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Local and landscape complexity support vegetation and spiders in Mediterranean olive agroforestry systems

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Abstract

Mediterranean olive landscapes face increasing threats from agricultural intensification, climate change, and biodiversity loss. These pressures raise urgent questions about whether such agroforestry systems can support ecological communities and maintain essential ecosystem functions necessary for productive, biodiverse, and sustainable land use. However, the specific features of olive groves that enhance functional biodiversity across spatial scales, trophic levels, and seasons remain unclear.

Therefore, we investigated how landscape composition (semi-natural habitat (SNH) cover, low vs. high and <30% vs. >30% within a 500 m buffer) and local grove features (terracing, mean tree diameter, canopy cover, and olive tree density) influence vegetation assemblages. We also examined how landscape composition and local vegetation variables (species richness, diversity, and cover) affect spider abundance in 12 organic olive groves in Tuscany, Italy, in both spring and autumn. We analysed seasonal data collected in spring and autumn between 2022 and 2024.

Our results show that both landscape composition (SNH cover) and local grove features influence vegetation diversity and spider assemblages. Specifically, we found that (i) plant species richness and vegetation diversity increased with higher SNH cover and local structural features (terracing and mean tree diameter), and (ii) spider abundance responded to landscape composition and local vegetation variables with distinct seasonal patterns. These findings highlight how the landscape composition, local structure, and seasonality influence biodiversity in Mediterranean olive groves. Preserving herbaceous cover and surrounding SNH cover in the landscape can strengthen ecosystem resilience and support key services, such as natural pest control, thereby promoting more sustainable agroecological management.

Keywords: *Agroecology; Arthropod diversity; Ecosystem functionality; Landscape composition; Organic farming; Semi-natural habitats; Sustainable land management; Vegetation structure.*

Zusammenfassung

Die mediterranen Olivenlandschaften sind zunehmend durch die Intensivierung der Landwirtschaft, den Klimawandel und den Verlust der biologischen Vielfalt bedroht. Diese Belastungen werfen dringende Fragen darüber auf, ob solche Agroforstsysteme ökologische Gemeinschaften unterstützen und die für eine produktive, biodiverse und nachhaltige Landnutzung notwendigen Ökosystemfunktionen aufrechterhalten können. Die spezifischen Merkmale von Olivenhainen, die die funktionale Biodiversität über räumliche Skalen, trophische Ebenen und Jahreszeiten hinweg verbessern, sind jedoch nach wie vor unklar.

Daher haben wir untersucht, wie die Landschaftszusammensetzung (Bedeckung durch naturnahen Lebensraum (SNH), niedrig vs. hoch und <30 % vs. >30 % innerhalb einer 500 m-Bufferzone) und lokale Merkmale der Haine (Terrassierung, mittlerer Baumdurchmesser, Kronendachbedeckung und Olivenbaumdichte) die Vegetationsgemeinschaften beeinflussen. Außerdem haben wir untersucht, wie sich die Landschaftszusammensetzung und lokale Vegetationsvariablen (Artenreichtum, Vielfalt und Bedeckung) auf die Spinnenpopulation in 12 biologischen Olivenhainen in der Toskana, Italien, im Frühjahr und Herbst auswirken. Wir haben saisonale Daten analysiert, die zwischen 2022 und 2024 im Frühjahr und Herbst erhoben wurden.

Unsere Ergebnisse zeigen, dass sowohl die Landschaftszusammensetzung (SNH-Bedeckung) als auch lokale Merkmale der Olivenhaine die Vegetationsvielfalt und die Spinnenpopulationen beeinflussen. Konkret haben wir festgestellt, dass (i) die Pflanzenartenvielfalt und die Vegetationsvielfalt mit einer höheren SNH-Bedeckung und lokalen Strukturmerkmalen (Terrassierung und mittlerer Baumdurchmesser) zunahmen und dass (ii) die Spinnenpopulationen auf die Landschaftszusammensetzung und lokale Vegetationsvariablen mit ausgeprägten saisonalen Mustern reagierten. Diese Ergebnisse verdeutlichen, wie die Landschaftszusammensetzung, die lokale Struktur und die Saisonabhängigkeit die Biodiversität in mediterranen Olivenhainen beeinflussen. Die Erhaltung der Krautbedeckung und der umgebenden SNH-Bedeckung in der Landschaft kann die Widerstandsfähigkeit des Ökosystems stärken und wichtige Funktionen wie die natürliche Schädlingsbekämpfung unterstützen, wodurch eine nachhaltigere agroökologische Bewirtschaftung gefördert wird.

Keywords: *Agroökologie; Arthropodenvielfalt; Ökosystemfunktionalität; Landschaftszusammensetzung; Ökologischer Landbau; Halbnatürliche Lebensräume; Nachhaltiges Landmanagement; Vegetationsstruktur.*

1. Introduction

Agricultural landscapes cover a third of the Earth's surface, and their expansion is one of the main drivers of global biodiversity loss (Newbold et al., 2020). Integrating agricultural systems into biodiversity conservation strategies is therefore particularly urgent in biodiverse regions with a long history of cultivation, such as the Mediterranean basin. In Italy, traditional farming systems, such as olive agroforestry systems, can reconcile agricultural productivity with the conservation of local biodiversity and cultural heritage (Raz et al., 2024). With over a million hectares of olive groves, conservation efforts in olive-cultivated landscapes can help protect native and endemic species and the ecosystem services that support productive, resilient, and sustainable food systems (Fekete et al., 2023).

Herbaceous vegetation and spiders are two key biological groups that support ecosystem services in olive groves (Rey et al., 2019; Picchi, 2020). Vegetation contributes to water retention, nutrient cycling, and soil stability (Case et al., 2020; Terzi et al., 2021). Moreover, vegetation is the basis of trophic networks, providing food, habitats, and favourable microclimatic conditions for higher trophic levels, particularly arthropods (Brunori et al., 2019; Schuldt et al., 2019). Amongst these, spiders are generalist predators that contribute to natural pest control; they are the most abundant predator group within olive tree canopies (Picchi et al., 2016; Wan et al., 2019). Understanding the ecological and structural features that promote vegetation and support spider-mediated services in olive groves is key to improving the resilience of agroecosystems and reducing reliance on external inputs (Paredes et al., 2019; Cuff et al., 2022). This knowledge could also inform agroecological policies and support the design of multifunctional landscapes that balance food production with the conservation of biodiversity and ecosystem services.

Olive groves can support diverse vegetation and spider assemblages through a combination of low-intensity management practices, local structural features, and broader ecological processes across the surrounding landscape (Picchi, 2020; Jiménez et al., 2023). At the landscape scale, the composition of surrounding habitats, particularly the presence of natural and semi-natural habitat (SNH) cover, influences both vegetation and spider assemblages in olive groves (Rey et al., 2019; Picchi, 2020). SNH cover present in agricultural landscapes can increase habitat quality and connectivity, act as stepping-stones for dispersal, and expand the regional species pool, thereby enhancing vegetation diversity and facilitating colonisation by spiders (Roschewitz et al., 2005; Baessler & Klotz, 2006; Picchi et al., 2020; Estrada-Carmona et al., 2022; Ganem et al., 2023).

Within the olive grove, local features such as tree density, canopy cover, and terracing generate microhabitat variation that increases habitat heterogeneity, fostering species-rich vegetation assemblages (Solomou et al., 2013; Terzi et al., 2021; Jiménez et al., 2023). These vegetation assemblages, in turn, provide sites for foraging, hunting, shelter, and overwintering for spiders. Vegetation abundance, species richness, and structural complexity contribute to the successful establishment of spider assemblages (Stenchly et al., 2012; Schuldt et al., 2019; Estrada-Carmona et al., 2022).

Notably, these interactions vary over time. Seasonal dynamics shape the influence of landscape composition and local grove features on herbaceous vegetation and spider assemblages (Zografou et al., 2016; Jiménez et al., 2023). Seasonal variation in vegetation phenology and prey availability modifies spider distribution, habitat use, and community composition (Ganem et al., 2023). Consequently, understanding biodiversity patterns in olive agroforests requires considering the combined effects of local grove features, the composition of the surrounding landscape, and seasonal variation in resource availability and species activity. Yet, the joint effects of these factors on functional biodiversity in olive groves remain largely understudied (Álvarez et al., 2019; Castro et al., 2021; Ganem et al., 2023; Jiménez et al., 2023).

This gap limits our ability to support biodiversity and ecosystem services in Mediterranean olive agroforestry systems. To address this, we investigated twelve organic olive groves in Tuscany, central Italy, guided by two research questions: (i) Do landscape composition (SNH cover) and local grove features that drive local habitat heterogeneity (e.g., mean tree density, canopy cover, terracing, and mean tree diameter) affect vegetation diversity, species richness, and abundance? And (ii) how do landscape composition and local vegetation variables (e.g., vegetation diversity, species richness, abundance, and structural complexity) affect spider abundance across seasons (spring and autumn)? Based on previous work on Mediterranean agroecosystems, we hypothesised that landscapes with higher SNH cover and olive groves with structural features that enhance local habitat heterogeneity would support richer and more diverse vegetation assemblages (Rey et al., 2019; Jiménez et al., 2023; Scordia et al., 2023; Wersebeckmann et al., 2024). We also expected that diverse, abundant vegetation and greater SNH cover would increase spider abundance with distinct patterns in spring and autumn (Álvarez et al., 2019; Paredes et al., 2019; Tobisch et al., 2023; Ganem et al., 2023).

2. Materials and methods

This study was designed to assess the impact of the landscape composition and the local grove features on vegetation and spider assemblages in Mediterranean olive agroforestry systems. To identify the ecological factors underlying vegetation and spider diversity and abundance, field surveys were conducted across 12 organic olive groves in Tuscany. These surveys combined standardised vegetation and spider sampling with detailed recording of grove structural features, soil conditions, and the composition of the surrounding landscape. Statistical models were then applied to evaluate the effects of landscape-scale SNH cover and grove-scale features on biodiversity indicators.

2.1 Study area and study sites

The study was conducted in the foothills of the Monti Pisani massif, located in the central-northern part of Tuscany, Italy. Research sites were situated around the villages of Calci (43.7263° N, 10.5137° E), Agnano (43.7379° N, 10.4861° E), and Vicopisano (43.6832° N, 10.5756° E; Figure 1). The Monti Pisani massif, with its highest peak, Monte Serra, at 917 m.a.s.l., lies within the Mediterranean bioclimatic region and is characterised by a sub-Mediterranean climate (Bertacchi et al., 2004). During the coldest months, the temperature ranges from -3 °C to 18 °C; during the warmest months, the average temperature is 22°C (Bertacchi et al., 2004). In terms of vegetation, the region is characterised by a mosaic of sclerophyllous and deciduous forests, Mediterranean macchia, garrigue, olive groves, and SNH, largely composed of pine forests and abandoned olive groves (Bertacchi et al., 2004).

