickets sampled in the central Apennines in 1992 [36] and to a lesser extent in 1960–1968 [58,59]. Based on the accurate description of the localities and the existing maps, we re-visited the same stands and established 37 new phytosociological relevés in 2016–2017. In addition to using maps and detailed

information about the relevés' headers, the new sampling fieldwork was personally performed by one of the researchers that had collected vegetation data in 1992 to guarantee the quality of the new data. Relevés were located in the subalpine belt [60,61], which is widely distributed in the analyzed mountains. In particular, we considered a lower subalpine belt (from 1750 up to 2100 m a.s.l.) and an upper subalpine belt (from 2100 up to 2420 m a.s.l.).

Data collection in the relevés was performed following the same sampling protocol (considering plant community type, plot size, previous species lists, and estimates of dominant species cover) [62], and the plant communities were sampled using the classic phytosociological approach and the Braun-Blanquet scale of abundance/dominance [63,64]. The original abundance and cover values of the Braun-Blanquet scale were transformed according to the ordinal transformation of van der Maarel, and the nomenclature followed Bartolucci et al. [65]. The collected specimens were identified according to the Flora Europaea [66,67], Flora d'Italia [68,69], and recent monographic works.

To investigate changes in species composition over time, we analyzed species abundance in the examined period. Changes in the ecological features of the vegetation were evaluated using Ellenberg indicator values [53], and changes in structure were evaluated using the life-form categories of Raunkiaer [51].

The ecological features were assessed using Ellenberg indicator values [53] of temperature (T), moisture (U), soil nutrients (N), and luminosity (L) adapted for Italian flora by Pignatti [70] (see the Ellenberg ecological values of the analyzed vascular plants in Table A1). Ellenberg [53] compiled a universally applicable numerical indicator value system for central European vascular plants that has been widely used and has also been refined, extended, and adopted for other regions [53,71]. According to the Ellenberg approach, each plant species is assigned an ordinal number, called an indicator value, between 1 and 9 (and 1–12 for moisture) that describes its preference along ecological gradients. Such values are assigned based on field experience, on coincident recordings of species and environmental variables, and on experimental tests. Plant stands (and their sites) are then positioned on these gradients by calculating (weighted) averages of the indicator values of the species that occur. Compared to physical and chemical measurements, Ellenberg indicator systems circumvent the problem of measuring those resource fractions that are accessible to plants and can be integrated over the spatial and temporal variability of sites [72]. To compare the ecological indicator values of the sampled flora for the different dates, we used weighted average (WA) values because they are reliable predictors of site conditions; WA values per plot were calculated using quantitative data (the frequency of each plant group in each habitat type).

To analyze changes in vegetation structure, we examined the Raunkiaer life-form categories [51] that classify plants according to the position of buds in relation to the ground surface, which is a good surrogate for the strategy adopted to survive during less favorable seasons. The following categories were distinguished: chamaephytes (C), geophytes (G), hemicryptophytes (H), phanerophytes (P), and therophytes (T). Moreover, as hemicryptophytes are the most abundant, we also explored the temporal changes in their sub-categories (Hscap: scapose, Hcaesp: caespitose, Hrept: reptant and Hros: rosulate; sensu Pignatti [70]).

### 2.3. Data Analysis

To explore the main temporal trends in floristic composition, we analyzed a matrix of 107 taxa (including species and subspecies, Table A1) observed in 74 relevés through detrended correspondence analysis (DCA) using the Bray-Curtis distance, and we projected the two analyzed periods in the ordination space (T1: old relevés, mainly assessed in 1992, and T2: new relevés assessed in the years 2016/17). Species with only one record of presence were excluded. Then, we compared the composition of vegetation plots surveyed in the two temporal groups (T1 and T2) and also explored the differences in *Pinus mugo* communities growing at different elevation ranges (lower subalpine belt: 1750–2100 m a.s.l. vs. upper subalpine belt: 2100–2420 m a.s.l.) using one-way analysis of similarities (ANOSIM) (9999 permutations). ANOSIM is a non-parametric procedure to test for differences between two or

more groups based on any distance measure that is converted to ranks [72]. We then identified the species that mostly contributed to the differentiation of the two temporal groups (T1 and T2) using a similarity percentage procedure (SIMPER, [72]).

