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Tree - open grassland mosaics drive the herbaceous structure and diversity in Mediterranean wood pastures

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Abstract

Mediterranean wood pastures are seminatural savannahlike agroecosystems that result from traditional silvopastoral practices, which shaped these systems into a mosaic of trees and open grassland. However, traditional silvo-pastoral uses are declining with the implications that this may have on the herbaceous layer, which is a very diverse and valuable resource. Here, we aim at assessing the influence of the tree – open grassland mosaic on the structure, diversity, and composition of the herbaceous layer. Specifically, assessing the canopy effect (a) under representative Iberian canopy types, considering traditional *Quercus* species stands and *Pinus pinea* plantations at different locations; and (b) along seasonality. For that purpose, we carried out vegetation surveys in Mediterranean wood pastures of the south SouthWest of the Iberian Peninsula. Our results show that the different components of the herbaceous layer performed differential responses to the presence/absence of tree canopies, as for instance shows the dominance of grasses under the canopy, while legumes and forbs were favoured in the open grassland. Also, the study plots differed in their composition of species and species richness, with a certain a reduction in the species richness in the plot dominated by *P. pinea* compared to plots dominated by *Quercus* species. The canopy effect was more pronounced at the more environmentally constrained location. Such canopy effects were generally more pronounced in spring than in autumn. In conclusion, it is highly advisable preserve the tree – open grassland mosaic and traditional *Quercus* species stands to maximize and preserve plant specific and functional diversity and ecosystem functionality.

1. Introduction

Mediterranean wood pastures, also called dehesas in Spain and montados in Portugal, are semi-natural savannah-like agroecosystems that result from silvo-pastoral practices, in which an herbaceous and an arboreal layer — mostly *Quercus* species — coexist (Ibañez et al. 2021). They are one of the largest agroforestry systems in Europe (Eichhorn et al. 2006), and are particularly abundant in the South-West of the Iberian Peninsula (Olea et al. 2005).

Mediterranean wood pastures have traditionally provided pasture and acorns for livestock, timber, and cork, and those traditional silvo-pastoral uses shaped these systems into a mosaic of trees and open grassland creating diverse ecological niches (Sankaran et al. 2004). In particular, wood pastures are extraordinarily rich in plant diversity (Marañon 1985; Moreno et al. 2016), and have been typified as habitat of community interest by the EU Habitats directive (6310 Dehesas with evergreen *Quercus* spp) for their singularity and potential to preserve biodiversity.

However, those traditional silvo-pastoral uses are nowadays changing. Mediterranean wood pastures are suffering simultaneously processes of intensification and abandonment (Peco et al. 2000). Traditional grazing practices are replaced by intensive farming and plantations of fast-growing trees, mostly *Eucalyptus* and *Pinus* species (Costa Pérez et al. 2006; Costa et al. 2011); while less productive pastures are abandoned, which results in shrub encroachment and loss of diversity (Peco et al. 2000).

All these land use changes drive important modifications in the tree-open grassland mosaic. The tree-open grassland mosaic which is the predominant intrinsic structure of Mediterranean wood grasslands, and in turn directly influences on all the other ecosystem compartments, including the herbaceous vegetation at the intra-ecosystem scale. To this regard, it is known that once plant species have passed the filters from the regional to the ecosystem scales, they still need to establish inside the ecosystem, and this establishment is the result of assembly, competition, and facilitation process, in interaction with the ecosystem intrinsic dynamics and structure (Sebastià et al.; Rodríguez et al. 2018). In wood grasslands the tree-open grassland structure has already been described as a relevant intra-ecosystem driver of the herbaceous productivity (Moreno et al. 2007; Gea-Izquierdo et al. 2009; Hussain et al. 2009) and plant diversity (Peco et al. 2006; Marañón et al. 2009; Lopez-Carrasco et al. 2015; Rossetti et al. 2015; López-Sánchez et al. 2016a; López-Sánchez et al. 2016b), for instance. Yet, how that canopy effect influences over all the herbaceous layer compartments (above and belowground biomass, and litter) as well as whose specific and functional diversity and composition has been less explored. Even less explored is the canopy effect under representative Iberian canopy types, considering traditional *Quercus* species stands and *Pinus pinea* plantations, a common tree plantation replacing traditional canopies (Costa Pérez et al. 2006); and how those canopy effects evolve along seasonality.

For that, we raise the following questions (i) are the different components of the herbaceous layer structure, composition and diversity affected in the same way by the tree - open grassland mosaic? (ii) is the canopy effect similar between representative Iberian canopy types? and (iii) how does the canopy effect evolve along seasonality? To answer these questions, we considered insightfully all the herbaceous layer compartments, and addressed the canopy effect under *Quercus* species stands and *Pinus pinea* plantations and along seasonality.

2. Methodology

2.1 Study sites and sampling design

Study sites were the same as described in Ibañez et al. (2021), distributed in two locations in the South-West of the Iberian Peninsula (Fig. 1): Sierra Morena mountains (SM, 37° 39’ 50” N, 5° 56’ 20” W, 296 m a. s. l.), and Doñana Natural Park (DN, 37° 15’ 34” N, 6° 19’ 55” W, 30 m a. s. l.). Both locations have Mediterranean climate regime (Peel et al. 2007) with warm, dry summers, and mild winters. However, SM is slightly cooler and wetter than DN, with mean annual temperature in SM of 16.8 ºC and in DN of 18.1 ºC, and mean annual precipitation in SM of 648 mm and in DN of 543 mm.

SM soils have a texture between sandy clay loam and clay. DN soils are sandier than SM, with a sandy loam texture. Total soil N (0-30 cm depth) is quite low in both locations, but lower in DN (0.06 – 0.20% N) than in SM (0.85% N Ibañez et al., 2021). Grasslands in both locations are dominated by herbaceous annual species, including grasses (i. e. *Bromus hordeaceus*), non-legume forbs (i. e. *Erodium moschatum*), and legume forbs (i. e.

Trifolium subterraneum). Both locations are extensively grazed at similar stocking rates: SM grazed by cattle and Iberian pigs (0.36 LSU ha^{-1}), and DN grazed by cattle and goat (0.40 livestock units (LSU) ha^{-1}), both typical stocking rates in Mediterranean grazing systems.

Study plots were selected according to their tree composition, representing typical canopy types of Iberian wood pastures. One pure *Quercus ilex* stand, in the SM location (SM-ilex), and one pure *Quercus suber* stand in the DN location (DN-suber), both the most abundant stands in the Iberian Peninsula (Costa Pérez et al. 2006); one *Q. ilex* and *Q. suber* mixed stand (DN-mixed), the next most abundant; and a pure *P. pinea* stand (DN-pinea. Fig. 1.c), a common tree plantation replacing traditional *Quercus* canopies (Costa Pérez et al. 2006). Plot tree densities (trees ha^{-1}) are on the average for the region (Costa Pérez et al. 2006): 34 ± 1 in SM-ilex, 26 ± 1 in DN-mixed, 26 ± 4 in DN-suber, and 48 ± 6 in DN-pinea. In the DN-mixed plot, we discriminated between both *Quercus* species (*Q. suber* and *Q. ilex*) to establish sampling points. However, preliminary comparative analysis in the DN-mixed plot on microenvironmental conditions and vegetation characteristics under the canopy of both *Quercus* species indicated no relevant differences. DN-mixed plot results are then always presented, combining both tree species.

