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Environmental and land use determinants of grassland patch diversity in the western and eastern Alps under agro-pastoral abandonment

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Abstract

Agro-pastoral decline in European mountain areas has recently caused changes to traditional landscapes with negative consequences on semi-natural grassland conservation and the associated biodiversity and ecosystem services. In the Italian Alps, grassland patches enclosed in a forest matrix are progressively disappearing. Two alpine valleys (Pesio and Pejo), having similar land-use history, were chosen as representative of management conditions of western and eastern Italian Alps, respectively. This study aims at interpreting the effect of abandonment on grassland patch plant diversity, considering land cover changes of the last 60 years, and assessing the role of ecological, topographic, management and landscape configuration on current grassland species richness. The total area of grassland patches has declined by 54% and 91% at Pesio and at Pejo, respectively. Actual grassland patch species richness was mostly influenced by ecological factors, such as quantity of light, soil moisture and reaction, then by topographic features, especially slope, and finally by management intensity. Landscape factors exerted a slightly significant effect on plant diversity. In the two valleys, differences on management practices were detected. Even though in the western valley the conservation of several grazing activities contributed to slow down the process of patch reduction, many species-rich grasslands were generally under-grazed. Conversely, in the eastern valley, despite a denser road network, the stronger decline of grassland patch extension was linked to the hay making decline. At the same time, overuse of grassland patches near farms reduced plant species richness. As a conclusion, plant species richness was weakly related to the area of grassland patches and current and historical landscape configuration were of relatively lower importance than ecological, topographic and management factors, when evaluated at patch-level.

Keywords: grazing; *Festuco-Brometea*; hay-making; *Molinio-Arrhenatheretea*; biodiversity management; landscape ecology

Introduction

European mountain regions were traditionally dominated by semi-natural ecosystems, where natural and anthropogenic disturbance regimes coexisted and interacted for centuries (Naveh 1995). After a period of biogeographical differentiation and an increase of plant diversity due to climatic variation (Ozenda 1994), the alpine region experienced more than seven thousand years of agro-pastoral activity (Bätzing 2005). Human activity has led to forest fragmentation and grassland patch establishment in a mosaic structure, with semi-natural open habitats of high biodiversity and ecological value (Gellrich et al. 2007).

The European Habitats Directive (92/43/EEC) has identified alpine semi-natural grasslands as important habitats, since the preservation of many plant and animal species is strongly dependent on their maintenance. In these habitats, environmental factors alone, such as topography, climate and soil, cannot explain the complex variability of plant species richness and composition, which is also influenced by past and current land-use pattern (Gehrig-Fasel et al. 2007).

Mechanization and agricultural intensification of some of these grasslands is often limited by physical constraints (e.g. slope). Moreover, in southern alpine regions, the Latin cultural model (*sensu* Bätzing in Fisher et al. 2008) characterised by farming systems usually small-scale and intensive, with concentrated settlements, cultivated crops and terraces (Bartaletti 2004; Niedrist et al. 2009), dominates. These two conditions have created a complex patchy mosaic of open areas scattered in a matrix of forests, with different densities according to silvicultural and grazing practices (Sitzia and Trentanovi 2011).

Throughout the last decades, a trend of abandonment of marginal agricultural and forest lands has caused a steady decline in the regularity of land-use practices in many Italian alpine areas (e.g. Tattoni et al. 2011; Nascimbene et al. 2013). These changes are due to depopulation or reduction of primary sector labour force (Bätzing et al. 1996; MacDonald et al. 2000; Sitzia et al. 2010). One of the most evident consequences has been the natural reforestation of former mesophilic nutrient-rich meadow and pasture communities and dry nutrient-poor calcareous pastures, belonging to *Molinio-Arrhenatheretea* and *Festuco-Brometea* plant communities, respectively. Most of the remaining meadows and pastures are fragmented into a system of small patches, which are increasingly subjected to management abandonment (Grossi et al. 1995). The reduction of the number and size of grassland patches has been causing a subsequent loss of many ecosystem services, such as the capability to produce food, to preserve biodiversity, cultural heritage and landscape attractiveness (Dullinger et al. 2003; Hunziker and Kienast 1999; Probo et al. 2013; Tocco et al. 2013).

The analysis of grassland abandonment and its effects on vegetation should be studied at multiple scales, such as: (i) at landscape level, quantifying how the land cover changes have occurred, considering the socio-economic context and the environmental conditions, and (ii) at local level, assessing current and past spatial configuration of grassland patches, their plant species richness and the factors determining their biodiversity. A comprehensive analysis has to be performed to check the cross-regional explanatory meaning of patch origin, dynamics, size, shape, and spatial configuration of grassland biodiversity when compared with the contribution of environmental and management factors (Forman and Godron 1981; Williamson 2003; Dainese and Sitzia 2013).

We selected two case studies representative of western and eastern alpine districts belonging to the Latin cultural model and sharing a common past history of land-use, but constrained by different environmental and management conditions. Both districts have been subject to exploitation of forest resources. The minimum extent of forests was reached in both valleys in the eighteenth and nineteenth centuries, for the need of agro-pastoral areas and mining and textile manufacturing. Since that period, the surface of forests has constantly increased due to agro-pastoral abandonment. Therefore, the present work compared two alpine valleys with the aims of (i) quantifying their spatial and temporal land cover changes (from 1954 to nowadays), (ii) comparing the two valleys to the patch-level and determining the factors affecting current grassland species richness and composition.

Materials and Methods

Study area

Two valleys, Pesio in the western and Pejo in the eastern Alps, were selected as representative of the main management situations in the Italian Alps. The Pesio Valley (Piedmont Region, north-western Italy) was selected as representative of sub-Mediterranean outer calcareous western Alps,

while the Pejo valley (Trento Province, north-eastern Italy) as representative of continental siliceous eastern Alps (Ozenda 1985).