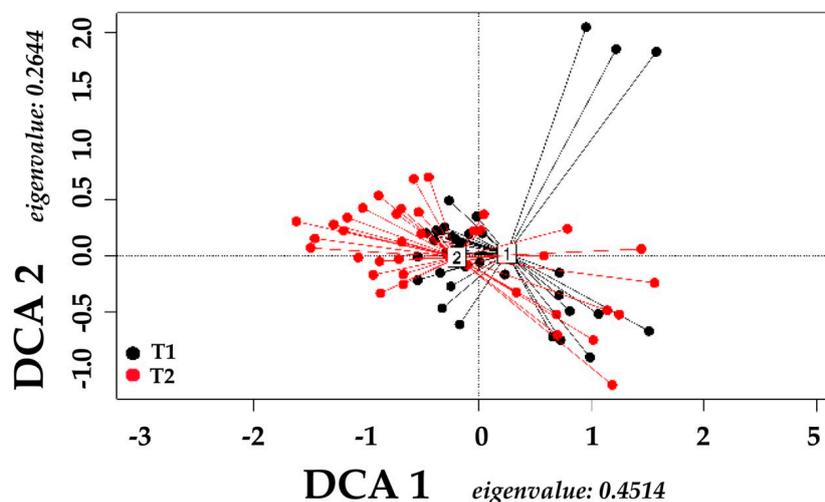
To detect temporal changes in the ecology of the analyzed vegetation, we used Ellenberg bioindicator values of temperature (T), moisture (U), soil nutrients (N), and luminosity (L). For each relevé, we calculated the mean indicator value weighted according to species frequency, as reported in Evangelista et al. [16].

Similarly, to detect temporal changes in community structure, life-form abundances were calculated using presence/absence data for each relevé.

Moreover, we performed a permutational multivariate analysis of variance of species cover, mean Ellenberg indicator values, and life forms (PERMANOVA, 9999 randomizations) based on Gower distances [73], including the effect of the year (factor with two levels) and the elevation range (factor with two levels) as grouping variables. We also included the interaction between year and elevation range, which allowed us to test whether the effect of the temporal groups varied with altitude. The Mann-Whitney post hoc test was used to determine which variables (ecological and structural) varied between the old and new relevés; this is a non-parametric test, which means that the distributions can be of any shape. The two-tailed (Wilcoxon) Mann-Whitney U test can be used to test whether the medians of two independent samples are different. All analyses were performed in the R statistical computing program (R Core Team 2014) using the Vegan package [74] and PAST (paleontological statistics software for education and data analysis) [75].

### 3. Results

The DCA revealed differences in floristic composition between the two analyzed periods. Eigenvalues for the DCA axes were 0.4514 for DCA1 and 0.2644 for DCA2, thus clearly discriminating between the two different time periods (Figure 2).



**Figure 2.** Detrended correspondence analysis using species as the explanatory variables. Black dots represent the relevés sampled in T1 (1992); red dots represent the relevés sampled in T2 (2016/2017); lines (blank and red) link the relevés with the respective centroids (numbered squares 1 and 2).

The ANOSIM confirmed these trends and revealed that differences in species composition among the old and the new relevés of *Pinus mugo* shrublands (T1 and T2) were significant (ANOSIM R value = 0.116, nT1 37, nT2 = 37,  $p = 0.001$ ).

According to the similarity percentage analysis, 21 of the 107 species contributed 50% of the observed temporal differences in vegetation composition. Of these, 15 increased and six decreased over time (Table 1).

**Table 1.** The contribution of plant species (contr. %) to the observed differences between plant communities in the two time periods (T1: 1992 and T2: 2016/17) assessed by the similarity percentage procedure (SIMPER, [72]). For each taxon, the life forms (L. form: C: chamaephytes, G: geophytes and hemicryptophytes, H, subdivided into Hcaesp: caespitose, Hrept: reptant, Hros: rosulate and Hscap scapose), the Ellenberg ecological indicator values for temperature (T), and the vegetation belt where the species occur (V. belt: 1 = lower subalpine; 2 = upper subalpine) are also reported.