Field work was carried out in spring (05/04/2016 –10/04/2016) and autumn (13/12/2016-17/12/2016), coinciding with the most productive moments of the system, to capture vegetation seasonal variability and canopy effects that may be season dependent. Study treatments were, therefore, established according to plot (SM-ilex, DN-mixed, DN-suber, and DN-pinea), season (spring and autumn), and canopy (open grassland, OG, and under the canopy, UC). Sampling points of the UC treatment were always placed at 1 m distance from the selected tree trunk, and sampling points of the OG treatment were placed at a minimal distance of 3 m from the selected tree, clearly outside the canopy. Sampling points were systematically placed following the north orientation with respect to the tree trunks (Ibañez et al. 2021). For each treatment level, we selected 3–4 samples, totalling 73 sampling points.

2.2 Vegetation sampling and calculation of diversity indexes

At each sampling point, we hammered a metal collar that defined the sampling area (diameter = 25 cm), and we harvested the herbaceous vegetation at ground level rooted within each metal collar. Thereafter in the laboratory, we separated aboveground biomass (AGB) from litter (dead plant material detached from the herbaceous vegetation and tree leaves on soil surface). Also, we separated the AGB into plant species. Species were then attributed to the given plant functional type (PFT): grasses, non-legume forbs (hereafter “forbs”), and legume forbs (hereafter “legumes”). Both levels of analysis (species and PFT) provided complementary information (Zhou et al. 2017), providing the first information about the species distribution *per se*, while the latter provided a mechanistic link between vegetation and a given ecosystem function (Petchey and Gaston 2006).

On the other hand, we determined the belowground biomass (BGB) by extracting a soil core of 9 cm^2 surface and 0 – 10 cm depth at each sampling point. Soil cores were afterwards washed and filtered with a 0.2 mm pore size in the laboratory. All vegetation samples were oven dried at 60 ºC until constant weight. Dry weight of all vegetation samples was converted to grams of dry weight per square meter (g DW m^{-2}).

Finally, we considered diversity indexes, including species richness (SR) and species evenness. SR was defined as the number of species per sample. Species evenness (Equation 1) is defined as a measure of the distribution of the relative abundance of species, and lies between 0 for monospecific plots to 1 for a plot in which all species are equally represented (Kirwan et al., 2007):

$$Evenness = \frac{2S}{S-1}\sum_{i<j} P_i P_j \quad \textit{(Equation 1)}$$

Where S is the number of species in the community matrix, and P_iP_j the pairwise interactions between species, meaning the product of the relative abundance of the *ith* and *jth* species (Equation 1).

2.3 Data analysis: structure, composition, and diversity of the herbaceous layer

All data analyses were performed using R software (R Core Team 2020). We performed generalized linear models (GLMs) on our response variables — herbaceous structural components (AGB, litter and BGB), PFT composition (forbs, grasses, and legumes), and diversity indexes (SR and evenness) — as function of plot, season, and canopy, and the corresponding interactions. For that, we considered the nature of our data (absolute abundances, counts, bounded data, etc.), and we transformed the data to fit a normal distribution (when it was possible) or selected the best distribution to fit the data (Table 1).

Note that legumes tend to have a patchy distribution (Schwinning and Parsons 1996), which results in a sever negatively skewed data distribution that resembles a Pearson distribution, frequently taking a value of 0, in combination with comparatively lower values of presence than absence (Figure S1). However, note that we want to model legumes absolute abundance (not counts), and this makes their modelling a challenge, since the data do not easily fit into a given distribution. For that reason, we performed the modelling of legumes in two steps. First, we modelled the presence/absence of legumes using a binomial distribution; and then we modelled legumes absolute abundance according to a gamma distribution only when they appear.

Final models were selected by a stepwise procedure based on the Akaike information criterion (AIC) using the stepAIC function, MASS package (Venables and Ripley 2002). Also, we calculated the proportion of deviance explained by each GLM ($D_{squared}$, equivalent to R^2_{Adj} for GLMs) using the Dsquared function, modEvA package (Guisan and Zimmermann 2000). Finally, we calculated the proportion of variance explained by each explanatory variable using the dominanceAnalysis function of the dominanceanalysis package (Bustos Navarrete and Coutinho Soares 2020).

On the other hand, we described the influence of plot, season, and canopy on species composition by canonical correspondence analysis (CCA) to represent the community on a given number of dimensions (Sandau et al. 2014). We performed the CCA on species absolute abundance using the cca function of the vegan package (Oksanen et al. 2018). Significance of the CCA terms (plot, season, and canopy) and significance of the CCA axes were both tested using the anova.cca function, also of the vegan package. Afterwards, means and standard errors of the first three significant ($p < 0.001$) axes were calculated and plotted for each level of the terms included as predictors (plot, season, and canopy). Also, we selected the species with the highest CCA scores within each axis (CCA1-CCA3, top five negative and top five positive), and the four species closest to the axes (0, 0) for representation purposes, and to unravel specific similarities and dissimilarities in the species composition between treatments.

3. Results

3.1 General structure of the herbaceous layer

The structure of the herbaceous layer was dependent on the particular plot, season, and the presence/absence of the tree canopy (Fig. 2). The AGB was mainly driven by season and plot (Fig. 3), being lower in all DN plots compared to the SM-ilex plot (plot effects, Table 2); and lower in autumn compared to spring (season effect, Table 2). Also, there was a tendency to lower AGB under the canopy than in the open grassland in all DN plots (canopy effect, Table 2), but not in the SM-ilex plot (Fig. 2).

Litter was markedly higher under the canopy than in the open grassland in spring, but this difference between the canopy and the open grassland almost disappeared in autumn (season x canopy effect, Table 2 and Fig. 2), being this season x canopy interaction a strong driver of litter's variability (Fig. 3). BGB was quite variable among treatments, and it was only significant the interaction between plot and canopy with a slightly lower BGB in the DN-mixed plot under the canopy than in the open grassland (plot x canopy, Table 2).

3.2 Herbaceous plant functional types

PFT composition also changed among plots, season, and canopy (Fig. 4). Forb biomass was lower in all DN plots than in the SM-ilex plot (DN plots effects, Table 3). Forb biomass decreased in autumn compared to spring, specially in the DN-pinea plot (plot x season effect, Table 3), being this interaction a strong driver (Fig. 3). Forbs biomass also decreased under the canopy compared to the open grassland (canopy effect, Table 3). Grass biomass was also lower in all DN plots compared to the SM-ilex plot (significant DN plots effects, Table 3 and Fig. 4), being plot as a strong driver of grasses variability (Fig.3). Unlike forbs, grasses increased under the canopy compared to the open grassland, but such diffrence between the under the canopy and the open grassland was lower in autumn than in spring (season x canopy effect, Table 3), when the biomass of grasses equalized between both microenvironments (Fig. 4). Legumes presence/absence was stonlgy driven by the canopy (Fig. 3 and Table 3), with a lower presence of legumes under the canopy than in the open grassland (Fig. 4). Legumes absolute abundance was stronlgy driven by season and canopy (Figs. 3-4), which was much lower in autumn than in spring (season effect, Table 3), and lower under the canopy than in the open grassland (canopy effect, Table 3).

3.3 Herbaceous species diversity and composition

Species evenness (Fig. 5.a) was only dependent on season, being lower in autumn than in spring (season effect, Table 4). Species richness (SR) was driven by plot, season and canopy (Fig. 3). SR decreased in the DN-pinea plot compared to the other plots (plot DN-pinea effect, Table 4), specially in autumn (Fig. 5.b). SR was also lower in autumn than in spring (season effect, Table 4); and lower under the canopy than in the open grassland (canopy effect, Table 4).

CCA on species absolute abundance had a constrained inertia of 1.87 over a total of 10.50, representing a 17.8% of explained variance, with plot, season, canopy, and season x canopy as explanatory terms. The anova.cca by terms showed that all the terms included in the CCA were significant ($p < 0.001$), and the anova.cca by axes showed that the first four axes out of six were also significant (CCA1 – CCA3, $p < 0.001$, and CCA4, $p = 0.04$).