The Pesio valley study site (44°13' N, 7°40' E) is located within the Marguareis Regional Park. The elevation range is from 850 to 2050 m a.s.l., the average temperature in Certosa di Pesio, located in the bottom of the valley (860 m a.s.l.), is 8°C and the average monthly temperatures range from 0.7°C in January to 17°C in July. The average annual rainfall is 1457 mm, with two peaks; one in May and the other in November. Population density decreased from 76 residents/km² in 1881 to the current 40 residents/km². The montane and subalpine belts are composed of a mixture of sycamore maple (*Acer pseudoplatanus* L.), common ash (*Fraxinus excelsior* L.), and European beech (*Fagus sylvatica* L.) forests enclosing grassland patches, which are still grazed during the seasonal transhumance on the way to the upper alpine pastures in late spring and on the way back in autumn. Residual meadows, in the valley floor, are currently and extensively mowed one or two times/year.

The Pejo valley study site (46°21' N, 10°41' E) is located within the border of the Stelvio National Park. The elevation range is from 1250 to 2080 m a.s.l., the average annual temperature in Pejo (1565 m a.s.l.) is 7°C and the average monthly temperatures range from -1°C in January to 15°C in July. The average annual rainfall is 856 mm, mainly concentrated in summer. In the Pejo valley, the population density is more or less unchanged since 1921 (10.8 residents/km² to the current 11.8 residents/km²). However, population maintenance was mainly due to the increase of tourism and to the decrease of the agricultural employment. The current montane and subalpine altitudinal belt consists of a mixture of larch (*Larix decidua* Mill.) and spruce (*Picea abies* (L.) H. Karst.) forests and enclosed remnant grassland patches, known as *maggenghi*, which are now only partly managed with mowing and grazing activities (Niedrist et al. 2009).

During the second post-war period, these two valleys were affected by widespread socio-economic changes which led to the abandonment of mountain agriculture and landscape transformation over large surfaces (Patella 1969; Pedrotti 1988; Garbarino et al. 2014). Agro-pastoral changes have included the reduction in the number of farms, available manpower and domestic herbivores reared and the intensification of the remaining agriculture within smaller areas.

Land cover changes

To assess landscape changes in both valleys, historical aerial photographs were scanned and orthorectified at 1 m resolution. Subsequently, five land cover types were detected with manual photo interpretation, within a buffer of 1 km (Sitzia and Trentanovi 2011) around current grassland patch centroids: forests, grasslands, rocks, water, and urban (Figure 1).

In the grassland land cover type, which included valley bottom meadows, grassland patches and alpine pastures (i.e. pastures above the treeline), grassland patches were defined and retained as the polygons, below the potential timberline, larger than 0.1 ha with a density of trees lower than 20%, and at least 10 m wide (Sitzia and Trentanovi 2011). Interpretation of photos and all the other spatial analyses were performed using the GIS software ESRI® ArcMap™ 10 (ESRI 2011). A landscape transition matrix was performed to assess land cover changes from 1954 to 2006 at Pejo and from 1954 to 2012 at Pesio.

Grassland patch vegetation

The past and present grassland patches were extracted from both sites. Total plant species richness was measured from the beginning of June to the end of August at the flowering phenological stage for the dominant graminoids and each site was walked through and all vascular plant species were recorded. The time spent at each site was adjusted to be proportional to the area of the site, approximately 30 min per ha (Cousins et al. 2007). Species nomenclature followed Landolt et al. (2010). In order to identify the prevalent grassland communities, the phytosociological optimum was associated to each vascular plant species at the class level, including all subordinated syntaxa

(Aeschimann et al. 2004). Two representative phytosociological grassland classes in the study sites were selected: the (i) *Molinio-Arrhenateretea* class, representing semi-natural mesophilic grasslands, and the (ii) *Festuco-Brometea* class, representing semi-natural dry grasslands. For each plant species recorded in the botanical surveys, the chorology and the distribution area were assigned according to Aeschimann et al. (2004) and plant species were divided in three groups: (i) species exclusively present at Pesio, (ii) exclusively present at Pejo valley (iii) and present in both valleys.

