

Diversity and floristic patterns of mediterranean grasslands: the relative influence of environmental and land management factors

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Abstract Managed grasslands are normally ecosystems with high species diversity. They are associated with traditional extensive livestock grazing. Land-use changes, in particular gradual abandonment or grazing intensification, lead to major changes in floristic patterns of these grasslands, some included in priority habitats of the EU Habitats Directive. In order to analyse these patterns of change, Mediterranean grasslands of eastern areas of mainland Portugal were studied aiming to: (1) establish ecological gradients underlying their floristic patterns; (2) examine the relative importance of both environmental and land-use factors on their floristic composition; (3) assess how floristic composition and species richness are affected by land-use factors. Vegetation sampling was carried out from 2008 to 2009 following phytosociological procedures. Canonical Correspondence Analysis was

Nomenclature: Botanical nomenclature follows Aedo and Herrero (2005), Benedí et al. (2009), Castroviejo et al. (1986, 1993a, b, 1997a, b, 2008), Devesa et al. (2007), Franco (1984), Franco and Rocha Afonso (1994, 1998), Morales et al. (2010), Muñoz Garmendia and Navarro (1998), Nieto Feliner et al. (2003), Paiva et al. (2001), Talavera et al. (1999, 2000, 2010, 2012) and also Díaz Lifante and Benito (1996) for *Asphodelus*, Franco (1971) for *Tuberaria*, *Geraniaceae* and *Linaceae*, Oliveira (2005) for *Arrhenatherum*, Pizarro (1995) for *Ranunculus* and Vázquez and Barkworth (2004) for *Celtica*. The bioclimatological, biogeographical and syntaxonomical typology was checked according to Rivas-Martínez et al. (2002a, b, 2011) and Rivas-Martínez (2007) and Costa et al. (2012).

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applied. Variation partitioning was used to assess the relative influence of land-use variables. Richness, legumes cover, endemic species and bryophytes cover were compared in four land-management regimes: unmanaged; extensive grazing by sheep; extensive grazing by cattle and sheep; frequent soil tillage. Significant differences were found in floristic and diversity patterns, revealing the importance of grazing as a management tool for maintaining or improving floristic diversity. From our findings slight extensive grazing can contribute to both maintenance of species diversity and to the increase in legumes cover and thus to palatability and economic value of studied grasslands. Interactions between herbivores and grasslands, considering also their influences on soil properties, have an important role in the equilibrium states which promote biodiversity and conservation of the services of these ecosystems.

Keywords Floristic composition · Conservation · Habitats · Species richness · Traditional land-use · Variation partitioning

Introduction

It is estimated that grasslands cover 40.5 % of earth's surface (excluding Greenland and Antarctica) (White et al. 2000) while managed grazing is related to more than 25 % of the global land surface (Asner et al. 2004). These ecosystems are strongly related in their nature and individual characteristics (such as species diversity) to the intensity of land-use (e.g. Gustavsson et al. (2007). However, it is known that grassland composition, functioning and services can be strongly affected by anthropic disturbance, namely by overgrazing (e.g. White et al. 2000). In effect, grasslands are considered as ecosystems where some of the largest changes in biodiversity are expected to take place due to land-use impact, and expected climate changes may intensify the impacts of these disturbances (Aguiar 2005).

The importance of biological diversity maintenance in semi-natural grasslands is generally recognized (e.g. Eriksson et al. 2002; Klimek et al. 2007). For example, Tilman and Downing (1994) based on long-term field studies, showed that primary productivity in plant communities with higher species diversity recovers more completely from an environmental shock (e.g. drought). Similar relations between plant diversity and productivity were found, for example in the BIOTEPH experiment made by Hector et al. (1999) and Huston et al. (2000). At the same time, the services that humans derive from biodiversity and the consequences of changes in biodiversity in the resilience of ecosystems to environmental change are recognized in several studies (e.g., Chapin et al. 2000). Grime et al. (2000) evaluated responses of grasslands to simulated climate change and found that disturbed grasslands linked to modern human activity may be more vulnerable than older traditional grasslands.

Traditional livestock grazing seems to replicate the natural grazing processes that gave rise to natural grasslands, which are considered a positive contribution to the preservation of biodiversity and endangered species associated with these habitats (e.g. McNaughton 1984; Pykälä 2000; Scholz 1975). Along these lines, some studies suggest that in managed grasslands, grazing can contribute to the maintenance of plant diversity for example through the increasing of forbs under conditions that would otherwise promote lower species diversity (Collins et al. 1998; Olff and Ritchie 1998). Moreover, the eventual

reduction of competitive dominant species by low grazing intensity is referred to in several studies (e.g. Belsky 1992). Although disturbance is an important factor in the creation and maintenance of species richness, high grazing intensities are normally regarded as a negative factor on species diversity (Hobbs and Huenneke (1992). In addition, Olff and Ritchie (1998) stressed the importance of distinguishing the effects of different herbivore types, according to their body size, for example.