The 12 olive groves selected for the study have an average plot size of 1.262 ± 523 m². Six of the sites are surrounded by a high proportion of SNH (>30%) and six by a lower proportion (<30%) within a 500 m buffer around the olive groves (see Figure 1). The sites covered an elevational range of 14–218 m above sea level and shared similar climatic conditions and comparable organic management practices. The ground cover vegetation was mown twice a year: once in May, before summer, to reduce the risk of fire, and once in October, to facilitate the harvesting process. Six of the olive groves were terraced, and the remaining six were not terraced.

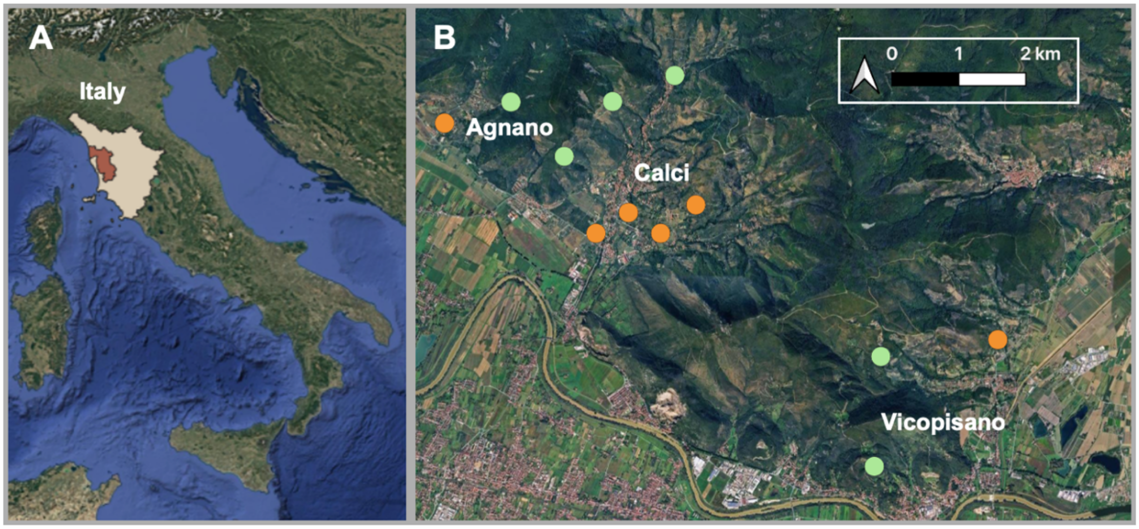

Figure 1. Map of study sites in Italy. (A) Region of Tuscany (light beige surface) and the province of Pisa (dark red surface), where the study was conducted. **(B)** Twelve Olive groves located in the Monti Pisani, in the communes of Calci, Vicopisano, and Agnano. Six of the selected olive groves have a low percentage of surrounding SNH (<30%; shown as orange points), and the remaining six have a high percentage of surrounding SNH (>30%; shown as green points).

2.1.1 Landscape composition

To assess the effect of the landscape composition on the local vegetation and spider assemblages, we studied olive groves with different amounts of surrounding SNH cover. SNH categories (high and low) were classified for each olive grove using GIS software (QGIS.org, 2024. QGIS Geographic Information System. QGIS Association. www.qgis.org). Around each site, a 500 m buffer was created using the *Buffer* tool in QGIS. Land cover data was obtained from an open-access vector layer provided by Regione Toscana (2007-2019). This buffer was intersected with the land cover layer using the *Intersection* tool in QGIS, yielding information on land cover types and their areas within the buffer. Land cover was categorised as water bodies, utilised agricultural area, wooded/semi-natural area, and artificial area. Olive grove locations were determined via GPS. The area of each land cover type within the 500 m buffer zone was calculated using the *Field Calculator* tool in QGIS. Olive groves were then classified as having high or low SNH based on the proportion of "Wooded semi-natural area" within the buffer. This classification serves as an indicator of surrounding land-use intensity, as wooded and semi-natural areas are typically subject to lower human disturbance.

2.1.2 Local grove features

We measured soil pH in each olive grove using four soil samples per site, diluted with distilled water and tested with pH strips (Jiménez et al., 2023). Soil moisture was evaluated in four trees per grove using an SM150 Soil Moisture Kit (Delta-T Devices, UK), with three measurements taken around each tree in a triangular pattern, resulting in 12 measurements per grove. The results are presented in Table S1 (Supplementary Material).

In addition to the soil data, we assessed the surface type (terraced vs. non-terraced), the mean tree diameter, the canopy cover, and the abundance of olive trees. The mean tree diameter was measured at three points: the stem base (where the first branches diverge), the largest first-order branch and the largest second-order branch, all measured in centimetres. Canopy cover was estimated by measuring the maximum horizontal extension from the trunk to the canopy edge in centimetres. Olive tree abundance was calculated using QGIS.

2.2 Seasonal variability

To account for seasonal variations in vegetation and spider assemblage dynamics, we conducted vegetation surveys in autumn 2023 and spring 2024, and spider surveys in spring 2022, 2023 and 2024, as well as autumn 2022 and 2023. During these years, spring temperatures ranged from 9 °C to 22 °C and autumn temperatures from 15 °C to 27 °C. The average annual temperature remained relatively stable during the sampling years, with slight variations: 16.3 °C in 2022, 16.1 °C in 2023 and 16.5 °C in 2024. Annual precipitation increased over the years: 618.6 mm in 2022, 1023.2 mm in 2023 and 1149.9 mm in 2024 (Meteostat, 2024).

2.3 Vegetation sampling

We sampled herbaceous vegetation using the quantitative methods outlined by Terzi et al. (2021). At each farm, we positioned six rectangular grids (4 m × 1 m) using GPS coordinates: two under the tree canopy (where root systems and management practices can affect vegetation composition), two between olive tree rows, and two at the edge of the farm. In total, we surveyed 72 grids (24 m² per farm). We identified all herbaceous species within the sampling grids at the family, genus, or species level. We conducted identification in the field if diagnostic features were present (e.g. flowers or vegetative parts); otherwise, we collected voucher specimens and identified them later in the herbarium, following Mayer (2015). Throughout the manuscript, the term “vegetation” refers specifically to this herbaceous layer. We visually estimated vegetation cover using the Braun-Blanquet scale (Terzi et al., 2021), which assigns each species to a cover class representing the percentage of the sampling grid it occupies. These classes were converted to proportional values (0-1) for analysis. Because cover was estimated separately for each species, and species can overlap horizontally within the same grid, the summed total cover per grid could exceed 1 (100%), reflecting vegetation layering rather than ground area.

2.3.1 *Woody vegetation, shrub cover, and vegetation structural complexity*

Woody vegetation was surveyed across the entire area of each olive grove using transects, recording species or genus, height, and abundance of all non-crop woody vegetation. Shrub cover was determined by shrub length, as shrub width and height were homogeneous across groves. Accordingly, we expressed shrub cover as linear cover, calculated for each olive grove (mean ± SD: 0.03 ± 0.02 m/m²) by dividing the total linear extent of shrubby vegetation (m) by the grove's total surface area (m²). This provides a consistent measure of shrub cover, reflecting the proportion of the grove occupied by shrubs.

In addition to shrub cover, we calculated the vegetation structural complexity for each olive grove. To estimate structural complexity, we obtained the average height of each plant species from the FloraVeg database (floraveg.eu 2022–2025). For each grove, we calculated the mean height across all recorded species (grove-level mean) and then measured the absolute difference between each species' height and the grove-level mean. Structural complexity was defined as the sum of these differences, with higher values indicating greater vertical heterogeneity in vegetation structure.

2.4 *Spider sampling*

We sampled spiders using pitfall traps (glass jars filled with propylene glycol, each covered with a PVC roof) to target ground-dwelling spiders. Four traps were installed per olive grove and left in place for one week per replicate; eight replicates were conducted across seasons and years. After collection, all adult spiders were sorted and identified by Andrea Piccinini (University of Bologna) to family, genus or species level.

2.5 *Statistical analysis*

All statistical analyses were conducted in R version 4.3.0 (R Core Team, 2024), with visualisations created using the *ggplot2* package (Wickham, 2016). We assessed the distribution and variance of the response variables using the Shapiro–Wilk test (*Shapiro.test* function from the *stats* package) and Levene's test (*leveneTest* function in the *car* package; Fox, 2019). Based on the landscape composition and local grove features described in Sections 2.1.1 and 2.1.2, we selected a set of ecologically relevant predictors for inclusion in our models (Table 1). To avoid redundancy and ensure interpretability, we evaluated collinearity amongst the predictors using correlation tests (*cor* function, *stats* package) and excluded highly correlated variables. We then performed Principal Component Analysis (PCA) separately for local and landscape predictors, as well as for the combined dataset, using the *prcomp* function (*stats* package). Finally, linear models were fitted to assess which principal component axes explained variation in vegetation diversity metrics and spider abundances across sites. We used Wilcoxon rank-sum tests to compare spider species richness and abundance across seasons in farms with low and high SNH cover (spider abundance showed equal variance but was not normally distributed).

Table 1. Ecologically relevant predictors of vegetation diversity, species richness, abundance, and spider abundance

Model predictors	Ecological relevance	Predicted effect
Landscape composition		
Semi-natural-habitat (SNH) low <30% vs high >30%	Structurally complex landscapes support more species than simple landscapes, implying that habitat patches in complex landscapes receive a higher diversity of potential colonists from the overall species pool than patches of the same size and quality in less complex landscapes (Tscharnke et al. 2012).	↑ Predictor for vegetation and spiders
Local grove features		
Olive tree density	Understory species diversity, including shrubs and herbs, is higher in sites with lower tree density. Vegetation exhibits greater species richness at lower tree densities (Scordia et al., 2023).	↓ Predictor for vegetation
Mean tree diameter	Mean tree diameter, a proxy for tree age, has been associated with greater understory vegetation diversity (Massaccesi et al., 2018). In olive groves, larger and older trees indicate longer establishment times, allowing more time for plant species to colonize.	↑ Predictor for vegetation
Canopy cover	Canopy cover stabilizes microclimatic conditions influencing vegetation composition and vegetation diversity. It fosters niches for diverse species and indirectly drives herbaceous vegetation production and richness (Cohen et al., 2015; Zangy et al., 2021).	↑ Predictor for vegetation
Olive grove surface (terraced/not terraced)	Traditional terraced cultivation, such as dry-stone walls, creates a structured landscape mosaic that supports diverse flora and fauna (Wersebeckmann et al., 2024).	↑ Predictor for vegetation
Vegetation structural complexity Shrub cover (linear cover in m)	Vegetation structural complexity influences spider communities, offering structures for web attachment and favourable microclimatic conditions (Batáry et al., 2011; Stenchly et al., 2012; Schuldt et al., 2019).	↑ Predictor for spider abundance
Vegetation diversity, species richness, and abundance	Vegetation diversity and abundance positively influence spider communities providing essential resources for spiders and attracting prey (Stenchly et al., 2012; Paredes et al., 2013; Paredes et al., 2019; Castro et al., 2021; Tobisch et al., 2023).	↑ Predictor for spider abundance

We then fitted separate Generalised Linear Models (GLMs) and Generalised Linear Mixed Models (GLMMs) with the g*lmer* function from the *lme4* package (Bates et al., 2015) to assess the effects of landscape composition and local grove features on vegetation and spider assemblages. For vegetation models, we used single-predictor models, as one of the local grove features (terracing) was highly correlated with our predictor for landscape composition (SNH cover). All models were compared, and the best-fitting model for each response variable was identified based on Akaike information-theoretic criteria (AIC). The model performance was evaluated through residual diagnostics, employing the *DHARMa* package (Hartig, 2024). Residuals were simulated using the *simulateResiduals* function, and diagnostic tests were conducted, including checks for uniformity (Kolmogorov–Smirnov), overdispersion and outliers. Sampling year and site were included as random effects in all models to account for temporal and spatial variation.