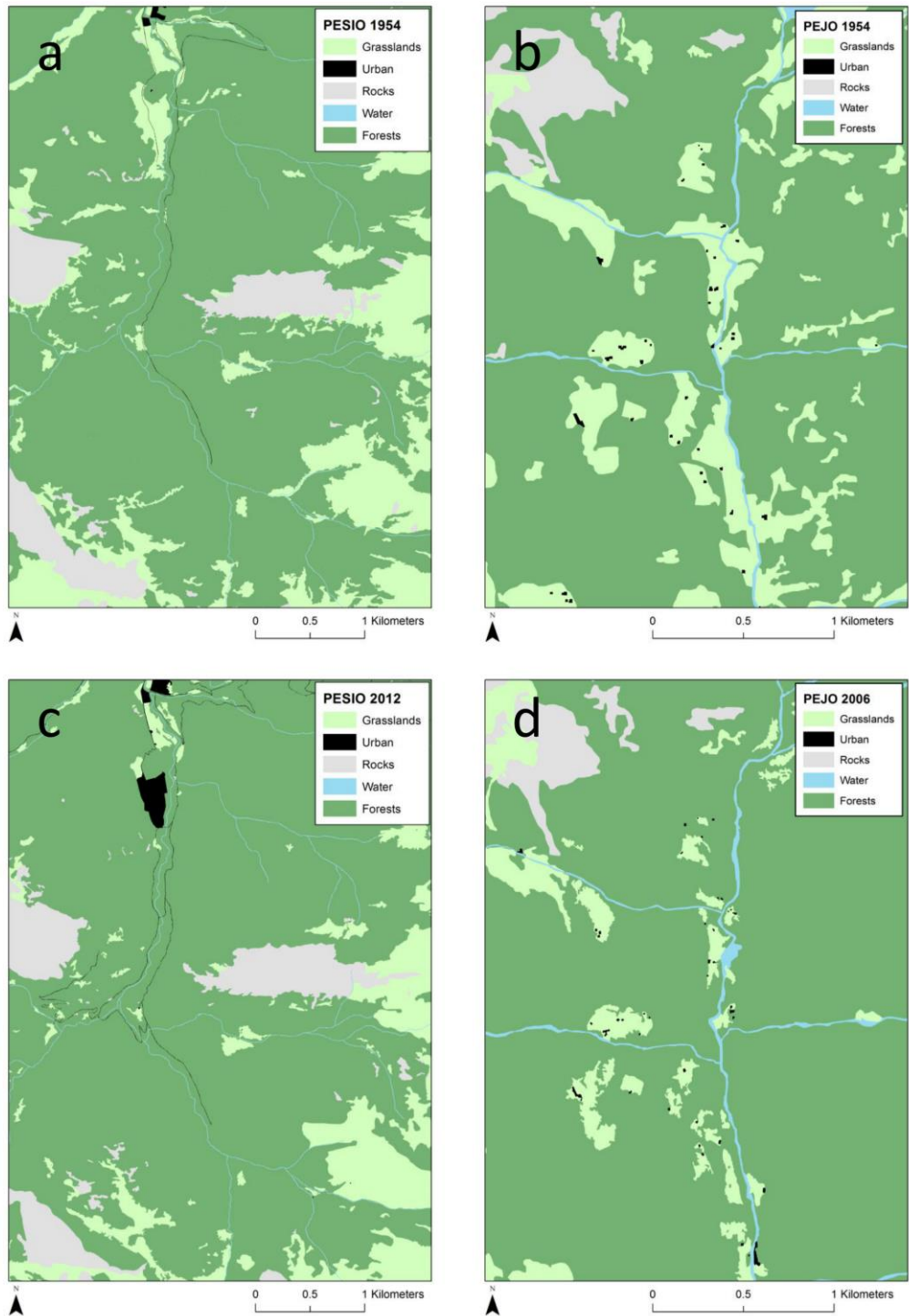


Figure 1 – Maps of the two study sites in two different years with 5 land-use classes: [a] the Pesio valley in 1954, [b] the Pejo valley in 1954, [c] the Pesio valley in 2012 and [d] the Pejo valley in 2006.

The following indicator values of Landolt (2010) were also attributed to each species: light (L), indicating the light quantity received by a species in its habitat; soil moisture (F), as the average quantity of soil moisture in a species habitat; soil reaction (R), indicating soil pH, and nutrient value (N), indicating soil nutrient content. The mean value of each indicator, based on the list of species of each grassland patch, was calculated to determine the mean ecological conditions of each patch (Lonati et al. 2013; Vacchiano et al. 2015). Furthermore, the standard deviation of each indicator was calculated to determine the degree of ecological variations within each patch.

Bare ground and rock layers percentage cover were visually estimated for each grassland patch. The average soil depth within each patch was assessed by randomly inserting a 1 m pole from ten to 25 times for each patch, depending on patch size and measuring the height of the insertion.

The overall grassland management intensity was calculated as the mean between the estimation of the grazing intensity and the number of mowings on a scale ranging from 0 (lowest intensity values) to 5 (highest values). Grazing intensity, obtained from a visual evaluation of forage consumption, was estimated using a scale ranging from 0 to 5. The number of mowings in each patch was recorded by direct interviews to farmers. The litter cover was also visually estimated and classified in five groups: low (0-20%), medium (21-40%), frequent (41-60%), abundant (61-80%), very abundant (81-100%).

Elevation, slope, southness and roughness were extracted for each patch from a Digital Elevation Model (DEM) with a 5×5 m cell size. Southness, an index of south-facing aspect, was measured as a linear transformation of aspect ($180^\circ - |\text{aspect} - 180^\circ|$) (Chang et al. 2004). A roughness index was determined from the DEM slope variation according to the Wilson et al. (2007) method. The distances between patches and roads and between patches and farm buildings were calculated, as a proxy for accessibility.

In order to assess grassland changes at a landscape level, the area, the perimeter and the Shape Index (SI, a measure of the complexity of patch shape compared to a standard square shape) of grassland patches were calculated. The SI was determined with Patch Analyst extension for ESRI® ArcMap™ 9.3 (Rempel et al. 2012). The maximum nearest neighbour distance among grassland patches and all the other grassland patches within a 1-km radius was calculated. Within this distance the proportion of grassland area for every patch was calculated as an index of connectivity (Kindlmann and Burel 2008; Sitzia and Trentanovi 2011).

Statistical analysis

In order to assess vegetation differences between the two valleys, a canonical correspondence analysis (CCA) was used to create a species–environment model using grassland patch species as response variables and environmental variables as predictors. The overall CCA model significance was tested using Monte Carlo permutation tests (499 iterations) and by evaluating canonical coefficients and intra-set correlations (Ter Braak 1986). In order to perform a more parsimonious CCA analysis, only the most abundant plant species were retained and used, i.e. species occurring in at least 10% of patches. Topographic features (elevation, slope, southness, roughness), landscape metrics (area, perimeter, shape index, connectivity) and the distance from roads and farm buildings were considered as environmental variables. Predictor variables were checked for avoiding mutual correlation ($r > |0.80|$), which may cause unstable canonical coefficients (Dirnböck et al. 2003), thus the roughness was excluded because of its correlation with the slope ($r = 0.98$). The CCA was performed with CANOCO 4.5 (Ter Braak and Šmilauer 2009).

In order to detect the factors that most affected species richness, a two-step analysis was performed.

Firstly, species-area curves with linear regression models were calculated for (i) total plant species richness, (ii) the number of species belonging to the *Molinio-Arhenatheretea* and (iii) to the *Festuco-Bometea* phytosociological classes for each valley. When necessary, data were log-

