

Taxonomic and functional diversity in Mediterranean pastures: Insights on the biodiversity–productivity trade-off

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Summary

1. Agricultural intensification is one of the main causes of biodiversity loss worldwide. The inclusion of semi-natural features in agricultural landscapes is suggested as a means of enhancing farm biodiversity, but this practice may have potential negative effects on yield production. Moreover, little evidence exists for effects of semi-natural features on other components of biodiversity, such as functional diversity. Yet this could provide a more comprehensive understanding of biodiversity–productivity trade-offs.

2. Here, we report the effects of semi-natural woody vegetation on taxonomic and functional diversity, and biomass production of herbaceous species at the field and farm scales by sampling 50 fields, ranging from 0 to 90% woody vegetation cover, on nine similarly managed farms in central-western Spain.

3. We found significant differences in herbaceous species richness among farms. Both taxonomic and functional β -diversity exhibited significant negative relationships with herbage production, highlighting the trade-off between biodiversity and productivity in these agroecosystems.

4. Woody vegetation cover had a significant negative relationship with biomass production and a unimodal relationship with species richness at the field scale. At high values of woody vegetation cover, species richness and functional diversity indices were decoupled, suggesting that at this extreme of the

woody vegetation gradient, only herbaceous species with contrasting trait values were present. Our results showed both convergent and divergent patterns of trait values, suggesting that different assembly processes are acting concurrently along the gradient of woody vegetation.

5. *Synthesis and applications.* Our result indicates that management of woody vegetation may indeed increase both taxonomic and functional diversity, but this may come at the expense of key ecosystem services or other management goals, namely, herbage production. Optimization of the trade-off between herbage diversity and productivity can be reached with a woody vegetation cover of c. 30% at the field scale.

Key-words: community assemblage, wood pastures, functional dispersion, functional traits, null models, semi-natural vegetation, ecosystem services, taxonomic diversity, biodiversity–productivity trade-off

1. Introduction

Semi-natural features are of key importance for biodiversity conservation in agricultural landscapes (Wezel *et al.* 2014). The positive effects that semi-natural features can exert on farm species richness of different taxa have been commonly highlighted in the literature (Billeter *et al.* 2008). Proximity to semi-natural features, such as field margins, hedgerows, shrub patches or woodlots, has a positive effect on species richness at the landscape scale (Hendrickx *et al.* 2007). However, semi-natural features represent an opportunity cost in land use for yield productivity (Green *et al.* 2005). Minimization of the trade-off between biodiversity conservation and yield production is the basis for managing the abundance of semi-natural features in agroecosystems (Rey Benayas & Bullock 2015). The assessment of the effects of semi-natural features on

biodiversity levels has been based mostly upon taxonomic diversity indices, while other components of biodiversity, such as functional diversity, have received much less attention (Cadotte 2011). Yet, metrics of functional diversity can provide a more mechanistic link between biodiversity and ecosystem functioning (de Bello *et al.* 2010). Compared to approaches that are solely based upon species richness (Cadotte 2011), assessing how semi-natural features affect functional diversity could add new ecological understanding to the trade-off between biodiversity conservation and yield production.

Functional diversity, i.e. the range and relative abundance of functional traits in a given community, plays an important role in understanding the links between community composition and ecosystem processes (Tilman *et al.* 1997). For instance, functional traits are better predictors than species composition in modelling variables of pastoral importance, such as forage yield and quality (Jouven, Carrère & Baumont 2006; Pontes *et al.* 2007; Ansquer *et al.* 2009). Commonly, as stated by the “mass ratio hypothesis” (Grime 1998), the traits of the most abundant species in the community largely determine ecosystem processes, such as rates of decomposition and mineralization or primary productivity (de Bello *et al.* 2010). Increasing trait dissimilarity between species in a community can also explain ecosystem processes, such as pollination, or their maintenance at multiple times (de Bello *et al.* 2010). This complementarity effect suggests that ecosystem processes are determined by multiple, functionally different, species assemblages (Tilman *et al.* 1997), whereas the mass ratio hypothesis asserts that selection effects are more important. Nevertheless, the joint contribution of complementarity and selection effects can explain variation in ecosystem processes (e.g. Laliberté, Norton & Scott 2013). To what extent that semi-natural features will affect ecosystem processes depends upon how they modify functional diversity levels.

Environmental conditions and grazing exert non-random effects on the functional structure of herbaceous communities in Mediterranean grasslands (Peco *et al.* 2005). The potential for semi-natural features, such as woody vegetation, to affect functional diversity and, ultimately, productivity, of local herbaceous communities may be related to their modifying effects on environmental conditions, or on the availability of abiotic resources both below- and above-ground. By inducing changes in soil resources (e.g. nutrients and water) and light availability (Rolo, López-Díaz & Moreno 2012), woody vegetation can be an important source of environmental heterogeneity in Mediterranean grasslands (Lopez-Pintor, Gomez Sal & Rey Benayas 2006). As a result, woody vegetation can alter floristic composition of the understorey herbaceous communities, compared to adjacent open spaces, thereby resulting in marked differences in plant nutrition and productivity (Rolo *et al.* 2014). Yet it is relatively unclear as to how these changes relate to functional diversity levels. For instance, changes in environmental conditions that are promoted by woody vegetation may result in a reduction of the functional trait space (convergence; Grime 2006), because only species bearing trait values that are adapted to the local conditions can co-exist (i.e. environmental filtering; Laliberté, Norton & Scott 2013). In contrast, these changes in environmental conditions may result in an increase in the functional trait space (divergence; Grime 2006), because co-existing species may try to avoid overlapping niches (i.e. niche complementarity; Laliberté, Norton & Scott 2013). How these assembly processes relate to biomass production through complementarity or selection effects remains largely untested in grasslands.