Taxon	contr. %	Mean Increase %			L. form	T	V. belt
		T1	T2				
<i>Poa alpina</i> subsp. <i>alpina</i>	2.649	0.351	0.595	H Caesp	3	1,2	
<i>Valeriana montana</i>	2.476	0.351	0.514	H Scap	4	1,2	
<i>Campanula scheuchzeri</i> s.l.	2.449	0.541	0.595	H Scap	2	2	
<i>Leucopoa dimorpha</i>	2.449	0.514	0.568	H Caesp	4	2	
<i>Pulsatilla alpina</i> subsp. <i>millefoliata</i>	2.434	0.432	0.514	H Scap	3	2	
<i>Doronicum columnae</i>	2.304	0.162	0.432	G	4	2	
<i>Hypericum richeri</i> subsp. <i>richeri</i>	2.298	0.189	0.432	H Scap	6	1,2	
<i>Orthilia secunda</i>	2.252	0.297	0.378	C	5	1,2	
<i>Hippocrepis comosa</i> subsp. <i>comosa</i>	2.211	0.297	0.432	H Caesp	7	1,2	
<i>Thymus praecox</i> subsp. <i>polytrichus</i>	2.162	0.216	0.405	C	6	1	
<i>Trifolium pratense</i> subsp. <i>semipurpureum</i>	1.947	0.135	0.378	H Scap	6	1	
<i>Helianthemum nummularium</i> subsp. <i>grandiflorum</i>	1.843	0.216	0.297	C	4	2	
<i>Ranunculus pollinensis</i>	1.701	0.027	0.351	H Scap	3	2	
<i>Carex kitaibeliana</i>	1.595	0.135	0.27	H Caesp	4	1	
		Mean Decrease %					
<i>Hieracium murorum</i> s.l.	2.341	0.405	0.351	H Scap	4	1,2	
<i>Silene multicaulis</i> subsp. <i>multicaulis</i>	2.292	0.378	0.324	H Caesp	4	1	
<i>Brachypodium genuense</i>	1.933	0.297	0.27	H Caesp	6	2	
<i>Phyteuma orbiculare</i>	1.792	0.892	0.703	H Scap	3	1	
<i>Ranunculus breyninus</i>	1.745	0.378	0	H Scap	3	1	
<i>Epipactis atrorubens</i>	1.645	0.27	0.162	G	6	1	
<i>Gentiana dinarica</i>	1.556	0.243	0.189	H Ros	3	1	

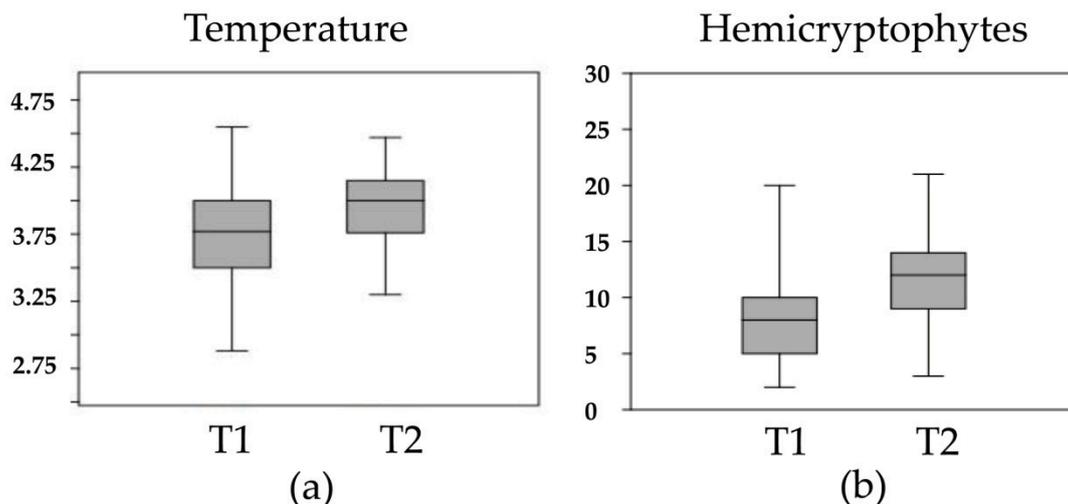
The PERMANOVA test showed that the ecological Ellenberg bioindicator values (T: temperature, U: moisture, N: soil nutrients, L: luminosity) and structural variables (life forms) were significantly affected by time and elevation range, but not by their interaction (Table 2).