Besides the influence of grazing on species diversity, several authors have also identified and stated that artificial fertilization can introduce changes in the floristic composition of grasslands (Aguilar 2005). Experiments made by Tilman (1987) revealed that nitrogen addition contributes to a reduction in plant diversity, promoting the dominance and biomass of few species which contributes to limitations in light availability for other species. Jacquemyn et al. (2003) also identified relations between nitrogen supply rates and light availability, stating that grazing can minimize the effects of nitrogen supply. Other authors have also identified high nitrogen fertilization of grasslands as a negative factor for species diversity changing extremely their floristic composition (e.g. Maurer et al. 2006). In the study area, fertilizations and mobilizations have been applied for many years, which leads us to pay particular attention to its possible influence in floristic composition.

Olff and Ritchie (1998) identified larger herbivores as more efficient seed dispersers, recognizing their partial role in the increase of plant diversity. However, they also found that a high density of large herbivores, such as the case of intensive livestock grazing, can determine unselective grazing and create widespread erosion and other negative soil disturbances (compression of soil aggregates, compactation), causing a reduction in plant diversity. Nevertheless, they point out that environmental factors are much more influential on floristic patterns than the type of herbivore. Therefore, the influence of herbivores in plant diversity is strongly dependent on environmental factors along with grazing intensity and type of herbivores (Olff and Ritchie 1998).

Assessing the effects of land management on floristic patterns has been a central concern of recent ecological research (e.g. Blasi et al. 2010; Catorc and Gatti 2010; Klimek et al. 2007). Due to the interactions between both environmental factors and land-use factors, it is necessary to clarify the relative importance of each one.

A case study, within an extensive area of eastern mainland Portugal, was conducted in order to identify and characterize the ecological gradients behind the floristic and diversity patterns in annual and perennial grasslands. Some of these are classified as priority habitats under the EU Habitats Directive (6220*“Pseudo-steppe with grasses and annuals of the *Thero-Brachypodietea*”) (EC 2007), namely subtype 3 (San Miguel 2008) that, in Portugal, corresponds to subtype 1 “annual neutrophyllous-basophyllous grasslands” (ICNF 2006), in which we include the pioneer and ephemeral basophilous annual communities identified in the studied territory. Other communities are included in the same habitat, subtype 4 “grasslands of high perennial grass” (ICNF 2006).

In the study area the managed grasslands traditionally correspond to a rotation between extensive grazing (for shorter or longer periods) and crop rotations with regular ploughing and artificial fertilization. Long rotations of 3/4–5 or even more years between cereals (mainly wheat and/or oats), forage, and fallow, together with extensive grazing characterize the traditional type of land management in the study area. Simultaneously all the grasslands in the study area have been subjected to several types of more or less disturbing land-uses over the last 100 years, determining that studied grasslands express quite clearly the influence of agriculture, grazing, fire, etc.

It was therefore in this context that the following questions were addressed: (1) Which are the ecological gradients underlying the floristic patterns of grasslands in southeastern

and the centre-east of mainland Portugal?; (2) What is the relative importance of both environmental and land-use factors on their floristic composition? (3) How are species richness and floristic composition affected by land-management types?

Materials and methods

The research area

Field research covered a total area of approximately 28,700 km² in central eastern and southeastern mainland Portugal (Fig. 1) mainly on siliceous and calcareous substrata (much less present in the study area). Soil types in the study area resulted from siliceous material, mainly schist and granite rocks over large areas.

Within the study area, grasslands were surveyed in areas with mesomediterranean thermotype and subhumid ombrotype (according to the bioclimatical system of Rivas-Martínez et al. (2011) with altitudes between 47 and 734 m.a.s.l., in the Western Mediterranean Subregion, Mediterranean West Iberian Province (Carpetan-Leonese and

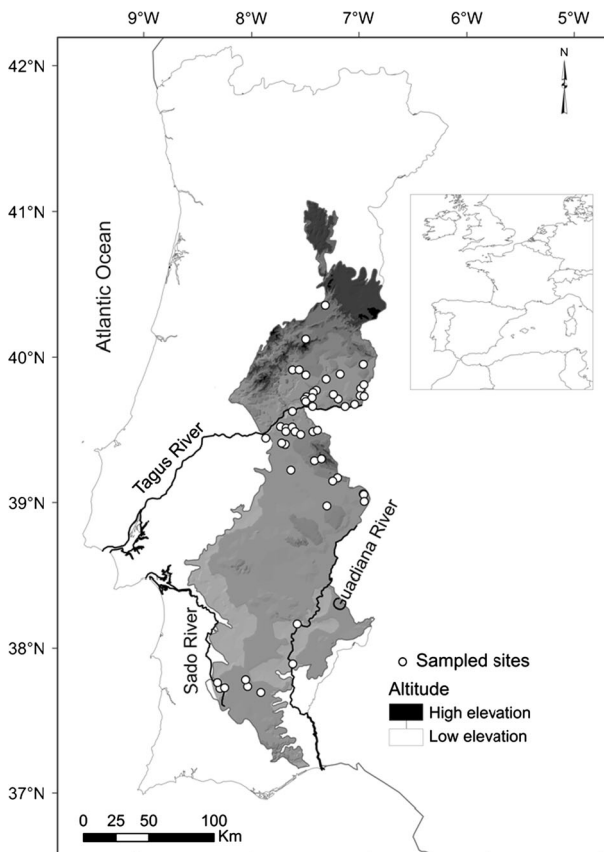


Fig. 1 Researched area in eastern Portugal and the location of sampled grassland sites

Lusitan-Extremadurean Subprovinces), according to the biogeographic typology of Rivas-Martínez (2007) and Rivas-Martínez et al. (2011).