In considering the deliberate incorporation of woody vegetation as a management strategy in agroecosystems (Rey Benayas, Bullock & Newton 2008), it is necessary to understand its effects at the farm scale, given that managers' actions are conducted over their entire farms. Identifying

when the spatial scale of influence of ecological processes matches the managerial scale can help to inform management decisions over the extent of a farm (Pelosi, Goulard & Balent 2010). Yet, it is assumed that farmers have limited possibilities for increasing biodiversity at the farm level (Schneider *et al.* 2014). For instance, many factors that act at the landscape scale, such as landscape heterogeneity, habitat fragmentation and connectivity, are beyond a single farmer's management options, but would influence plant diversity within a given farm. However, Gonthier *et al.* (2014) have recently shown that within-farm management can affect plant diversity to a greater extent than can landscape complexity. Understanding how variation in biodiversity among farms (β -diversity) is explained by differences in woody vegetation cover may help support decisions at the farm scale, with direct implications for biodiversity.

Our study aims to assess changes in herbage production and diversity along a woody vegetation gradient and evaluate how these changes relate to differences in functional diversity. We employed a trait-based approach to determine how the functional structure of the herbaceous community varies with woody vegetation cover and to examine how processes that control coexistence in plant communities are related to productivity. Specifically, we first assessed how patterns of productivity *versus* taxonomic and functional diversity varied, depending upon the cover of woody vegetation at the field scale. We expected directional changes in these variables along a woody vegetation gradient because of the modifying effects of woody vegetation on environmental conditions. We then examined non-random community assembly processes (trait divergence *versus* convergence) along a woody vegetation gradient using null models to study the relative importance of different processes affecting productivity (complementarity *versus* environmental filtering) at the field scale. We hypothesized that increasing woody vegetation presence would promote trait divergence because of the increase in environmental heterogeneity.

Finally, we examined patterns of variation in taxonomic and functional diversity (β -diversity) to evaluate how processes acting at the field scale drive differences in community structure among farms. We hypothesized that farms with more woody features would contribute to high β -diversity than farms with fewer woody features.

2. Materials and methods

2.1 Study region and site selection

The study area was north of Plasencia and located in the Tierras de Granadilla district (40°06'N 6°29'W), which forms part of the Extremadura region of central-western Spain. The regional climate is Mediterranean, with a mean annual temperature of 16.1 °C. Mean total annual rainfall is 756 mm. The agrarian landscape in the region is dominated by Iberian *dehesas*, one of the major types of low-input farming systems that are encountered across Europe (Paracchini *et al.* 2008). Iberian *dehesas* are grazed woodlands where a scattered tree layer is embedded in a pasture matrix with interspersed shrub patches. The dominant tree and shrub species were holm oak *Quercus ilex* L. and gum rockrose *Cistus ladanifer* L., respectively. The pasture layer primarily consists of annual native species, including *Chamaemelum mixtum* (L.) All., *Echium plantagineum* L., *Festuca ampla* Hack., *Ornithopus compressus* L., *Poa bulbosa* L., *Tolpis barbata* (L.) Gaertn., *Trifolium glomeratum* L., and *Tuberaria plantaginea* (Willd.) M.J. Gallego.

Within the study region, a set of farms was selected based on CORINE Land Cover maps (Coordination of Information on the Environment; European Environment Agency 2010) and cadastral maps to ensure that silvopastoral land use was similar across farms. Eighteen farms were selected *a priori*, where livestock husbandry was the main activity. From this initial set of

Table 1 Main characteristics of sampled *dehesa* farms: area (ha), number of fields, woody vegetation cover (% \pm SE) and type of livestock present

Farm	Area (ha)	Number of Fields	Field area (mean and range, ha)	Woody vegetation cover (% \pm SE)	Livestock
Farm 1	835	9	42 (4.8 – 184)	34.8 \pm 10.0	Cattle, Pigs
Farm 2	232	5	9 (0.3 – 42)	6.0 \pm 2.4	Cattle
Farm 3	347	5	5 (0.5 – 21)	3.2 \pm 3.0	Cattle, Horses
Farm 4	604	7	25 (3.2 – 102)	47.0 \pm 10.9	Cattle, Pigs, Sheep
Farm 5	449	4	14 (2.0 – 40)	20.8 \pm 17.3	Cattle, Pigs, Horses
Farm 6	150	5	12 (0.5 – 27)	2.0 \pm 2.0	Cattle, Sheep, Goats, Horses
Farm 7	154	6	9 (0.5 – 43)	36.2 \pm 12.3	Cattle, Sheep
Farm 8	758	5	21 (2.1 – 62)	58.2 \pm 15.2	Cattle
Farm 9	753	4	37 (4.0 – 102)	11.8 \pm 4.2	Cattle, Pigs, Sheep