transformed to ensure the normality and homoscedasticity of residuals. Secondly, to avoid the effect of area, the residuals from the species-area relationship were modelled to consider other sources of variation (Price 2004), such as ecological, management, topographic and landscape factors. Thus, the residuals from linear regressions of total plant species richness, number of species belonging to the *Molinio-Arrhenatheretea* and to the *Festuco-Brometea* phytosociological classes for each valley were used as dependent variables in Generalized Linear Models (GLMs). A backward stepwise model was used in order to select the most parsimonious model using the stepAIC function of the MASS package (Venables and Ripley 2002) of the R statistical software, version 3.1.2 (R Core Team 2014). Analyses were performed separately for each valley to consider regional differences. We decided not to perform a unique analysis, with site considered as a random effect, due to the small number of its levels, since at least six levels are required for obtaining sensible estimates of standard deviations for simple random effect terms (Bates 2010). Predictors were ecological parameters (L, F, R, N Landolt's indicator values, bare ground and rock cover percentage and soil depth), management variables (management intensity, litter cover, distance from roads and from farm buildings), topographic features (elevation, slope, southness and roughness) and landscape metrics (area, perimeter, shape index and connectivity) of the grassland patches. For the total species richness analysis, the standard deviation and the mean value of Landolt indicator values were used to assess the ecological variations within each patch, while for the phytosociological class analysis only the mean value was considered to evaluate the specific mean ecological conditions affecting class species richness. Predictors were standardized (Z-scores) to examine the effect of each factor by scrutinizing model parameters (β coefficients). A correlation analysis of predictor variables was used to exclude any highly collinear predictors ($r > |0.80|$), thus the roughness was excluded because of its correlation with the slope ($r = 0.98$). The amount of deviance (D^2) explained by each GLM was calculated with the following equation: $D^2 = [(\text{Null-Deviance} - \text{Residual Deviance}) / \text{Null-Deviance}]$.

Results

Land cover changes

Forest was the dominant land cover type (Table 1) and increased its percentage over the study period in both sites. Grasslands decreased especially due to forest encroachment (-28% at Pesio and -53% at Pejo), the Urban class increased from 7.2 ha to 23.4 ha (+225%) at Pesio and from 28.1 ha to 70 ha (+150%) at Pejo. On the whole, the landscape transition matrix showed that 15.5% and 22.3% of the landscape at Pesio and Pejo, respectively, changed throughout the study period (Table 1).

In the Pesio valley, 47 and 61 grassland patches were found from aerial photographs in 1954 and 2012, respectively. The total area of the grassland patches was 110.62 ha in 1954, with an average extension of 2.35 ha per patch, and 59.23 ha in 2012, with an average of 0.97 ha (Table 2). In the Pejo valley, 32 and 59 patches were found in 1954 and 2006, respectively. The total area was 852.55 ha in 1954, with an average extension of 26.64 ha per patch and 77.84 ha in 2006, with an average of 1.32 ha.

The total area of grassland patches declined by 46% and 91% in the Pesio and in the Pejo valley (Table 2), respectively. In the Pesio valley, 20 patches in 2012 originated from the fragmentation of 9 bigger patches in 1954. In the Pejo valley, 37 patches in 2006 originated from the fragmentation of 11 bigger patches in 1954.

Table 1 – Transition matrices showing land cover changes in the two study sites. Values are expressed in hectares and in percent (in brackets) relative to the total area of the class in 1954. The total area value in the row indicates the area of the land-use class in 1954, while the total area value in the column indicates the area of the land-use in 2012 for the Pesio valley and in 2006 for the Pejo valley. The percentage indicates the percentage area of the 1954 land-use class (row) which shifted to the current land-use class (column).

	Grassland	Urban	Rock	Water	Forest	Total area
Pesio 1954 to 2012						
Grassland	574.4 (63 %)	12.6 (1 %)	74.2 (8 %)	0.0 (<1 %)	254.9 (28 %)	916.1 (25 %)
Urban	1.0 (15 %)	3.4 (47 %)	0.0 (<1 %)	0.0 (<1 %)	2.7 (38 %)	7.2 (<1 %)
Rock	25.3 (10 %)	0.0 (<1 %)	162.2 (66 %)	0.0 (<1 %)	58.2 (24 %)	245.7 (7 %)
Water	0.0 (<1 %)	0.0 (<1 %)	0.0 (<1 %)	21.8 (100 %)	0.0 (<1 %)	21.8 (1 %)
Forest	64.4 (3 %)	7.3 (<1 %)	32.1 (1 %)	0.0 (<1 %)	2389.1 (96 %)	2493.0 (68 %)
Total area	665.1 (18 %)	23.4 (1 %)	268.6 (7 %)	21.8 (1 %)	2704.9 (73 %)	3683.8 (100 %)
Pejo 1954 to 2006						
Grassland	658.7 (42 %)	48.5 (3 %)	12.0 (1 %)	18.1 (1 %)	821.5 (53 %)	1558.8 (35 %)
Urban	4.7 (17 %)	18.9 (67 %)	0.1 (<1 %)	0.3 (1 %)	4.2 (15 %)	28.1 (1 %)
Rock	8.4 (5 %)	0.0 (<1 %)	146.1 (82 %)	2.6 (1 %)	21.4 (12 %)	178.5 (4 %)
Water	3.6 (6 %)	1.3 (2 %)	1.0 (2 %)	41.8 (70 %)	11.7 (20 %)	59.5 (1 %)
Forest	46.2 (2 %)	1.2 (<1 %)	13.9 (1 %)	5.4 (<1 %)	2581.4 (97 %)	2648.1 (59 %)
Total area	721.7 (16 %)	70.0 (2 %)	173.1 (4 %)	68.1 (2 %)	3440.1 (77 %)	4472.9 (100 %)

Table 2 – Mean value and standard deviation value of landscape metrics (area, perimeter and shape index) and slope of grassland patches of the Pesio Valley for 1954 and 2012 and of the Pejo Valley for 1954 and 2006. For both valleys the loss of patch area during the study period was calculated and expressed in percentage of total area.

	Total area (ha)	Average area (ha)	Area st. dev. (ha)	Average perimeter (m)	Perimeter st. dev. (m)	Average shape index	Shape index st. dev.	Average slope (degrees°)	Slope st. dev. (degrees°)
Pesio Valley									
1954	110.62	2.35	3.48	985	829.94	1.76	0.88	25.46	10.05
2012	59.23	0.97	1.41	593	427.76	1.79	0.53	22.11	10.28
Area loss (%)	46 %								
Pejo Valley									
1954	852.55	26.64	55.965	5751	8768.6	3.23	1.53	21.77	4.85
2006	77.84	13.19	1.750	897	701.33	2.36	0.58	19.64	5.71
Area loss (%)	91 %								

The shape index in the Pesio and Pejo valleys slightly increased and considerably decreased, respectively, from 1954 to the present (Table 2). The average slope of grassland patches decreased in both valleys during the study period, from 25.46° to 22.11° and from 21.77° to 19.64° at Pesio and at Pejo, respectively (Table 2).