They occupy large areas of arable land, livestock grazing and clearings of forest mosaics.

Sampling design and data collection

Field sampling was carried out from spring (March) to summer (July) in 2008 and 2009, on 110 grassland sites (Fig. 1), representing different land management systems, from agriculture rotation crops combined or not with extensive grazing systems to mesic grasslands without management for more than 10 years.

Grasslands were surveyed following the phytosociological method of Braun-Blanquet (1964, 1979) modified by Géhu and Rivas-Martínez (1981). The minimum area method was used in line with Mueller-Dombois and Ellenberg (1974) and the representative plot size of homogeneous floristic composition was standardised, as recommended by Chytrý and Otýpková (2003), Otýpková and Chytrý (2006) and Dengler et al. (2009), in order to reduce potential effects of different plot sizes in classifications and ordinations and also to allow the comparison of the species richness between plots. Thus, the minimum representative area was 16 m² for these studied grasslands. Each taxon's percentage cover was recorded to allow multivariate analysis (Podani 2006). Bryophytes' percentage cover was also recorded for each relevé.

Explanatory variables were recorded for each sampling plot, and they were assigned into two groups: (i) environmental, (ii) land-use. The environmental variables included: continuous variables such as thermotypes and ombrotypes (Monteiro-Henriques 2012), altitude, slope, rock/stone cover, soil humidity and pH; and categorical variables such as aspect (NE; N, NW, W, SW; S, SE, E) geological substrata (schist, granite, sandstones calcareous), soil texture (clay, sandy, loamy, stony-clay and sandy-clay). Land-use influence was evaluated by comparison between four land management types (LMT): LMT1 (21 relevés)—unmanaged/native grasslands—without any use for more than 10 years; LMT2 (42 relevés)—rotation crops (3–5 years) with extensive grazing by sheep; LMT3 (22 relevés)—rotation crops (3–5 years) with extensive grazing by cattle and sheep (cattle are dominant); LMT4 (25 relevés)—grassland areas subjected to frequent soil tillage without grazing.

Data analysis

The data set, which included 110 relevés and 260 species, was subjected to ordination procedures using CANOCO 4.5 software (ter Braak and Šmilauer 2002). A previous Detrended Correspondence Analysis (DCA) was applied to test if species have a unimodal response to ecological variables, which can be detected if the gradient lengths exceed 2 SD (Jongman et al. 1995). As that was the case, relationships between a species' occurrence and the main explanatory variables were assessed through CCA and partial CCA (pCCA). Applying logarithmic transformations is commonly used to improve normality of data (e.g. McDonald 2009; Osborne 2010). Thus, in order to improve the normality of data, log transformation was used ($\log(x + 1)$), also in line with Lepš and Šmilauer (2003). In order to detect collinearity between explanatory variables, a forward selection was used (Borcard et al. 1992; Heikkinen et al. 2004), performed by the Monte Carlo permutation test (9,999 permutations), which allowed the exclusion of variables that did not contribute significantly ($p < 0.05$) to the ordination pattern. This test was also used to calculate statistical

differences in the floristic pattern composition between the four above mentioned LMTs. Furthermore, variance inflation factors for the explanatory variables were examined to detect collinearity.

Variation partitioning as a tool for spatial variation analysis with multivariate ecological data (Borcard et al. 1992, Borcard and Legendre 1994) was used to decompose the floristic variation between the two groups of explanatory variables: environmental (E) and land-use (LU). It isolates the contribution to floristic pattern of pure “E”, pure “LU” and the interaction between the two. The pCCA was used to assess the relative contribution to each of the different sets of explanatory variables. It allows variance partitioning between several user-defined groups of explanatory variables (two groups: Borcard et al. 1992; Heikkinen and Birks 1996).

Floristic composition was analysed from the point of view of legumes cover (nutritional value), endemic/protected species cover (conservation value) and bryophytes cover, which are indicators of habitat quality according to Carroll et al. (2000).

In order to clarify statistical differences of both α diversity and legumes abundance, the mean values of both plant species richness and legumes cover between the four LMT were tested by PERMANOVA tests (Anderson and Gorley 2007) in the PRIMER package (Clarke and Gorley 2007). It allows testing of sampling designs using multivariate data (Anderson and ter Braak (2003). More details of PERMANOVA tests can be found, for example in Anderson (2001, 2005) and McArdle and Anderson (2001).

Species with high fidelity to the target site group (resulting from the classification/ordination) are considered as its diagnostic species. Fidelity (understood as a measure of concentration of a species' occurrence or cover within one group in relation to other groups of relevés) was assessed using the coefficient *phi* (Sokal and Rohlf 1995; Chytrý et al. (2002) applied to all groups standardised to equal size. Fisher's exact test was applied to test statistical significance (Chytrý et al. 2002; Tichý and Chytrý 2006) of species to a group. Fidelity was then used to identify diagnostic species that are finally presented in a synoptic table. Only fidelity values of species with significance ($p < 0.05$) are displayed. These analyses were performed using the software JUICE 7.0.33 (Tichý 2002).