farms, we selected a subset of nine farms according to two criteria (Table 1). First, the structure (proportion of wood and open pasture) and farm size had to be typical of the region, while reducing between-farm variability that was associated with vegetation type, slope and soil fertility. To achieve this goal, all selected farms were on gently sloping terrain (< 3%), with *Q. ilex* being the main tree species. Soils were classified as Dystric Cambiosols (García Navarro & López Piñero 2002). Second, the percentage of woody vegetation cover for each farm had to be different, which resulted in a gradient of woody vegetation cover among farms. The nine farms that were selected ranged from 2 to 60% woody vegetation cover.

2.2 Vegetation sampling protocol

The entire study area per farm was mapped and all fields within a farm were identified and delimited using aerial photographs and field surveys. Field identification followed a standard mapping procedure based on the dominant Raunkiaer life-forms, edaphoclimatic conditions, and management practices (Bunce *et al.* 2011). In those fields with a minimum width of 50 m, in 2010 (April to June), one quadrat of 10 \times 10 m was randomly placed well away from the edges (~ 5 m). All plant species, including woody species, were identified in each quadrat. The

abundance of each species was visually estimated in 5% increments. Rare species were assigned a generic abundance value of 1%. Fields were subsequently classified as: (i) open pastures that lacked woody vegetation, and which were dominated by annual species (vegetative period from October to May), by perennial species (dried in summer for 3–4 months), or by a mixture of both (number of fields = 20) (hereafter referred to as “open habitat”); (ii) shrub-encroached pastures of 1.5–3 m height, with 10 to 90% shrub cover, consisting mostly of *Cistus* spp., *Retama sphaerocarpa* (L.) Boiss., *Genista hirsuta* Vahl. and *Cytisus* spp., but also *Thymus* spp., and *Lavandula* spp., with or without presence of a sparse tree layer (hereafter referred to as “shrub habitat,” number of fields = 9); (iii) wood pastures with typically 10–30 mature oak trees per ha, with 10 to 70% canopy cover having stem diameters at breast height of 30–60 cm and heights of 6–8 m (hereafter referred to as “tree habitat,” number of fields = 19). Total woody vegetation cover per farm was computed as the average of woody species abundance per field (hereafter referred to as “woody cover”).

At the end of May 2010, herbage yield was visually estimated in each field (i.e. near the peak of green biomass and before livestock grazing) using the comparative yield method of Haydock & Shaw (1975), which allowed for precise estimates of actual yield (Redjadj *et al.* 2012). Two separate components were involved: destructive (cutting and weighing) and non-destructive (visual estimates) quadrats. First, three 0.25 m² (50 × 50 cm) reference quadrats were selected within each field. These three quadrats were established on low- (referred to as standard one), intermediate- (standard two) and high-yielding (standard three) areas to define a range that captured most of the biomass variation within each field. Herbage was harvested at ground level in each quadrat, dried (65 °C for 48 h) and weighed. Vegetation occurring along two perpendicular transects of 20 m was then visually estimated using the previously established

yield rating (standards one to three). In each transect, an individual, trained observer estimated herbage yield every second metre in 50×50 cm quadrats (10 per transect). Herbage yield for the 20 quadrats that was visually observed per field was then obtained by substituting its ratings by the corresponding dry mass obtained within the reference quadrats.

2.3 Functional traits

Five key functional traits (specific leaf area, maximum plant height, leaf dry matter content, seed length and leaf length) were selected to describe the 280 species that were recorded. Mean trait values per species across all observations were compiled from the TRY data base (<http://www.try-db.org>, Kattge *et al.* 2011) and data sources contained therein (Appendix S1 in Supporting Information), and bibliographic sources (Castroviejo 2012). Trait selection was based upon the known importance of various traits in plant life-history strategies, responses to environment or land-use change, and forage productivity (Díaz *et al.* 2004; Ansquer *et al.* 2009). Plant height and leaf length are related to resource availability, especially light, and competitive environments, with high plant height and leaf length indicating competitive advantages through greater access to light (Westoby *et al.* 2002; Gubsch *et al.* 2011). Specific leaf area (SLA) and leaf dry matter content (LDMC) relate to resource-use strategies, with low specific leaf area and high leaf dry matter content values indicating a conservative strategy with low relative growth rates (Westoby *et al.* 2002). Seed mass affects seedling survival and colonization capacity of species, i.e. species with larger seeds having less seed outputs but with high seedling survival (Westoby *et al.* 2002). Missing values constituted ~13.7% of the data set and only one species was represented by only one trait value. Unobserved values were estimated by means of dissimilarity imputation (Taugourdeau *et al.* 2014). This imputation method relies upon the

functional proximity between species to calculate new data and has been shown to be a robust option for computing functional diversity indices in data sets that have a maximum of 30% missing values (Taugourdeau *et al.* 2014).