Grassland patch vegetation

The overall species richness of the grassland patches of both valleys consisted in 682 plant species. In the Pesio and Pejo valleys, 609 and 253 species were detected, respectively, and 180 species were recorded in both valleys (i.e. 26.4% of the total number of species). The chorological analysis highlighted that 94% of the species were potentially present in both valleys. *Molinio-Arrhenatheretea* and *Festuco-Brometea* were the dominant phytosociological classes, with 88 species and 78 species for the Pesio valley and with 63 species and 25 species for the Pejo valley, respectively.

The CCA (Figure 2a) showed a clear separation of the two valleys along the first two axes (eigenvalue (λ) axis 1=0.31, λ axis 2=0.15). The patches of the Pesio valley were generally located further from roads and farm buildings. The upper patches were also distinguished by high connectivity values, mainly due to the proximity of alpine pasture. The Pejo patches were characterized by a higher perimeter and shape index values and were closer to roads and farm buildings, mainly in south-facing sites (Figure 2a). The main difference was assessed within the first axis, which highlighted the dominant presence of woody and shade demanding species in the Pesio valley (Figure 2b). These species belonged to the *Vaccinio-Piceetea excelsae* (e.g., *Rhododendron ferrugineum* L., *Vaccinium myrtillus* L.), *Fagetea sylvaticae* (e.g., *Acer pseudoplatanus* L., *Fagus sylvatica* L) and *Crataego-Prunetea* (*Sorbus aucuparia* L., *Rosa canina* L.). Elevation and slope gradients were highlighted in both valleys. Lower elevation patches were dominated by species belonging to the *Festuco-Brometea* (e.g., *Salvia pratensis* (Rafn) Godr., *Galium verum* L.), *Trifolio Geranietea* (*Agrimonia eupatoria* L., *Hypericum perforatum* L.) and *Molinio-Arrhenatheretea* class, particularly belonging to the *Cynosurion* alliance (*Cynosurus cristatus* L., *Bellis perennis* L.), which is typical of intensively used pastures, and *Arrhenatherion* (e.g., *Knautia arvensis* (L.) Coult.), of mesophilic and eutrophic meadows. Higher elevation patches were dominated by grassland species, belonging to the *Juncetea trifidi* (e.g., *Campanula scheuchzeri* Vill., *Phyteuma betonicifolium* Vill.,), *Elyno-Seslerietea varia* (e.g., *Lotus alpinus* (DC.) Ramond., *Carduus defloratus* L.) and *Nardetea strictae* class (e.g., *Luzula multiflora* (Ehrh.) Lej., *Carex leporina* L.). At the highest elevations, species belonging to the *Molinio-Arrhenatheretea* class had their phytosociological optimum in the *Trisetum-Polygonum* alliance, which is typical of meadows mowed once a year, (e.g., *Polygonum bistorta* L., *Chaerophyllum villarsii* W. D. J. Koch) and in the *Poion alpinae* alliance (e.g., *Phleum rhaeticum* (Humphries) Rauschert, *Poa alpina* L.), characteristic of intensively used alpine pastures.