2.5.1 Vegetation models

We fitted separate single-model GLMs to assess the effects of landscape composition (SNH cover) and local olive features, including (i) terracing (terraced vs. non-terraced), (ii) mean tree diameter, (iii) canopy cover and (iv) olive tree abundance on plant species richness (total number of species recorded), vegetation abundance, and vegetation diversity (Hill–Shannon–Wiener diversity index, sensitive to species turnover; Chao et al., 2014; Roswell et al., 2021). Species richness was modelled with a Poisson distribution, while vegetation abundance and diversity were modelled using a Gamma distribution. Due to high collinearity between SNH cover and terracing, landscape and local predictors were modelled separately.

2.5.2 Spider models

We fitted separate GLMMs to assess the effects of landscape composition (SNH cover) together with individual vegetation variables on spider abundance, including (i) vegetation abundance, (ii) plant species richness, (iii) vegetation diversity, (iv) vegetation structural complexity and (v) shrub cover (see Table 1 for ecological relevance of predictors). Models were fitted separately for spring and autumn, reflecting seasonal patterns rather than direct seasonal comparisons. Poisson distributions were used for spider abundance, and random effects accounted for spatial and temporal variation.

To explore the predictive behaviour of the spider–vegetation models, we simulated 100 values for each vegetation variable (vegetation abundance, species richness, vegetation diversity, structural complexity, and shrub cover) across their documented ranges. Then, we paired each value with randomly drawn values for SNH cover, year, and site from the original dataset, generating realistic combinations of predictor variables. We used the simulated datasets as input for the GLMMs, which predicted spider abundances across the gradients using the *predict* function.

3. *Results*

Our results reveal strong biodiversity patterns shaped by both the landscape composition and the local features of the olive groves. Based on single-predictor models, plant species richness and vegetation diversity were higher in groves surrounded by higher SNH cover. Species richness increased on terraced farms, and vegetation abundance and diversity were positively associated with mean tree diameter. Spider abundance responded differently to landscape composition and vegetation variables in spring and autumn: in spring, abundance declined with higher vegetation structural complexity and plant species richness, particularly in high-SNH groves. Whereas in autumn, spider abundance increased with vegetation abundance and species richness, with SNH cover having no significant effect. These findings highlight the importance of both spatial context and seasonal patterns in structuring biodiversity within Mediterranean olive groves.

3.1 Vegetation

Across the 12 study sites, we documented 314 plant taxa, belonging to 205 genera and 61 vascular plant families (see Table S2, Supplementary Material). From these, 262 of the taxa were identified to the species level, and 52 of the taxa were identified to the genus level. The families with the highest number of recorded species were Asteraceae (46 taxa), Poaceae (32 taxa), and Fabaceae (32 taxa). Notably, Apiaceae, Caryophyllaceae, and Plantaginaceae were present in all olive groves. The remaining families comprise the remaining taxa, with each contributing 20 or fewer species.

The vegetation was dominated by annual species belonging to the families Asteraceae, Poaceae, and Fabaceae. In addition, several species typically associated with the SNH of the Monti Pisani were recorded across the study sites (see Figure S1, Supplementary Material). From deciduous and sclerophyll forests, we identified the species *Quercus ilex* L. (Fagaceae), *Fraxinus ornus* L. (Oleaceae), and *Robinia* sp. L. (Fabaceae). Common to the Mediterranean macchia, we documented the species *Cistus salviifolius* L. (Cistaceae), *Erica arborea* L. (Ericaceae), and *Arbutus unedo* L. (Ericaceae). From the garrigue, we recorded the species *Myrtus communis* L. (Myrtaceae), *Smilax aspera* L. (Smilacaceae), *Rhamnus alaternus* L. (Rhamnaceae), and *Spartium junceum* L. (Fabaceae).

3.1.1 Effects of landscape composition (SNH cover) on vegetation

Plant species richness was higher in olive groves surrounded by higher SNH cover (χ^2 = 12.266, estimate = -0.17297, p = 0.0004**; AIC= 103.96), with an average of 149 species (95% CI: 128–176), compared to 126 species (95% CI: 113–151) in olive groves surrounded by lower SNH cover (Figure 2).

Vegetation diversity was also higher in olive groves surrounded by higher SNH cover ($\chi^2 = 0.4456$, estimate = -0.38661023, $p = 0.016$**; AIC= 82.005), with a mean diversity value of 47.12 versus 34.07 in olive groves surrounded by lower SNH cover. Vegetation abundance did not differ between high- and low-SNH groves (Figure 2).

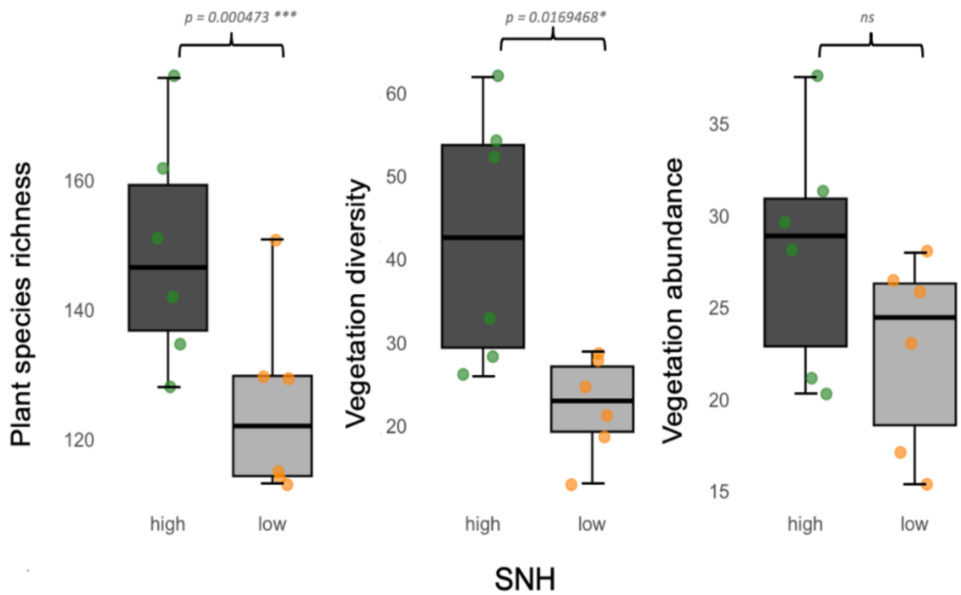

Figure 2. Effects of SNH cover on plant species richness, vegetation diversity, and abundance. Green dots indicate sites surrounded by high SNH cover, and orange dots indicate sites surrounded by low SNH cover. Significance values are based on GLMs (see Table S3, Supplementary Material).

3.1.2 Effects of local features of olive groves on vegetation

Plant species richness was best explained by terracing ($\chi^2 = 15.578$, estimate = 0.19503, p = <0.0001***; AIC=101.28), with terraced farms supporting a higher number of species than non-terraced ones (mean = 150 species, 95% CI: 128–176 vs. mean = 124 species, 95% CI: 113–142). Terraced farms also hosted indicator species such as *Umbilicus rupestris* and species from the genus *Sedum* sp., that were absent in non-terraced farms (see Figure S2, Supplementary Material). Amongst the local factors examined, mean tree diameter was the best predictor of vegetation diversity (χ^2 = 0.5104293, estimate = 0.007822596, p = <0.0001***; AIC= 81.02) and vegetation abundance (χ^2 = 161.4, estimate = 0.005912, p = 0.033*; AIC=78.697; Table S3, Supplementary Material). By contrast, canopy cover and soil characteristics showed no significant relationship with vegetation abundance, diversity, or species richness (Table S3, Supplementary Material).

3.2 Spiders

We sampled a total of 1,262 spider individuals, representing 130 taxa across 31 families (see Table S4 in Supplementary Material for taxonomic details). Of these, 124 taxa were identified to the species level, while six were identified to the genus level. The families with the highest species richness were Gnaphosidae and Linyphiidae, each comprising 22 species. In terms of spider abundance, *Thomisidae* was the most represented family, followed by *Lycosidae* and *Araneidae*.

3.2.1 Effects of landscape composition (SNH cover) on spider abundance across seasons

In spring, the best-fitting model describing spider abundance included SNH cover (estimate = 0.31668, p = 0.003**; AIC = 298.6; Table S5, Supplementary Material), together with vegetation structural complexity. Spider abundance was significantly higher in olive groves surrounded by low-SNH cover compared with those surrounded by high-SNH cover (Figure 3).

In autumn, the best-fitting model included the SNH cover (estimate = –0.14989, p = 0.023 (ns); AIC = 171.9; Table S5, Supplementary Material) together with vegetation abundance. We didn't find a significant difference in spider abundance on farms surrounded by high versus low SNH cover during this season.

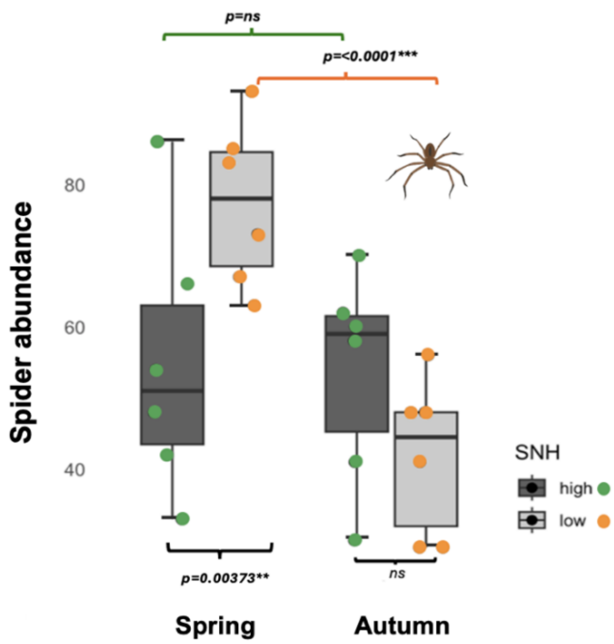

Figure 3. Seasonal spider abundance in olive groves with high vs. low SNH cover. Differences between high and low SNH cover within each season were tested with GLMMs, while seasonal differences (spring vs. autumn) within each SNH category were assessed with Wilcoxon rank-sum tests.

