

Mediterranean cork oak wooded grasslands: synergies and trade-offs between plant diversity, pasture production and soil carbon

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Abstract Mediterranean wooded grasslands that emerge from silvopastoral activities are multifunctional systems that result in high biodiversity and offer ecosystem services such as forage production and soil carbon sequestration. During 3 years, ten grazed wooded grassland fields were studied in the Berchidda–Monti long-term observatory, located in NE Sardinia, Italy, with the aim of exploring the synergies and trade-offs between biodiversity and selected ecosystem services. Positions below and outside the canopy of three cork oak trees in each field were randomly selected to compare seasonal pasture production, pasture utilization rate by animals, botanical composition, biodiversity indicators (Shannon index and plant species richness) and soil organic carbon. In

in the two positions; in two winters out of three it was greater below the trees than outside, and in spring it was greater outside than below the trees. While plant species richness and Shannon index were not significantly influenced by the position, the overall wooded grassland plant species richness was 31% higher than that outside of the tree crown. The soil organic carbon content in the 0-40-cm soil layer was also higher below the trees. Our findings highlight that if the main purpose of the wooded grasslands is to provide forage for grazing animals rather than conserving and/or enhancing plant diversity and soil fertility, the presence of trees constrains the overall forage productivity, although the greater forage availability in winter under the trees can contribute to improve the seasonal distribution of forage production.

autumn, dry matter production of pasture was similar

Keywords Biodiversity indicators · Ecosystem services · Habitat heterogeneity · Pastoral value · Scattered trees

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Introduction

Grassland ecosystems are traditionally perceived as forage suppliers (Nieto-Romero et al. 2014) but their relevance for the provisioning of ecosystem services to society (MEA 2005) is increasingly receiving the attention of international organizations (e.g. FAO



2017) and scientific communities (e.g. Pilgrim et al. 2010 and references therein). Grasslands also provide regulating services such as climate regulation since they can act as carbon sinks (Seddaiu et al. 2013), the control of water flow (Hönigová et al. 2012), soil erosion regulation (Bazzoffi 2009) and pollination (Bagella et al. 2013a). Grasslands are ecosystems with high species diversity (Ribeiro et al. 2014), hence, their maintenance plays an important role for biodiversity conservation that enables ecological functioning (Kyriazopoulos et al. 2016).

The relationship between plant diversity and productivity in grassland systems has been investigated under several environmental and management conditions often with contrasting findings (e.g. Tilman et al. 2012; Klaus et al. 2013; Rolo et al. 2016). Manipulative experiments involving randomly assembled communities have generally shown positive relationships between plant diversity and primary productivity (Craven et al. 2016 and references therein), while observational studies of natural or semi-natural grasslands have often highlighted negative or no relationship (Loreau et al. 2001; Chanteloup and Bonis 2013). The manipulation of plant species composition has effects on natural vegetation dynamics and the experimental conditions can seldom well represent "real" agricultural conditions (Petersen et al. 2012). More observational studies are therefore needed. Soil fertility features such as pH, and organic C, phosphorus and potassium contents are often the most important factors influencing plant species diversity in grasslands. Acidic soils are usually species-poor while higher diversity is associated with low organic C, phosphorus and potassium contents (Bagella et al. 2013b; Merunková and Chytrý 2012).

Grassland systems studies often are focused on assessing the delivery of one or two ecosystem services at a time (e.g. Pilgrim et al. 2010), thus neglecting the complex, dynamic interactions among multiple ecosystem services. The assessment of single ecosystem services or pair-wise interactions between ecosystem services can likely lead to unexpected trade-offs or to undesirable declines in others (Bennet et al. 2009). When considering grassland systems, the evaluation of the trade-offs and synergies among different ecosystem services is even less documented.

Wooded grasslands, defined as herbaceous grasslands with scattered trees, are grassland ecosystems characterized by a high level of heterogeneity in terms

of biodiversity and soil proprieties due to the presence of trees which determine different ecological conditions (Moreno et al. 2016). In the Mediterranean area, wooded grasslands have emerged from a continuous selection of both the woody and grass vegetation operated by traditional agro-silvo-pastoral activities practiced over centuries. They are widely known for their positive role in the provision of a distinct microclimate (Moreno et al. 2005), soil fertility (Moreno et al. 2007), and soil C sink capacity (Howlett et al. 2011). Scattered trees in grasslands are recognized as keystone structures for biodiversity contributing to disproportional high plant richness given the relatively small area occupied (Manning et al. 2006; Moreno et al. 2016). However, studies on the relationship between plant diversity, pasture production and soil features for wooded grasslands are still rare. Rossetti et al. (2015) reported some 50% more top soil C under than beyond adult cork oak tree canopies, while plant species richness was slightly lower under the tree than in the open grassland. In the Spanish Dehesa habitat, Moreno et al. (2016) showed that wooded grasslands had similar plant species richness than the adjacent open pastures at plot scale. Our hypothesis was that, while soil fertility is expected to be higher underneath the tree canopy, the pasture production and quality are negatively affected by the presence of trees, while trees can provide benefits on the overall wooded grassland plant diversity.

The objective of this study was to assess the influence of scattered adult cork oak trees on plant biodiversity, soil organic carbon, pasture production and intake by animals in order to gain insights on synergies and tradeoffs among these features in Mediterranean grasslands.

Materials and methods

Study area

The study area is located in the Long-Term Observatory of Berchidda–Monti, Sardinia, Italy (40°47′0″N 09°10′0″E, 320 m a.s.l). The climate is Mediterranean pluviseasonal oceanic, low mesomediterranean. The mean annual rainfall is 632 mm, 70% occurring from October to March and the aridity index is 0.53. The mean annual temperature is 14.2 °C. During the 3-year study, the rainfall amount in autumn and winter



was 28% higher and 40% lower respectively in the first and second year than the pluriannual average (449 mm) while mean temperatures were similar to the long term means (13.2, 7.8 and 22.8 °C respectively in autumn, winter and spring).

The soil is classified as Typic Dystroxerept (USDA 2010). Soil texture in the Ap horizon is sandy loam with average pH of 5.7, an organic C content of 2.3% and total N content of 0.2% (Seddaiu et al. 2013). The natural potential vegetation is mainly represented by *Quercus suber* L. forests referable to *Violo dehnhardtii-Quercetum suberis* association (Bagella and Caria 2011). The landscape is characterized by a wide variety of land uses such as cork oak forests, grasslands, vineyards, with cork oak wooded grasslands representing the dominant land use type covering 30% of the Berchidda–Monti observatory.