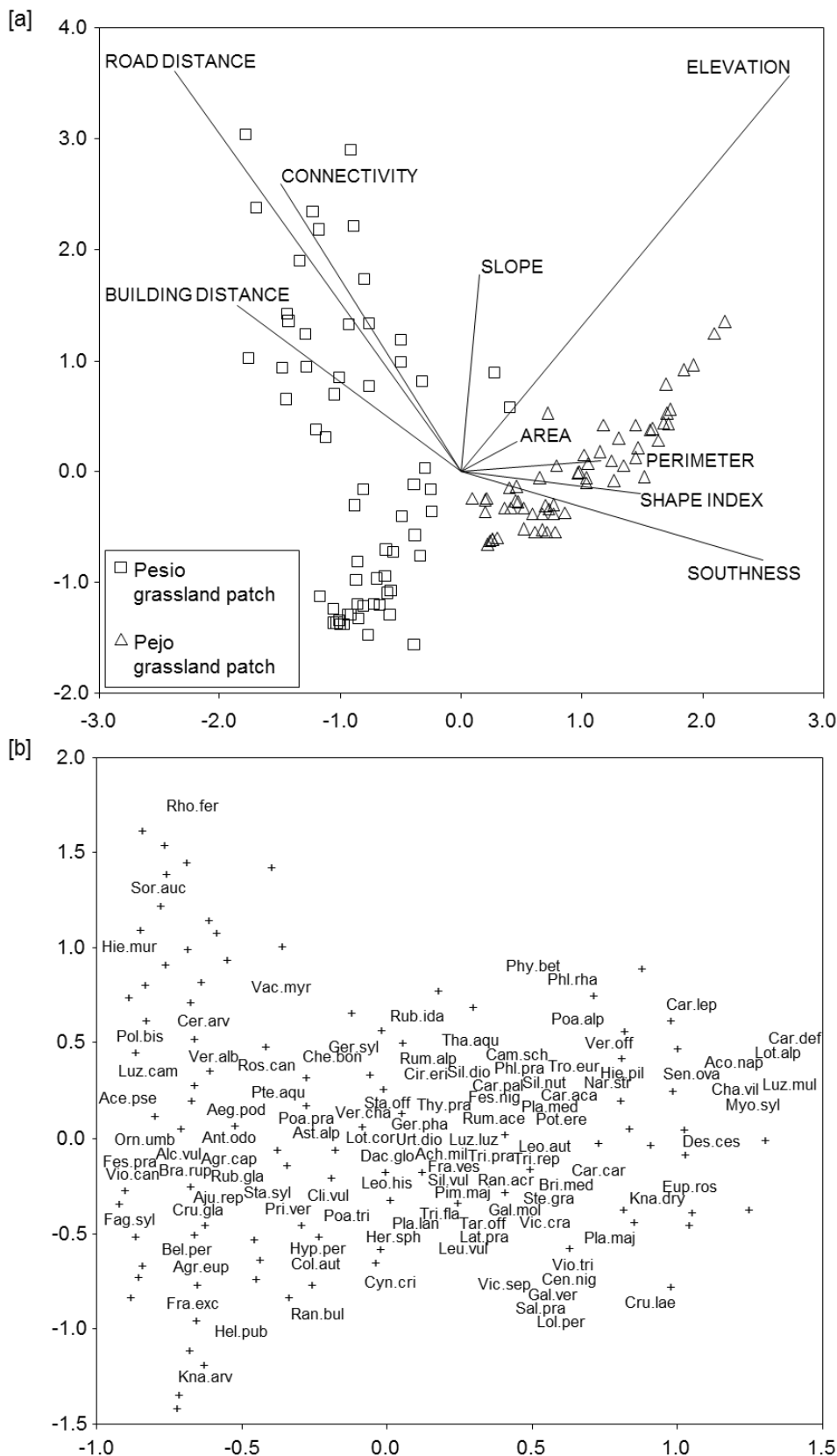


Figure 2 – CCA ordination diagram of [a] sample patches and [b] species (species labels were centered on scores, with minor adjustment to avoid text overlap).

Species-area linear regressions highlighted that patch area was positively, but weakly, related to total species richness, number of the *Molinio-Arrhenatheretea* species and number of the *Festuco-Brometea* species in both valleys (Table 3).

Table 3 – Species-area linear regressions of total species richness, the number of *Molinio-Arrhenatheretea* species and the number of *Festuco-Brometea* species of the Pesio and Pejo valleys, respectively.

	R ²	Signif. ^a
Pesio Valley		
Total species richness	0.392	***
<i>Molinio-Arrhenatheretea</i> number of species	0.182	**
<i>Festuco-Brometea</i> number of species ^b	0.084	*
Pejo Valley		
Total species richness ^b	0.144	**
<i>Molinio-Arrhenatheretea</i> number of species	0.066	*
<i>Festuco-Brometea</i> number of species ^b	0.068	*

^a ‘****’ p <0.001; ‘***’ p <0.01; ‘*’ p <0.05

^b Log-transformed data

Generalized Linear Models showed that species diversity was mainly affected by ecological, topographic, management and landscape factors. The total species richness of both valleys was more influenced by ecological, topographic and management features than by landscape features (Table 4). Mean soil moisture and light emerged as being the most influential variables at Pesio, but also pH variation exerted a positive significant influence on the total number of plant species. The intensity of agro-pastoral management had a strong negative influence on species richness at Pejo, while mean soil pH and variation of light quantity positively affected total plant biodiversity. In both valleys, the rock cover negatively affected total species richness. On the contrary, soil depth and litter cover had an opposite effect between the two valleys.

Total species richness was reduced by an increase in soil depth and was increased by litter cover at Pesio, whereas soil depth and litter cover were positively and negatively correlated with total species richness, respectively, at Pejo. Moreover, shape index had a positive influence on plant biodiversity at Pesio, while slope and southness had a positive influence on plant diversity at Pejo.

Species belonging to the *Molinio-Arrhenatheretea* phytosociological class were mostly affected by ecological, topographic and management features both in the Pesio and Pejo valleys (Table 4). Soil moisture and light quantity exerted the main influence in the Pesio valley, while soil pH was the most significant ecological factor affecting mesophilic grassland species at Pejo. These species were negatively correlated with elevation at Pesio and were positively affected by slope and southness at Pejo. Intensity of agro-pastoral management determined an opposite effect between the two valleys, as it was positively and negatively related to the *Molinio-Arrhenatheretea* species in the Pesio and in the Pejo valleys, respectively. Furthermore, litter cover negatively affected mesophilic grassland species at Pesio, while soil depth had a positive influence. The current grassland patch connectivity was positively associated with the total number of species belonging to *Molinio-Arrhenatheretea* phytosociological class only at Pesio.

The total number of species belonging to *Festuco-Brometea* phytosociological class was strongly influenced by ecological variables in both valleys (Table 4). In the Pesio valley, light quantity and soil moisture were positively and negatively correlated with the number of semi-natural dry grassland species, respectively, whereas in the Pejo valley these species were positively affected by soil reaction and negatively influenced by soil nutrient content. Moreover, in the Pesio valley the rock cover had a negative effect on the number of *Festuco-Brometea* species and in the Pejo valley slope and southness had a positive relation. Within the same valley, the intensity of agro-pastoral management and the current grassland patch connectivity were both negatively correlated with dry grassland species richness.

Table 4 - Stepwise GLMs of Pesio and Pejo valleys on the species-area linear regression residuals of total species richness, the number of *Molinio-Arrhenatheretea* specie and the number of *Festuco-Brometea* species as dependent variable, and ecological (L – light quantity; F – soil moisture; R – soil reaction; N – soil nutrient content; rock cover; bare ground cover; soil depth), management (management intensity, litter cover, distance from roads), topographic (elevation, slope, southness) and landscape features (SI – shape index, connectivity) as predictors. D² is the amount of deviance explained by each model.

Predictors	Pesio valley			Pejo valley		
	Total species richness	<i>Molinio-Arrhenatheretea</i>	<i>Festuco-Brometea</i>	Total species richness	<i>Molinio-Arrhenatheretea</i>	<i>Festuco-Brometea</i>
D ²	0.52	0.76	0.81	0.65	0.75	0.72
Ecological						
L ^a	16.69**	6.92**	0.17***	0.04***		
L ^b	5.82 ^{n.s.}				0.95 ^{n.s.}	
F ^a	19.43**	10.6**	-0.16***	0.04***	2.90***	0.12***
R ^a	7.37 ^{n.s.}	2.47 ^{n.s.}			0.93 ^{n.s.}	-0.06***
R ^b	8.87*					
N ^a				0.02 ^{n.s.}		
N ^b				-0.03**		
Rock cover	-8.39**	-1.54 ^{n.s.}	-0.11***	-0.02 ^{n.s.}		
Bare ground cover			0.05 ^{n.s.}			
Soil depth	-6.07*			0.02*	1.60**	
Management						
Management intensity		2.54*		-0.05***	-1.83***	-0.03*
Litter cover	4.72*	1.14 ^{n.s.}		-0.03*	-2.16***	
Distance from roads			0.06 ^{n.s.}			
Topographic						
Elevation		-4.92***	-0.08 ^{n.s.}			
Slope				0.03**	1.82**	0.07***
Southness				0.02*	0.69 ^{n.s.}	0.03*
Landscape						
Connectivity		4.04**		-0.02 ^{n.s.}		-0.04**
SI	5.97*	1.15 ^{n.s.}				