In particular, the post hoc Mann-Whitney U comparisons revealed major differences between the old and new datasets (T1: 1992 and T2: 2016–2017) in the temperature indicator value (T) and the hemicryptophyte life form (H). The median T indicator value increased from 15.68 to 21.8 (Mann-Whitney  $z = -2.4505$ ,  $n_{T1} = 37$ ,  $n_{T2} = 37$ ,  $p = 0.0143$ ), and the H median value increased from 13.77 to 23.73 (Mann-Whitney  $z = -3.995$ ,  $n_{T1} = 37$ ,  $n_{T2} = 37$ ,  $p = 0.0002$ ) (Figure 3). The increase in T was mainly related with an increase in the frequencies of some thermophilic species (Ellenberg T values 4–6).

**Table 2.** Results of permutational multivariate analysis of variance (PERMANOVA). Effect of the time period (T1: 1992 and T2: 2016–2017) and the vegetation belt (lower subalpine and upper subalpine) on species abundance, mean Ellenberg indicator values, and life forms. Asterisks indicate significant results.

Source	Sum of Squares	Df	Mean Square	F. Model	R2	Pr (> F)
Time	0.09777	1	0.097765	4.3227	0.05327	<b>0.003 **</b>
Elevation Range	0.15007	1	0.150068	6.6352	0.08177	<b>0.002 **</b>
Interaction	0.00432	1	0.004324	0.1912	0.00236	0.920
Residual	1.58318	70	0.022617	0.86261		
Total	1.83534	73		1.00000		

\*\*  $p < 0.01$ .



**Figure 3.** Box plots comparing (a) the Ellenberg ecological value (temperature;  $p = 0.0143$ ) and (b) frequency of the main category hemicryptophyte life-form (H;  $p = 0.0002$ ) of the analyzed data (T1: 1992 and T2: 2016–2017). Both differences are significant according to a post hoc Mann-Whitney U test.

Indeed, based on percent similarity, some common grass and forb species of the subalpine and montane belts ( $T = 3$ – $6$ ) and the alpine belt ( $T = 2$ ) have increased in abundance (Table 1). In contrast, some typical species of open grasslands and juniper shrublands of the subalpine and montane belts ( $T = 3$ – $6$ ) have decreased in abundance (for a complete list of sampled taxa and the respective ecological values, see Table A1).

Regarding life-forms, only hemicryptophytes showed significant differences (Figure 3), likely because grasses and forbs are the most abundant plant species in *Pinus mugo* undergrowth, and their change in abundance was more noticeable. We observed that only the scapose hemicryptophytes varied significantly, with an increase between the old and new relevés from 12.9 to 24.6 (median value, Mann-Whitney  $z = -4.7164$ ,  $n_{T1} = 37$ ,  $n_{T2} = 37$ ,  $p = 0.0001$ ).

#### 4. Discussion

The present re-visitation study highlights that relevant changes have occurred in the floristic composition, structure (life forms), and ecological characteristics (Ellenberg indicator values) of *Pinus mugo* scrubs in the central Apennines during the last decades. As observed in the Alps [27,76], such changes should be related to a recent increase in *Pinus mugo* thicket cover, which occurred following the abandonment of traditional grazing activities in combination with global warming processes. In the central Apennines, the abandonment of traditional grazing and agroforestry activities began after the 1950s [28,41,77] and accelerated in the investigated mountain areas after their inclusion in the national parks system [16,55]. As in other European mountains [26,27,29,30], land use has deeply changed, and the previous landscape that was characterized by *Pinus mugo* stands scattered over a matrix of secondary grasslands has been replaced by dense *Pinus mugo* shrublands [28]. Similar to what was recently reported for the period of 1960–1990 [50], in the past three decades, we have observed a decline in some subalpine and treeline species that characterize the early stages of *Pinus mugo* community succession, such as *Brachypodium genuense* grasslands and scattered *Juniperus communis* shrublands [35,36,38].