Based on Wilcoxon rank-sum tests, spider abundance in low-SNH groves was significantly lower in autumn than in spring (81 to 35 individuals; p < 0.001**). In contrast, abundance in olive groves surrounded by high SNH cover remained stable across seasons (59 in spring vs. 54 in autumn, ns). Spider species richness didn't differ significantly between olive groves surrounded by high and low SNH cover (mean=52 vs. 41 species, respectively, ns) across seasons.

3.2.2 Effects of local features of olive groves on spider abundance across seasons

In spring, the best-fitting model for spider abundance indicated that higher vegetation structural complexity and SNH cover were associated with lower spider abundance (vegetation structural complexity: estimate = –0.15168, p = 0.007**; AIC = 298.6; species richness: estimate = –0.010521, p = 0.014*; AIC = 299.2; Figure 4, Table S5). Associations with vegetation diversity and abundance were weak or non-significant.

In autumn, the best-fitting model indicated that spider abundance increased with vegetation abundance (estimate = 0.06153, p = 0.006**; AIC = 171.9). A separate model also revealed a positive effect of plant species richness on spider abundance (estimate = 0.017768, p = 0.026*; AIC = 173.6). Relationships with vegetation diversity, structural complexity, and shrub cover were weak or non-significant (Figure 4, Table S5 Supplementary Material).

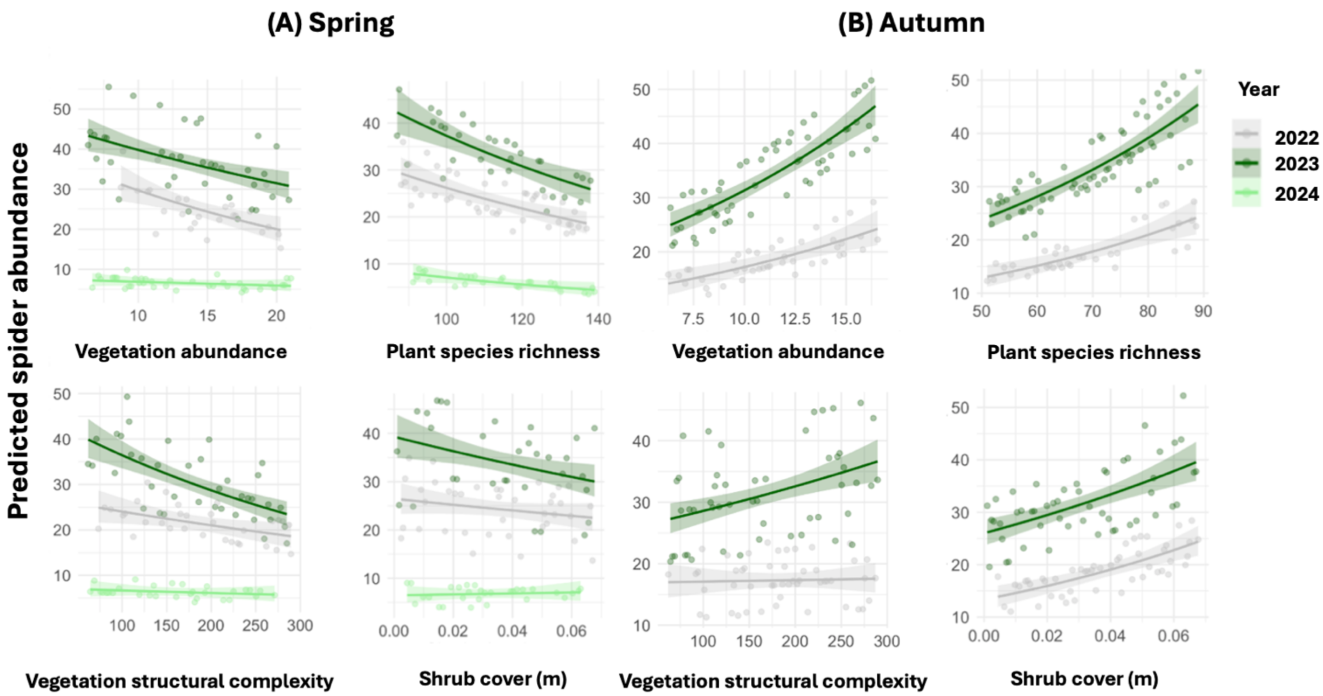

Figure 4. Predicted relationships between spider abundance and vegetation variables in spring and autumn. Effects of vegetation abundance, species richness, structural complexity, and shrub cover on spider abundance based on GLMMs, shown for (A) spring and (B) autumn with 95% confidence intervals (shaded).

4. ***Discussion***

4.1 Vegetation

We documented 314 plant taxa across the 12 study sites, confirming that traditionally managed organic olive groves can support high levels of vascular plant diversity (Radić Lakoš et al., 2014; Rey et al., 2019; Jiménez et al., 2023). As expected in agricultural landscapes subject to seasonal disturbance, the vegetation was dominated by annual species belonging to the Asteraceae, Poaceae and Fabaceae families. However, we also recorded species that are usually found in relatively undisturbed habitats or SNH in the Mediterranean, including characteristic taxa of sclerophyllous forests, Mediterranean macchia, and garrigue. This suggests that olive groves host diverse plant assemblages and have the potential to contribute to the conservation of native Mediterranean vegetation, enhancing ecological connectivity with adjacent SNH. The presence of fleshy-fruited native species, such as *Myrtus communis*, *Rubus ulmifolius*, *Smilax aspera*, *Rubia peregrina* and *Rhamnus alaternus*, further suggests potential biotic interactions, including endozoochorous seed dispersal, between the olive groves and the surrounding habitats (Jiménez et al., 2023). These findings emphasise the importance of traditionally managed olive agroforestry systems as key landscape elements that can enhance connectivity with the surrounding SNH, while also providing habitat for native vegetation that is increasingly threatened by agricultural intensification and urban expansion.

In agroecosystems, herbaceous vegetation plays a crucial role in providing vital ecosystem services such as erosion control, water retention, and nutrient cycling (Case et al., 2020). These functions are particularly important in regions such as Italy and the broader Mediterranean region, which are already experiencing severe climate and land degradation impacts (Newbold et al., 2020; Tsiakiris et al., 2024). In addition to these services, vegetation supports functional biodiversity by forming the basis of trophic networks (Brunori et al., 2019; Schuldt et al., 2019). To preserve vegetation-mediated ecosystem services, it is essential to understand the key factors promoting plant diversity in olive agroecosystems. Identifying local and landscape drivers of vegetation diversity is key to sustaining resilient, olive-based farming systems in Italy and for contributing to the preservation of biodiversity and ecosystem services across Mediterranean landscapes.

4.1.1 Effects of landscape composition (SNH cover) on vegetation

Our findings support the importance of the surrounding landscape's composition in shaping plant diversity within olive agroecosystems, confirming previous research in Mediterranean olive groves (Rey et al., 2019; Jiménez et al., 2023). Specifically, olive groves embedded in landscapes with higher

SNH cover support significantly richer and more diverse vegetation. This is likely driven by the combined effects of increased dispersal from a broader species pool in the surrounding landscape (Estrada-Carmona et al., 2022) and management practices linked to olive groves within more complex landscapes with higher SNH cover (Brunori et al., 2019). Landscapes with a greater SNH cover present fewer dispersal obstacles and maintain a larger pool of species capable of colonising olive groves (Baessler & Klotz, 2006; Rey et al., 2019). Management practices such as reduced mechanisation in traditional olive groves, which are typically surrounded by SNH cover, allow a richer understorey vegetation to persist (Estrada-Carmona et al., 2022; Jiménez et al., 2023). Together, these factors enhance the potential of olive groves to promote biodiversity by improving species movement and ecological connectivity (Rey et al., 2019). These findings emphasise the need to broaden agricultural policy and conservation planning: while current measures mainly target field-level practices, integrating landscape-scale strategies is crucial to supporting multifunctional agroecosystems and protecting biodiversity in Italian and Mediterranean farming systems.

4.1.2 Effects of local features of olive groves on vegetation

Structural features of the olive groves were positively associated with the local vegetation characteristics (vegetation diversity, species richness, and abundance) in single-predictor models. Terraced farms supported higher plant species richness and vegetation diversity. These patterns are consistent with previous studies of Mediterranean olive groves and other terraced agroecosystems, which highlight the importance of local structural heterogeneity in supporting vegetation assemblages (Solomou et al., 2013; Wersbeckmann et al., 2023). Terraces can create microhabitats by modifying soil depth, moisture retention, and sun exposure (Wersbeckmann et al., 2023). The presence of succulent indicator species, such as *Umbilicus rupestris* and *Sedum* sp., in terraced farms supports the hypothesis that groves with structurally complex terrain provide microclimatic niches that support greater plant diversity (Solomou et al., 2013). In addition, vegetation abundance and diversity increased with mean tree diameter. Larger trees are generally older, which may create more stable belowground conditions and enhance soil biochemical processes (Massaccesi et al., 2018). These factors could help explain why groves with larger trees appear to provide more opportunities for vegetation to colonise and persist.

These associations may also reflect co-variation with management intensity, as terraces and older trees are often linked to more traditional practices, including reduced mechanisation and less intensive mowing, which can favour diverse and abundant understorey vegetation (Cohen et al., 2015). Despite the conservation benefits of traditional olive groves, they face increasing risk of abandonment due to declining profitability (Wersbeckmann et al., 2023). From a management perspective, these results emphasise the ecological importance of preserving structural features such as terraces and mature trees in cultural landscapes. Targeted conservation strategies are therefore needed to maintain these traditional features, which play an important role in supporting biodiversity in Mediterranean olive agroecosystems.

Other structural features, including canopy cover, tree density, and soil characteristics, were not significantly associated with vegetation cover, diversity, or species richness in the models. This contrasts with previous research showing that canopy cover and tree density influence understory assemblages through effects on light availability and resource competition (Cohen et al., 2015; Scordia et al., 2023). The lack of association may reflect the structural uniformity of the study sites, as traditional olive groves typically employ regular pruning and low tree densities, reducing variability in canopy architecture and limiting competitive effects on herbaceous vegetation.

4.2 Spiders

Consistent with previous research in the Monti Pisani region, where up to 148 species of spider have been documented in olive groves (Picchi et al., 2016), we recorded 131 species of spider across the 12 study sites. These findings reinforce the potential of traditionally managed organic olive groves to support abundant and diverse spider populations. Our results demonstrate that the abundance of spiders in groves is influenced by the proportion of SNH cover in the surrounding area and local structural features, with different associations observed in spring and autumn. Spiders are key natural predators that provide the essential ecosystem service of natural pest control in organic systems, where synthetic pesticides are avoided (Paredes et al., 2013; Picchi, 2020). Therefore, maintaining stable and abundant spider populations can strengthen crop resilience against pest outbreaks and mitigate the impact of pests on yield (Paredes et al., 2019). The importance of sustaining spider populations and the ecosystem services they provide is emphasised by the growing demand from consumers for organic products free of pesticides.