Experimental layout

The study was carried out in ten wooded grassland fields within a range of different grazing management systems and tree cover (mean 27% of tree cover; range 16-37%). All fields belonged to private farms and were managed using business as usual practices. The fields were intended to be homogenous areas of managed permanent grassland (i.e. same type of grazing animals, grazing management, and same agricultural inputs, if any) usually fenced, and not ploughed or sown for at least 10-20 years. Grazing animals were dairy sheep and/or beef cattle with stocking rates ranging respectively from 0.7 to 1.5 LU ha⁻¹ and from 0.8 to 1.0 LU ha⁻¹. In each field, three cork oak trees were randomly selected. Only scattered trees of each field were included in the randomization, therefore clusters of trees that are usually found in the proximity of rocks and/or at the edge of the fields were excluded. For each selected tree, surveys were made at two positions, identified by considering the horizontal projection of the canopy onto the ground: a position fully below the tree canopy projection in the North-East orientation and a position (mainly unshaded) outside the tree canopy (OT). The North-East orientation for the positions below the tree was taken also because the dominant wind in the study area is from South-West and the trees have typically flag-shape crowns.

Seasonal and annual pasture dry matter production and intake, animal utilization rate, plant biodiversity (vegetation composition and biodiversity indicators) and soil organic C content were measured in both positions. Overall, all the studied variables were measured at each sampling date in a total of 60 sampling units (10 fields \times 3 trees \times 2 positions).

Pasture production and intake were considered as indicators of provisioning ecosystem services associated to the grassland-based systems such as meat and milk, and soil C stock as an indicator of the regulating services (MEA 2005).

Data collection

Plant biodiversity

Vegetation surveys were performed four times: early and late spring 2013 and early and late spring 2014 at each sampling unit. Data were taken inside a 2 m × 2 m quadrat randomly located within each sampling unit. Inside each quadrat a list of the rooted vascular plant species was compiled and their abundance was estimated following Braun-Blanquet (1951). Plant identification and nomenclature follow the free online application for plant identification http://dbiodbs. units.it/carso/chiavi_pub21?sc=624. For each species, the maximum frequency value found between the two sampling dates within each year was considered and then averaged between years for data processing. The mean yearly value for each field and for each sampling position within the field was used for building a species/cover matrix for data analysis.

Pasture production and herbage intake

Pasture dry matter production was evaluated at about monthly intervals from October 2012 to May 2015, using movable grazing exclusion cages (1 m \times 1 m) (Frame 1981). At each sampling date, the aboveground phytomass (P) on 0.5 m² areas was cut inside (i) and outside (o) the cages. The herbage production was calculated as ($Pi_{\rm tn}-Po_{\rm tn-1}$) and the herbage intake by animals as ($Pi_{\rm tn}-Po_{\rm tn}$) where $Pi_{\rm tn}$ is the phytomass cut inside the cage at time n, $Po_{\rm tn-1}$ and $Po_{\rm tn}$ are the phytomass cut outside the cage respectively at time n-1 and n. After herbage cutting, all the cages were moved to another area for the following cut. Herbage samples were oven-dried at 65 °C until constant weight. Seasonal dry matter production was calculated by summing up the monthly production



from October to December for autumn, from January to March for winter and from April to June for spring. No pasture growth was observed in summer (from July to September) as expected in Mediterranean grasslands dominated by annual species (e.g. Gutman et al. 1990; Cosentino et al. 2014). Pasture utilization rate was calculated as the ratio between herbage intake and herbage production.

Soil organic carbon

In May 2014, for each sampling unit, three soil samples were collected with an auger (5 cm diameter) at three depths (0–20, 20–40 and 40–60 cm) and for each depth samples were pooled. A LECO CHN 628 elemental analyzer was used to determine C content. The C stocked (Mg ha⁻¹) by each soil layer was calculated as the product of its C concentration (g kg⁻¹), bulk density (kg dm⁻³) and thickness (dm). To determine the bulk density of the fine earth, soil cylinders of 493 cm³ (height: 10.8 cm; diameter: 7.7 cm) were used to collect horizontal soil cores from each layer.

Data analysis

Plant cover-abundance data from vegetation surveys were transformed to numeric values according to van der Maabel (1979) prior to statistical analysis. In order to detect in which way the plant assemblage surveys were related each other a cluster analysis was performed and differences between groups were tested using the ANOSIM function with the software Primer 7 (Anderson et al. 2008). Species richness was quantified using presence/absence data from the species/cover matrix. At field scale, the γ diversity was quantified as the cumulative number of species in both positions below and outside of the tree canopy. The α diversity below and outside of the trees was considered as the cumulative number of species in such position. The total γ diversity was the total number of species found in all the fields. The β diversity was quantified following the Whittaker (1972) approach ($\beta = \gamma/\alpha$) at the field scale and as a whole. The number of shared and unique species to both positions was also calculated. Diversity was estimated as Shannon-Wiener index (H') (Pielou 1969):



where p_i is the proportion of the *i*th species.

Pastoral value (PV) was assessed according to Daget and Poissonet (1971) using the specific indices (Is) reported by Roggero et al. (2002), which indicate the agronomic value of each species contributing to CSP_i , i.e. the percentage contribution of each species to plant cover (Table 3 in Appendix):

$$PV = 0.2 \sum_{i=1}^{i=n} CSP_i * Is_i$$

CSP_i was calculated as the percentage ratio between the species cover assigned to each species and the sum of the cover of all species. Data on seasonal dry matter production and intake and pasture utilization rate were analysed with the PROC MIXED procedure in SAS (SAS Institute 1999), suitable for analyzing mixed effects and repeated measures with non-constant variance and any covariance structure models.

Data on annual dry matter production and intake, PV, plant species richness (α -diversity), Shannon index and soil organic C were analysed according to a one-way ANOVA with the sampling positions as treatments using SAS. Data on soil organic C content for each soil depth were analysed according to a one-way ANOVA with the sampling positions as treatments using SAS. Homogeneity of variances was verified using the Cochran C-test, and data were appropriately transformed when necessary. Means were separated according to the least significant difference using Fisher's protected test (Gomez and Gomez 1984).

By applying the software CANOCO v4.5 for Windows (Ter Braak and Smilauer 2002), a Canonical Correspondence Analyses (CCA) was performed using Hill's scaling with a focus on sample distances, to test relationships between plant species cover and eight explanatory variables, i.e. PV, C stock, seasonal average dry matter and intake (spring, summer and winter). Variables with variation inflation factors ≥ 20 were removed from the analysis to prevent high collinearity (McCune et al. 2002). Prior to submitting to the CCA, plant cover values were square-root-transformed and down-weighted for rare species. The statistical significance of axes 1 and 2 was



tested by a Monte Carlo test with 499 permutations under the full model.