The first CCA axis (CCA1, 30% of total explained variance) captured mainly differences in species composition between spring and autumn (CCA1, Fig. 6). In spring, species as *Hordeum leporinum*, *Trifolium cherleri*, *Trifolium glomeratum*, and *Medicago doliata* (positive side of the CCA1, Fig. 7.a) were much more abundant than in autumn. On the contrary, species as *Myosotis ramosissima*, *Genista hirsuta*, *Hypochaeris glabra*, *Cerastium glomeratum*, and *Silene gallica* (negative side of the CCA1, Fig. 7.a) were only found in autumn. Species as *Vulpia membranacea*, *Carex divulsa*, *Ornithopus pinnatus*, *Lathyrus cicera*, and *Galium aparine* (close to the axis CCA1, Fig. 7.a) were not especially abundant, but could be found in both seasons.

The second axis (CCA2, 24% of total explained variance) explained mainly differences in species composition between plots: on one side SM-ilex and DN-suber, and on the other side DN-mixed and DN-pinea plots (Fig. 6.a). SM-ilex and DN-suber being especially abundant in *Lolium perenne* (negative side of the CCA2, Fig. 7.b), and DN-pinea being especially abundant in *Stachys arvensis* (positive side of the CCA2, Fig. 7.b).

Finally, the third axis (CCA3, 15% of total explained variance), captured differences in species composition between under the canopy and the open grassland dependent on season (CCA3, Fig. 6.b). In the open grassland legumes as *M. doliata* and *T. glomeratum* (Fig. 7.c) were highly abundant in spring (negative side of the CCA3 and positive side of the CCA1, Fig. 7.c); while in autumn there was presence of a group of forbs, including *Taraxacum officinale*, *Leontodon longirrostris*, and *Crepis capillaris* (negative side of the CCA3 and negative side of the CCA1, Fig. 7.c). Conversely, under the canopy and in spring *Carex divulsa* was specially abundant, and some other species as *Urtica urens*, *L. cicera*, *Brassica barrelieri, G. aparine*, were

also present, but in low proportion (positive side of the CCA3, Fig. 7.c). Under the canopy and in autumn, *Geranium molle* was specially abundant, together with many other species in lower proportion.

4. Discussion

4.1 The tree – open grassland mosaic as driver of the herbaceous layer composition

Tree canopies were important spatial drivers of the herbaceous layer at the intra-ecosystem scale, both in terms of structure (specially increasing the litter under the canopy, Fig.2), diversity and composition (Figs. 4-7). However, in line with our first question, the different herbaceous components were not affected in the same way by the tree - open grassland mosaic (Fig. 3), differences that were especially notable on the PFT (Fig. 4) and species distribution (Figs 6-7). The microenvironment created under the canopy favoured the dominance of some species, mainly grasses, while the open grassland favoured the presence of legume and non-legume forbs. Previous studies have also described dominance of grasses under the canopy (Olsvig-Whittaker et al. 1992; Gea-Izquierdo et al. 2009), while the presence of forbs and legumes is limited under the canopy (Gea-Izquierdo et al. 2009; Marañón et al. 2009; Lopez-Carrasco et al. 2015). Species of high light demand — as is the case of legumes, with enhanced photosynthesis (Ibañez et al. 2020) — are limited in their growth under the canopy, affected by light constraints, litter accumulation, and competition with species tolerant to these conditions (Marañón 1986; Marañón et al. 2009). Hence, the accumulated litter may influence in different ways the growth of the different life forms, negatively affecting forbs and legumes — dicots — while not having a negative impact on the growth of grasses — monocots — with dense erect leaves (Barrantes Díaz 1986; Roldán Ruiz 1993; Sebastià 2007).

Also, the higher litter input under the canopy (Fig. 2) increased soil N content (Ibañez 2019), and that could favour the growth of grasses, at the expense of forbs and legumes. In agreement, Song et al. (2011) found that grasses increased their biomass at high N availability at the expense of forbs (Song et al. 2011). Moreover, results reported by Ibañez (2019) from the same study plots, suggested that grasses could be more efficient than forbs in terms of N acquisition and use. Grasses usually have fibrous roots (Weaver 1958; Schenk and Jackson 2002; Pirhofer-Walzl et al. 2012), trait that may be facilitating N absorption from the most superficial soil layers and from symbiotically fixed N sources (Pirhofer-Walzl et al. 2012). Therefore, these differences in the N uptake could represent an important competitive advantage for grasses, displacing other species under the canopy at higher soil N availability. This fact also agrees with the lower species richness (SR), and the tendency to a lower evenness observed under the canopy in comparison to the open grassland (Fig. 5).

Overall, these indicates that some species, mainly legumes, are more vulnerable to changes in the tree coverage than others (Fig. 3), and this could drive changes in the plant specific and functional composition at the intra-ecosystem scale. Changes that in turn may have several ecosystem functional implications, as for instance in terms of forage provision (i.e. Dewhurst et al. 2009; Sturludottir et al. 2014; Adams et al. 2016; Barneze et al. 2020), soil nitrogen (Debouk et al. 2020) and carbon (Rodríguez et al. 2021) cycling among others, which suggests that it is highly advisable preserve the tree – open grassland mosaic to preserve plant specific and functional diversity and maximize ecosystem's functionality.

Regarding the BGB compartment, we did not detect any clear pattern in the BGB distribution either driven by the presence/absence of tree canopies, season, or plot. This results are contrary to what expected, since some authors have described differences in the root density between the understory and the open grassland (Moreno et al. 2005); as well as a seasonal pattern in the fine root biomass (López et al. 2001). In our results, one possible reason for the lack of any observed pattern could be the depth at which we sampled (0-10 cm) that could have been not enough to detect differences. Yet, it is worth mentioning that our results show the magnitude of the BGB compartment, which is of a magnitude much bigger than the ABG (Figure 2) and deserves further attention in future studies.

4.2 The canopy effect under representative Iberian canopy types

In line with our second question, the canopy effect differed between canopy types when comparing *Quercus* species and *P. pinea* stands. This was observed on the certain reduction of SR in the plot dominated by *P. pinea* (DN-pinea) in comparison to plots dominated by *Quercus* species (specilally in autumn, Table 4 and Fig. 5.b), diffrence that was most likely caused by a lower presence of forbs (Table 3 and Fig 4). This reduction in the SR could be related with the tree litter characteristics, which may be driving soil properties, and this in turn SR. The litter of *P. pinea* is known for its mulching capacity, and allelopathic properties, both factors lowering the understory growth (Valera-Burgos et al. 2012). Also, the litter of *P. pinea* has been reported to be poorer in N content than litter of *Quercus* species (Fioretto et al. 2008; Sheffer et al. 2015), and this could lower soil N content and availability. Indeed, N availability for plants in the DN-pinea plot was reported the lowest among the study plots (Ibañez 2019). Factors that combined could decrease SR in the DN-pinea, driving this difference in the SR between *P. pinea* and *Quercus* species dominated plots.

Our study plots also performed diffrences in their composition of herbaceus species, in addition to the variability associated to seasonality (Figs. 6-7). The mosaic of trees drove an heterogeneous distribution of the herbaceous species, with some species being dependent on the specific microclimatic conditions (Figs. 6-7). This combined with the PFT distribution mediated by the presence/absence of tree canopies (discussed in Section 4.1), interestingly, indicates that although SR decreased under the canopy (Fig. 5.b), the tree – open grassland mosaic allowed the growing of an increased variety of species, increasing plant specific and functional diversity at the ecosystem scale. Hence, it is worth mentioning that Mediterranean wood pastures are ecosystems of high conservation value, whose diversity and preservation is dependent on such tree - open grassland mosaic, which in turn is directly linked to the presence of grazer animals and traditional silvo-pastoral activities.