Results

Ecological gradients

The Monte Carlo permutation test ($p < 0.05$) allowed the identification of the following explanatory variables for the ordination model (see correlations with axis 1 and axis 2 in parenthesis): grazing by sheep (−0.1521; 0.1115), grazing by cattle and sheep (−0.2225; 0.3110), soil tillage (0.1202; 0.7161), sandy texture (−0.1548; 0.3600), altitude (−0.3313; −0.7161), soil humidity (−0.2093; −0.6534), stony-clay texture (0.1477; 0.4271), calcareous (0.7350; 0.0856), schist (−0.3237; 0.1924), granite (−0.1717; 0.0677), calcareous sandstones substrata (0.6142; −0.0139), rock/stone cover (0.4309; −0.1875), thermotype (0.12228; 0.2096) and annual mean precipitation (−0.3124; −0.2867). The two first axes of the CCA accounted for 40 % of the species-environmental cumulative percent of variance. The CCA ordination diagram (Fig. 2) shows the relation of the floristic patterns with the identified explanatory variables. The species-key factors correlation was 0.955 for axis 1 and 0.912 for axis 2, which indicates a good relationship between species and the selected explanatory variables. Particularly relevant is the separation between the relevés of basophilous and of siliceous substrata along axis 1. Axis 2, displays the different

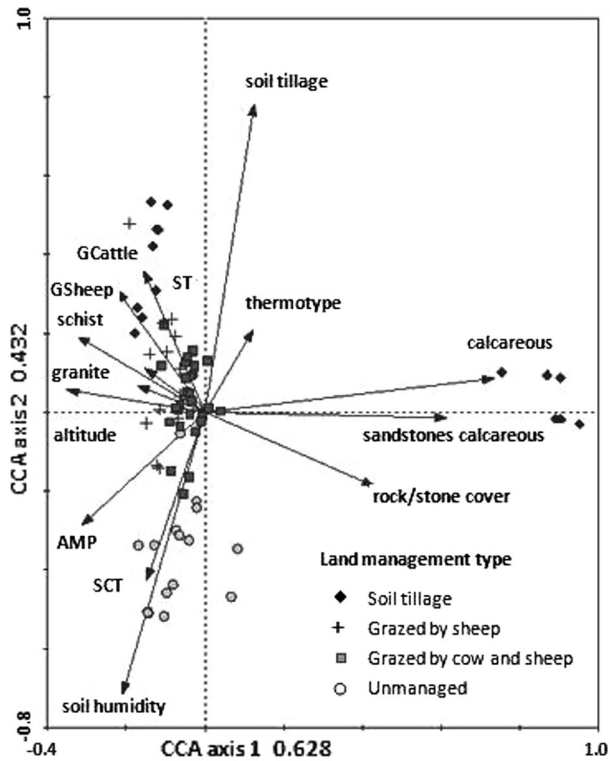


Fig. 2 Canonical correspondence analysis. Biplot with samples and explanatory environmental variables selected using Monte Carlo permutation test ($p < 0.05$). AMP annual mean precipitation, GCattle grazing by cattle and sheep, GSsheep grazing by sheep, ST sandy texture, SCT stony-clay texture

some influence of climate, soil characteristics and soil management (e.g. soil tillage). Also evident is the differentiation between unmanaged and grazed plots. Axis 3, although not shown in Fig. 2, displays thermotype (0.2535), sandy texture (0.3251), rock/stone cover (0.3805).

From these results the importance of environmental variables like pH and climate as primary factors of differentiation is clear. Land management is also differentiated with particular relevance to soil tillage. Grazed plots are also separated between unmanaged and grazed, but the grazing type is not clearly differentiated.

Partitioning the variance of species composition

Results of variation partitioning of species composition accounted for 27.4 % of total explained variation, while 72.6 % remained unexplained. Most of the explained variation in species composition corresponds to the variables related to environmental gradients (18.6 %). The pCCA of pure land-use variables accounted for 4.8 % of the total variance, while the joint effect of environmental and land-use accounted for 4 %. Thus, the variance accounted for shared environmental and land-use variables is much smaller than the pure environmental variance. This means that the two sets of variables are largely independent