The long-term vegetation analysis also revealed an increase in the abundance of warm-adapted species (e.g., those with an ecological optimum in lower subalpine and montane belts), especially in *Pinus mugo* stands in the upper subalpine belt, such as *Valeriana montana*, *Leucopoa dimorpha*, *Doronicum columnae*, *Hypericum richeri* subsp. *richeri*, *Hippocrepis comosa* subsp. *comosa*, *Orthilia secunda*, and *Thymus praecox* subsp. *polytrichus*. Such variation is most likely related to the increase in mean

annual temperatures that occurred in the study area [33], which probably enhanced the spread of thermophilous species in the *Pinus mugo* scrub at the highest elevations. A similar increase in warm-adapted species was observed by Gottfried et al. [22] in the high-elevation summits of Europe in response to climate warming, and such floristic and ecological changes were interpreted as a process of thermophilization. Other authors have described an increase in species richness in European summits over time and an upward immigration of species from the lower vegetation belts [5,7,10,11,13–15,18,34,78–80]. In our case, the observed thermophilization process was related to the increase in cover of a set of warm-adapted species that were already present in *Pinus mugo* scrubs in the historical relevés. Similar gains in cover were described in alpine vegetation of the central Italian Alps by Cannone and Pignatti [25], who attributed changes in species composition and cover changes to a range-filling process characterized by the expansion of species within the same elevation belt. Our findings showed that a range-filling process has occurred and is ongoing in Mediterranean *Pinus mugo* stands, as species that increased in abundance were already present in the old relevés.

Moreover, it is worth noting that *Pinus mugo* stands in the central Apennines mainly grow on steep calcareous slopes [35] with soils that are rich in debris. These environmental conditions allow good and patchy lighting in the *Pinus mugo* undergrowth that, when coupled with global warming, likely promoted the growth and spread of thermophilous hemicryptophytes, particularly the scapose type. Scapose hemicryptophytes are the smallest forb species occurring in *Pinus mugo* stands, and they are able to increase their cover according to two main strategies: by filling the gaps in vegetation cover in the patchily lit underbrush and by taking advantage of the new climatic conditions that permit a longer growing season and warmer temperatures [81,82].

On the other hand, some cold-adapted herbaceous species common in lower alpine grasslands, such as *Poa alpina* subsp. *alpina*, *Campanula scheuchzeri* s.l., *Pulsatilla alpina* subsp. *millefoliata*, and *Ranunculus pollinensis*, also increased in frequency in *Pinus mugo* stands at higher altitudes. These species may find favorable environmental conditions in shaded undergrowth where summer temperatures tend to be lower than in open grasslands at the same altitudes [83,84].

Our findings also highlighted that the *Pinus mugo* scrubs in calcareous Mediterranean high mountains share several herbaceous plants with the neighboring grasslands in the same vegetation belt, which is consistent with the observations of Wild and Winkler [34], who interpreted the mixed presence of shrubs and grasses in krummholz to be a consequence of the competition-colonization (CC) trade-off, which is the mechanism that allows the coexistence of different contrasting life forms. In this specific case, the authors affirmed that the superiority of krummholz is attenuated by the ability of grasses to reduce the sexual reproduction of shrubs, thus weakening their dominance.

As assessed by other authors [27,31], *Pinus mugo* will most likely colonize the vigorous high-growing grasslands of many subalpine abandoned pastures at relatively low rates, even under the favorable climatic conditions of southern European mountains.