On the other hand, there are climatic differences between the two study locations (DN *vs.* SM), and this climatic-driven variability has also to be considered as a possible source of variability on the canopy effect when comparing the two locations. Thus, the canopy effect tent to differ between the two locations (DN *vs.* SM), as suggests the neutral canopy effect on the AGB in the SM-ilex plot in contrast with the AGB decrease observed under the canopy in all DN plots (Fig. 2). This suggests that the magnitude of the drivers behind the canopy effect on the AGB production might differ depending on local conditions, including environmental conditions and competition/facilitation professes.

Several studies have described that although under the canopy there is less light available (Hussain et al. 2009; Seddaiu et al. 2018) and litter mulching the soil (Marañón et al. 2009), the canopy can create a favourable environment, with increased soil moisture (Holmgren et al. 1997), higher nutrient availability (Gallardo et al. 2000; Gallardo 2003) and amelioration of extreme summer temperatures (Marañón et al. 2009), which may result in an enhanced productivity of the herbal layer (Moreno et al. 2007; Gea-Izquierdo et al. 2009).

However, this increase in the productivity under the canopy was not detected in our study plots, which even decreased in the DN plots, even though the environment under the canopy in our locations presented higher soil water content, lower soil temperature (Ibañez et al. 2021), and higher soil C and N content (Ibañez 2019) than in the open grassland. Accordingly, some authors have reported that competition for water resources between trees and the herbaceous layer could be limiting the productivity, especially in the most arid Mediterranean wood pastures, or when soil texture does not promote much water retention (Moreno 2008; Gea-Izquierdo et al. 2009). Plants could only profit from the increase in soil fertility mediated by the canopy without water stress, the canopy effect being dependent on water availability (Gea-Izquierdo et al. 2009; López-Sánchez et al. 2016a) and this might be the case in our locations (DN *vs.* SM). The DN location is drier than SM, with higher temperatures, lower precipitation, and sandier soils (Section 2.1); and competition for water resources could be here a limiting factor (combined with light availability and litter mulching the soil), especially during dry periods within the growing season, which are frequent under the irregular Mediterranean climate. Conversely, in the SM location, the reduced environmental constraints (slightly cooler and wetter than DN) may allow a certain compensation between the drivers that might be reducing the biomass production under the canopy (i. e. reduced light availability), and the drivers favouring productivity (i. e. increased soil fertility), which results on a neutral canopy effect on the AGB (Fig. 2).

Also, the presence of grazer animals may be driving the general structure of the herbaceous layer, and some of those differences in the canopy effect between locations (DN *vs.* SM). The stocking rate was very similar in both locations (Section 2.1), but the productivity in the DN location was lower than in SM (Fig. 2), and the livestock impact on the AGB might be higher in DN, wherein livestock visiting the under the canopy microenvironment, looking for shadow, acorns, and fresh herb, could be more frequent.

These differential canopy effect on the AGB production between locations (DN *vs.* SM), interestingly links with the results reported on greenhouse gas exchange (Ibañez et al. 2021), and C and N dynamics (Ibañez 2019) from the same study plots. The authors reported that CO_2 exchange (Ibañez et al. 2021), and N uptake rates by plants (Ibañez 2019) under the canopy did not differ so much from the open grassland in SM, in contrast to the strong differences found in DN. Overall suggesting that SM seemed to be less environmentally constrained than DN, where the canopy effect was more pronounced. Ultimately, this differential canopy effect between locations (DN *vs.* SM) becomes relevant in terms of management to estimate the optimum tree coverage, since it will be dependent not only on the primary ecosystem service (i. e. forage provision) but also on local conditions. Also, this result illustrates the possible mid-long-term evolution of the fresher Mediterranean wood pastures, which will be warmer and dryer under the future climate change scenario, and highlights the relevance of trees specially under restrictive environmental conditions.

4.3 The canopy effect along seasonality

In line with our third question, seasonality interacted with the tree – open grassland mosaic to drive the herbaceous layer structure and composition. First, this was shown by the big amount of litter that was present under the canopy in spring, but no longer present in autumn (season x canopy effect, Table 1). This result shows how the organic matter input evolves along seasonality, driven by tee canopies, and suggests a rapid incorporation of the litter into the soil along the year, in addition to the relevance of trees as sources of soil fertility in Mediterranean wood pastures (Howlett et al. 2011; Gómez-Rey et al. 2013; Pulido-Fernández et al. 2013; Andivia et al. 2015).

Second, the canopy also interacted with seasonality and drove the distribution of species, mainly of grasses and legumes, with a lower difference between under the canopy and the open grassland in autumn compared to spring (season x canopy effect, Table 2). Results that underscore the dynamisms of the herbaceous layer composition along seasonality, and the relevance of recording seasonal dynamics to capture canopy effects that are season dependent.

Conclusion

Our study shows how the different components of the herbaceous layer perform differential responses to the tree-open grassland mosaic, as for instance shows the dominancy of grasses under the canopy, while legumes and forbs were favoured in the open grassland. Also, the canopy effect differed between canopy types when comparing *Quercus* species and *P. pinea* stands, since *P. pinea* dominated plots presneted a certain reduction in their herbaceus species richcness compared to plots dominated by *Quercus* species. These results suggest that it is highly advisable preserve open grassland spaces and traditional *Quercus* species stands to maximize and preserve plant specific and functional diversity. Our results also point out that that the canopy efect might be dependent on local environmental conditions, in addition to the seasonal variabilty, as showed the reduction on the AGB under the canopy compared to the open grassland at the more environmentally constrained location of DN; while such canopy effect was neural at the cooler

and wetter location of SM. This suggests that the optimum tree coverage might be dependent, not only on the primary ecosystem service (i. e. forage provision), but also on local conditions. Facts that may be considered to manage and guarantee ecosystem services provision and conservation of Mediterranean wood pastures.

Declarations

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Competing interests

The authors declare that they have no competing interests.

Availability of data and material

The datasets generated during the current study are available from the corresponding author on reasonable request.

Author contributions

MI conceived the ideas, designed methodology, collected, and analysed the data, and wrote the manuscript. CC conceived the ideas, designed methodology, collected the data, and reviewed the manuscript. MJL designed methodology, executed project administration and funding acquisition, and reviewed the manuscript. M-TS conceived the ideas, designed methodology, executed project administration and funding acquisition, and reviewed the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Ethics approval

Not applicable.

Consent to participate

Not applicable.

Consent for publication

Not applicable.

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Tables

Table 1. Study variables, data characteristics, transformation applied to fit a normal distribution (if applicable) and distribution, p-value of the distribution test.

Study variable	Data characteristics, transformation, and distribution	p-value
Aboveground biomass (AGB)	Absolute abundance, square root transformation, normal distribution	Shapiro-Wilk normality test, p = 0.06237
Litter	Absolute abundance, ln+1 transformation, normal distribution	Shapiro-Wilk normality test, p = 0.1366
Below ground biomass (BGB)	Absolute abundance, square root transformation, normal distribution	Shapiro-Wilk normality test, p = 0.7975
Forbs	Absolute abundance, exponential distribution	Kolmogorov-Smirnov test p = 0.2163
Grasses	Absolute abundance, log10 transformation, normal distribution	Shapiro-Wilk normality test, p = 0.1084
Legumes	Presence / absence, binomial distribution	Binomial test p > 0.05
	Absolute abundance, gamma distribution	Gamma test, p = 0.8471
Evenness	Bounded between 0 to 1, Weibull distribution	Weibull p = 0.012, This is the distribution with lowest AIC
Species richness (SR)	Counts, normal distribution	Shapiro-Wilk normality test, p = 0.05623, but Shapiro-Wilk normality test on the model residuals p-value = 0.1514

Table 2. Modelling of the herbaceous layer structure in dry weight (DW), including aboveground (AGB) and litter biomass, as function of plot, season, and canopy. Season with spring as reference level, plot with SM-ilex as reference level, and canopy with open grassland (OG) as reference level. Parameter estimates (Par.), standard error (SE), t and p-value.

