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The influence of the soil management systems on aboveground and seed bank weed communities in olive orchards

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Abstract

The biodiversity of farmed landscapes is, in the context of agricultural intensification, a key aspect with regard to improving the sustainability of agroecosystems. Olive groves are undergoing rapid changes because of the spread of intensive farming systems, which may have negative environmental impacts. This paper reports a survey on the aboveground flora and seed banks in five olive groves located in Andalusia (Southern Spain). In this study, the following three management systems have been compared: no-tillage, with the mowing of spontaneous weedy vegetation; no-tillage, with the mowing of planted cover crops (*Poaceae*); and conventional tillage practices. Results showed that coverage and an abundance of vegetation are favored by spontaneous weedy vegetation with mowing management, while the richness of aboveground species was affected by landscape diversity and the presence of edges, which increases the richness and diversity of aboveground flora species in olive groves. Seed bank composition showed a low relationship with aboveground flora in the three cover crop management systems. The multivariate analysis performed pointed to those seed species that have a major influence on the aboveground flora communities of each of the three agricultural systems. The seed bank was clearly impoverished in terms of both abundance and species richness after the long-term conventional tillage practices. We conclude that the intensive long-term conventional tillage dramatically reduces weed communities in olive orchards and the subsequent ecosystem services provided by them.

Keywords: biodiversity; cover crop; *Olea europaea*; seed bank; soil management; weeds

Table S1 List of weed species identified during fieldwork. Management systems: 1 = bare ground, 2 = natural cover crops and 3 = planted cover crops.

Table S2 List of seed species identified during fieldwork. Management systems: 1 = bare ground, 2 = natural cover crops and 3 = planted cover crops. % of seeds = proportion of the identified 45 seeds in the germinated seeds (531).

Table S3 Results of sequential test of distance-based linear model for selection of seed <<Query: ‘seedbank’ has been changed to ‘seed bank’ across the file to maintain consistency. Please confirm if this is fine. Ans: Ok>>bank species of 2014 that could be included in the best model.

1 INTRODUCTION

The effects of the recent intensification of agriculture on biodiversity are a major concern in rural landscapes dominated by agriculture with regard to improving farm sustainability and the provision of ecosystem services (Cohen et al., 2015). The impact of agriculture on biodiversity depends on the practices and their type, frequency and intensity (Nascimbene, Marini, Ivan, & Zottini, 2013). Of these practices, weeding and ploughing reduce herbaceous plant diversity more than mowing, sowing or grazing (Cohen et al., 2015). However, other conventional agricultural practices, such as fertilization and irrigation, have a direct positive effect on herbaceous biomass (Grime, 1979).

One example of agricultural intensification is the implantation of new intensive olive orchard systems as a result of both the enlargement and the intensification of farming (Gómez et al., 2018). An increased demand for olive oil has resulted in significant conversion of open arable land or even traditional rainfed olive groves into intensive irrigated olive groves (Ramos & Santos, 2009). This new intensive olive faming is characterized by a high density of trees, irrigation, yearly fertilization and pruning, the use of biocides for pest and weed control, frequent soil tillage (once to three times per year) and mechanized harvesting (Metzidakis, Martinez-Vilela, Nieto, & Basso, 2008). These practices have incorporated new production techniques with a considerable input of energy and water at the expense of natural resources (Guzmán & Alonso, 2008). Moreover, the Common Agricultural Policy (CAP) encouraged the enlargement and intensification of olive systems during the last two decades, which led to certain sustainability problems, such as soil erosion (Gómez, Sobrinho, Giráldez, & Fereres, 2009), the overexploitation of water resources, diffuse water pollution, reservoir clogging, simplification of the agricultural landscape (Parra-López, Groot, Carmona-Torres, & Rossing, 2009), a contribution to climate change (Rodríguez-Entrena, Barreiro-Hurlé, Gómez-Limón, Espinosa-Goded, & Castro-Rodríguez, 2012) and the loss of biodiversity (Carpio, Castro, Mingo, & Tortosa, 2017; Carpio, Oteros, Tortosa, & Guerrero-Casado, 2016; Gómez-Limón, Picazo-Tadeo, & Reig-Martínez, 2012).