We computed independent univariate and multivariate metrics of functional diversity from the generated trait data matrix. With respect to univariate metrics of functional diversity, we calculated the range, which was the difference between maximum and minimum value of each trait in a given field per farm (Swenson 2014). With respect to multivariate metrics of functional diversity, we calculated functional dispersion (Laliberté & Legendre 2010), which collectively summarizes various ecological traits within a given community and its deviation from a random community (see below) that can be interpreted in a manner similar to that of the univariate metrics (Swenson 2014).

2.4 Data analysis

2.4.1 Diversity metrics at the field scale

To assess the differences among habitats (open, shrub, and tree) on herbage production and species richness, we used linear mixed-effects models that included farm as a random effect. We parameterized both models including the open habitat as the reference level (i.e. represented by the intercept parameter) to facilitate comparison between open and woody habitats. Species richness (count data) was modelled assuming a Poisson distribution (log-link) and included the number of fields that were sampled per farm as an offset. Taxonomic and functional diversity metrics and herbage yields were modelled as a function of woody cover. We added a quadratic term to the regression to test for non-linear relationships between variables.

We used a null model approach to test the effect of habitat on patterns of trait values. Null

models allow the comparison of observed communities with randomly assembled communities of equal species richness (Gotelli & Graves 1996). To generate the random communities, we performed an individual-based randomization of species abundance across farms. A matrix describing the cover of each herbaceous species that was observed at the field scale was randomly permuted (999 times) across farms. For each randomization, univariate (range) and multivariate functional diversity (functional dispersion) metrics were calculated. We used a standardized effect size (SES) to compare the deviation of observed values relative to the null model assemblage. SES is a metric that is widely used to infer assembly rules (Gotelli & McCabe 2002), which is calculated as the ratio of the difference between the observed value and the mean of the null distribution, to the standard deviation (SD) of the null distribution:

$$SES = (\text{Observed-Null}) / SD (\text{Null})$$

The null hypothesis is that the average SES is zero. Thus, an SES value that is significantly higher than zero indicates a higher than average expected value in a random community (trait value divergence indicative of niche complementarity), while an SES value that is significantly lower than zero indicates a lower than average expected value in a random community (trait value convergence indicative of environmental filtering). Calculation of SES values using output from a null model is a commonly used method for comparing functional diversity of different communities, while removing biases that are associated with differences in species richness (Swenson 2014). We used linear mixed-effect models including farm as a random effect and excluding the intercept (i.e. adding a -1 term to the model) to assess if mean SES values per habitat significantly deviated from zero.

Also, we computed community-level weighted mean (CWM) per field, which was calculated as:

$$CWM = \sum_{i=1}^n p_i \text{trait}_i$$

where p_i and $trait_i$ are respectively the relative abundance and the trait value for species i and n is the total number of species. This index estimates the most probable attribute that a species drawn at random from a community would display (Swenson 2014). We used linear mixed-effects models that included farm as a random effect to assess the differences in CWM among habitats (open, shrub, and tree).

2.4.2 Diversity metrics at the farm scale

Since the number of sampled fields for each farm was not equal across farms, species richness was a rarefied sample-based estimate to the smallest number of fields sampled per farm. Rarefaction curves were constructed based on 100 random replicates using the software EcoSim (Acquired Intelligence Inc., Jericho, VT, USA). Species richness values were considered significantly different among farms when 95% confidence intervals of the rarefied values did not overlap. To compare variation in species composition and functional diversity among farms (β -diversity), we computed a multivariate dispersion index per farm (Anderson, Ellingsen & McArdle 2006) using Bray-Curtis distance. This metric is a permutation-based multivariate extension of Levene's test of homogeneity of variance. It computes the average distance between individual observation units (fields) to their group centroid (all fields within a farm). One advantage of this metric is that it yields a unique value per group (farm), which allowed us to model it against the gradient of woody cover. The functional diversity data matrix was based on CWM values. Values of β -diversity were regressed against herbage production and woody cover. To verify if species composition and functional diversity significantly differed among farms, we performed permutational MANOVA (999 permutations) using Bray-Curtis distance. All analyses were carried out in the R statistical environment (v3.1.1, R Development Core Team 2013) using the packages *vegan* (Oksanen *et al.* 2013), *nlme* (Pinheiro *et al.* 2014) and *FD* (Laliberté &

Legendre 2010).

3. Results

3.1 Effect of woody vegetation at the field scale

A total of 280 herbaceous species were found in the 50 sampled fields belonging to the nine farms. Species richness was significantly higher in shrub and tree habitats compared to open habitats ($P < 0.001$ for both), whereas herbage production was significantly lower under shrubs ($P = 0.024$) and marginally significantly lower under trees ($P = 0.054$) (Fig. 1). Shrub and tree