4.2.1 Effects of landscape composition (SNH cover) on spider abundance across seasons

Spider abundance in olive groves varied with the landscape composition in a season-specific manner. In autumn, no significant association was detected between spider abundance and SNH cover. This suggests that other factors, such as the local vegetation or seasonal resource availability, may play a more prominent role in shaping spider assemblages during this season (Paredes et al., 2019). In spring, spider abundance was greater in groves embedded within landscapes with lower SNH cover. In landscapes with higher SNH cover, spiders may instead utilise alternative suitable habitats adjacent to olive groves (Álvarez et al., 2019; Ganem et al., 2023), whereas in low-SNH landscapes, olive groves can serve as important refuges when ground vegetation is at its seasonal peak (Picchi et al., 2016; Paredes et al., 2019).

Spider abundance was relatively stable across seasons in sites with high-SNH, whereas abundance in sites with low-SNH declined from spring to autumn. This pattern suggests that SNH could buffer spider assemblages, support more stable populations, and reduce seasonal fluctuations (Paredes et al., 2023; Ganem et al., 2023). These findings highlight that the influence of the surrounding landscape composition on spider populations can vary across the year. This variation emphasises the need to consider seasonal dynamics when evaluating the ecological value of the composition of the landscape (SNH cover) for conserving functional biodiversity and ecosystem services in olive cultivated landscapes. Because our models analysed each season independently, we cannot draw a direct comparison of spider abundance between spring and autumn. Future studies could include multiple seasons within a single modelling framework to compare temporal variation and potential seasonal influences of landscape composition on spider assemblages.

4.2.2 Effects of local features of olive groves on spider abundance across seasons

In spring, spider abundance showed either no significant association or a negative association with local vegetation metrics. This contrasts with our initial hypothesis, the autumn results, and previous studies that reported positive associations between understory vegetation and spider abundance in agroforestry systems (Gómez et al., 2018; Paredes et al., 2019; Castro et al., 2021). One explanation may be the interaction between landscape composition and vegetation: groves surrounded by higher SNH cover also supported more diverse and abundant vegetation, while spider abundance was greater in groves with lower SNH cover during this season. Thus, including both vegetation and landscape variables in the same model may have masked the effect of vegetation on spider abundance. Seasonal shifts resource distribution across the landscape may also drive spiders, as highly mobile predators, to move from olive groves to more suitable habitats in spring (Estrada-Carmona et al., 2022).

In autumn, spider abundance was positively correlated with higher vegetation abundance, plant species richness, and shrub cover. This result agrees with previous studies, showing that vegetation in agroecosystems provides essential resources for spiders, including foraging substrates, overwintering refuges, and stable microhabitats (Stenchly et al., 2012; Picchi, 2020). These vegetation metrics are especially important during the cooler months when resources in the surrounding landscape become scarce (Ganem et al., 2023). Understorey vegetation is therefore essential for sustaining spider assemblages and maximising their contribution to natural pest control, particularly when resources in the landscape are scarce (Cohen et al., 2015; Case et al., 2020; Cuff et al., 2022).

To better capture the effect of seasonal dynamics on spider abundance, we explored alternative model families in both GLMs and GLMMs, including different variance structures and interaction terms for the season. However, these models produced unstable estimates, likely due to uneven data representation across seasons and the complexity of ecological datasets. As a result, we fitted separate GLMMs for each season, which provided the most stable and interpretable solutions. While this methodological constraint limits the overall model complexity, it reflects the data limitations rather than insufficient consideration of analytical options. In addition to modelling constraints, our vegetation structural complexity measure may not fully capture local conditions, as it was derived from species height values in databases rather than field measurements. This likely underestimates structural heterogeneity in managed olive groves, highlighting the value of field-based vegetation data in ecological modelling. These limitations call for caution in interpreting seasonal differences in spider abundance; nevertheless, the patterns observed remain consistent with broader ecological implications and provide meaningful guidance for the sustainable management of olive agroecosystems.

Overall, these findings highlight the importance of both local and landscape-level factors, as well as their seasonal dynamics, in shaping spider populations in olive agroecosystems. Vegetation plays a central role in this context, as it provides the structural and functional basis for multi-trophic interactions, influencing higher trophic levels, such as spiders, that ultimately underpin key ecosystem services as natural pest control (Case et al., 2020). Effective management should prioritise maintaining diverse, abundant, and structurally complex understory vegetation within groves, alongside the conservation of natural and SNH in the surrounding landscape. Enhancing habitat complexity at multiple spatial scales is particularly important in organic agroecosystems, where spiders contribute to natural pest control and support both ecological sustainability and crop production.

5. *Conclusion*

This study demonstrates that both local grove features and surrounding landscape composition (SNH cover) significantly influence vegetation and spider assemblages in organic olive groves in Tuscany, Italy. Our findings show that (i) plant species richness and vegetation diversity increase with higher SNH cover and are positively affected by local features such as terracing and larger mean tree diameter; and (ii) spider abundance also responds to vegetation and landscape context, displaying distinct seasonal patterns. Overall, our results highlight the ecological potential of organic olive agroforestry systems to support biodiversity and sustain key ecosystem services. Ecosystem services mediated by vegetation and spiders, such as biological pest control, are shaped by the interaction of local grove features and landscape composition. Our findings underscore the importance of biodiversity-friendly management practices that promote local vegetation, preserve traditional features like terraces and mature trees, and maintain SNH cover in the surrounding landscape. Incorporating both spatial and seasonal factors into management and policy can enhance the multifunctionality and resilience of Italian and Mediterranean agroecosystems.

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7. *Supplementary Material*

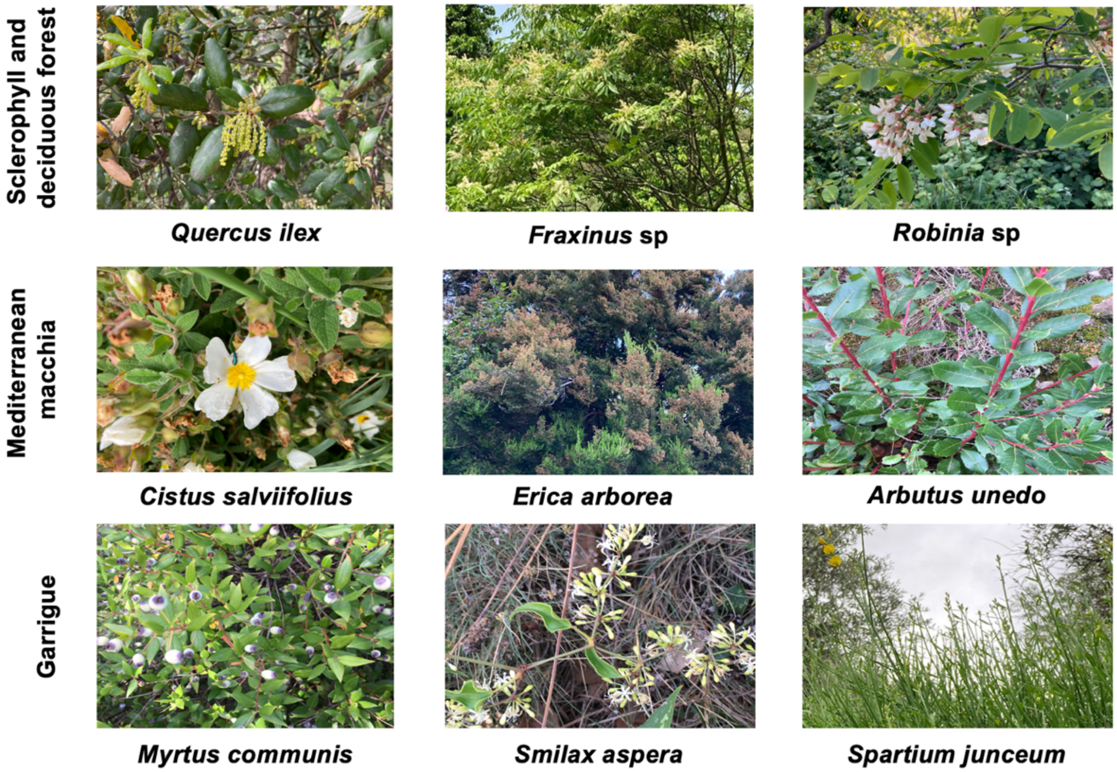

Figure S1. Plant species native to ecosystems of the Monti Pisani found in olive groves: sclerophyll and deciduous forests, Mediterranean macchia, and garrigue

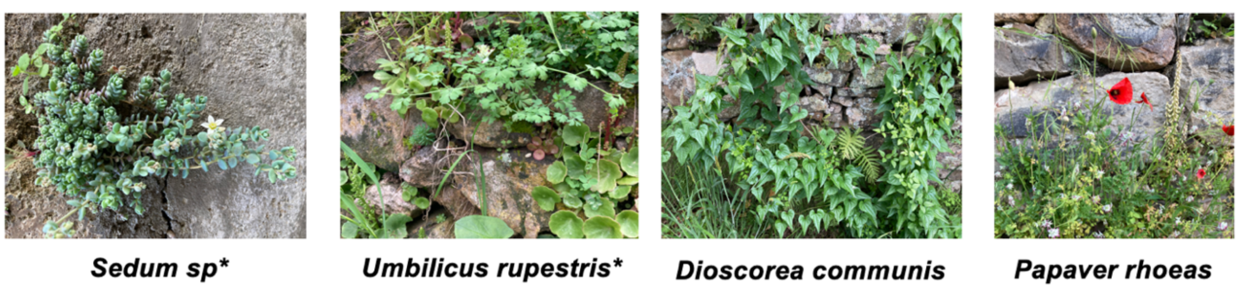

Figure S2. Plant species associated with terrace structures in olive groves, with indicator species marked (*)