	AGB				Litter				BGB			
	Par.	SE	t	p-value	Par.	SE	t	p-value	Par.	SE	t	p-value
(Intercept)	18.8	0.6	30.79	<0.001	2.8	0.2	11.75	<0.001	18	2	7.73	<0.001
Plot DN-mixed	−4.7	0.6	−7.39	<0.001					5	3	1.67	0.10
Plot DN-suber	−4.5	0.7	−6.02	<0.001					3	3	0.81	0.4
Plot DN-pinea	−5.0	0.7	−6.68	<0.001					−2	3	−0.72	0.5
Season	−5.9	0.5	−12.47	<0.001	0.4	0.4	1.08	0.3				
Canopy	−1.1	0.5	−2.33	<0.001	2.4	0.3	6.82	<0.001	3	3	0.92	0.4
Season x canopy					−2.0	0.5	−3.85	<0.001				
Plot DN-mixed x canopy									−11	4	−2.71	0.008
Plot DN-suber x canopy									−3	5	−0.68	0.5
Plot DN-pinea x canopy									−5	5	−0.98	0.3
$D_{squared}$	0.76				0.42				0.22			
Degrees of freedom	69				71				67			

Table 3. Modelling of plant functional type (PFT) composition in dry weight (DW), including forbs, grasses, and legumes, as function of plot, season, and canopy. Plot with SM-ilex as reference level, season with spring as reference level, and canopy with open grassland (OG) as reference level. Parameter estimates (Par.), standard error (SE), t and p-value.

	Forbs absolute abundance				Grasses absolute abundance				Legumes presence absence				Legumes absolute abundance			
	Par.	SE	t	p−value	Par.	SE	t	p−value	Par.	SE	t	p−value	Par.	SE	t	p−value
(Intercept)	5.7	0.4	15.21	<0.001	1.6	0.1	14.54	<0.001	1.6	0.8	2.04	0.04	4.3	0.3	13.39	<0.001
Plot DN-mixed	−0.6	0.4	−1.49	0.1	−0.4	0.1	−3.96	<0.001	0.1	0.8	0.15	0.9	−0.6	0.3	−1.68	0.10
Plot DN-suber	−1.1	0.5	−2.14	0.03	−0.3	0.1	−2.18	0.03	0.8	1.0	0.79	0.4	0.2	0.4	0.43	0.7
Plot DN-pinea	−0.5	0.5	−1.03	0.3	−0.4	0.1	−3.06	0.003	−0.2	0.9	−0.20	0.8	−1.3	0.4	−3.26	0.002
Season	−1.4	0.5	−2.83	0.005	0.2	0.1	1.72	0.09	1.3	0.6	2.10	0.04	−1.8	0.3	−7.08	<0.001
Canopy	−0.4	0.2	−1.72	0.09	0.4	0.1	3.59	<0.001	−2.4	0.7	−3.57	<0.001	−1.2	0.3	−4.43	<0.001
Plot DN-mixed x season	−0.2	0.6	−0.31	0.8												
Plot DN-suber x season	0.6	0.7	0.84	0.4												
Plot DN-pinea x season	−1.3	0.7	−1.79	0.07												
Season x canopy					−0.3	0.2	−2.00	0.05								
$D_{squared}$	0.54				0.32				0.23				0.48			
Degrees of freedom	66				68				69				47			

Table 4. Modelling of species evenness and species richness (SR), as function of plot, season, and canopy. Season with spring as reference level, plot with SM-ilex as reference level, and canopy with open grassland (OG) as reference level. Parameter estimates (Par.), standard error (SE), t and p-value.

	Evenness				SR			
	Par.	SE	t	p-value	Par.	SE	t	p-value
(Intercept)	−0.25	0.03	−9.04	<0.001	10.6	0.6	17.12	<0.001
Plot DN-mixed					−1.3	0.6	−1.97	0.05
Plot DN-suber					−0.6	0.8	−0.79	0.4
Plot DN-pinea					−1.7	0.8	−2.29	0.02
Season	−0.08	0.04	−1.96	0.05	−1.6	0.5	−3.28	0.002
Canopy					−1.6	0.5	−3.26	0.002
$D_{squared}$	0.05				0.28			
Degrees of freedom	72				69			

Figures

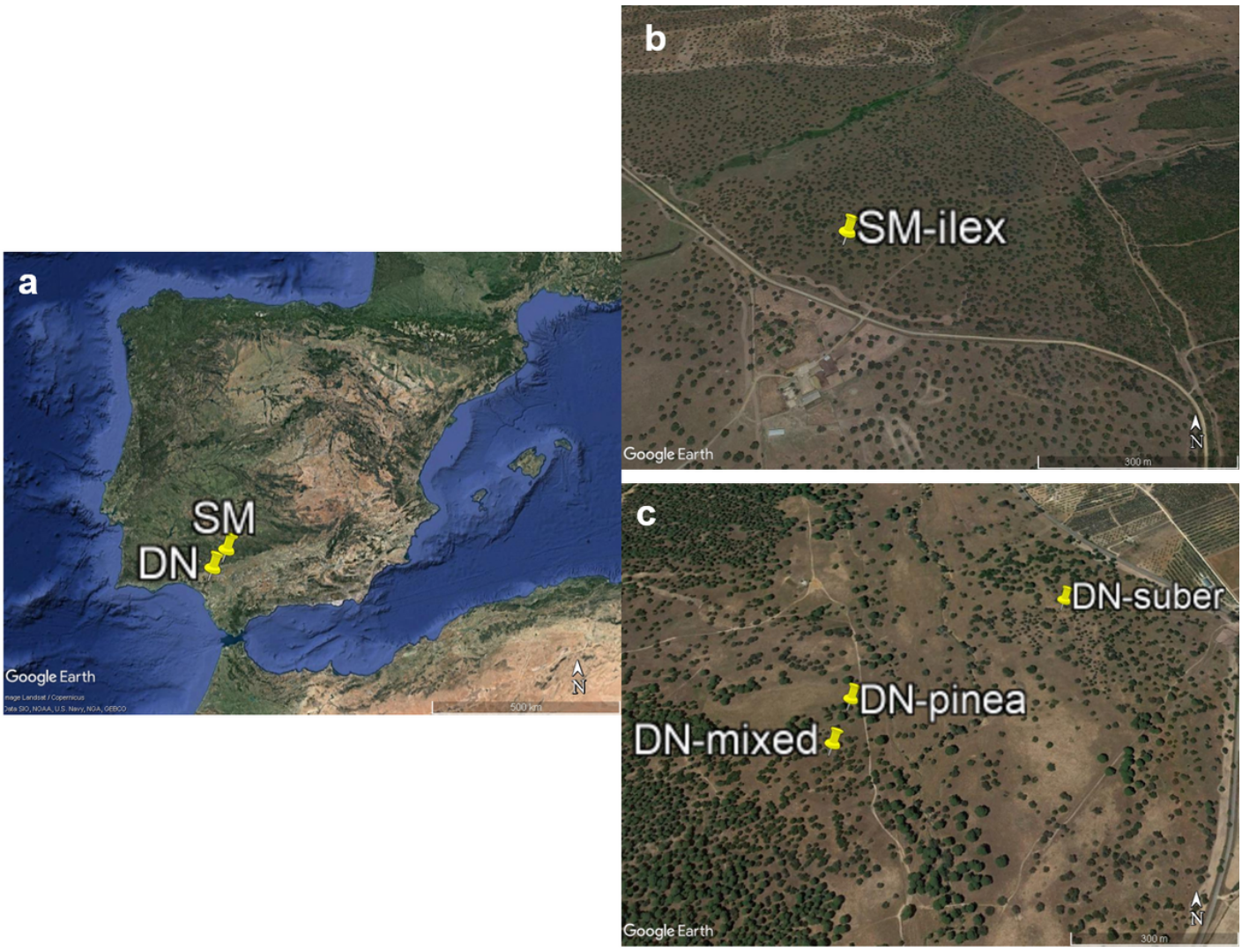


Figure 1

(a) Study sites geographical location in the Iberian Peninsula; and study plots aerial view: (b) SM-ilex; and (c) DN-mixed, DN-suber, and DN-pinea. Source: Google Earth, earth.google.com/web/