Results

As a whole, 177 plant taxa were detected, which represent the γ diversity of the studied wooded grasslands (Table 3 in Appendix). The cluster analysis showed a sharp separation in terms of plant assemblage composition between below and outside of the tree positions, that was confirmed by the ANOSIM analysis (r = 0.9; P = 0.001). Outside the tree canopy, the most abundant species were Trifolium subterraneum (mean cover 56%), Vulpia ligustica (20%), Anthemis arvensis (19%), and Avena barbata (18%). Below the tree canopy, the most abundant species were Vulpia ligustica (13%), Stellaria media (12%), Lolium rigidum (11%) and Geranium molle (10%). At field scale, the plant α diversity, β diversity and the Shannon index were not significantly influenced by the sampling position, while the number of species unique to this position was higher under the tree (Table 1). Overall, the presence of the scattered trees in the wooded pastures increased by 31% the total number of plant species in the wooded grassland.

The pasture dry matter production was significantly influenced by the season x sampling position interaction. Significant differences between the two positions were found each spring and in two winters out of three (Fig. 1, top). In spring, dry matter production was 55% higher outside than below the trees, while in winter it was 67% higher under the tree positions than in the open grassland. The maximum dry matter production was observed in spring, while the lowest in autumn, with spring production representing 73% (year 1),

83% (year 2) and 98% (year 3) of the total annual dry matter production in the positions outside the tree canopies, and respectively 37, 40 and 91% under the trees.

The dry matter intake was significantly influenced by the season \times sampling position interaction (Fig. 1, bottom). The dry matter intake of the grazing animals was always higher in the positions outside of the tree canopies than under the trees in the spring, while it was lower in the winter of 2012–2013 and 2013–2014. No significant differences were observed between the two positions for dry matter intake in autumn and in the winter of 2014–2015.

The seasonal pasture utilization rate outside of the tree canopy ranged between 0.60 in spring and 0.90 in autumn and below the trees it ranged between 0.49 in spring and 0.75 in autumn (Fig. 1, top). Significantly higher pasture utilization rates were observed outside than below the trees in two winters out of three.

The pasture mean annual dry matter production, pastoral value and herbage intake by animals were respectively 23, 19 and 30% higher outside than below the tree canopies (Table 2; Fig. 2).

Significant higher soil organic C content was found under the trees than outside of the trees in the 0–20 cm (+ 33%) and 20–40 cm (+ 18%) soil layers, while no significant differences were observed in the 40–60 cm layer (Figs. 2, 3). The soil organic C stock was also significantly higher below than outside of tree canopies (Table 2).

Among the eight explanatory variables included in the CCA (Fig. 4), two were removed because of the high inflation value. Pastoral value, C stock and spring production were significant variables, explaining overall 71% of the total variance. The higher spring dry matter production in the positions located outside

Table 1 Biodiversity indices and pastoral value (PV) below (BT) and outside (OT) of trees

Plant biodiversity	BT	OT	All
Average α biodiversity (field scale)	63.6a	61.7a	
γ biodiversity (across all fields)	146	135	177
β biodiversity $(γ/α)$	2.3a	2.2a	2.8
No. of species unique to BT or OT or shared	42a	31b	104
Average Shannon-Winner index	3.3a	3.1a	
PV	32.4b	42.5a	

Means followed by the same letters are not significantly different at P = 0.05



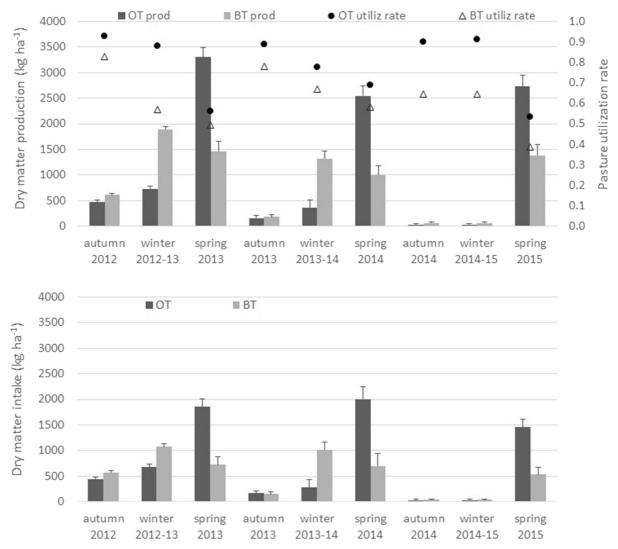


Fig. 1 Seasonal dry matter production (top, y-axis on the right) and intake (bottom) and pasture utilization rate (top, y-axis on the left) in relation to the positions below (BT) and outside (OT)

of the tree canopy in the wooded grasslands. Error bars indicate the standard errors

Table 2 Means and results of the analysis of variance for the mean annual dry matter production and intake, pastoral value (PV), and soil organic C stock in the 0–60 cm soil layer in relation to sampling position (BT below the tree, OT outside of the tree)

Variable	OT	BT	P value	CV (%)
Dry matter production (kg ha ⁻¹)	3461	2665	< 0.001	39.5
Dry matter intake (kg ha ⁻¹)	2665	1621	< 0.001	43.4
PV	42.5	32.4	< 0.001	16.3
Soil organic C stock 0-60 cm (Mg ha ⁻¹)	169	207	0.001	19.8

CV (%) coefficient of variation



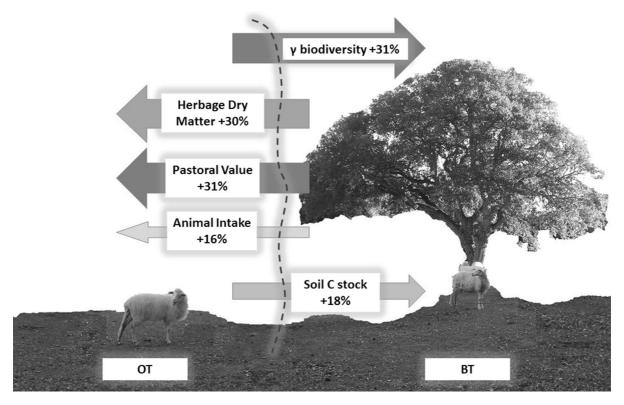


Fig. 2 Relative effects of scattered trees on γ biodiversity, herbage dry matter production, pastoral value, animal intake and soil C stock. OT outside of the tree canopy, BT below the tree canopy

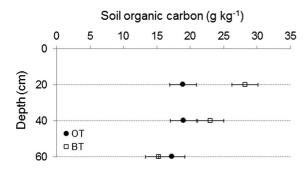


Fig. 3 Soil organic carbon content at three soil layers (0-20, 20-40, 40-60 cm) in relation to the sampling position (BT) below the tree, OT outside the tree). Error bars indicate standard errors

the tree positions was mainly related to the abundance of *Vulpia ligustica* and *Avena barbata* while the higher pastoral value was mainly related to *T. subterraneum*. Under the trees, the C stock corresponded to the frequencies of plant species with low *Is*, such as *Sherardia arvensis*, *Geranium molle* and *Rumex acetosa*.