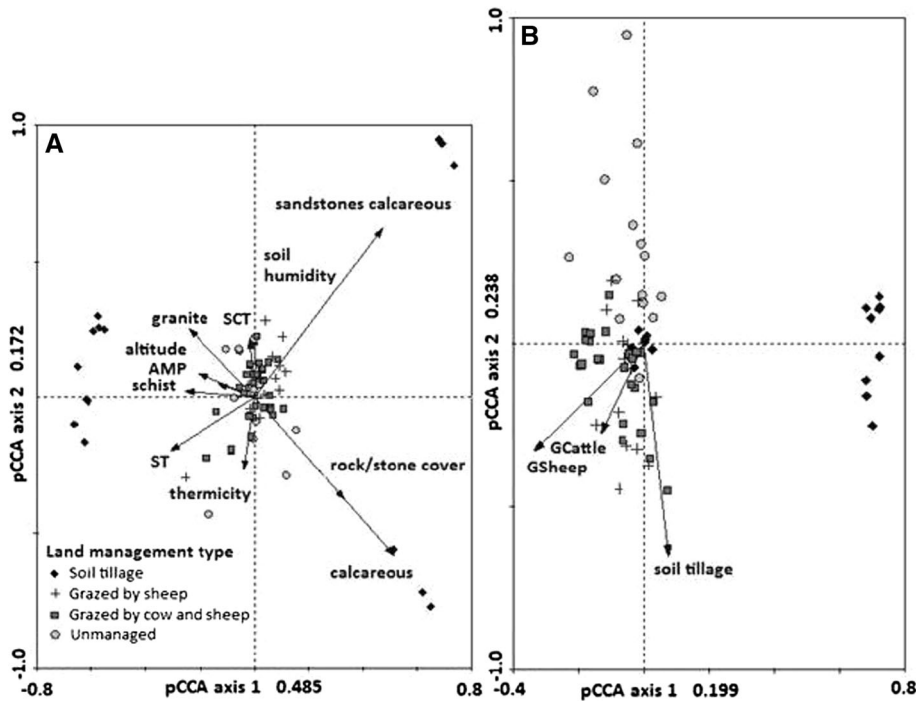


Fig. 3 Ordination biplots based on pCCA of floristic composition representing pure environmental (a) and pure land-use (b) components. *AMP* annual mean precipitation, *GCattle* grazing by cattle and sheep, *GSsheep* grazing by sheep, *ST* sandy texture, *SCT* stony-clay texture

in explaining floristic composition, and each set of variables is responsible for largely explaining specific aspects of species composition variation.

The pCCA biplots allow us to visualize the main gradients within each set of variables, both pure environmental (accounted for 40 % of the species-environmental cumulative percent of variance) and pure land-use components (accounted for 79.9 % of the species-environmental cumulative percent of variance, Fig. 3). The pCCA biplot of pure environmental component (Fig. 3a) confirms the separation between the grasslands on calcareous substrata from the ones on siliceous ones, as well as the factors related to soil texture.

The results of the pCCA of the pure land-use component (Fig. 3b) confirm the clear separation between the unmanaged grasslands and the grazed ones (axis 2), and between these three and the ones subjected to soil tillage (axis1).

Influence of the four LMT

Following the results of the pCCA, the differentiating effect of the pH was taken into consideration by considering two different data sets for soil tillage (4c and 4s).

In order to try to better differentiate the influence of the land management, simple and descriptive statistics of plant species richness, endemic species, legumes and bryophytes were analysed (Table 2 in Appendix S1) between the four LMT. Endemic species cover is null in the plots subjected to frequent soil tillage and clearly lower in the grazed plots than

in the unmanaged plots. Bryophytes cover is very high in the unmanaged grasslands, reduced in the grazed and tilled siliceous soils but also high in the tilled calcareous plots. Endemic species and bryophytes cover, due to the high absence found in the four LMT, were not considered in the statistical significance tests.

Statistically significant differences (Table 1) between the LMT were found for species richness (PERMANOVA, Pseudo-F = 6.1925, $p = 0.001$) and legumes cover (PERMANOVA, Pseudo-F = 3.018, $p = 0.028$).

Analysing the Table 2 in Appendix S1 and PERMANOVA pair-wise tests results (Table 1) as well as Fig. 4 (showing medians, interquartiles ranges, and outliers), it becomes evident that there is a continuous reduction of species between unmanaged and both LMT4 and 3. The latter show a stronger effect of disturbance than LMT2 and LMT1.

Summarizing, relevant differences in relation to species richness were found between LMT1 and LMT3, LMT4c and LMT4s (Table 1). Species richness of grasslands only grazed by sheep (LMT2) also differed from LMT4c and LMT4s. On the other hand, species richness of grasslands grazed by cattle and sheep also differed from LMT4c and LMT4s. Also relevant differences in relation to legumes cover were found between LMT1 and the others—3, 4c and 4s. Legume species cover of grasslands grazed by sheep is higher than in all other grasslands (Table 2 in Appendix S1) but significant differences were not found. Thus, one can point to a slight advantage of grazing by sheep in relation to species richness and endemic species occurrence.

Floristic patterns in the four LMT

Monte Carlo Permutation tests were used to evaluate the statistical significance of floristic patterns between the four LMT. Results of these tests revealed highly significant differences ($p < 0.01$) between the floristic patterns within all the LMT. These variations in floristic composition are shown in a synoptic table (Table 3 in Appendix S1) and Table 4 in Appendix S1) summarizes the phytosociological units that were recognized in each one of the LMT. Syntaxonomical typology is presented in Appendix S2.

The synoptic table allows us to discern which are the dominant species in the different LMT shown in the CCA diagram (Fig. 2), as well as the species with significant fidelity (Table 3 in Appendix S1). Species with significant fidelity value are marked in Table 3 in Appendix S1).

The unmanaged grasslands were dominated by *Agrostis castellana* and its diagnostic species were *Andryala integrifolia*, *Briza maxima*, *Asphodelus aestivus*, *Serapias cordigera* and *Serapias lingua* (Table 3 in Appendix S1) which corresponded to the perennial communities of *Gaudinio fragilis-Agrostietum castellanae* (Table 4 in Appendix S1) which is included in 6220* priority habitat, subtype 4 (ICNF 2006).