^a. average value

^b. standard deviation value

***: $n < 0.001$; **: $n < 0.01$; *: $n < 0.05$; ^{n.s.}: $n > 0.05$

Discussion

Land cover changes

In both valleys, the abandonment of agro-pastoral activities led to spontaneous reforestation, which mainly reduced the extension and the relative abundance of grasslands, particularly decreasing the area of grassland patches enclosed by forests. The extension of grassland patches in 1954 was much greater at Pejo than at Pesio, however, a more intense pattern of abandonment at Pejo led to a similar current grassland patch extension. The stronger decrease of both total and average grassland patch area observed at Pejo, as well as the higher fragmentation and the reduction in the shape index, could be explained by the abandonment of the hay making practice, which is currently confined to small residual areas, often located on the flattest sites. Slope was one of the most important factors causing the abandonment of semi-natural meadows and a long-term landscape simplification. This was mainly due to the transformation of hay-making practices in last the decades as farmers currently cut meadows on gentle slopes (Tasser et al. 2007; Marini et al. 2011). Thus, one spatial process that surely played an important role during the study period is the spontaneous reforestation of the less accessible grassland patches, which made patch boundaries more regular and curvilinear (Forman 1995), as demonstrated by the shape index reduction observed at Pejo. Conversely, in the Pesio valley the conservation of the grazing activity, linked to the transhumance towards alpine summer pastures, resulted in a slower decrease in the grassland patch area and in a lower fragmentation, allowing the maintenance of less accessible and steeper grassland patches (Dolek and Geyer 2002). Therefore, at Pesio the grazing activity maintained the original complexity of patches, as confirmed by the stability of the shape index during the study period.

Grassland patch vegetation

The CCA highlighted a sharp separation between the two valleys, due to the presence of several vegetation groups that were dominant in only one site, mainly because of management differences (Niedrist et al. 2009) and not related to biogeographical differentiations between western and eastern Italian Alps. The Pesio valley was characterized by patches far from roads and management structures, traditionally used during the seasonal transhumance towards upper alpine pastures. This practice allowed for the maintenance of a significant connection between grassland patches and the upper alpine pastures that represent an important source of biodiversity, as highlighted by the presence of many pasture species in grassland patches, which were typical of the alpine belt. In the Pesio valley, many fringe and tall herb species occurred due to land abandonment and as a consequence of current low stocking density and under-grazing, which concerned many middle-elevation patches. In the Pejo valley, the grassland patches were generally associated to warmer south-facing aspect, high area extension and jagged perimeter. Current grassland patches were usually close to roads and to farms buildings. These characteristics determined the maintenance of traditional hay making practice and the conservation of meadows. As patch grazing was often restricted in farms' paddocks, and livestock was moved towards alpine summer pastures on roads, the grassland connectivity was low.

Molinio-Arrhenatheretea and *Festuco-Brometeta* total plant species richness within grassland patches were positively, but weakly, associated to patch size, as reported by other authors (Krauss et al. 2004; Reitalu et al. 2009). In any case, the number of species was mainly influenced by factors other than patch size, such as environmental features (Reitalu et al. 2009). The results of stepwise GLMs highlighted that ecological, topographic variables and management intensity were the most important features influencing grassland biodiversity, as reported by other authors (Marini et al. 2007; Reitalu et al. 2009). The results of both valleys showed that grassland biodiversity within patches was fostered by the differentiation of favourable niches (Cousins and Eriksson 2002; Chytrý et al. 2003; Becker and Brändel 2007) due to the variation of local conditions. However, at

Pesio, the negative effect of soil depth was unexpected, as this parameter generally exerts an inverse influence on the amount of species (Cousins and Eriksson 2002). Cousins and Eriksson (2002) found a positive relationship between the total number of species and soil depth within acidic mesophilic grasslands, but, at Pesio, an inverse trend was detected. This result could be explained considering the steep slopes and the calcareous parent rock of several grassland patches with a reduced soil depth, which hosted a large amount of rupicolous species, mainly belonging to the *Festuco-Brometea* phytosociological class. In accordance with this result, Tyler (1996) found that soil depth had little influence on total species richness in calcareous alpine grasslands, even on extremely shallow soil (i.e. less than a couple of centimetres), due to the stronger influence of the parental rock (Hillier et al. 1990). These dry grasslands, present on almost the entire European continent on calcareous to neutral substrates, are among the most species-rich grassland communities (Calaciura and Spinelli 2008; Dengler et al. 2014). The positive effect of litter cover percentage on total species richness was also unforeseen and it could probably be related to the early secondary succession stages of many sites, due to recent changes in grazing management, such as the reduction of farms: -92 % during the last 50 years in the western Alps (ISTAT 2010) and -67 % in the Trento province (Fontana 2011). Consequently, an increase of fringe species and patch fragmentation has been produced, as confirmed by the positive effect of the shape index (SI). Where grazing was abandoned, the colonization of niche space for light capture was one of the most recurring phenomenon in grassland patches, due to the cessation of the competitive exclusion (den Boer 1986) for light made by dominant and fast-growing herbaceous species and to the possible establishment of low-growing, poorly competitive species (Roleček et al 2014). For this reason, the patch edges were temporarily colonized by light demanding woody species and shade-tolerant herb species that contributed to an increase in plant biodiversity during this first phase of the secondary succession with a contemporary increase of litter cover (Schmidt 2005). Instead, when the secondary succession proceeds to late stages, a marked reduction in total plant diversity is produced (Schmidt 2005). In the Pejo valley, total species richness was higher on steeper slopes due to a different meadow management in steep terrain, less suitable for intensive practices (Bennie et al. 2006). Steep slope was a typical feature of grassland patches far from farm buildings. Indeed over 15° of slope, mowing activity is generally unfeasible, thereby only extensive grazing can be performed to maintain grassland patches and their biodiversity. This is one of the main reasons to explain why management intensity was negatively related to total species richness, likely because several grasslands were over-used on many flat sites, close to farm buildings. Overgrazing can lead to a reduction of total species richness (Walz and Syrbe 2013), as with the increase of management intensity only the ruderal and competitor species can survive (Grime 2002), causing a loss of total species richness (Marini et al. 2008). Indeed, in the case of management that is too frequent and/or intense and ecological disturbances, only a few species have the necessary adaptations to survive (Dengler et al. 2014). In contrast, plant diversity is generally promoted in extensively fertilized meadows, where resources such as nutrients and soil moisture are limiting, as a result of niche overlaps, which enable the co-existence of distinct water- and nutrient-use strategies (Dengler et al. 2014). For this reason, steep slopes, which usually reduce management intensity, tend to host higher plant species richness (Marini et al. 2008).