Discussion

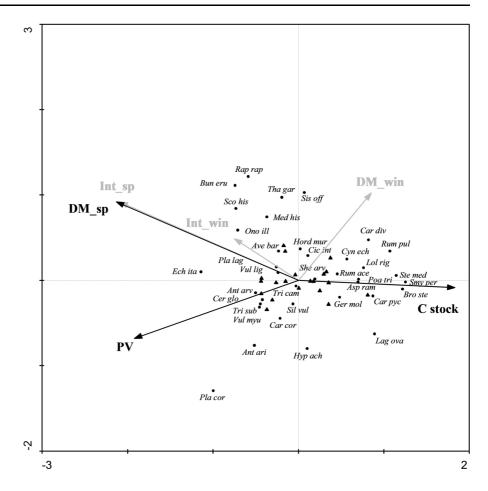
The effect of isolated trees on plant biodiversity

The importance of environmental heterogeneity in controlling biodiversity is widely recognized in ecology and its conservation is considered a priority because of the threat of biodiversity loss at global scale (Dufour et al. 2006; Questad and Foster 2008; Stein et al. 2014). The scattered trees in wooded grasslands are recognized to be beneficial for increasing environmental heterogeneity favoring the presence of different species and plant communities with respect to the open grasslands (Manning et al. 2006; Moreno et al. 2016).

We found that the plant species occurring under the scattered trees were responsible of about 24% of the γ diversity of the wooded grasslands (42 species unique to the below tree position out of a total of 177 species detected in the quadrats) and showed a higher γ diversity and a slightly higher β diversity below than outside the tree canopies. Under the tree canopies, no



Fig. 4 Triplot from the Canonical Correspondence Analysis (CCA). Triangles indicate the sampling units and three characters of the code are: the first is the farm, the second is the field and the third is the position (B below tree, O outside the tree); circles refer to plant species with a specific contribution higher than 10% at least in one sampling unit; significant and no significant explanatory variables are respectively in black and grey characters. The correspondence between codes and plant names is given in the Appendix



dominant species were observed, but the differences in plant cover repartition among species were not strong enough to result into significant changes of the Shannon-Winner indices between the two positions. This finding, as well as that related to the similar mean α diversity values in the two positions, is apparently in contrast with the results of previous studies on wooded grasslands, where both species richness and Shannon-Winner index significantly decreased from the open grassland to the positions under the tree canopies (Fernández-Moya et al. 2011; Rossetti et al. 2015). However, those findings were referred to a single field and a limited number of trees (i.e. six in both cases) whereas our study was based on more trees and several fields.

The dominance of *T. subterraneum* (plant cover higher than 50%) in the open grassland plant communities, confirms that this is habitat with high conservation interest, recognized as a priority habitat (6620* Pseudo-steppe with grasses and annuals of the Thero-

Brachypodietea) in the Annex 1 of the European Habitat Directive (Council of Europe 1992). Our results indicate that the habitat heterogeneity induced by the scattered trees is the most important driver of species richness in wooded grasslands, as already observed in other complex systems (Báldi 2008). This effect can be related to a higher diversity of the environmental conditions below the tree canopy with respect to the open grasslands and is confirmed by the other biodiversity indicators. Therefore the habitat heterogeneity, typical of wooded grasslands, supports habitat quality (i.e. habitat of conservation concern) and the floristic richness.

The effects of isolated trees on pasture production

The presence of the trees affected seasonal and annual pasture production, but the difference between areas under and outside the tree canopy was highly variable between years. In the driest year (342 mm of total



rainfall from autumn to spring), the annual yield was more than twice in the open areas than below the trees while in the wet years (more than 600 mm from autumn to spring) it was between + 12 and + 19%higher. This finding was related to the very low pasture production in dry autumns and winters when soil water content is more limiting under the tree (Moreno et al. 2013). In wet years a higher autumn and winter forage production under the tree was observed. Similar results were obtained by López-Carrasco et al. (2015) in the Spanish dehesas, where a lower yield of the herbaceous vegetation was observed under the tree cover than in the open pasture with less than 600 mm of annual rainfall. In wetter conditions (878 mm annual rainfall), the same authors did not detect significant differences in pasture yield in positions beneath or beyond the tree canopy projection. Other researchers have reported beneficial effects of isolated trees on herbage biomass (e.g. Moreno 2008) that was attributed to an indirect effect of the higher concentration of soil nutrients and more favorable soil and air temperature under the tree (Moreno et al. 2007; Casals et al. 2014). Moreno (2008) also reported a much greater forage yield under the tree canopy in more humid sites than in drier ones.

The higher pasture dry matter production under the tree canopy than in the open areas in winter and, at a lesser extent, in autumn, can be interpreted as the positive effect of the tree in maintaining better soil temperature conditions for seedling establishment and herbage growth. In a Central-western Spanish dehesa, Moreno et al. (2005) observed higher soil temperatures beneath oak trees during cold weather and lower values during warm conditions.

The effect of isolated trees on soil C content and stock

Scattered cork oak trees contributed to the increase in soil fertility along the soil profile (0–60 cm), expressed in terms of C content (+ 17%) or stock (+ 18%) under the tree canopy. The beneficial impact of trees on soil nutrient content and availability has been reported by several authors under different environmental and management conditions (e.g. Takimoto et al. 2009; Haile et al. 2010; Howlett et al. 2011). The C content in the soil profile, irrespectively

of the tree influence, was about two to three times higher than 1.0%, which is the lower limit for identifying the status of pre-desertification (CEC 2002). This finding suggests that the silvopastoral systems under study can help to ensure the long-term maintenance of satisfactory soil fertility levels and that the presence of scattered trees can provide a substantial contribution to the soil carbon sink of Mediterranean wooded grasslands.

The sharp decrease of C content from the upper soil layer (0–20 cm) to the underlying one in the positions below trees is consistent to what observed in Spanish wooded grasslands dominated by Quercus spp. (Pulido-Fernández et al. 2013). Wooded grasslands can integrate the benefits of the forest and grassland soils in accumulating C as soils under the tree canopy mostly accumulate C in the superficial horizons, while secondary grassland soils have the ability to distribute C stocks in a thicker horizon (Seddaiu et al. 2013). Such complementarity enhances the overall resilience of these systems towards disturbance factors. Moreover, the presence of scattered trees influences the soil organic C stocks up to distance of 6-8 m from the tree trunk (Simón et al. 2013; Rossetti et al. 2015), resulting in a higher C accumulation in the open grassland of the wooded pastures if compared to treeless pastures.