Thus, our results revealed a surprising increase in forb species in the undergrowth of *Pinus mugo* scrub, even though the krummholz stands are denser than in the past. *Pinus mugo* scrubs, which are characterized by richer and drier soils compared with those of the neighboring open grasslands, likely buffer the increase in aridity occurring in the open stands that are rich in calcareous debris. *Pinus mugo* stands seem to offer “mesic islands” in arid and nutrient-poor calcareous grasslands. A similar ability was assessed for other high-mountain shrubs, such as *Juniperus communis*, that develop “fertility islands” in nutrient-poor pastures [84]. The patchy mosaics of *Pinus mugo* stands and grasslands thus provide ecological niches for more mesic species whether they are cold- or warm-adapted, helping to maintain the great plant diversity of the Mediterranean calcareous high mountains [37,55].

## 5. Conclusions

This re-visitation study increased our knowledge of long-term changes in high calcareous mountain Mediterranean vegetation. The *Pinus mugo* underbrush in the central Apennines constituted

an unexpectedly inclusive environment for several hemicryptophytes, both warm- and cold-adapted ones, that increased in abundance in the last decades. *Pinus mugo* scrubs tend to present a patchy spatial pattern that gives rise to “mesic islands” in a matrix of arid grasslands. Based on our results, the increase in herbaceous species is more likely due to a range-filling process of grasses and forbs than to an upward/down-slope shift of species from other vegetation belts. In our case, the biotic interactions between shrubs and grasses and the abiotic heterogeneity seem to play an important role in shaping vegetation structure and ecology, and could buffer the short-term effects of climate change in the analyzed ecosystems.

Similar re-visitation analyses should be implemented in other Mediterranean high mountains, where the effect of global changes (e.g., climate, land cover, N deposition) is forecasted to be consistent, to detect local vegetation trends and adaptation strategies in alpine and subalpine ecosystems. The adopted re-visitation approach represents an adequate instrument where long-term series of ecological data describing natural ecosystems are unavailable, and the results can be combined with those from existing observation networks (e.g., the Long Term Ecological Research network). As historical vegetation plots are available in several countries of Europe, similar re-visitation studies should be extended to other mountains for exploring long-term changes at different scales. In this context, we are confident that new case studies can be done in the future to provide long-term information for increasingly larger areas.

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## Appendix A

**Table A1.** The complete list of species along with the corresponding ecological indicator values of light availability (L), temperature (T), soil moisture (U), soil fertility (N) [48], and species occurrence in the analyzed vegetation belts. The lower subalpine belt (from 1750 up to 2100 m a.s.l.) is indicated by 1, and the upper subalpine belt (from 2100 up to 2420 m a.s.l.) is indicated by 2.

Taxon	Ecological Indicator Value				Vegetation Belt
	L	T	U	N	
<i>Achillea barrelieri</i> s.l.	11	3	2	1	1,2
<i>Adenostyles australis</i>	6	2	7	4	1,2
<i>Anthemis cretica</i> subsp. <i>petraea</i>	10	3	2	1	2
<i>Anthoxanthum nipponicum</i>	8	2	5	4	1,2
<i>Anthyllis montana</i> subsp. <i>jacquinii</i>	10	6	3	3	1,2
<i>Anthyllis vulneraria</i> subsp. <i>pulchella</i>	8	5	3	3	1
<i>Arctostaphylos uva-ursi</i>	6	3	3	2	1,2
<i>Arenaria bertolonii</i>	7	4	3	1	1,2
<i>Armeria gracilis</i> subsp. <i>majellensis</i>	11	3	3	2	1,2
<i>Asperula cynanchica</i> s.l.	7	7	3	3	1
<i>Bellidiastrum michelii</i>	7	3	7	2	1,2
<i>Bellis perennis</i>	9	5	7	5	1,2

Table A1. Cont.