In order to avoid the negative effects of intensified agriculture, the CAP stimulates soil conservation practices in olive groves, such as not burning olive-suckering debris, shredding olive-pruning debris for use as inert soil cover and using cover crops under mower control (Rodríguez-Entrena & Arriaza, 2013). One example of these practices is ground flora cover, which consists of an intertree herbaceous vegetation strip, although it can also extend as a continuous covering across the crop (Paredes, Cayuela, Gurr, & Campos, 2015), which may be natural and spontaneous or cultivated vegetation (Simoes, Belo, Pinto-Cruz, & Pinheiro, 2014). In the case of cultivated cover, ground cover can be formed using a single species or a polyculture composed of legume and grass species (Guerrero-Casado, Carpio, Prada, & Tortosa, 2015). The use of cover crops within annual or woody crops could, therefore, support more weed diversity than crops growing in intensive agricultural habitats. Cover crops in olive orchards have been shown to play an important role in improving the multifunctionality of the crop growing in the Mediterranean area (Simoes et al., 2014). For instance, herbaceous cover crops in olive groves offer favorable conditions for many fauna taxa, such as arthropods, reptiles, mammals and birds (Carpio et al., 2017; Carpio, Castro, & Tortosa, 2018; Castro-Caro, Barrio, & Tortosa, 2015), as well as positive agronomic effects, such as reducing soil erosion (Gómez et al., 2018) or improving soil properties (Gómez et al., 2009). Previous studies have indicated that ground flora in olive groves should ideally combine adequate positive effects on the agroenvironment with only marginal negative competitive effects on the olive trees (Fracchiolla, Caramia, Lasorella, & Montemurro, 2013). Weed communities should, therefore, be integrally managed not as a mere “target” but as a community that is composed of individuals interacting with each other, with the crop and with all agroecosystem components (Fracchiolla et al., 2016).

The effects of different management practices on weed composition have been assessed in many cropping systems (Fried, Kazakou, & Gaba, 2012), including woody crops such as almond, citrus or apple orchards (Fracchiolla et al., 2016; Mas, Poggio, & Verdù, 2007; Minãrro, 2012; Shrestha, Knezevic, Roy, Ball-Coelho, & Swanton, 2002). However, little information is available about the use of herbaceous ground cover on weed communities and seed banks in olive groves (Huqi, Dhima, Vasilakoglou, Keco, & Salaku, 2009). The aim of this study is, therefore, i) to compare the influence of different soil management practices (conventional tillage; no-tillage, with the mowing of spontaneous weedy vegetation; and no-tillage, with the mowing of planted cover crops (*Poaceae*) on the diversity and composition of weed communities and soil seed banks; ii) to determine the relationship between aboveground flora and the seed bank in the three management systems; and iii) to explored the effect of patches of natural vegetation and landscape diversity on the diversity of aboveground flora and seed banks.

2 MATERIAL AND METHODS

2.1 Study area

This study was conducted in Andalusia (37°30′–37°58′N, 4°17′–4°56′W, at 159–369 m.a.s.l.<<Query: Please define m.a.s.l. Ans: meters above sea level>>), in the south of the Iberian Peninsula (Figure 1), which is characterized by a dry Mediterranean climate (an average annual rainfall of 526 ± 186 mm for the last 20 years and monthly mean temperatures of 8–26°C). Five study plots (mean surface ± *SD* = 7.1 ± 2.7 ha) were selected: no-tillage, with the mowing of spontaneous weedy vegetation, *n* = 2; no-tillage, with the mowing of planted cover crops, *n* = 1; and conventional tillage, *n* = 2. These categories were selected in order to compare conventional bare ground with no ground flora, spontaneous ground flora (multispecific) and a monospecific planted cover crop of *Poaceae* (*Bromus rubens*). The management of conventional olive groves is characterized by the regular use of the plow (e.g., consisting of three to four passes, 0.15 m deep, with a rotary tiller [5.5 h.p.] per year, starting after the first rain in late September or early October to control weeds in the streets of the olive groves) and herbicide-based weed control (glyphosate was applied [Piton, 0.36 kg a.e. L^{-1}, <<Query: Please define a.e. Ans: aerosol>>Dow AgroSciences, Indianapolis, Indiana] at 2.1 kg a.e. ha^{-1}), while the olive groves with covers crops (both types) are characterized by mowing, through tractor-driven rotary cutting with blades mounted on a horizontal axle, to cut weeds to a height of about 5 cm above the ground. The plots were integrated into an olive crop-dominated landscape, with more than 80% of total area, with the remaining 20% being devoted to vineyards, sunflower and cereal, in which agricultural intensification has eliminated most of the natural vegetation. The olive trees were 10–100 years old, and the distance between them varied by between 7 and 10 m.