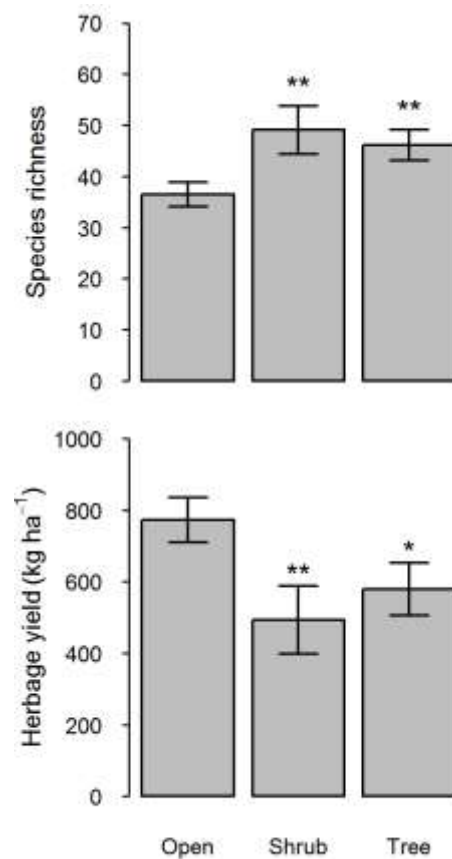


Figure 1 Mean values (\pm S.E.) of herbage yield (kg ha⁻¹) and herbaceous species richness per habitat type (open, shrub and tree). Asterisks denote a significant (** at $P < 0.05$) or marginally significant (* at $0.05 < P < 0.10$) difference between shrub or tree as compared to open habitat types.

habitats did not differ, either in terms of the number of species or in herbage production.

Table 2 Standardized effect sizes (SES \pm SE) and *P*-values per habitat type (open, shrub and tree) of range for univariate trait values (specific leaf area (SLA), maximum plant height, leaf dry matter content (LDMC), seed length and leaf length) and of dispersion for multivariate functional diversity metrics as compared to a null model. Significant differences from zero ($P < 0.05$) are depicted in bold

	Open		Shrub		Tree	
	SES	<i>P</i> -value	SES	<i>P</i> -value	SES	<i>P</i> -value
SLA	0.20 \pm 0.19	0.299	0.76 \pm 0.25	0.005	0.97 \pm 0.20	<0.001
Height	-0.96 \pm 0.20	<0.001	-0.55 \pm 0.28	0.051	-0.85 \pm 0.21	<0.001
LDMC	-0.41 \pm 0.14	0.006	-0.21 \pm 0.19	0.291	-0.26 \pm 0.15	0.086
Seed length	0.45 \pm 0.24	0.066	0.71 \pm 0.31	0.029	1.19 \pm 0.24	<0.001
Leaf length	-0.55 \pm 0.19	0.006	0.07 \pm 0.25	0.768	-0.34 \pm 0.19	0.081
Multivariate	-0.33 \pm 0.16	0.049	0.26 \pm 0.22	0.254	0.30 \pm 0.17	0.073

Differences in trait ranges were contingent upon the habitat that was considered (Table 2). Open habitats showed a significant reduction in ranges of maximum plant height ($P < 0.001$), leaf dry-matter content ($P = 0.006$) and leaf length ($P = 0.006$) relative to those of a random community, indicating convergence in trait values. These results were corroborated by the significant differences in CWM values between habitats. Open habitats showed significantly higher CWM values of height ($P = 0.031$) and lower CWM values of leaf dry matter content ($P = 0.002$) and seed length ($P < 0.001$) than tree habitats (Table 3). In contrast, shrub and tree habitats showed a significant increase in ranges of specific leaf area ($P = 0.005$ and $P < 0.001$, for shrub and trees, respectively) and seed length ($P = 0.029$ and $P < 0.001$, for shrub and trees, respectively) as compared to a random community, indicating divergence in trait values. Tree habitat also showed a significant reduction in the range of heights ($P < 0.001$). The multivariate index of functional diversity, functional dispersion, was significantly reduced in open habitats ($P = 0.049$) compared to a random community.

Table 3. Community weight mean values (CWM \pm SE) per habitat type (open, shrub and tree) of specific leaf area (SLA), maximum plant height, leaf dry matter content (LDMC), seed length and leaf length. Letters depict significant differences among habitat type at $P < 0.05$

	Open	Shrub	Tree
SLA	27.43 \pm 0.41 a	27.41 \pm 0.73 a	28.31 \pm 0.42 a
Height	34.29 \pm 1.50 a	29.86 \pm 2.66 ab	29.46 \pm 1.54 b
LDMC	199.5 \pm 2.1 b	206.5 \pm 3.7 ab	209.7 \pm 2.1 a
Seed length	1.97 \pm 0.08 b	2.52 \pm 0.15 a	2.53 \pm 0.08 a
Leaf length	83.02 \pm 4.43 a	76.09 \pm 7.85 a	78.42 \pm 4.53 a

The relationship between species richness and woody cover followed a hump-shaped pattern ($r^2 = 0.19$, $F_{2-47} = 6.6$ and $P = 0.003$) (Fig. 2). Species richness was highest at intermediate values of woody cover (~30%) and lowest at both extremes (maximum and minimum) of the woody cover gradient. Functional dispersion showed a significant positive relationship with woody cover ($r^2 = 0.40$, $F_{1-48} = 34.2$ and $P < 0.001$). In contrast, herbage production showed a significant negative relationship with woody cover ($r^2 = 0.27$, $F_{1-48} = 18.6$ and $P < 0.001$).