Taxon	Ecological Indicator Value				Vegetation Belt
	L	T	U	N	
<i>Betonica alopecuroides</i> subsp. <i>divulsa</i>	7	3	4	2	1,2
<i>Biscutella laevigata</i> subsp. <i>laevigata</i>	8	2	3	2	1,2
<i>Bistorta vivipara</i>	7	2	3	5	1,2
<i>Brachypodium genuense</i>	8	6	5	4	1,2
<i>Bromopsis erecta</i> s.l.	8	5	3	3	1,2
<i>Campanula scheuchzeri</i> s.l.	8	2	5	0	1,2
<i>Carduus chrysacanthus</i>	11	4	2	1	1,2
<i>Carex kitaibeliana</i>	10	4	2	1	1,2
<i>Carex macrolepis</i>	6	5	3	2	1,2
<i>Carlina acaulis</i> subsp. <i>caulescens</i>	7	5	4	2	1
<i>Carum heldreichii</i>	7	4	3	2	1,2
<i>Cephalanthera longifolia</i>	4	5	3	3	1,2
<i>Cerastium arvense</i> s.l.	8	4	4	4	1,2
<i>Cerastium tomentosum</i>	11	6	3	1	1
<i>Clinopodium alpinum</i> s.l.	9	4	5	2	1,2
<i>Crepis aurea</i> subsp. <i>glabrescens</i>	9	2	5	7	1,2
<i>Cynoglossum magellense</i>	10	4	3	3	1,2
<i>Daphne mezereum</i>	4	5	5	5	1,2
<i>Dianthus longicaulis</i>	8	7	3	4	1
<i>Doronicum columnae</i>	6	4	6	6	1,2
<i>Doronicum orientale</i>	6	4	6	6	2
<i>Dryas octopetala</i> subsp. <i>octopetala</i>	7	2	7	3	1,2
<i>Edraianthus graminifolius</i> subsp. <i>graminifolius</i>	10	3	3	2	1,2
<i>Epipactis atrorubens</i>	8	6	4	4	1,2
<i>Epipactis helleborine</i>	3	5	5	5	1
<i>Erysimum pseudorhaeticum</i>	9	7	2	3	1,2
<i>Euphrasia salisburgensis</i>	7	4	5	4	1
<i>Festuca circummediterranea</i>	11	6	1	2	2
<i>Festuca rubra</i> s.l.	8	4	4	3	1,2
<i>Festuca violacea</i> subsp. <i>italica</i>	8	2	4	4	1,2
<i>Galium anisophyllum</i>	9	3	3	2	1,2
<i>Galium corrudifolium</i>	11	8	2	2	1
<i>Gentiana dinarica</i>	9	3	4	2	1,2
<i>Gentiana lutea</i> subsp. <i>lutea</i>	8	4	4	2	2
<i>Globularia meridionalis</i>	11	3	2	1	1,2
<i>Gymnadenia conopsea</i>	8	4	4	3	1
<i>Helianthemum apenninum</i> subsp. <i>apenninum</i>	9	7	2	2	1,2
<i>Helianthemum nummularium</i> subsp. <i>grandiflorum</i>	9	4	4	2	1,2
<i>Helianthemum oelandicum</i> subsp. <i>alpestre</i>	9	4	3	2	1
<i>Helianthemum oelandicum</i> subsp. <i>incanum</i>	9	4	3	2	1,2
<i>Helictochloa praetutiana</i> subsp. <i>praetutiana</i>	8	4	6	3	1,2
<i>Hepatica nobilis</i>	4	6	4	4	1,2
<i>Hieracium bifidum</i> subsp. <i>stenolepis</i>	8	6	4	2	1,2
<i>Hieracium murorum</i> s.l.	4	4	5	2	1,2
<i>Hieracium pietrae</i>	9	2	4	2	2
<i>Hippocrepis comosa</i> subsp. <i>comosa</i>	9	7	2	2	1,2
<i>Hypericum richeri</i> subsp. <i>richeri</i>	6	6	6	4	1,2
<i>Juniperus communis</i>	8	2	4	4	1,2
<i>Koeleria splendens</i>	11	7	3	1	1
<i>Leontodon hispidus</i> subsp. <i>hispidus</i>	8	3	4	3	1,2
<i>Leucanthemum heterophyllum</i>	7	4	3	2	1,2
<i>Leucanthemum tridactylites</i>	9	4	3	2	1,2
<i>Leucopoa dimorpha</i>	11	4	2	1	1,2
<i>Linum capitatum</i> subsp. <i>serrulatum</i>	9	4	3	1	1,2
<i>Lotus corniculatus</i> subsp. <i>corniculatus</i>	7	5	4	2	1,2
<i>Luzula multiflora</i> subsp. <i>multiflora</i>	7	3	6	3	1

Table A1. Cont.