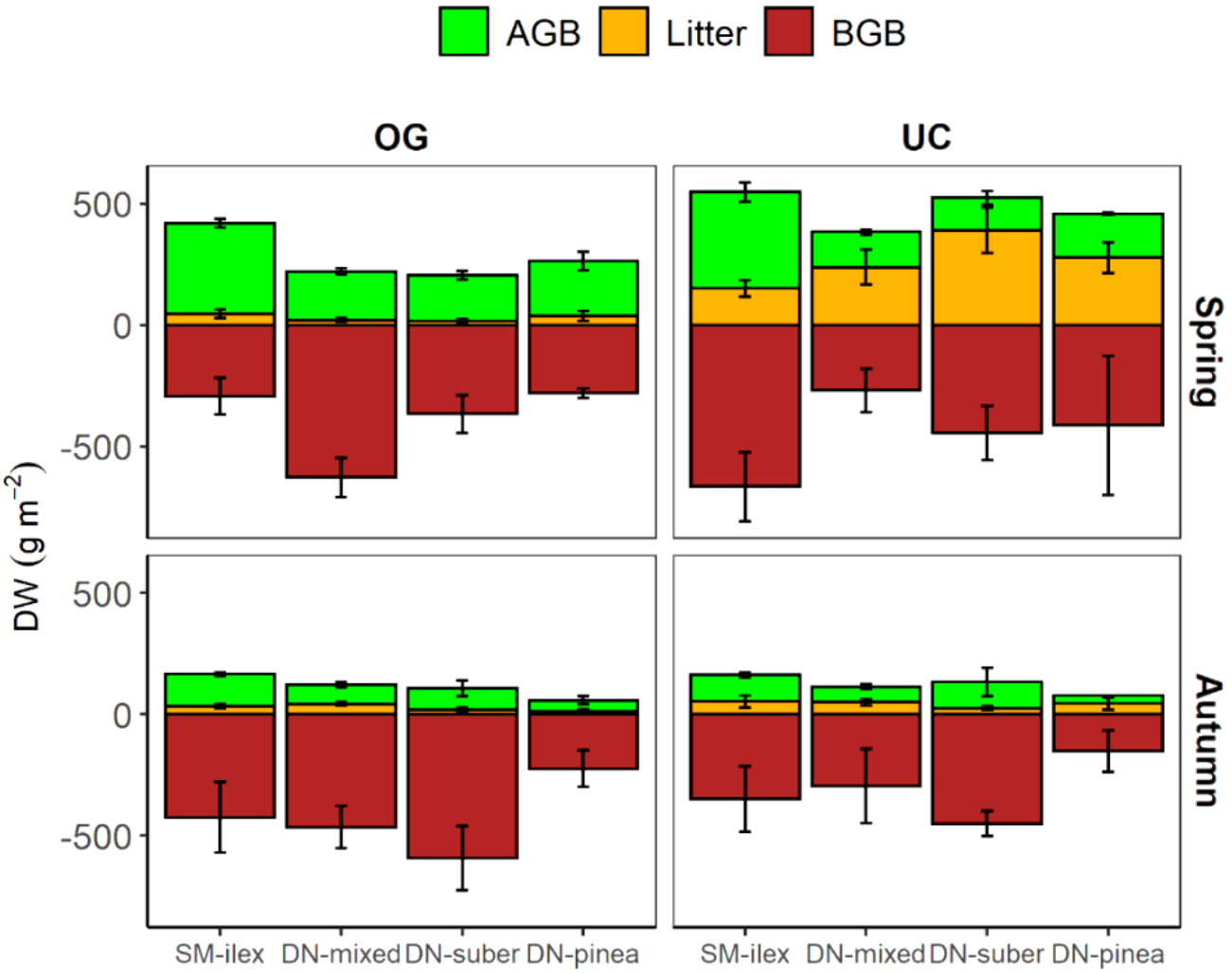


Figure 2

Dry weight (DW) mean ± 1 standard error of aboveground biomass (AGB), litter and belowground biomass (BGB) per plot, season, and canopy: open grassland (OG) and under the canopy (UC).