In LMT2 the fidelity index did not allow the identification of diagnostic species. Nevertheless some species like *Agrostis pourretii* and *Bromus hordeaceus* stand out as dominant species (Table 3 in Appendix S1). They include mainly associations and communities of *Stellarietea mediae* (it groups annual large biomass nitrophilous communities), less *Pulicario uliginosae-Agrostietum salmanticae* (association of *Isoeto-Nanojuncetea*—class that groups annual pioneer ephemeral communities periodically flooded) and less frequently *Gaudinio fragilis-Agrostietum castellanae* (dominant in unmanaged grasslands) (Table 4 in Appendix S1).

In LMT3, *Echium plantagineum* was the most frequently species found (Table 3 in Appendix S1). It includes mainly the association *Rumici angiocarpi-Coleostephetum myconis* (Table 4 in Appendix S1).

Table 1 PERMANOVA (pair-wise tests) results for species richness and legumes cover between the LMT

LMT	1	2	3	4c	4s
Plant species richness					
1		0.54	0.046*	0.016*	0.002**
2			0.078	0.01*	0.001**
3				0.281	0.003**
4c					0.033*
4s					
Legumes cover					
1		0.009**	0.004**	0.004**	0.01**
2			0.225	0.196	0.202
3				0.593	0.76
4c					0.877
4s					

c calcareous, s siliceous

Approximate probabilities (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$)

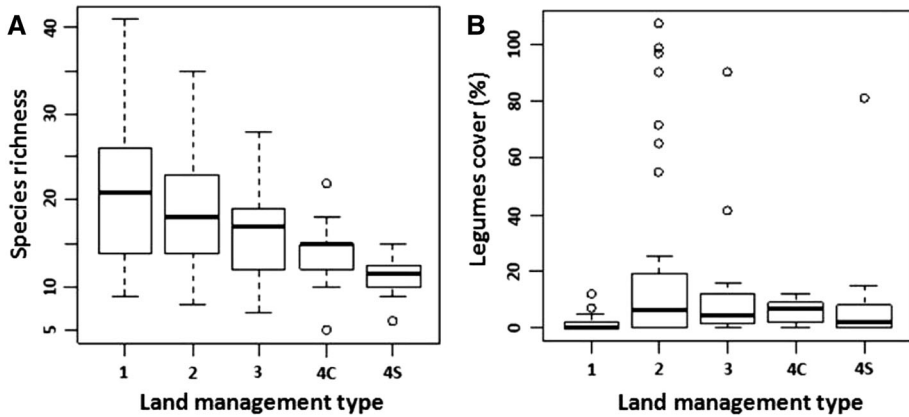


Fig. 4 Differences in plant species richness (a), and legume species cover (b) between the four LMT (c calcareous, s siliceous). The boxplots show median, interquartile range and outliers

In LMT4, *Stellarietea mediae* communities are dominant in siliceous substrata (Table 4 in Appendix S1), *Rumex bucephalopharus* subsp. *gallicus* and *Spergula arvensis* being the main diagnostic species (Table 3 in Appendix S1). In this LMT in calcareous substrata the main diagnostic species were *Brachypodium distachyon*, *Trifolium scabrum*, *Aegilops geniculata*, *Atractylis cancellata* subsp. *cancellata*, *Echinops strigosus*, *Crupina vulgaris* and *Linum strictum* (Table 3 in Appendix S1). These are common species in *Velezio rigidae*–*Astericetum aquaticae* association (Table 4 in Appendix S1), included in the 6220* priority habitat (subtype 3).

Discussion

Relationship between floristic patterns and ecological variables

Environmental variables related to substrate type, thermicity and humidity gradients have an important role in the identified floristic patterns. It is clear that the environmental component has an important role in determining the floristic composition patterns of the grasslands studied, particularly the substrate type which is in line with similar findings made by, for example, Sebastiá (2004). Grazing and soil tillage were also identified as significant explanatory factors in the ordination of the grasslands studied. Indeed, experiments made by Levine and Hille Ris Lambers (2009) confirmed that niche differences have an important role in the maintenance of species diversity and stability of communities. Abiotic condition diversity combined with some positive biotic interactions (e.g. low intensity grazing) seems to contribute to maintaining or even improving plant diversity which, accordingly to Chapin et al. (2000), contributes to better resilience and resistance of ecosystems to environmental change, such as drought, as suggested by Tilman and Downing (1994).

The decomposition of the explained variation in species composition into pure and shared variation components confirmed the relative importance of environmental site conditions. It was found that the pure environmental and land-use factors are strongly related to different floristic patterns and that the two sets of variables are largely

independent of each other. A moderate amount of unexplained variance was obtained which is a common occurrence in ordination models (Økland 1999), possibly due to some unmeasured or not assessed ecological variability such as some aspects of land-use history.

Relationship of species richness and floristic composition with LMT

Unmanaged grasslands revealed significantly higher species richness than in LMT3 and 4 (Table 1). They had the highest cover of bryophytes (Table 2 in Appendix S1) which are known as good indicators of habitat quality by, for example, Carroll et al. (2000). A study by Aude and Ejrnæs (2005) showed that bryophytes tend to decrease with fertilization which can help to understand the low bryophytes cover registered in our managed grasslands. However, species richness of unmanaged grasslands was not significantly different from the grasslands grazed by sheep (Table 1). These results suggest that extensive grazing only by sheep (LMT2) does not have a strong influence on the loss of species richness, which concur with the results of Collins et al. (1998).