Taxon	Ecological Indicator Value				Vegetation Belt
	L	T	U	N	
<i>Luzula sylvatica</i> subsp. <i>sieberi</i>	4	4	6	3	1,2
<i>Luzula sylvatica</i> subsp. <i>sicula</i>	4	4	6	5	1,2
<i>Moneses uniflora</i>	4	4	5	2	1,2
<i>Myosotis graui</i>	9	4	4	2	1,2
<i>Onobrychis viciifolia</i>	8	7	3	3	1
<i>Oreojuncus monanthos</i>	9	3	2	2	2
<i>Orthilia secunda</i>	4	5	5	2	1,2
<i>Pedicularis elegans</i>	9	3	3	2	1,2
<i>Phyteuma orbiculare</i>	8	3	5	2	1,2
<i>Petrosedum rupestre</i>	7	5	2	1	1
<i>Picris hieracioides</i> subsp. <i>hieracioides</i>	8	7	4	4	1,2
<i>Pilosella officinarum</i>	8	6	3	2	1,2
<i>Pinus mugo</i> subsp. <i>mugo</i>	8	3	2	3	1,2
<i>Plantago atrata</i> subsp. <i>atrata</i>	5	4	4	5	1,2
<i>Poa alpina</i> subsp. <i>alpina</i>	7	3	5	6	1,2
<i>Polygala alpestris</i> subsp. <i>alpestris</i>	8	2	4	2	1,2
<i>Polygala chamaebuxus</i>	6	4	3	3	1
<i>Potentilla crantzii</i> subsp. <i>crantzii</i>	9	2	5	0	1,2
<i>Prenanthes purpurea</i>	4	4	5	5	1,2
<i>Pulsatilla alpina</i> subsp. <i>millefoliata</i>	8	3	5	3	1,2
<i>Ranunculus breiofolius</i>	11	4	3	2	1
<i>Ranunculus breyninus</i>	9	3	4	3	1,2
<i>Ranunculus pollinensis</i>	11	3	3	1	1,2
<i>Ranunculus thora</i>	8	3	3	3	1,2
<i>Robertia taraxacoides</i>	11	5	4	1	2
<i>Rosa pendulina</i>	7	4	5	5	1
<i>Rumex nebroides</i>	8	7	4	4	1,2
<i>Sabulina verna</i> subsp. <i>verna</i>	9	7	2	0	1
<i>Salix retusa</i>	7	2	6	4	2
<i>Scabiosa columbaria</i> s.l.	8	5	4	2	1,2
<i>Scabiosa silenifolia</i>	11	4	3	2	1
<i>Senecio doronicum</i> subsp. <i>orientalis</i>	8	2	5	3	1,2
<i>Senecio squalidus</i> subsp. <i>rupestris</i>	7	4	4	5	1
<i>Sesleria juncifolia</i> subsp. <i>juncifolia</i>	10	4	2	4	1,2
<i>Sesleria nitida</i> subsp. <i>nitida</i>	11	5	2	1	1,2
<i>Silene acaulis</i> subsp. <i>bryoides</i>	9	1	5	1	1,2
<i>Silene multicaulis</i> subsp. <i>multicaulis</i>	11	4	2	2	1,2
<i>Thymus praecox</i> subsp. <i>polytrichus</i>	8	6	2	2	1,2
<i>Trifolium pratense</i> s.l.	7	6	4	3	1,2
<i>Trinia dalechampii</i>	10	4	3	2	1,2
<i>Urtica dioica</i> subsp. <i>dioica</i>	7	8	6	8	1,2
<i>Valeriana montana</i>	8	4	5	2	1,2
<i>Veronica aphylla</i> subsp. <i>aphylla</i>	8	2	5	2	2
<i>Viola eugeniae</i> s.l.	11	4	2	1	1,2

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