3.2 Patterns of taxonomic and functional diversity at the farm scale

Species richness estimates from sample-based rarefaction varied significantly among farms (Table 4). The farms with highest estimated number of species were around 117 (95% CI: 105–129), whereas the farm with the lowest number of species were about half of this value (~67; 95% CI: 57–77). Species composition and functional diversity varied significantly among farms ($F_{8-41} = 2.7$, $P = 0.025$ and $F_{8-41} = 2.4$, $P = 0.027$, respectively). Woody cover showed a significant positive relationship with functional dispersion ($r^2 = 0.63$, $F_{1-7} = 14.6$ and $P = 0.006$) and a hump-shaped pattern with species richness ($r^2 = 0.64$, $F_{2-6} = 5.3$ and $P < 0.047$), similar to results found at the field scale, but no relationship with herbage yield (Fig. 2). The farm with the lowest taxonomic β -diversity (~10% woody cover) also exhibited the lowest functional β -

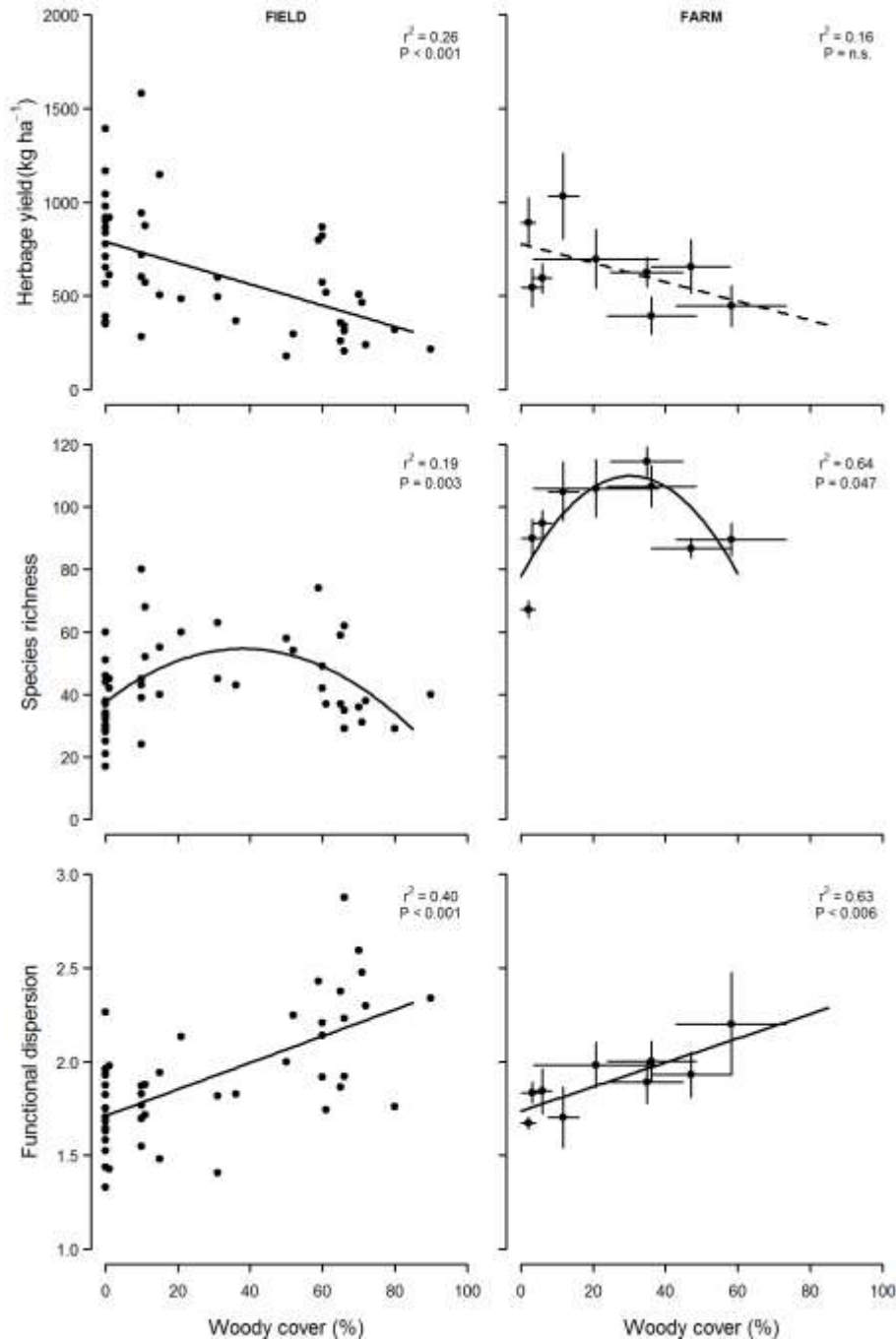


Figure 2 Relationship between herbage yield (kg ha⁻¹), species richness and functional dispersion against woody cover (% of shrubs and trees) at the field (left column) and farm (right column) scale. Error bars at the farm scale depict standard errors. Dashed lines indicate non-significant relationships between variables. Note that species richness at the farm scale depicts rarefied values per farm.