Floristic composition found in LMT1 was significantly different from all the other LMT, due to the fact that unmanaged plots are dominated by perennial communities almost non-existent in the grazed plots. Thus, species richness value in the grasslands grazed by sheep is more related to the presence of annual than of perennial species (Tables 3, 4 in Appendix S1). In addition, the highest diversity of communities was found in areas grazed by sheep (Table 4 in Appendix S1) which suggests that grazing by sheep may possibly contribute to maintain the vegetation mosaic better than grazing by cattle. Still, grazing retards the succession of the annual communities to perennial grasslands or to shrub seral stages. Thus, this reinforces that low intensity of extensive grazing can contribute to the maintenance of plant species diversity and control of perennial grassland seral stages. These results are in agreement with other studies of, for example, Casasús et al. (2007) and Pykälä (2003). On the other hand, these results seem to be in accordance with the intermediate disturbance hypothesis (IDH) which predicts that local species diversity be maximal at an intermediate level of disturbance in tropical rain forests (Connell 1978) verifying in the grasslands the same pattern.

Species richness was lower in grasslands grazed by both cattle and sheep than in the grasslands grazed only by sheep (Table 1) which seems to be in accordance with Olff and Ritchie (1998) who recognized that high grazing pressures can reduce plant species diversity. However, grazing exclusion has also been recognized as having a negative effect on plant species diversity (e.g. Peco et al. 2005).

Plant species richness of unmanaged grasslands was significantly higher than in the ones submitted to frequent soil tillage in siliceous substrata (Fig. 4; Table 2 in Appendix S1). These results suggest that LMT4 (soil tillage) has a higher impact on the loss of species richness in contrast with grazing or absence of management. On the other hand, LMT2 and LMT3 (grazing) also differed from LMT4, which reinforces the high impact of the frequent soil tillage and fertilizations in the loss of species richness. Soil tillage seems to be clearly detrimental to endemic species, while grazing shows no positive effect (with an average 60 % reduction in comparison to unmanaged plots), possibly explained by the known effects of frequent soil tillage and fertilizations in the seed bank, reducing the presence of legumes and the species richness as already proposed by several authors (e.g. Tilman 1987; Jacquemyn et al. 2003; Maurer et al. 2006). Results of Tables 1 and S1.1 in Appendix S1 show that species richness was very similar between unmanaged grasslands and those grazed only by sheep and differs significantly from those submitted to frequent soil tillage. All of these differences suggest that land management based on low intensity extensive

grazing with rotation crops (3/4–5 years) seems to be a better alternative to frequent soil tillage in order to ensure conservation of plant diversity.

In LMT4 significant differences were found, not only in terms of floristic composition but also of species richness, between calcareous and siliceous soil. Thus, calcareous grasslands submitted to frequent soil tillage had lower species richness than other siliceous grasslands submitted to other LMT. However, they presented a species richness significantly higher than siliceous grasslands submitted to the same LMT. This underlines the high species diversity recognized in 6220* habitat (subtype 3) by, for example, San Miguel (2008). Although subtype 3 of habitat 6220* is potentially rich in endemic species, the plots obtained in this study showed a total absence of endemic species, a result that can possibly be explained by the land management history, in this case, frequent soil tillage. These results seem to concur with Dutoit et al. (2005), Römermann et al. (2005) and San Miguel (2008), who postulate that floristic patterns of habitat 6220* (subtype 3) are expected to suffer loss of biodiversity if there is an intensification of either agricultural or pastoral activities or alternatively their abandonment. This abandonment of traditional management activities leads to ecological succession (as represented in Fig. 5), resulting in the replacement of these communities by perennial grasslands or shrub communities.

A study made by Rudmann-Maurer et al. (2008) suggested that low-intensity grazing can be considered as a valuable conservation alternative to abandonment since the latter led to a reduction in species richness. Also, Peco et al. (2005) and Wrage et al. (2011) have identified some positive effects of grazing in species diversity.

Legume species (mainly annual) cover in ungrazed grasslands (LMT1) was significantly lower than in the other LMT (Table 1; Fig. 4) in which the annual plants were generally dominant species. These results may be related to the low competitive ability of annual species in relation to perennial grasses. Indeed, these limit the light availability to the smaller species, namely legumes of *Trifolium* or *Medicago* genus. Nevertheless the absence of significant differences of legumes cover between LMT2 and LMT3 is probably linked to selective grazing of herbivores, as sheep and cattle, for example, differ in the type of bite (cows tend to tear the plants). On the other hand, these fine dynamics related to legumes abundance can be explained by soil nutrient balance (related e.g. with phosphorus) as addressed by Sánchez Rodríguez et al. (2006).

Future local experiments on a fine scale will be necessary to better control the unknown effects of environmental variability and to clarify the real influence of selective grazing such as its impact on the dominance of grass of perennial seral stages in relation to annual forbs or legumes cover. Moreover, a wider sampling program differentiated according to the different types of soil (basic or acidic), soil moisture and nutrient availability and considering the land-use history for at least the last 15–30 years, seems to be necessary in order to be able to better determine the real differentiating influence of grazing types and other land management practices.