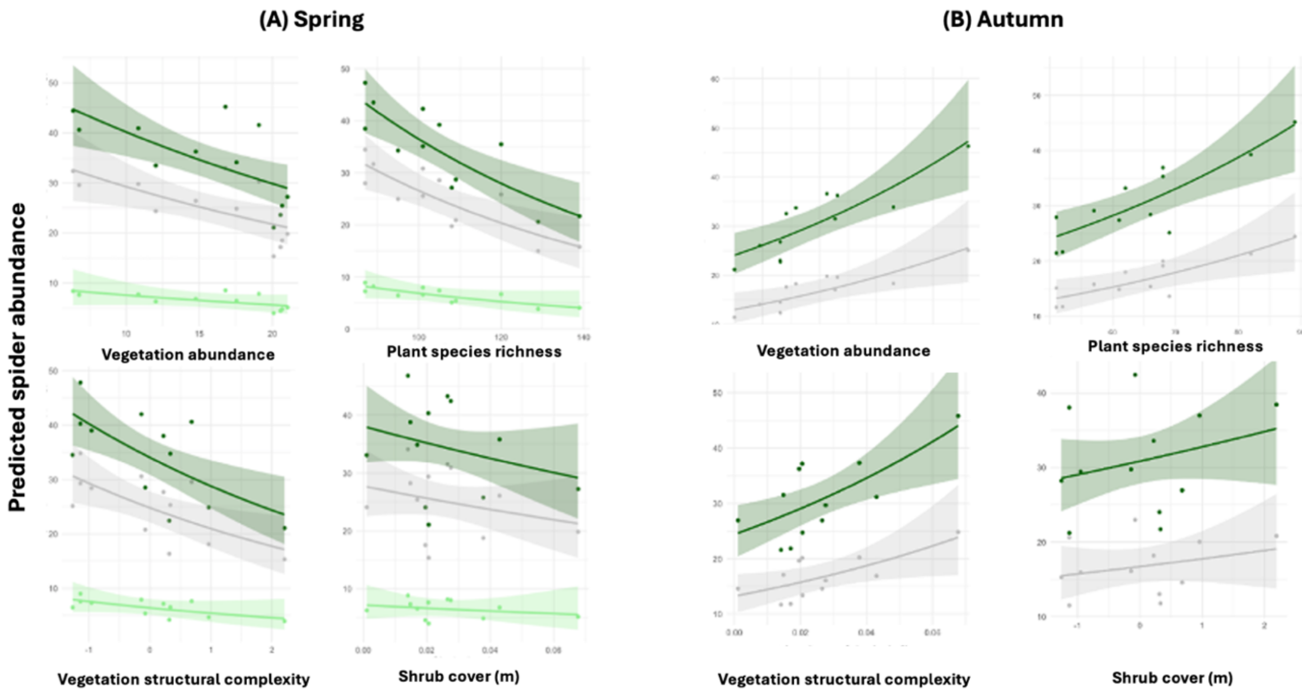

Figure S3. Association between spider abundances and vegetation variables in spring and autumn

(A) Predictions for data collected in spring, showing spider abundance as a function of vegetation abundance, species richness, structural complexity, and shrub abundance, with 95% confidence intervals (shaded areas). (B) Predictions for data collected in autumn, modelled using the same vegetation features as predictors, with 95% confidence intervals.

Table S1. Effect of soil pH and soil moisture on vegetation diversity, species richness, and abundance (linear models)

Predictor	Response variable	F	df	P-value
pH	Plant species richness	0.04824	1.10	0.831
Mean soil moisture	Plant species richness	1.785	1.10	0.211171
pH	Vegetation abundance	0.1334	1.10	0.723
Mean soil moisture	Vegetation abundance	1.467	1.10	0.2537
pH	Vegetation diversity	0.1744	1.10	0.685
Mean soil moisture	Vegetation diversity	0.9521	1.10	0.3522

Table S2. Plant species identified in olive groves: taxonomic classification and associated SNH cover

Order	Family	Species	SNH high	SNH low
Lamiales	Acanthaceae	*Acanthus mollis*		x
Asterales	Asteraceae	*Achillea ligustica*	x	
Rosales	Rosaceae	*Agrimonia eupatoria*	x	
Poales	Poaceae	*Aira caryophyllea*	x	x
Lamiales	Lamiaceae	*Ajuga reptans*	x	
Rosales	Rosaceae	*Alchemilla arvensis*		x
Asparagales	Amaryllidaceae	*Allium roseum*	x	
Asparagales	Amaryllidaceae	*Allium* sp.		x
Asparagales	Amaryllidaceae	*Allium triquetrum*	x	
Caryophyllales	Amaranthaceae	*Amaranthus* sp.		x
Asparagales	Orchidaceae	*Anacamptis papilionacea*	x	
Ranunculales	Ranunculaceae	*Anemone coronaria*	x	x
Asterales	Asteraceae	*Anthemis* sp.	x	x
Poales	Poaceae	*Anthoxanthum odoratum*	x	x
Apiales	Apiaceae	*Anthriscus sylvestris*	x	x
Brassicales	Brassicaceae	*Arabidopsis* sp.	x	
Ericales	Ericaceae	*Arbutus unedo*	x	
Caryophyllales	Caryophyllaceae	*Arenaria* sp.	x	x
Alismatales	Araceae	*Arisarum vulgare*	x	x
Piperales	Aristolochiaceae	*Aristolochia rotunda*		x
Asterales	Asteraceae	*Artemisia vulgaris*	x	x
Alismatales	Araceae	*Arum italicum*	x	x
Poales	Poaceae	*Arundo donax*		X
Asparagales	Asparagaceae	*Asparagus acutifolius*	x	x
Poales	Poaceae	*Avena barbata*	x	x
Poales	Poaceae	*Avena* sp.	x	X
Lamiales	Orobanchaceae	*Bellardia trixago*	x	x
Asterales	Asteraceae	*Bellis perennis*	x	x
Asterales	Asteraceae	*Bellis sylvestris*	x	x
Lamiales	Lamiaceae	*Betonica officinalis*	x	
Poales	Poaceae	*Brachypodium* sp.	x	
Poales	Poaceae	*Briza maxima*	x	x
Poales	Poaceae	*Briza media*	x	x
Poales	Poaceae	*Briza minor*	x	
Poales	Poaceae	*Bromus hordeaceus*	x	x
Poales	Poaceae	*Bromus sp.*	x	x
Poales	Poaceae	*Bromus tectorum*	x	x
Brassicales	Brassicaceae	*Bunias erucago*	x	x
Lamiales	Lamiaceae	*Calamintha nepeta*	x	x
Asterales	Asteraceae	*Calendula arvensis*	x	x
Brassicales	Brassicaceae	*Calepina irregularis*		x
Asterales	Campanulaceae	*Campanula erinus*		x
Asterales	Campanulaceae	*Campanula rapunculus*	x	x
Brassicales	Brassicaceae	*Capsella bursa-pastoris*	x	x
Brassicales	Brassicaceae	*Cardamine cf flexuosa*	x	x
Brassicales	Brassicaceae	*Cardamine cf hirsuta*	x	x
Asterales	Asteraceae	*Carduus pycnocephalus*		x
Asterales	Asteraceae	*Carduus* sp.	x	x
Poales	Cyperaceae	*Carex caryophyllea*	x	

Poales	Cyperaceae	*Carex divulsa*	x	x
Poales	Cyperaceae	*Carex hirta*		x
Poales	Cyperaceae	*Carex pendula*		x
Poales	Cyperaceae	*Carex sp.*	x	x
Poales	Poaceae	*Catapodium rigidum*	x	x
Rosales	Cannabaceae	*Celtis australis*		x
Asterales	Asteraceae	*Centaurea cyanus*	x	
Asterales	Asteraceae	*Centaurea nigrescens*	x	x
Asterales	Asteraceae	*Centaurea scabiosa*	x	
Gentianales	Gentianaceae	*Centaurium erythraea*	x	x
Gentianales	Gentianaceae	*Centaurium tenuiflorum*		x
Caryophyllales	Caryophyllaceae	*Cerastium glomeratum*	x	x
Caryophyllales	Amaranthaceae	*Chenopodium album*	x	x
Asterales	Asteraceae	*Chondrilla juncea*	x	x
Asterales	Asteraceae	*Cichorium intybus*	x	x
Asterales	Asteraceae	*Cirsium* sp.	x	
Malvales	Cistaceae	*Cistus salviifolius*	x	
Ranunculales	Ranunculaceae	*Clematis flammula*	x	x
Ranunculales	Ranunculaceae	*Clematis vitalba*	x	x
Lamiales	Lamiaceae	*Clinopodium vulgare*	x	x
Asterales	Asteraceae	*Coleostephus myconis*	x	x
Solanales	Convolvulaceae	*Convolvulus arvensis*	x	x
Asterales	Asteraceae	*Crepis sancta*	x	x
Asterales	Asteraceae	*Crepis sp.*	x	x
Asterales	Asteraceae	*Crepis vesicaria*	x	x
Solanales	Convolvulaceae	*Cuscuta campestris*		x
Poales	Primulaceae	*Cyclamen hederifolium*	x	
Lamiales	Plantaginaceae	*Cymbalaria muralis*		x
Poales	Poaceae	*Cynodon dactylon*	x	x
Poales	Poaceae	*Cynosorus echiantus*	x	x
Poales	Cyperaceae	*Cyperus eragrostis*		x
Poales	Cyperaceae	*Cyperus longus*		x
Fabales	Fabaceae	*Cytisus villosus*	x	x
Poales	Poaceae	*Dactylis glomerata*	x	x
Malvales	Thymelaeaceae	*Daphne gnidium*	x	
Apiales	Apiaceae	*Daucus carota*	x	x
Caryophyllales	Caryophyllaceae	*Dianthus sp.*	x	x
Solanales	Convolvulaceae	*Dichondra micrantha*	x	x
Poales	Poaceae	*Digitaria sanguinalis*	x	x
Dioscoreales	Dioscoreaceae	*Dioscorea communis*	x	x
Dipsacales	Caprifoliaceae	*Dipsacus sp.*		x
Asterales	Asteraceae	*Dittrichia viscosa*	x	x
Brassicales	Brassicaceae	*Draba muralis*	x	
Ericales	Ericaceae	*Erica arborea*	x	
Asterales	Asteraceae	*Erigeron bonariensis*	x	x
Asterales	Asteraceae	*Erigeron sp.*	x	x
Asterales	Asteraceae	*Erigeron sumatrensis*	x	x
Geraniales	Geraniaceae	*Erodium sp.*	x	x
Apiales	Apiaceae	*Eryngium campestre*	x	
Celastrales	Celastraceae	*Euonymus europaeus*	x	x
Malpighiales	Euphorbiaceae	*Euphorbia helioscopia*	x	x
Malpighiales	Euphorbiaceae	*Euphorbia peplus*	x	x
Poales	Poaceae	*Festuca sp.*	x	x