Synergies and trade offs between production, plant diversity and soil organic C in wooded grasslands

A detrimental effect of the scattered trees was observed on annual pasture production and PV, whereas soil C stock was enhanced. Moreno et al. (2013) examined the relationships between trees and understorey plants in a dehesa system, highlighting that understorey plant production is related to canopycaused gradients of aboveground and belowground resources such as radiation, nutrients and water. In particular, trees compete for soil moisture and solar radiation with the understorey plants and the higher soil nutrient concentration below the tree canopy is not sufficient to offset the reduction of the other limiting factors. Other studies have attempted to analyze the relative weight of the multiple factors influencing the responses of pasture yield to the presence of scattered trees. Bagella et al. (2017) showed a sharp effect of



fertilization on the botanical composition of oligotrophic Mediterranean grasslands. García-Barrios and Ong (2004) highlighted a more important role of solar radiation reduction than soil fertility and water availability, while Moreno (2008) concluded that Mediterranean wooded pastures seem to be more nutrient-limited than water or radiation-limited. Our findings suggest that the different vegetation beneath and beyond the trees is one of the most important driver affecting the herbage palatability and, in turn, grazing behavior. We found a constant lower pasture utilization rate below the tree canopy than in the open areas, particularly in winter, when grazing pressure is higher than in other seasons due to the unbalance between pasture growth rates and animal nutritive requirements. Although a higher pasture growth was observed in winter underneath the trees, animals tended to graze less efficiently (0.63 vs. 0.85 of pasture utilization rate respectively for the below and outside of the tree positions). This was mainly associated to the lower forage quality under the tree as indicated by the lower PV. Areas underneath the tree often represent a resting site for animals after grazing since they are cooler in the summer being protected from solar radiation. This behavior also affects the palatability of the herbaceous communities below the trees as animals can damage the vegetation by trampling and smearing with dung and urine. Furthermore, the higher fertility levels under the tree canopy favored the presence of nitrophylous species (De Miguel et al. 2013; Rossetti et al. 2015) characterized by low palatability (Roggero et al. 2002).

The sharp distinction of pastoral plant communities between the two positions was associated with differences in pasture production, intake and PV. These results confirm what reported by Bagella et al. (2013b) about *T. subterraneum* and annual grasses such as *A. barbata* and *V. ligustica* that are key species in the open grassland to ensure herbage quality and productivity in spring.

Conclusions

Scattered trees in Mediterranean cork oak wooded grasslands significantly enhanced pasture plant biodiversity, by introducing a micro-habitat that was associated with higher soil C stocks, but lower pasture productivity and quality (as estimated by PV) in spring than in the open grassland. Therefore, maintaining scattered trees in the Mediterranean cork oak grasslands can be more beneficial to the society in terms of regulating services than to farmers in terms of provisioning services. If the main purpose of the wooded grasslands is to produce forage for grazing animals rather than conserving and/or enhancing plant diversity and soil fertility, the presence of scattered trees in the grassland constrains the overall productivity, although the greater forage availability in winter under the trees can be an added value for such silvopastoral farming systems. Our findings have relevant implications for designing effective conservation policies of such habitats, given the declining net farmer income associated with cork production and other provisioning services in these Mediterranean agro-ecosystems.

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Appendix

See Table 3.



Table 3 List of plant taxa with relative specific index (Is), codex used in the triplot from CCA (Fig. 3) and indication of presence (1) or absence (0) in BT (below the tree) and OT (outside the tree)

Is	Taxon	Codex	BT	OT
1	Achillea ligustica All.		1	0
1	Agrostis pourretii Willd.		0	1
0	Aira caryophyllea L.		0	1
1	Ammoides pusilla (Brot.) Breistr.		0	1
1	Anagallis arvensis L.		1	1
0	Andryala integrifolia L.		1	1
0	Anthemis arvensis L.	Ant arv	1	1
2	Anthoxanthum aristatum Boiss.		1	1
0	Aphanes floribunda (Murb.) Rothm.		0	1
0	Arisarum vulgare Targ Tozz.		1	0
0	Asparagus acutifolius L.		1	0
1	Asperula laevigata L.		1	0
1	Asphodelus ramosus L.	Asp ram	1	1
4	Astragalus pelecinus (L.) Barneby	·	0	1
3	Avena barbata Pott ex Link		1	1
3	Avena fatua L.		0	1
0	Bartsia trixago L.		1	0
1	Bellis perennis L.		1	1
2	Briza maxima L.		1	1
2	Briza minor L.		1	0
2	Bromus hordeaceus L.		1	1
2	Bromus scoparius L.		1	1
1	Bromus sterilis L.	Bro ste	1	0
1	Bunias erucago L.	Bun eru	1	1
0	Calamintha nepeta (L.) Savi	Buil Old	1	0
0	Calendula arvensis L.		0	1
0	Capsella rubella Reut.		1	1
1	Cardamine hirsuta L.		1	1
0	Carduus pycnocephalus L.	Con myo	1	1
0	Carex divulsa Stokes	Car pyc Car div	1	1
0	Carlina corymbosa L. Carthamus lanatus L.	Car cor	1	1
0			1	1
0	Centaurea calcitrapa L.	G 1	0	1
0	Cerastium glomeratum Thuill.	Cer glo	1	1
2	Chenopodium album L.		1	0
2	Chondrilla juncea L.	·	1	1
4	Cichorium intybus L.	Cic int	1	1
1	Convolvulus arvensis L.		1	1
0	Corrigiola litoralis L.		0	1
2	Crepis vesicaria L.		1	1
0	Cynara cardunculus L.		0	1
4	Cynodon dactylon (L.) Pers.		0	1
3	Cynosurus cristatus L.		1	0
2	Cynosurus echinatus L.	Cyn ech	1	1
3	Dactylis glomerata L.		1	0
3	Dasypyrum villosum (L.) P. Candargy, non Borbas		1	1
1	Daucus carota L.		1	1