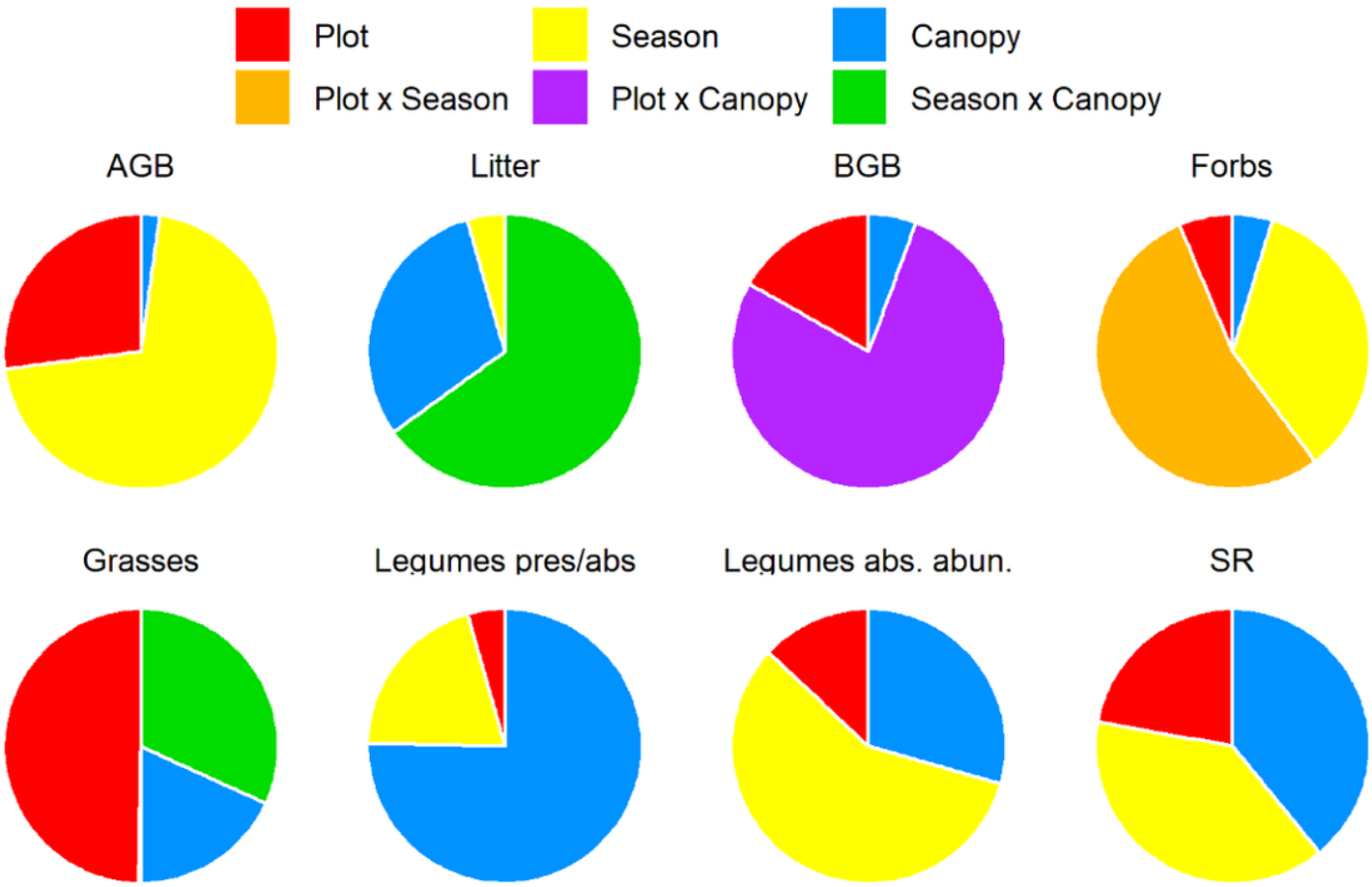


Figure 3

Proportion of variance explained by the explanatory terms included in the models of each response variable: Aboveground biomass (AGB), litter and belowground biomass (BGB, Table 2); forbs, grasses, and legumes presence/absence, and absolute abundance (Table 3); and species richness (SR, Table 4).

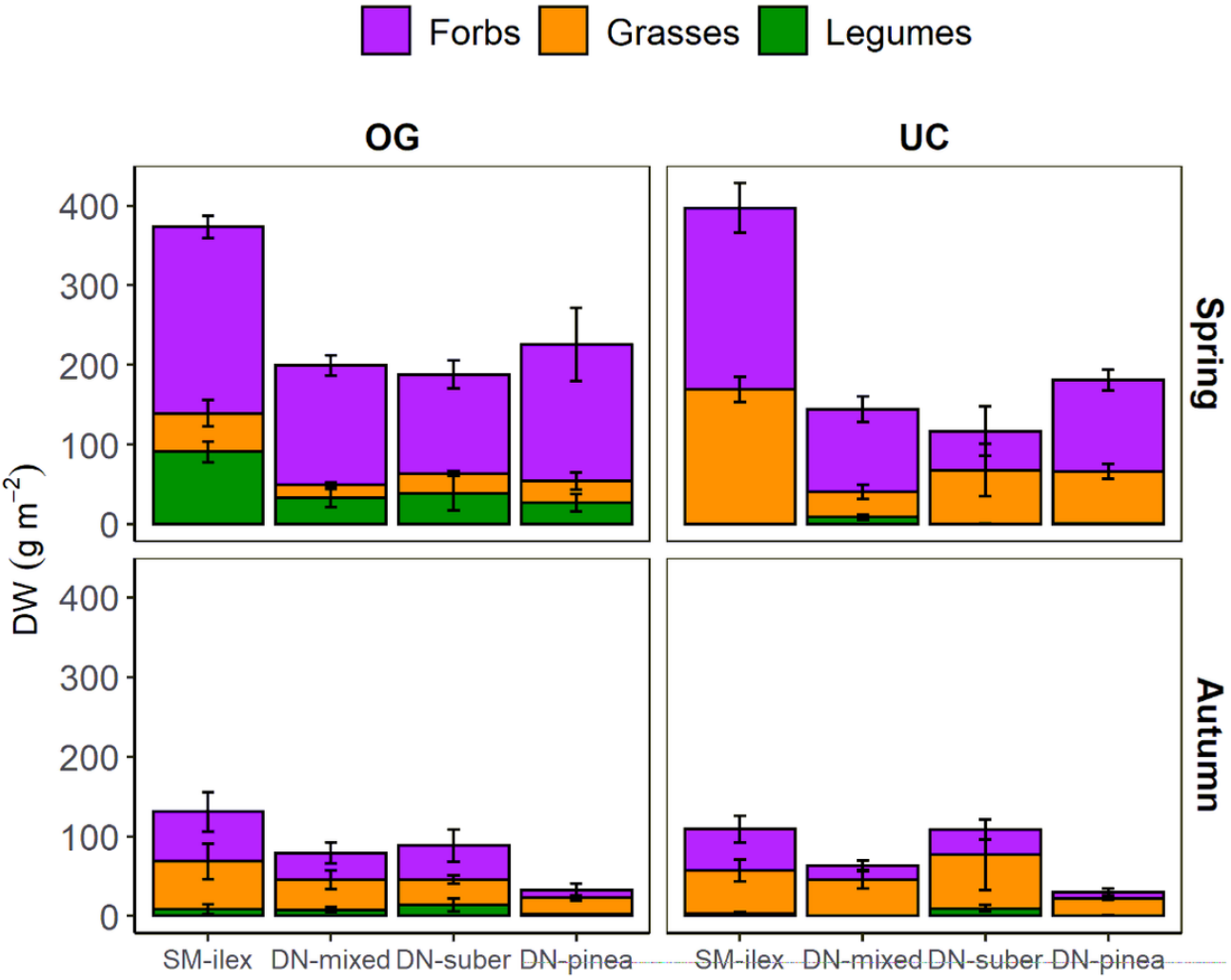


Figure 4

Dry weight (DW) mean ± 1 standard error of plant functional types (PFT: forbs, grasses, and legumes) per plot, season, and canopy: open grassland (OG) and under the canopy (UC).