Relationship of species composition and LMT

Floristic compositions of all management types were significantly different from each other, according to Monte Carlo permutations tests. These floristic differences can be understood in the synoptic table (Table 3 in Appendix S1 and Table 4 in Appendix S1). These results indicate that some species do not tolerate frequent soil tillage. In addition perennial grasslands that were not found in LMT4 were residually identified in the extensive grazing management types 2 and 3. Annual communities of *Stellarietea mediae*, that have the ability to spread and to compete under high anthropic pressure (Fig. 5), occur

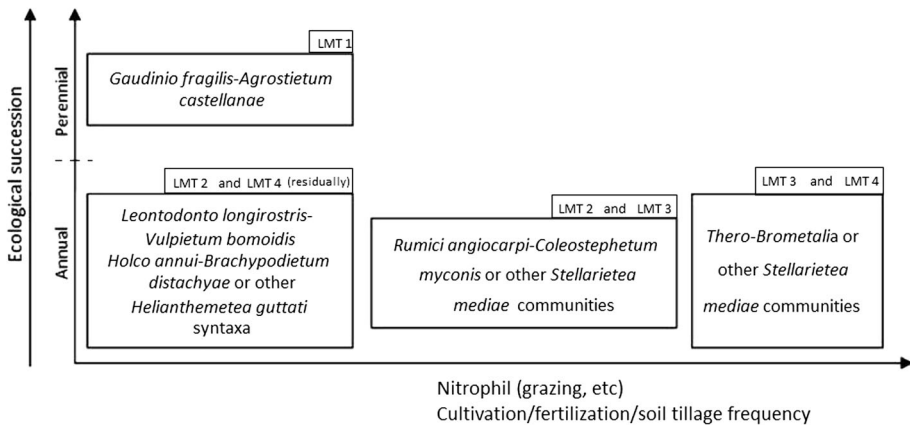


Fig. 5 Dynamic scheme of the communities identified in the four LMT in acid soils

frequently in LMT4 and LMT3 (Table 4 in Appendix S1). In our study area, grazing activities are frequently related to crop rotation, subjected to frequent fertilizations and mobilizations, which favours annual large biomass nitrophilous species in relation to perennial species (that are unrelated to soil tillage), thus introducing strong floristic composition differences in relation to the unmanaged grasslands. These findings lead us to consider the increase of characteristic species of *Stellarietea mediae* communities as indicators of high land-use pressures.

Our results in Tables 3 and 4 of Appendix S1 show a progressive substitution of perennial grasslands by *Stellarietea mediae* communities from unmanaged grasslands to frequent soil tillage as represented in Fig. 5 (which synthesises grasslands dynamic in acid soils). *Stellarietea mediae* communities are known as annual nitrophilous or semi-nitrophilous vegetation that spread in various substrate rich in nitrogenous matter (Costa et al. 2012). The latter shows a dynamic scheme that synthesizes the frequency of communities between the four LMT and the land-use gradients identified in our results and also the successional dynamics identified.

Conclusions

It was found that the pure environmental and land-use factors are largely independent, thus they are strongly related to different floristic patterns, revealing a general pattern associated. Each set of variables explains specific aspects of species composition variation.

Unmanaged grasslands revealed significantly higher species richness than the grazed by cattle and sheep and the grasslands submitted to frequent soil tillage. However, their high values of species richness, bryophytes and endemic species cover contrasted with their low legumes cover in comparison with the grazed grasslands. In addition, species richness of plots grazed by sheep was not significantly different from unmanaged plots. Thus, we conclude that slight extensive grazing by sheep maximizes diversity and can contribute to both maintenance of species diversity and to the increase in legumes cover and thus to palatability and economic value of these grasslands.

The results revealed that soil tillage has a higher impact on the loss of species richness in contrast with grazing or absence of management. Soil tillage in the priority habitat 6220 (subtype 3) clearly eliminated the endemic species and reduced the legumes cover. *Agrostis castellana* was a key species in unmanaged grasslands and annual nitrophilous or semi-nitrophilous species cover increased with human pressure.

In this context, we suggest some measures in order to improve and ensure the conservation of plant diversity in the study area: low intensity extensive grazing in the unmanaged (native grasslands) also included in 6220* habitat (subtype 4); reducing soil tillage and fertilizations in cropland alternating with fallow periods in which low intensity grazing can be practiced in order to allow the colonization of perennial herbaceous stages in siliceous substrata; in the 6220* habitat (subtype 3), related to calcareous substrata, replacing soil tillage and fertilizations with grazing in order to maintain its annual characteristic species and avoid its evolution to perennial seral stages.

Although the relation between nitrogen and the dominance and biomass of few species, as stated by Tilman (1987), correctly managed grazing can interfere with the biomass of dominant species, allowing light availability to other small species, thus promoting the maintenance or even increase of species diversity. We conclude, therefore, that biotic interactions such as herbivory in grasslands, considering also their influences on soil properties, can promote biodiversity and conservation of the services of these ecosystems.

Future local experiments on a fine scale will be necessary to better control the unknown effects of environmental variability and to clarify the real influence of selective grazing such as its impact on the dominance of grass of perennial seral stages in relation to annual forbs or legumes cover. Moreover, a wider sampling program differentiated according to the different types of soil (basic or acidic), soil moisture and nutrient availability and considering the land-use history for at least the last 15–30 years, seems to be necessary in order to be able to better determine the real differentiating influence of grazing types and other land management practices.

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