Table 3 continued

Is	Taxon	Codex	BT	OT
0	Dipsacus ferox Loisel.		1	1
0	Echium italicum L.		0	1
0	Echium plantagineum L.		0	1
0	Epilobium tetragonum L.		0	1
0	Erodium cicutarium (L.) L'Her.		1	1
0	Eryngium campestre L.		1	1
0	Euphorbia helioscopia L.		1	1
0	Euphorbia peplus L.		1	0
0	Filago gallica L.		0	1
0	Filago vulgaris Lam.		1	1
0	Fumaria capreolata L.		1	0
0	Galactites elegans (All.) Soldano		1	1
0	Galium aparine L.		1	0
1	Galium parisiense L.		1	1
2	Gaudinia fragilis (L.) P. Beauv.		1	1
1	Geranium lucidum L.		1	0
1	Geranium molle L.	Ger mol	1	1
2	Geranium purpureum Vill.		1	0
2	Hedypnois cretica (L.) Dum.Cours.		1	1
2	Hordeum bulbosum L.		1	1
2	Hordeum murinum L.	Hor mur	1	1
3	Hyoseris radiata L.		1	1
0	Hypericum humifusum L.		1	0
1	Hypochaeris achyrophorus L.		1	1
3	Hypochaeris glabra L.		1	1
3	Hypochaeris radicata L.		1	1
0	Isoetes duriei Bory		1	1
1	Kickxia cirrhosa (L.) Fritsch		1	1
1	Lagurus ovatus L.		1	1
3	Lamarckia aurea (L.) Moench		0	1
4	Lathyrus angulatus L.		1	0
3	Lathyrus aphaca L.		1	0
4	Lathyrus cicera L.		1	1
2	Leontodon tuberosus L.		1	1
0	Linaria pelisseriana (L.) Miller		1	1
5	Lolium multiflorum Lam.		1	1
5	Lolium rigidum Gaudin	Lol rig	1	1
3	Lotus conimbricensis Brot.		0	1
3	Lotus edulis L.		1	1
2	Lotus hispidus DC.		1	1
1	Luzula forsteri (Sm.) DC.		1	0
4	Medicago arabica (L.) Huds.		1	1
5	Medicago murex Willd.		1	1
4	Medicago orbicularis (L.) Bartal.		0	1
4	Medicago polymorpha L.	Med his	1	1
1	Molineriella minuta (L.) Rouy		0	1
0	Muscari comosum (L.) Mill.		1	1
1	Myosotis pusilla Loisel.		0	1



Table 3 continued

Is	Taxon	Codex	BT	OT
2	Oenanthe pimpinelloides L.		1	0
4	Olea europaea L.		1	0
0	Onopordum illyricum L.	Ono ill	1	1
4	Ornithopus compressus L.		1	1
4	Ornithopus pinnatus (Mill.) Druce		1	1
0	Orobanche amethystea Thuill.		0	1
0	Papaver dubium L.		0	1
0	Petrorhagia prolifera (L.) Ball et Heywood		1	1
0	Phedimus stellatus (L.) Raf.		1	1
1	Plantago bellardii All.		0	1
2	Plantago coronopus L.		1	1
2	Plantago lagopus L.	Pla lag	1	1
2	Plantago lanceolata L.		1	0
2	Poa annua L.		1	1
2	Poa infirma Kunth		1	1
4	Poa trivialis L.	Poa tri	1	0
1	Polycarpon tetraphyllum L.		1	1
0	Pulicaria odora (L.) Rchb.		1	0
2	Quercus suber pl. L.		1	1
0	Ranunculus muricatus L.		1	0
0	Ranunculus paludosus Poir.		1	1
0	Ranunculus parviflorus L.		1	1
0	Ranunculus sardous Crantz		1	0
2	Raphanus raphanistrum L.	Rap rap	1	1
2	Reichardia picroides (L.) Roth		1	1
2	Rhagadiolus stellatus (L.) Gaertn.		1	0
0	Romulea ligustica Parl.		1	1
0	Romulea ramiflora Ten.		1	1
1	Rostraria cristata (L.) Tzvelev		0	1
1	Rubus ulmifolius Schott		1	0
1	Rumex acetosa L.	Rum ace	1	1
2	Rumex bucephalophorus L.		0	1
0	Rumex pulcher L.	Rum pul	1	1
0	Salvia verbenaca L.		0	1
3	Sanguisorba minor Scop.		1	1
2	Scandix pecten-veneris L.		1	1
0	Scolymus hispanicus L.	Sco his	1	1
0	Senecio vulgaris L.		1	1
0	Sherardia arvensis L.	She arv	1	1
0	Silene gallica L.		1	1
1	Silene vulgaris (Moench) Garcke	Sil vul	1	1
0	Silybum marianum (L.) Gaertner.		1	1
1	Sisymbrium officinale (L.) Scop.	Sis off	1	1
0	Smyrnium perfoliatum L.	Smy per	1	1
4	Sonchus arvensis L.		1	1
0	Sonchus asper (L.) Hill		1	1
1	Sonchus bulbosus (L.) N. Kilian & Greuter		1	0
1	Sonchus oleraceus L.		1	0



Table 3 continued

Is	Taxon	Codex	BT	OT
1	Spergula arvensis L.		0	1
0	Stachys arvensis (L.) L.		1	1
0	Stellaria media (L.) Vill.	Ste med	1	0
0	Thapsia garganica L.	Tha gar	1	1
0	Tillaea vaillantii Willd.		0	1
1	Tolpis umbellata Bertol.		0	1
0	Torilis arvensis (Hudson) Link		1	0
2	Torilis nodosa (L.) Gaertner		1	0
2	Trifolium arvense L.		1	0
2	Trifolium bocconei Savi		1	1
2	Trifolium campestre Schreb.	Tri cam	1	1
3	Trifolium cherleri L.		1	1
3	Trifolium glomeratum L.		1	1
5	Trifolium incarnatum L.		1	0
5	Trifolium michelianum Savi		1	0
4	Trifolium nigrescens Viv.		1	1
3	Trifolium resupinatum L.		1	0
2	Trifolium scabrum L.		1	1
3	Trifolium stellatum L.		1	0
5	Trifolium subterraneum L.	Tri sub	1	1
3	Trifolium tomentosum L.		1	1
2	Triticum ovatum (L.) Raspail		0	1
2	Urospermum dalechampii (L.) F.W. Schmidt		1	1
0	Urtica pilulifera L.		1	0
2	Valerianella microcarpa Loisel.		1	1
0	Verbascum blattaria L.		0	1
0	Verbascum pulverulentum Vill.		1	1
1	Veronica peregrina L.		1	1
4	Vicia hybrida L.		1	0
2	Vicia lathyroides L.		1	1
4	Vicia sativa L.		1	0
0	Vulpia bromoides (L.) Gray		1	1
2	Vulpia ligustica (All.) Link	Vul lig	1	1
2	Vulpia myuros (L.) C.C. Gmel.	Vul myu	1	1