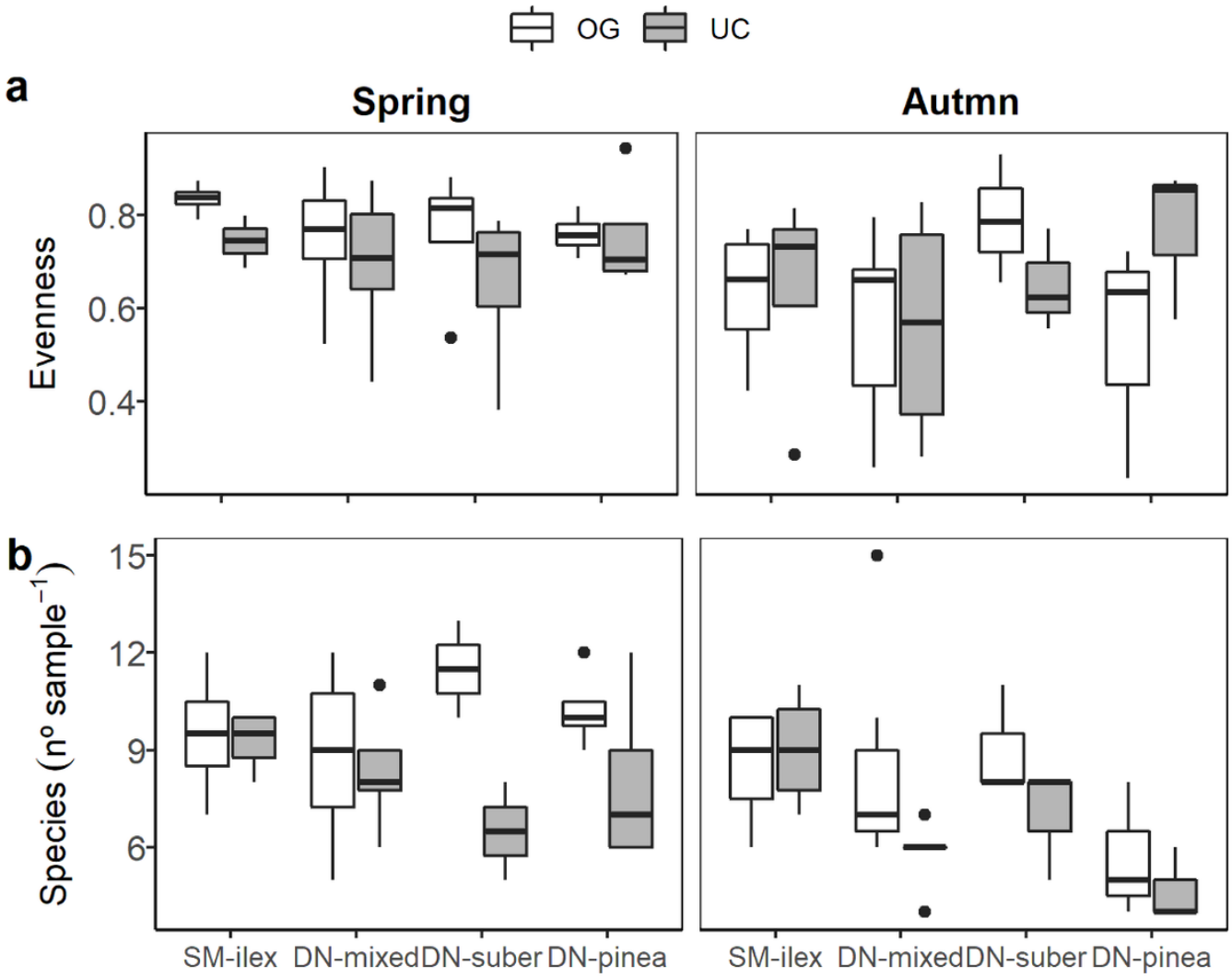


Figure 5

(a) Species evenness; and (b) species richness (SR) per plot, season, and canopy: open grassland (OG) and under the canopy (UC). Boxplot's midline indicates the median; upper and lower limits of the box indicate the third and first quartile; whiskers extend *up to* 1.5 times the interquartile range from the top/bottom of the respective box, and dots represent data beyond the whiskers.

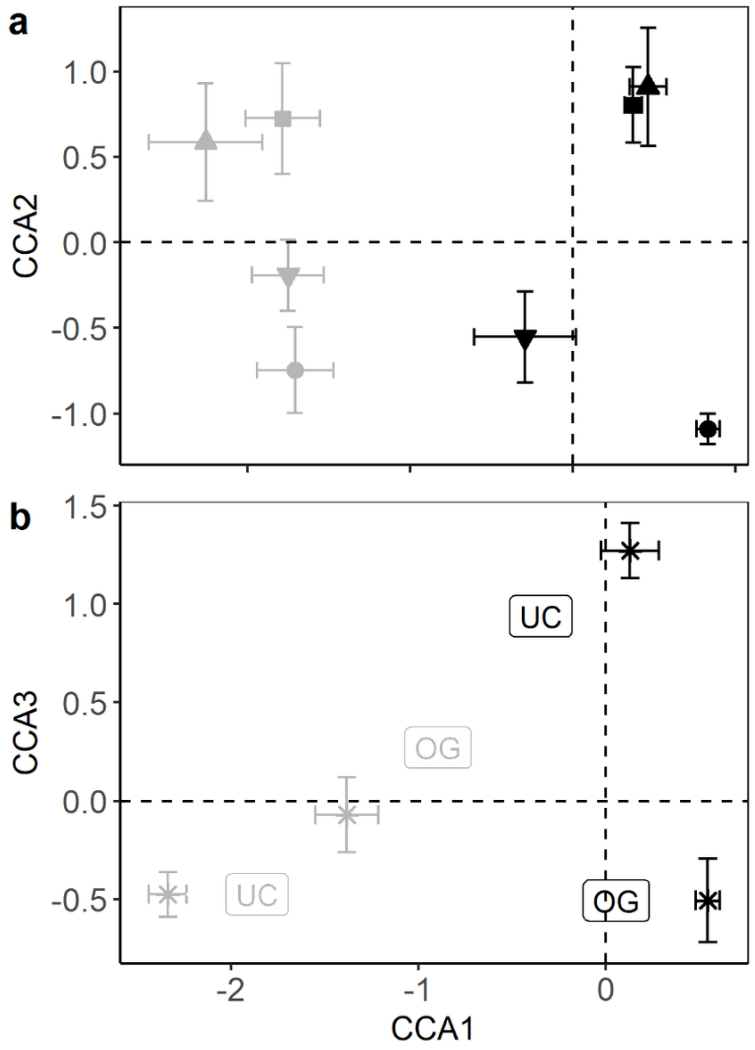


Figure 6

Canonical correspondence analysis (CCA): (a) axis 1 (CCA1) *vs.* axis 2 (CCA2) per season (black: spring, grey: autumn) and plot (●● SM-ilex, ■■ DN-mixed, ▼▼ DN-suber, ▲▲DN-pinea); and (b) CCA1 *vs.* axis 3 (CCA3) per season and canopy (OG: open grassland, UC: under the canopy). Sites mean scores ± 1 standard error.

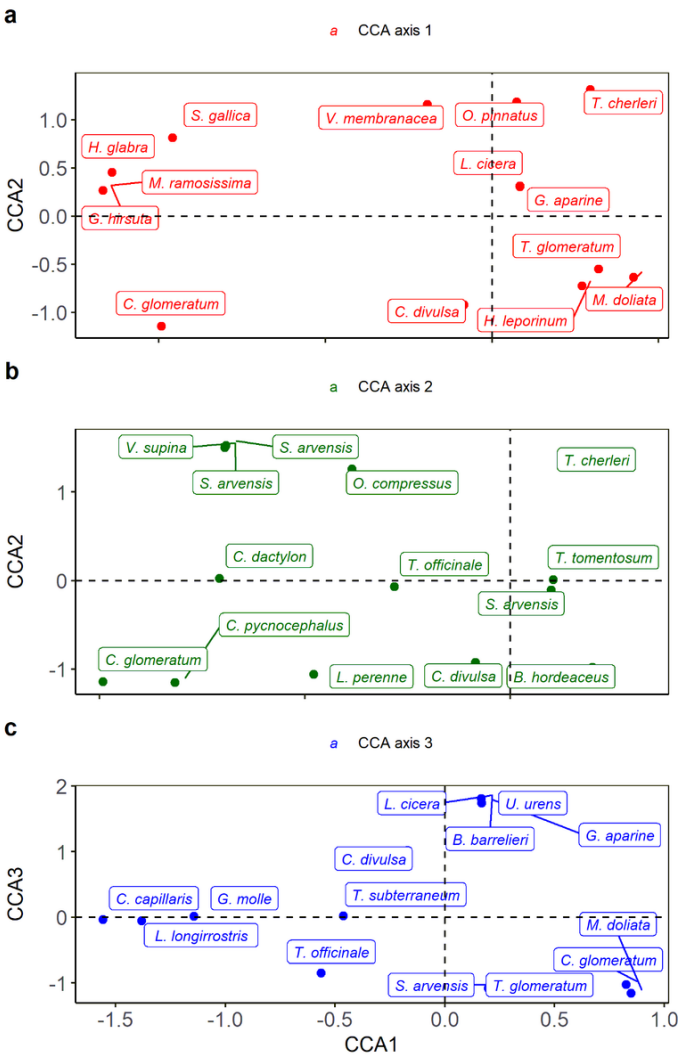


Figure 7

Species CCA scores. Species selected according to (a) axis 1 (CCA1); (b) axis 2 (CCA2); and (c) axis 3 (CCA3).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- histograms.tiff