Ranunculales	Ranunculaceae	*Ficaria verna*	x	x
Apiales	Apiaceae	*Foeniculum vulgare*	x	x
Lamiales	Oleaceae	*Fraxinus ornus*	x	
Ranunculales	Papaveraceae	*Fumaria capreolata*	x	x
Ranunculales	Papaveraceae	*Fumaria officinalis*	x	x
Asterales	Asteraceae	*Galactites tomentosus*	x	x
Gentianales	Rubiaceae	*Galium aparine*	x	x
Gentianales	Rubiaceae	*Galium mollugo*	x	x
Gentianales	Rubiaceae	*Galium sp.*	x	x
Gentianales	Rubiaceae	*Galium verrucosum*	x	
Geraniales	Geraniaceae	*Geranium molle*	x	x
Geraniales	Geraniaceae	*Geranium purpureum*	x	x
Geraniales	Geraniaceae	*Geranium rotundifolia*	x	x
Geraniales	Geraniaceae	*Geranium sp.*	x	x
Asterales	Asteraceae	*Glebionis segetum*	x	
Lamiales	Lamiaceae	*Glechoma hederacea*	x	
Apiales	Araliaceae	*Hedera helix*	x	x
Asterales	Asteraceae	*Hedypnois rhagadioloides*	x	
Malvales	Cistaceae	*Helianthemum nummularium*	x	
Boraginales	Boraginaceae	*Heliotropium europaeum*	x	
Brassicales	Brassicaceae	*Hirschfeldia incana*	x	x
Poales	Poaceae	*Holcus lanatus*	x	x
Poales	Poaceae	*Hordeum murinum*	x	x
Asterales	Asteraceae	*Hyoseris radiata*	x	x
Malpighiales	Hypericaceae	*Hypericum perforatum*	x	x
Asterales	Asteraceae	*Hypochaeris achyrophorus*	x	x
Asterales	Asteraceae	*Hypochaeris glabra*	x	x
Asterales	Asteraceae	*Hypochaeris radicata*	x	x
Asterales	Asteraceae	*Jacobaea erratica*	x	x
Poales	Juncaceae	*Juncus conglomeratus*	x	x
Poales	Juncaceae	*Juncus sp.*	x	x
Lamiales	Plantaginaceae	*Kickxia sp.*	x	x
Asterales	Asteraceae	*Lactuca sp.*		x
Poales	Poaceae	*Lagurus ovatus*	x	
Lamiales	Lamiaceae	*Lamium amplexicaule*	x	x
Lamiales	Lamiaceae	*Lamium purpureum*	x	x
Fabales	Fabaceae	*Lathyrus annuus*	x	x
Fabales	Fabaceae	*Lathyrus cicera*	x	x
Fabales	Fabaceae	*Lathyrus ochrus*	x	x
Laurales	Lauraceae	*Laurus nobilis*		x
Lamiales	Lamiaceae	*Lavandula sp.*	x	
Asterales	Asteraceae	*Leontodon tuberosus*	x	x
Asparagales	Asparagaceae	*Leopoldia comosum*	x	
Lamiales	Plantaginaceae	*Linaria pelisseriana*	x	x
Lamiales	Plantaginaceae	*Linaria vulgaris*	x	x
Malpighiales	Linaceae	*Linum bienne*	x	x
Malpighiales	Linaceae	*Linum strictum*	x	
Poales	Poaceae	*Lolium perenne*		x
Dipsacales	Caprifoliaceae	*Lonicera sp.*	x	
Fabales	Fabaceae	*Lotus ornithopodioides*	x	x
Fabales	Fabaceae	*Lotus sp.*	x	x
Poales	Juncaceae	*Luzula campestris*	x	
Poales	Juncaceae	*Luzula forsteri*	x	

Ericales	Primulaceae	*Lysimachia arvensis*	x	x
Ericales	Primulaceae	*Lysimachia foemina*	x	x
Myrtales	Lythraceae	*Lythrum salicaria*		x
Malvales	Malvaceae	*Malva multiflora*		x
Malvales	Malvaceae	*Malva sylvestris*	x	x
Fabales	Fabaceae	*Medicago arabica*	x	x
Fabales	Fabaceae	*Medicago orbicularis*	x	x
Fabales	Fabaceae	*Medicago polymorfa*	x	x
Fabales	Fabaceae	*Medicago sp.*	x	
Poales	Poaceae	*Melica minuta*	x	
Lamiales	Lamiaceae	*Melissa sp.*	x	x
Lamiales	Lamiaceae	*Mentha sp.*		x
Lamiales	Lamiaceae	*Mentha suaveolens*	x	
Malpighiales	Euphorbiaceae	*Mercurialis annua*	x	
Lamiales	Plantaginaceae	*Misopates orontium*	x	x
Boraginales	Boraginaceae	*Myosotis arvensis*	x	x
Boraginales	Boraginaceae	*Myosotis ramosissima*	x	x
Myrtales	Myrtaceae	*Myrtus communis*	x	x
Lamiales	Orobanchaceae	*Odontites vernus*		x
Apiales	Apiaceae	*Oenanthe pimpinelloides*	x	x
Lamiales	Lamiaceae	*Origanum vulgare*	x	x
Asparagales	Asparagaceae	*Ornithogalum sp.*	x	
Fabales	Fabaceae	*Ornithopus compressus*	x	x
Lamiales	Orobanchaceae	*Orobanche minor*	x	
Lamiales	Orobanchaceae	*Orobanche variegata*	x	x
Santalales	Santalaceae	*Osyris alba*	x	x
Oxalidales	Oxalidaceae	*Oxalis articulata*	x	x
Oxalidales	Oxalidaceae	*Oxalis corniculata*	x	x
Oxalidales	Oxalidaceae	*Oxalis pes-caprae*	x	
Oxalidales	Oxalidaceae	*Oxalis stricta*	x	x
Ranunculales	Papaveraceae	*Papaver rhoeas*	x	x
Lamiales	Orobanchaceae	*Parentucellia viscosa*	x	x
Rosales	Urticaceae	*Parietaria sp.*	x	
Poales	Poaceae	*Paspalum dilatatum*	x	x
Malpighiales	Passifloraceae	*Passiflora caerulea*	x	
Caryophyllales	Caryophyllaceae	*Petrorhagia dubia*	x	x
Caryophyllales	Caryophyllaceae	*Petrorhagia prolifera*	x	
Saxifragales	Crassulaceae	*Phedimus stellatus*		x
Asterales	Asteraceae	*Picris hieracioides*	x	x
Apiales	Apiaceae	*Pimpinella sp.*	x	x
]Lamiales	Plantaginaceae	*Plantago bellardii*	x	
Lamiales	Plantaginaceae	*Plantago coronopus*	x	
Lamiales	Plantaginaceae	*Plantago lagopus*	x	x
Lamiales	Plantaginaceae	*Plantago lanceolata*	x	x
Lamiales	Plantaginaceae	*Plantago major*		x
Lamiales	Plantaginaceae	*Plantago sp.*	x	x
Poales	Poaceae	*Poa annua*	x	x
Poales	Poaceae	*Poa bulbosa*	x	x
Poales	Poaceae	*Poa pratensis*	x	x
Caryophyllales	Caryophyllaceae	*Polycarpon tetraphyllum*	x	x
Caryophyllales	Polygonaceae	*Polygonum aviculare*	x	x
non_vascular	Fern	*Polypodium sp.*	x	
Caryophyllales	Portulacaceae	*Portulaca oleracea*	x	x

Rosales	Rosaceae	*Potentilla reptans*	x	x
Rosales	Rosaceae	*Prunus avium*	x	x
Rosales	Rosaceae	*Prunus sp.*	x	x
Fagales	Fagaceae	*Quercus ilex*	x	
Fagales	Fagaceae	*Quercus pubescens*	x	x
Fagales	Fagaceae	*Quercus sp.*	x	x
Ranunculales	Ranunculaceae	*Ranunculus bulbosus*	x	x
Ranunculales	Ranunculaceae	*Ranunculus muricatus*	x	x
Brassicales	Brassicaceae	*Raphanus raphanistrum*	x	x
Asterales	Asteraceae	*Reichardia picroides*	x	x
Asterales	Asteraceae	*Rhagadiolus stellatus*	x	x
Rosales	Rhamnaceae	*Rhamnus alaternus*		x
Rosales	Rosaceae	*Rosa sp.*		x
Fabales	Fabaceae	*Robinia sp.*	x	
Gentianales	Rubiaceae	*Rubia peregrina*	x	x
Rosales	Rosaceae	*Rubus ulmifolius*	x	x
Caryophyllales	Polygonaceae	*Rumex acetosa*	x	x
Caryophyllales	Polygonaceae	*Rumex acetosella*	x	x
Caryophyllales	Polygonaceae	*Rumex crispus*	x	x
Caryophyllales	Polygonaceae	*Rumex pulcher*	x	x
Lamiales	Lamiaceae	*Salvia officinalis*	x	
Lamiales	Lamiaceae	*Salvia verbenaca*		x
Dipsacales	Viburnaceae	*Sambucus nigra*	x	
Rosales	Rosaceae	*Sanguisorba minor*	x	x
Asterales	Asteraceae	*Scolymus sp.*	x	
Lamiales	Scrophulariaceae	*Scrophularia peregrina*	x	x
Saxifragales	Crassulaceae	*Sedum album*	x	x
Saxifragales	Crassulaceae	*Sedum cepaea*	x	x
Saxifragales	Crassulaceae	*Sedum rubens*	x	x
Asterales	Asteraceae	*Senecio sp.*	x	x
Asterales	Asteraceae	*Senecio vulgaris*	x	x
Asparagales	Orchidaceae	*Serapias cordigera*	x	
Asparagales	Orchidaceae	*Serapias lingua*	x	x
Asparagales	Orchidaceae	*Serapias neglecta*	x	x
Poales	Poaceae	*Setaria sp.*	x	x
Poales	Poaceae	*Setaria verticilata*	x	x
Gentianales	Rubiaceae	*Sherardia arvensis*	x	x
Caryophyllales	Caryophyllaceae	*Silene flos-cuculi*	x	x
Caryophyllales	Caryophyllaceae	*Silene gallica*	x	
Caryophyllales	Caryophyllaceae	*Silene italica*	x	x
Caryophyllales	Caryophyllaceae	*Silene latifolia*	x	x
Caryophyllales	Caryophyllaceae	*Silene sp.*	x	x
Caryophyllales	Caryophyllaceae	*Silene vulgaris*	x	x
Brassicales	Brassicaceae	*Sisymbrium sp.*	x	
Liliales	Smilacaceae	*Smilax aspera*	x	x
Solanales	Solanaceae	*Solanum lycopersicum*		x
Solanales	Solanaceae	*Solanum nigrum*	x	x
Asterales	Asteraceae	*Sonchus arvensis*		x
Asterales	Asteraceae	*Sonchus asper*	x	x
Asterales	Asteraceae	*Sonchus bulbosus*	x	x
Asterales	Asteraceae	*Sonchus oleraceus*	x	x
Asterales	Asteraceae	*Sonchus sp.*	x	x
Poales	Poaceae	*Sorghum halepense*	x	x