References

- Anderson M, Gorley R, Clarke K (2008) PERMANOVA for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth
- Bagella S, Caria MC (2011) Vegetation series: a tool for the assessment of grassland ecosystem services in Mediterranean large-scale grazing systems. Fitosociologia 48:47–54
- Bagella S, Salis L, Marrosu GM, Rossetti I, Fanni S, Caria MC, Roggero PP (2013a) Effects of long-term management practices on grassland plant assemblages in Mediterranean cork oak silvo-pastoral systems. Plant Ecol 214:621–631. https://doi.org/10.1007/s11258-013-0194-x
- Bagella S, Satta A, Floris I, Caria MC, Rossetti I, Podani J (2013b) Effects of plant community composition and flowering phenology on honeybee foraging in Mediterranean sylvo-pastoral systems. Appl Veg Sci 16:689–697. https://doi.org/10.1111/avsc.12023
- Bagella S, Sitzia M, Roggero PP (2017) Soil fertilisation contributes to mitigating forest fire hazard associated with *Cistus monspeliensis* L. (rock rose) shrublands. Int J Wildland Fire 26(2):156–166. https://doi.org/10.1071/wf16114
- Báldi A (2008) Habitat heterogeneity overrides the species—area relationship. J Biogeogr 35:675–681. https://doi.org/10. 1111/j.1365-2699.2007.01825.x
- Bazzoffi P (2009) Soil erosion tolerance and water runoff control: minimum environmental standards. Reg Environ



- Change 9:169–179. https://doi.org/10.1007/s10113-008-0046-8
- Bennett EM, Peterson GD, Gordon LJ (2009) Understanding relationships among multiple ecosystem services. Ecol Lett 12:1394–1404. https://doi.org/10.1111/j.1461-0248.2009.
- Braun-Blanquet J (1951) Pflanzensoziologie: grundzüge der vegetationskunde. Springer-Verlag
- Casals P, Romero J, Rusch GM, Ibrahim M (2014) Soil organic C and nutrient contents under trees with different functional characteristics in seasonally dry tropical silvopastures. Plant Soil 374:643–659. https://doi.org/10.1007/ s11104-013-1884-9
- CEC (Commission of the European Communities) (2002)
 Towards a thematic strategy for soil protection. In: Communication from the Commission to the Council, the European Parliament, the Economic and Social Committee and the Committee of the Regions. Brussels, p 35
- Chanteloup P, Bonis A (2013) Functional diversity in root and above-ground traits in a fertile grassland shows a detrimental effect on productivity. Basic Appl Ecol 14:208–216. https://doi.org/10.1016/j.baae.2013.01.002
- Cosentino SL, Porqueddu C, Copani V, Patanè C, Testa G, Scordia D, Melis R (2014) European grasslands overview: Mediterranean region. Grassland Sci Eur 19:41–56
- Council of Europe (1992) Council Directive 92/43/EEC, Official Journal L. 206, 22/07/1992, pp 7–50. http://eur-lex.europa.eu/legal-content/EN/TXT/HTML/?uri=CELEX: 31992L0043&from=EN
- Craven D, Isbell F, Manning P, Connolly J, Bruelheide H, Ebeling A, Roscher C, van Ruijven J, Weigelt A, Wilsey B, Beierkuhnlein C, de Luca E, Griffin JN, Hautier Y, Hector A, Jentsch A, Kreyling J, Lanta V, Loreau M, Meyer ST, Mori AS, Naeem S, Palmborg C, Wayne Polley H, Reich PB, Schmid B, Siebenkas A, Seabloom E, Thakur MP, Tilman D, Vogel A, Eisenh N (2016) Plant diversity effects on grassland productivity are robust to both nutrient enrichment and drought. Philos T Roy Soc B 371:20150277. https://doi.org/10.1098/rstb.2015.0277
- Daget P, Poissonet J (1971) Une méthode d'analyse phytologique des prairies: critères d'application. Ann Agron 22:5–41
- De Miguel JM, Acosta-Gallo B, Gómez-Sal B (2013) Understanding Mediterranen pasture dynamics: general tree cover vs specific effects of individual trees. Rangeland Ecol Manag 66:216–223. https://doi.org/10.2111/REM-D-12-00016.1
- Dufour A, Gadallah F, Wagner HH, Guisan A, Buttler A (2006)
 Plant species richness and environmental heterogeneity in
 a mountain landscape: effects of variability and spatial
 configuration. Ecography 29:573–584. https://doi.org/10.
 1111/j.0906-7590.2006.04605.x
- FAO (2017) Sustainably manage forests, combat desertification, halt and reverse land degradation, halt biodiversity loss. http://www.fao.org/sustainable-development-goals/goals/goal-15/en/
- Fernández-Moya J, San Miguel-Ayanz A, Cañellas I, Gea-Izquierdo G (2011) Variability in Mediterranean annual grassland diversity driven by small-scale changes in fertility and radiation. Plant Ecol 212:865–877. https://doi. org/10.1007/s11258-010-9869-8

- Frame J (1981) Herbage mass. In: Hodgson J, Baker R, Davies A, Laidlaw A (eds) Sward measurements handbook. The British Grassland Society, Maidenhead, pp 39–67
- García-Barrios L, Ong CK (2004) Ecological interactions, management lessons and design tools in tropical agroforestry systems. Agrofor Syst 61:221–236. https://doi.org/ 10.1023/B:AGFO.0000029001.81701.f0
- Gomez KA, Gomez AA (1984) Statistical procedures for agricultural research. Wiley, New York
- Gutman M, Seligman NG, Noy-Meir I (1990) Herbage production of Mediterranean grassland under seasonal and yearlong grazing systems. J Range Manag 43:64–68. https://doi.org/10.2307/3899124
- Haile SG, Nair VD, Nair PKR (2010) Contribution of trees to carbon storage in soils of silvopastoral systems in Florida, USA. Glob Change Biol 16:427–438. https://doi.org/10.1111/j.1365-2486.2009.01981.x
- Hönigová I, Vačkář D, Lorencová E, Melichar J, Götzl M, Sonderegger G, Oušková V, Hošek M, Chobot K (2012) Survey on grassland ecosystem services. Report of the European Topic Centre on Biological Diversity. Nature Conservation Agency of the Czech Republic, Prague
- Howlett DS, Moreno G, Mosquera-Losada MR, Nair PKR, Nair VD (2011) Soil carbon storage as influenced by tree cover in the Dehesa cork oak silvopasture of central-western Spain. J Environ Monit 13:1897–1904. https://doi.org/10.1039/c1em10059a
- Institute SAS (1999) SAS/STAT user's guide, version 8, vol 2. SAS Institute, Cary
- Klaus VH, Hölzel N, Boch S, Müller J, Socher S, Prati D, Fischer M, Kleinebecker T (2013) Direct and indirect associations between plant species richness and productivity in grasslands: regional differences preclude simple generalization of productivity-biodiversity relationships. Preslia 85:97–112
- Kyriazopoulos AP, López-Francos A, Porqueddu C, Sklavou P (2016) Ecosystem services and socio-economic benefits of Mediterranean grasslands. Options 114:13
- López-Carrasco C, López-Sánchez A, San Miguel A, Roig S (2015) The effect of tree cover on the biomass and diversity of the herbaceous layer in a Mediterranean dehesa. Grass Forage Sci 70:639–650. https://doi.org/10.1111/gfs.12161
- Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston M, Raffaelli D, Schmid B, Tilman D, Wardle DA (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294:804–808. https://doi.org/10.1126/science.1064088
- Manning AD, Fischer J, Lindenmayer DB (2006) Scattered trees are keystone structures—implications for conservation. Biol Conserv 132:311–321. https://doi.org/10.1016/j.biocon.2006.04.023
- McCune B, Grace JB, Urban DL (2002) Analysis of ecological communities. MjM software design, Gleneden Beach
- MEA (Millenium Ecosystem Assessment) (2005) Ecosystems and human well-being: a framework for assessment. Island Press, Washington
- Merunková K, Chytrý M (2012) Environmental control of species richness and composition in upland grasslands of the southern Czech Republic. Plant Ecol 213:591–602. https://doi.org/10.1007/s11258-012-0024-6