Table 4. Species richness (95% confidence interval) and β -diversity (centroids \pm S.E.) values per farm. Species richness represent rarefied sample-based values to the smaller number of fields sampled per farm. Letters depict significant differences among farms based on non-overlapping confidence interval values. β -diversity represents within-farm heterogeneity of species composition (Taxonomic) or community-level weighted means of trait values (Functional). Letters depict significant differences among farms at $P < 0.05$

Farm	Species Richness	Taxonomic β -diversity	Functional β -diversity
Farm 1	115 (104 - 125) c	0.47 \pm 0.02 cd	18.58 \pm 1.71 c
Farm 2	94 (83 - 106) bc	0.47 \pm 0.04 cd	12.88 \pm 2.62 abc
Farm 3	90 (80 - 100) b	0.43 \pm 0.03 bcd	17.60 \pm 3.07 bc
Farm 4	87 (78 - 96) b	0.43 \pm 0.02 c	14.05 \pm 2.04 bc
Farm 5	117 (105 - 129) c	0.47 \pm 0.06 bcd	21.65 \pm 8.01 abc
Farm 6	67 (57 - 77) a	0.35 \pm 0.04 ab	11.49 \pm 2.22 ab
Farm 7	107 (96 - 117) bc	0.50 \pm 0.04 d	18.94 \pm 2.38 c
Farm 8	90 (81 -98) bc	0.44 \pm 0.05 bcd	18.03 \pm 3.47 bc
Farm 9	105 (97 -113) c	0.32 \pm 0.02 a	6.40 \pm 1.48 a

diversity, despite including a large number of species (105; 95% CI: 97–113.). Herbage production exhibited significant negative relationships (Fig. 3) with taxonomic ($r = -0.86$, $F_{1,7} = 24.2$ and $P = 0.018$) and functional β -diversity ($r = -0.70$, $F_{1,7} = 8.8$ and $P = 0.017$). Woody cover showed a weak positive relationship with both β -diversity indices ($P = 0.283$ and 0.352 , for taxonomic and functional β -diversity, respectively).

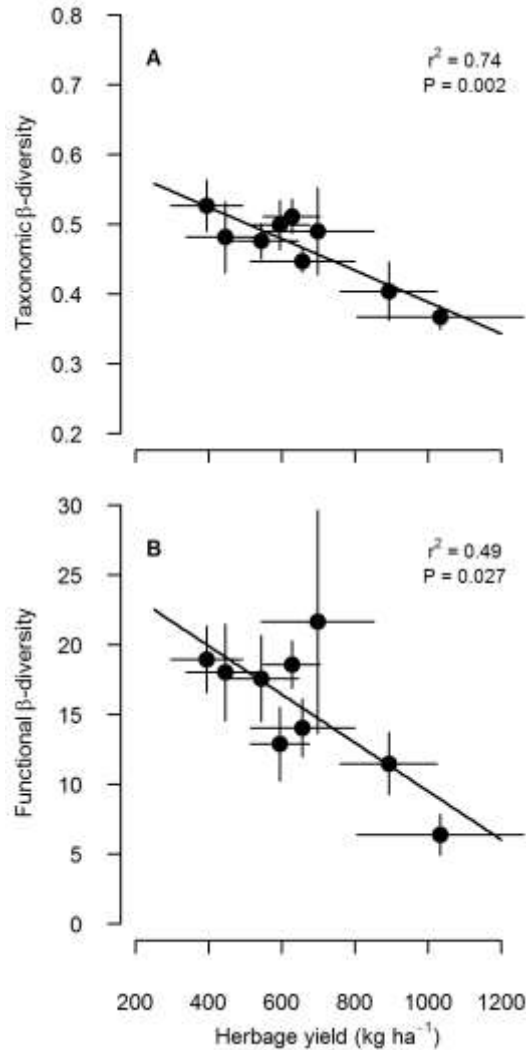


Figure 3 Relationship between herbage yield (kg ha⁻¹) and (a) β -diversity, for species composition, and (b) functional β -diversity, based on community weighted mean trait values, at the farm scale. Error bars depict standard errors.

4. Discussion

Our results conformed to expectation that herbaceous community diversity and productivity in agroecosystems vary along a woody vegetation gradient. Trees and shrubs showed similar negative effects on herbage productivity, which declined linearly as the cover of woody vegetation increased at the field scale. These results are consistent with previous findings

reporting semi-natural features as elements that are detrimental to herbage yield, not only through land-use opportunity costs (Green *et al.* 2005), but also through direct yield reductions (Rolo, López-Díaz & Moreno 2012). Nevertheless, we found that woody vegetation was positively related to functional diversity and that the assembly processes determining the functional structure of herbaceous communities were dependent upon the habitat type. These results indicate that the management of woody vegetation can have the potential to enhance biodiversity levels, but it is important to optimize the cover of woody vegetation and to consider the scale of management, in order to minimize yield losses.