Molinio-Arrhenatheretea species richness in both valleys was also mainly influenced by ecological and management factors. At Pesio, the results highlighted that soil moisture and light quantity had the most important effect, as reported by other authors (Kuzemko 2011), as water availability and light are essential factors for semi-natural mesophilic grassland. Moreover, elevation was negatively related to mesophilic grassland vegetation, as this group of species is generally located in the valley floor, at relatively low elevation (Kuzemko 2011). On the contrary, current connectivity and management intensity had a positive influence, due to the remarkable effect of grazing and mowing on landscape features (Lindborg and Eriksson 2004), as the reduced connectivity among grassland patches can negatively influence the spillover of grassland species and decrease the chance of

dispersal among the remaining grassland patches (Zulka et al. 2014). Intermediate-intensity grazing is considered a management technique allowing the co-existence of many grassland specialist species, according to the Intermediate Disturbance Hypothesis, which suggests that species richness should peak at intermediate densities of management (Grime 1973; Connell 1978). At Pejo, the *Molinio-Arrhenatheretea* species were mainly affected by soil reaction, as it was the main cause of the diversity of these species in nutrient-demanding grasslands on siliceous soil (Becker et al. 2012). The relationship with soil depth, management intensity, litter cover percentage, and slope could be explained considering that these grassland species were favoured by mesophilic conditions, which occurred preferably at moderate slope sites with balanced soil nutrient content. On more gentle slopes and accessible sites, the high management intensity increased nitrogen soil content and led to the colonization of nitrophilous species, as *Urtica* and *Rumex* spp. and to the reduction of *Molinio-Arrhenatheretea* species. Besides fertilization, the cutting regime of the hay meadows was likely to affect grassland plant diversity. Hay cutting had a short-term effect by removing above-ground biomass periodically, and so influencing plant dispersal, competition and germination conditions. In experimental long-term monitoring studies, the positive effect of haymaking once a year was confirmed, while hay-making twice a year showed a reduction of *Molinio-Arrhenatheretea* species richness after fertilization cessation (Bakker et al. 2002).

Festuco-Brometea species richness in the Pesio valley was positively affected by light and negatively affected by soil moisture and rock cover percentage, as highlighted in literature (Dengler et al. 2012). This vegetation unit is dominated by species producing high amounts of litter, generally located on steep and sunny sites (Dengler et al. 2012; Sutcliffe et al. 2015), with reduced soil water availability, as was confirmed by the Pejo valley results. Furthermore, the negative effect of nutrient content, of management intensity and of current connectivity underlined that intensive management activities had to be avoided for *Festuco-Brometea* species conservation (Marini et al. 2007). This relationship between *Festuco-Brometea* species and management activity in the Pejo valley was confirmed also by the negative influence of the connectivity, which highlighted that semi-natural dry grassland occurred in isolated patches, less accessible and generally not easily managed. South-facing patches on sloping ground generally showed few changes in plant species diversity, maintaining a more stress-tolerant and light-demanding flora (Bennie et al. 2006). Nevertheless, patch gaps with prevalence of *Festuco-Brometea* species could be maintained over a long-term period only by grazing activity (Sitzia and Trentanovi 2011; Garbarino et al. 2014).

Conclusion

In both valleys, the abandonment of agro-pastoral activities led to spontaneous reforestation and to the decrease of grassland patches, with a negative consequence on plant biodiversity.

The analysis of the Pesio and of the Pejo valley highlighted two different patterns of land-use and abandonment, which were representative of the western and eastern Alps, respectively. The grassland patches of the Pesio valley were rapidly used during the seasonal summer transhumance. The vegetation assessment showed the dominance of extensive grazing practice, as many fringe species were detected in grassland patches. Reduction of time spent driving livestock to the higher pastures led to the underuse of these transitional areas, with negative consequences on grassland patch biodiversity. Conversely, in the Pejo valley, hay making practices combined with pasture was relatively more diffuse, mainly due to a denser road network between farm buildings and grasslands. Nevertheless, a different gradient of management intensities was identified, as intensive practices were carried out mostly near farm buildings, whereas extensive practices were carried out in steep and less accessible sites.

Species richness and composition of vascular plants in grasslands were predominantly controlled by local factors, and only secondarily by factors operating at the landscape-scale. Ecological features

and agro-pastoral activities produced the most favourable effect on the maintenance of grassland plant diversity and species richness pool both at local and landscape level.

The results of the study highlighted the need for adapting management to the environmental, socio-economic and landscape context through a correct agro-pastoral planning. Conservation approaches should promote a range of agro-pastoral practices in order to maintain grassland patch biodiversity through the regulation of livestock stocking rates and mowing activities (number and timing of cuts). In the Pesio valley, a pastoral plan ought to be carried out with the main purpose of increasing the stocking rate in under-grazed patches. In the Pejo valley, a reduction of management practices that are too intensive, has to be realized near farms buildings, whereas an intensification of grazing activities has to be performed in steep and less accessible sites, where mowing activity is unfeasible.

Similar studies can be very helpful in addressing conservation policies for grassland plant communities based on management intervention, aiming at biodiversity conservation. Considering the high value of European union grassland habitats in Italy (Biondi et al. 2009), it is important to direct grazing and mowing interventions towards a landscape approach in order to prevent further grassland reduction.

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