Fabales	Fabaceae	*Spartium junceum*	x	
Asparagales	Orchidaceae	*Spiranthes spiralis*	x	x
Poales	Poaceae	*Sporobolus sp.*	x	
Lamiales	Lamiaceae	*Stachys arvensis*	x	x
Caryophyllales	Caryophyllaceae	*Stellaria media*	x	x
Caryophyllales	Caryophyllaceae	*Stellaria sp.*	x	x
Asterales	Asteraceae	*Taraxacum sp.*	x	x
Rosales	Rubiaceae	*Theligonum cynocrambe*	x	x
Lamiales	Lamiaceae	*Thymus sp.*	x	
Asterales	Asteraceae	*Tolpis sp.*	x	x
Apiales	Apiaceae	*Tordylium apulum*	x	x
Apiales	Apiaceae	*Torilis sp.*	x	x
Asterales	Asteraceae	*Tragopogon porrifolius*		x
Fabales	Fabaceae	*Trifolium alexandrinum*	x	x
Fabales	Fabaceae	*Trifolium angustifolium*	x	x
Fabales	Fabaceae	*Trifolium arvense*	x	x
Fabales	Fabaceae	*Trifolium campestre*	x	x
Fabales	Fabaceae	*Trifolium glomeratum*	x	x
Fabales	Fabaceae	*Trifolium medium*	x	x
Fabales	Fabaceae	*Trifolium nigrescens*	x	x
Fabales	Fabaceae	*Trifolium pratense*	x	x
Fabales	Fabaceae	*Trifolium repens*	x	x
Fabales	Fabaceae	*Trifolium sp.*	x	x
Fabales	Fabaceae	*Trifolium stellatum*	x	x
Fabales	Fabaceae	*Trifolium subterraneum*	x	x
Fabales	Fabaceae	*Ulex europaeus*	x	
Rosales	Ulmaceae	*Ulmus minor*		x
Saxifragales	Crassulaceae	*Umbilicus rupestris*	x	x
Asterales	Asteraceae	*Urospermum dalechampii*	x	x
Rosales	Urticaceae	*Urtica dioica*	x	x
Rosales	Urticaceae	*Urtica sp.*	x	x
Caryophyllales	Caryophyllaceae	*Vaccaria hispanica*	x	
Dipsacales	Caprifoliaceae	*Valeriana eriocarpa*	x	
Dipsacales	Caprifoliaceae	*Valeriana locusta*	x	x
Lamiales	Scrophulariaceae	*Verbascum blattaria*	x	x
Lamiales	Scrophulariaceae	*Verbascum sinuatum*		x
Lamiales	Verbenaceae	*Verbena officinalis*	x	x
Lamiales	Plantaginaceae	*Veronica arvensis*	x	x
Lamiales	Plantaginaceae	*Veronica cymbalaria*	x	x
Lamiales	Plantaginaceae	*Veronica persica*	x	x
Lamiales	Plantaginaceae	*Veronica sp.*	x	x
Fabales	Fabaceae	*Vicia cracca*	x	
Fabales	Fabaceae	*Vicia hirsuta*	x	x
Fabales	Fabaceae	*Vicia hybrida*	x	x
Fabales	Fabaceae	*Vicia lutea*	x	x
Fabales	Fabaceae	*Vicia sativa*	x	x
Fabales	Fabaceae	*Vicia sp.*	x	x
Fabales	Fabaceae	*Vicia tetrasperma*	x	x
Gentianales	Apocynaceae	*Vinca major*	x	
Vitales	Vitaceae	*Vitis vinifera*		x
Poales	Poaceae	*Vulpia sp.*	x	x

Table S3. Best-fitting GLMs of vegetation diversity, species richness, and abundance predicted by landscape composition (SNH cover) and local grove features (terracing, mean tree diameter, canopy cover, olive tree density)

The best fitting models, based on AIC, are marked in **bold.** Marginally and significant effects (0.05 < p < 0.1) are marked in *italic* and statistical significance is denoted as follows: (*** p < 0.001; ** p < 0.01; * p < 0.05; • p < 0.1; n.s. p > 0.1). Models were compared based on AIC, with site code included as a fixed effect. The direction of effects is indicated by arrows (↑ positive, ↓ negative).

Response	Model type / data distribution	Effect	Estimate	z-value	AIC	X^2	*p-value*
Plant species richness	GLM / Poisson	**Terracing**	**0.19503**	**3.937**	**101.28**	**15.578**	↑ ***8.23e-05 *****
		SNH cover (low)	-0.17297	-3.496	103.96	12.266	↓ *0.0004* ***
		Tree density	5.192663166	3.479355	104.2498	11.976818	↑ *0.0005****
		Mean tree diameter	0.002975408	3.080437	106.7071	9.519562	↑ *0.002***
Vegetation abundance (across seasons)	GLM / Gamma	**Mean tree diameter**	**0.005912**	**2.0073605**	**78.69718**	**161.4**	↑ ***0.033* ***
		Tree density	7.609661025	1.9622754	79.21115	0.19847191	↑ 0.041*
		SNH cover (low)	-0.21356956	-1.591574	80.58261	0.13657661	0.111
		Canopy cover	-0.00127377	-0.594160	82.72334	0.02491914	0.526
Vegetation diversity (Hill – Shannon)	GLM / Gamma	**Mean tree diameter**	**0.007822596**	**2.565945**	**81.02155**	**0.5104293**	↑ ***0.008*****
		SNH cover (low)	-0.38661023	-2.395256	82.00506	0.4456374	↓ *0.016**
		Canopy cover	-0.00428757	-1.638520	84.19326	0.2814527	0.080
		Terracing	0.270794155	1.348826	84.96220	0.2164763	0.174

Table S4. List of all spider species identified in sampling sites and category of SNH cover (high or low)

Species	High SNH	Low SNH
Agraecina lineata		x
Agroeca cuprea		x
Agyneta cf. affinis		x
Agyneta cf. mollis		x
Agyneta rurestris	x	x
Alopecosa albofasciata	x	x
Anelosimus vittatus	x	x
Araneus angulatus/circe	x	x
Araniella cucurbitina		x
Araniella opistographa		x

Arctosa cf. personata	x	
Argenna subnigra	x	
Aulonia albimana		x
Bassaniodes bufo	x	
Chalcoscirtus infimus	x	
Cheiracanthium mildei	x	x
Clubiona comta	x	
Cresmatoneta mutinensis		x
Cybaeodes marinae	x	x
Cyclosaconica sp.	x	
Cyclosa sp.	x	x
Cyrtarachne ixoides		x
Diplocephalus graecus	x	x
Dipoena melanogaster		x
Dysdera cf. lantosquensis	x	x
Dysdera crocata	x	x
Dysdera lantosquensis	x	x
Ebrechtella tricuspidata		x
Eidmannella pallida		x
Enoplognatha testacea	x	
Episinus angulatus		x
Eratigena fuesslini	x	
Erigone autumnalis	x	x
Erigone cf. atra		x
Erigonella ignobilis		x
Euophrys frontalis	x	x
Euophrys gambosa	x	x
Euophrys herbigrada	x	x
Euophrys innotata	x	x
Euophrys rufibarbis	x	x
Euophrys sulphurea	x	x
Euryopis episinoides	x	x
Evarcha jucunda	x	x
Frontinellina frutetorum	x	
Gibbaranea gibbosa	x	x
Gnaphosa alacris	x	x
Hahnia sp.	x	x
Haplodrassus signifer	x	x
Heliophanus flavipes	x	x

Heliophanus tribulosus		x
Heser nilicola		x
Hogna radiata	x	x
Kochiur aulica	x	x
Lasaeola sp.		x
Lathys umilis		x
Leptodrassus albidus		x
Liophrurillus flavitarsis	x	x
Macaroeris nidicolens		x
Marisprozelotes barbatus	x	x
Marisprozelotes mutabilis	x	x
Mecopisthes nicaeensis		x
Metellina mengei	x	
Micaria coarctata	x	x
Micaria cyrnea	x	
Micaria micans		x
Neaetha membrosa	x	
Nemesia sp.	x	x
Neoscona adianta	x	x
Neoscona subfusca	x	x
Neottiura sp.	x	
Nigma flavescens		x
Nigma puella	x	x
Nomisia exorspta	x	x
Nuctenea sp.	x	
Nurscia albomaculata		x
Oecobius maculatus	x	
Oliosargelasius sp..	x	x
Ozyptila confluens	x	x
Ozyptila pauxilla	x	
Ozyptila sanctuaria	x	x
Ozyptila trux	x	
Pachygnatha degeeri	x	x
Paidiscura pallens		x
Palliduphantes liguricus	x	x
Palliduphantes pallidus	x	
Pardosa proxima		x
Pardosa tenuipes		x
Pelecopsis elongata	x	x

Pelecopsis inedita	x	x
Phaeocedus vankeeri		x
Philodromus albidus	x	x
Philodromus aureolus	x	
Philodromus praedatus		x
Philodromus rufus	x	x
Phlegra bresnieri	x	x
Phrurolitus festivus	x	x
Phrurolitus minimus	x	
Phylloneta impressa		x
Pimoa rupicola	x	
Pisaura mirabilis	x	
Platnickisp tincta		x
Porrhoclubiona leucaspis	x	x
Pseudicius badius		x
Pulchellodromus bistigma	x	
Runcinia grammica		x
Salticus mutabilis		x
Scotophaeus validus	x	
Scytodes thoracica	x	x
Segestria florentina		x
Setaphis carmeli	x	x
Silhouettella loricatula	x	
Simitidion simile	x	x
Styloctetor romanus		x
Synema globosum	x	
Tenuiphantes tenuis	x	x
Tetragnatha sp.		x
Thanatus atratus		x
Theridion mystaceum	x	x
Titanoeca flavicoma		x
Tmarus piger	x	
Tmarus staintoni	x	x
Trachelas minor		x
Trachyzelotes pedestris	x	
Trichoncus affinis	x	x
Triconcus hackmani	x	x
Trichoncus sordidus	x	x
Trochosa hispanica	x	

Trochosa ruricola	x	x
Walckesperia corniculans	x	
Xysticus kochi	x	x
Zelotes atrocaeruleus	x	
Zelotes fulvaster	x	x
Zelotes hermani	x	x
Zelotes oblongus	x	
Zelotes tenuis	x	x
Zilla diodia	x	
Zodarion vicinum	x	x
Zora sp.		x
Zygiella x-notata	x	

Table S5. Best fitting GLMMs of spider abundance predicted by landscape composition (SNH cover) and grove vegetation variables (vegetation diversity, species richness, abundance, structural complexity, and shrub cover)

Spider abundances were analysed separately by sampling season and by sampling method. The direction of effects is represented by arrows (↑ positive, ↓ negative). Best fitting model is shown in **bold** and statistical significance is denoted as follows: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; • $p < 0.1$; ns. $p > 0.1$.

Season	Response	Effect	AIC	Estimate	z-value	p-value
Spring	**Spider abundance**	**SNH cover (low)**	**298.6**	**0.31668**	**2.900**	↑ **0.003 ****
		Vegetation structural complexity		**-0.15168**	**-2.659**	↓ **0.007 ****
		SNH cover (low)	301.2	0.27390	2.065	↑ 0.038 *
		Vegetation abundance (spring)		-0.02306	-1.795	↓ 0.072 .
		SNH cover (low)	299.2	0.189972	1.438	0.150
		Plant species richness (spring)		-0.010521	-2.436	↓ 0.014 *
		SNH cover (low)	300.9	0.219575	1.560	0.118
		Vegetation diversity		-0.011291	-1.922	↓ 0.054 .
Autumn	**Spider abundance**	**SNH cover (low)**	**171.9**	**-0.14989**	**-1.193**	**0.232**
		Vegetation abundance (autumn)		**0.06153**	**2.729**	↑ **0.006 ****
		SNH cover (low)	173.6	0.051656	0.278	0.781
		Plant species richness (autumn)		0.017768	2.219	↑ 0.026 *
		SNH cover (low)	176.7	-0.150862	-0.859	0.391
		Vegetation diversity		0.007006	0.995	0.320
		SNH cover (low)	177.4	-0.22831	-1.451	0.147
		Vegetation structural complexity		0.04212	0.531	0.596