4.1 Patterns of taxonomic and functional diversity along a woody vegetation gradient

Our results showed that at high woody vegetation cover, taxonomic and functional diversity were decoupled. Patterns of taxonomic and functional diversity have been shown to follow different trajectories in response to land-use change (Mayfield *et al.* 2010). Nevertheless, this decoupled pattern indicates that any reduction in woody cover would be accompanied by a reduction in functional diversity, but also by an increase in species richness and herbage yield. A reduction in functional diversity might compromise provisioning of ecosystem services other than herbage yield (e.g. pollination or nutrient cycling, Cadotte 2011). However, the unimodal relationship between woody vegetation cover and species richness suggests that the conservation potential, in terms of number of species, would be maximal at intermediate values of the range (~30% woody cover). Similar patterns have been found for birds (Sirami *et al.* 2009) and mammals (Blaum *et al.* 2007), suggesting that our results are in accordance with the intermediate landscape-complexity hypothesis (Jonsson *et al.* 2015). This hypothesis suggests a maximum conservation potential would be observed in landscapes with intermediate complexity rather than in clearer

(i.e. extremely simplified landscapes with very low amounts of semi-natural habitat) or in more complex (i.e. extremely complicated landscapes with very high amounts of semi-natural habitat) landscapes (Tschardt *et al.* 2012). In this way, maintaining low to intermediate values of woody vegetation could be a feasible tool for promoting heterogeneity at the field scale and enhancing both taxonomic and functional diversity levels of Mediterranean grasslands.

4.2 Community assembly processes and herbage yield

The importance of a trait-based approach to manage variables of pastoral importance, such as forage yield and quality in grasslands, is being increasingly advocated (Jouven, Carrère & Baumont 2006; Pontes *et al.* 2007; Ansquer *et al.* 2009). Our results support this view and suggest that a further understanding of the processes that mediate functional trait responses to environmental conditions (i.e. woody vegetation presence) can provide insight into the linkages between biodiversity and ecosystem processes. We observed that herbaceous communities growing in open habitats, where the highest yields were achieved, had convergent trait values, suggesting that environmental filtering is the main process structuring these communities. Indeed, our results showed that these herbaceous communities contain few species with high values of height, and low LDMC and seed lengths. Thus, management strategies that aim to maximize herbage yield in these systems could be optimized by focusing on a particular set of species with similar trait values that were close to the aforementioned. This strategy contrasts with the commonly found positive effect of biodiversity on biomass production (Duffy 2009). However, most biodiversity–ecosystem function studies are based on controlled experiments, with little support for more “natural” conditions (Duffy 2009), and great difficulties in terms of applicability to specific management practices (Doherty, Callaway & Zedler 2011). In contrast,

strategies that are based upon low levels of biodiversity to promote one function may not guarantee the temporal stability in the provisioning of this function (Tooker & Frank 2012). The need for high levels of biodiversity has been increasingly recognized to maintain multiple functions at multiple times and places (Isbell *et al.* 2011). Promoting the presence of woody vegetation in Mediterranean grasslands may reconcile the two approaches (i.e. low–high biodiversity). We observed that under both woody vegetation types, herbaceous communities showed mainly divergent trait values, suggesting that increased levels of biodiversity are promoted by niche complementarity, which may support herbage productivity in the long-term (Cardinale *et al.* 2007). Moreover, woody vegetation can lead to the establishment of subordinate species, which might provide for additional functions under current or future conditions (Isbell *et al.* 2011).

4.3 Between-farm differences in productivity are related to different levels of taxonomic and functional diversity

Contrary to expectation, we found that there was a lack of association between woody cover and β -diversity values. This result was not consistent with the effect of woody vegetation at the field scale, suggesting that other factors than woody cover contribute to variation in biodiversity among farms. When considering the whole farm, the effect of woody vegetation on diversity levels could have been confounded with other emerging properties, such as on-farm management practices, i.e. grazing intensity (Gabriel *et al.* 2010) or the spatial configuration of habitats (Hendrickx *et al.* 2007).

We found a negative relationship between herbage productivity and β -diversity at the farm scale, both in terms of taxonomic and functional β -diversity. This relationship suggests that highly

productive farms, where woody cover was minimal, had herbaceous communities that were dominated by a few abundant species with a similar set of traits, as would be expected from environmental filtering. In contrast, higher values of β -diversity on less productive farms suggest the presence of more complex and heterogeneous herbaceous communities, as would be expected from niche complementarity. These results suggest that processes driving productivity gradients (i.e. the effect of woody vegetation on local communities) can generate spatial variation of taxonomic and functional diversity among communities.

Together with the results observed at the field scale, it is apparent that the management of woody cover as a means of enhancing biodiversity conservation in Mediterranean grasslands must consider different scales of management. On one hand, it has been recommended that allowing for the presence of many small patches of woody vegetation can promote the conservation of biodiversity, while minimizing yield losses (Rey Benayas, Bullock & Newton 2008). Our results expand upon this strategy, and suggest that spatial variation in biodiversity could be promoted within a farm, if different fields were managed to achieve a productivity gradient (i.e. through changing woody cover). On the other hand, when considering only a single field for management, intermediate levels of woody vegetation can promote a positive effect on biodiversity, while minimizing yield losses. Further experimentation may help to disentangle the role of woody vegetation and clarify whether the maintenance of low to intermediate levels of woody vegetation can increase both taxonomic and functional diversity of herbaceous communities in Mediterranean grasslands.

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Data accessibility

Data available from the Dryad Digital Repository: doi: 10.5061/dryad.hh76j (Rolo *et al.* 2016).

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