- Moreno G (2008) Response of understorey forage to multiple tree effects in Iberian dehesas. Agric Ecosyst Environ 123:239–244. https://doi.org/10.1016/j.agee.2007.04.006
- Moreno G, Obrador J, García E, Cubera E, Montero M, Pulido F (2005) Consequences of dehesa management on tree-understorey interactions. In: Mosquera-Losada MR, Riguero-Rodriguez A, McAdam J (eds) Silvopastoralism and sustainable land management. CAB International, Oxon, pp 263–265
- Moreno G, Obrador JJ, García A (2007) Impact of evergreen oaks on soil fertility and crop production in intercropped dehesas. Agric Ecosyst Environ 119:270–280. https://doi. org/10.1016/j.agee.2006.07.013
- Moreno G, Bartolome JW, Gea-Izquierdo G, Cañellas I (2013) Overstory-understory relationships. In: Campos P, Huntsinger L, Oviedo JL, Starrs PF, Diaz, M, Standiford RB, Montero G (eds) Mediterranean Oak woodland working landscapes. Dehesas of Spain and Ranchlands of California. Landscape Series, vol 16. Springer, New York, pp 145–179
- Moreno G, Gonzalez-Bornay G, Pulido F, Lopez-Diaz ML, Bertomeu M, Juárez E, Diaz M (2016) Exploring the causes of high biodiversity of Iberian dehesas: the importance of wood pastures and marginal habitats. Agrofor Syst 90:87–105. https://doi.org/10.1007/s10457-015-9817-7
- Nieto-Romero M, Oteros-Rozas E, González JA, Martín-López B (2014) Exploring the knowledge landscape of ecosystem services assessments in Mediterranean agroecosystems: insights for future research. Environ Sci Policy 37:121–133. https://doi.org/10.1016/j.envsci.2013.09.003
- Petersen U, Wrage N, Kohler L, Leuschner C, Isselstein J (2012)
 Manipulating the species composition of permanent grasslands—a new approach to biodiversity experiments.
 Basic Appl Ecol 13:1–9. https://doi.org/10.1016/j.baae. 2011.10.003
- Pielou EC (1969) An introduction to mathematical ecology. An introduction to mathematical ecology. Wiley, New York
- Pilgrim ES, Macleod CJ, Blackwell MS, Bol R, Hogan DV, Chadwick DR, Cardenas L, Misselbrook TH, Haygarth PM, Brazier RE (2010) Interactions among agricultural production and other ecosystem services delivered from European temperate grassland systems. Adv Agron 109:117–154
- Pulido-Fernández M, Schnabel S, Lavado-Contador JF, Miralles Mellado I, Ortega Pérez R (2013) Soil organic matter of Iberian open woodland rangelands as influenced by vegetation cover and land management. CATENA 109:13–24. https://doi.org/10.1016/j.catena.2013.05.002
- Questad EJ, Foster BL (2008) Coexistence through spatiotemporal heterogeneity and species sorting in grassland plant communities. Ecol Lett 11:717–726. https://doi.org/ 10.1111/j.1461-0248.2008.01186.x
- Ribeiro S, Fernandes JP, Espírito-Santo MD (2014) Diversity and floristic patterns of mediterranean grasslands: the

- relative influence of environmental and land management factors. Biodivers Conserv 23:2903–2921. https://doi.org/10.1007/s10531-014-0754-y
- Roggero PP, Bagella S, Farina R (2002) Un Archivio dati di Indici specifici per la valutazione integrata del valore pastorale. Rivista di Agronomia 36:149–156
- Rolo V, Rivest D, Lorente M, Kattge J, Moreno G (2016) Taxonomic and functional diversity in Mediterranean pastures: insights on the biodiversity–productivity tradeoff. J Appl Ecol 53:1575–1584. https://doi.org/10.1111/ 1365-2664.12685
- Rossetti I, Bagella S, Cappai C, Caria MC, Lai R, Roggero PP, da Silva PM, Sousa JP, Querner P, Seddaiu G (2015) Isolated cork oak trees affect soil properties and biodiversity in a Mediterranean wooded grassland. Agric Ecosyst Environ 202:203–216. https://doi.org/10.1016/j.agee. 2015.01.008
- Seddaiu G, Porcu G, Ledda L, Roggero PP, Agnelli A, Corti G (2013) Soil organic matter content and composition as influenced by soil management in a semi-arid Mediterranean agro-silvo-pastoral system. Agric Ecosyst Environ 167:1–11. https://doi.org/10.1016/j.agee.2013.01.002
- Simón N, Montes F, Díaz-Pinés E, Benavides R, Roig S, Rubio A (2013) Spatial distribution of the soil organic carbon pool in a Holm oak dehesa in Spain. Plant Soil 366:537–549. https://doi.org/10.1007/s11104-012-1443-9
- Stein A, Gerstner K, Kreft H (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecol Lett 17:866–880. https://doi.org/10.1111/ele.12277
- Takimoto A, Nair VD, Nair PKR (2009) Contribution of trees to soil carbon sequestration under agroforestry systems in the West African Sahel. Agrofor Syst 76:11–25. https://doi.org/10.1007/s10457-008-9179-5
- Ter Braak CJF, Smilauer P (2002) CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5). Ithaca, NY, USA. www.canoco.com
- Tilman D, Reich PB, Isbell F (2012) Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. P Natl Acad Sci USA 109:10394–10397. https://doi.org/10.1073/pnas.1208240109
- USDA (2010) Keys to soil taxonomy, 11th edn. Soil survey staff, United States Department of Agriculture, Natural Resources Conservation Service, Washington, DC, USA. https://www.nrcs.usda.gov/Internet/FSE_DOCUMENTS/nrcs142p2_050915.pdf
- van der Maabel E (1979) Transformation of cover-abundance values in phytosociology and its effects on community similarity. Vegetatio 39:97–114. https://doi.org/10.1007/BF00052021
- Whittaker RH (1972) Evolution and measurement of species diversity. Taxon 21:213–251