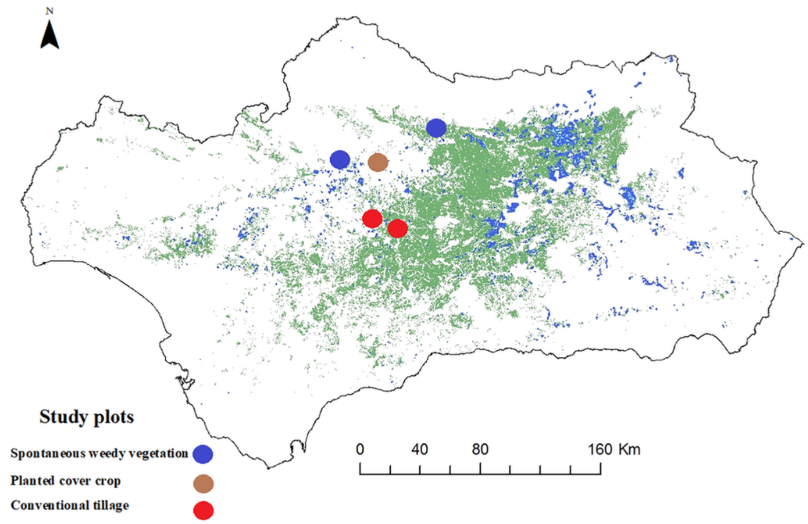

Figure 1 Study plots (colored points) and the distribution of unirrigated olive groves (green areas) and irrigated olive groves (blue areas) in Andalusia (Spain)

2.2 Vegetation sampling

The samples of aboveground flora<<Query: Please confirm if the edits made to the sentence 'The samples of aboveground flora...' are fine. Ans: ok>> were collected during three samplings repeated in spring (April, May and June) in 2014 and 2015 (Figure 2). In the Mediterranean climate, characterized by dry and hot summers and cold winters, this period (spring) is the period of maximum diversity of flora and the period of maximum emergence and flowering of species, which allows its identification (Cowling, Rundel, Lamont, Arroyo, & Arianoutsou, 1996). The abundance and diversity of aboveground<<Query: Please confirm if the edits made to the sentence 'The abundance and diversity of aboveground...' are fine. Ans: ok>> flora (weed) was sampled along two linear transects (100 m in length) in two rows of olive trees in 10-points 0.5 m^2 plots separated by 10 m in each row (Guerrero-Casado et al., 2015). All the weed species at these sampling points were identified; the total number of individuals was recorded; and the total ground coverage at a particular point was estimated visually as a proportion of an area, which was always calculated by the same observer. The Shannon diversity index for the weed community and the surface covered by aboveground flora were calculated at the sampling point level per month (2 transect × 10-point × 5 states × 3-month × 2 year = 600 sampling points).

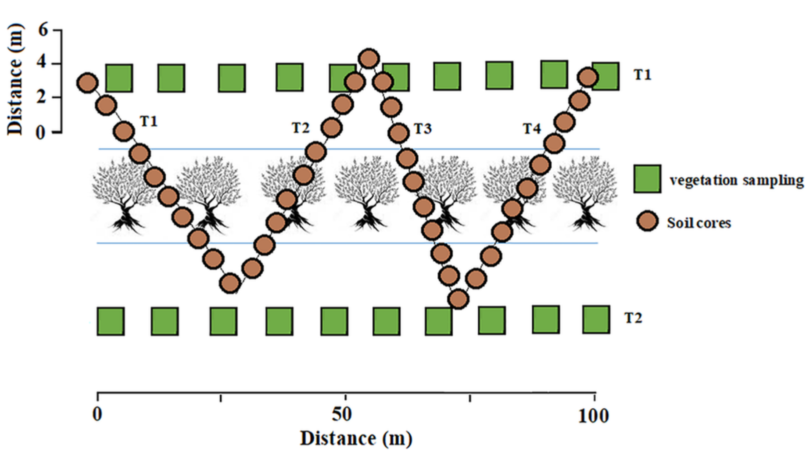

Figure 2 Sampling design used to survey plant species in the aboveground vegetation (20 quadrant 0.5 × 0.5 m) and soil seed bank (40 soil cores) in zigzagging transects, spanning both sides of the olive groves (*n* = 5 study plots)

2.3 Seed bank sampling

The soil seed bank in each field site was sampled in March 2014 when the soil was still bare and had no vegetation, prior to control practice (Fracchiolla et al., 2016). Soil samples were taken using cylindrical soil cores (7.62 cm diameter × 15.24 cm depth) from four zigzagging transects in each study plot in the same places as the aboveground vegetation (Figure 2). Ten soil seed bank samplings per transect were evenly spaced (in zigzags) between the transects of the vegetation surveys (40 cores per site in total) (Figure 2). These cores were stored (<2 days) at 4°C in darkness until processing. The samples collected for the seed bank were disaggregated in water with sodium hexametaphosphate (15 g/L at pH = 7) (Crowe, 1985) and were sieved in a 500-μm mesh.

Once dry, the samples were sieved in 4 to 0.2 mm sieves. Seeds larger than 4 mm were counted and identified using a magnifying glass, while seeds <4 mm were sown in plastic trays (57 × 42 × 8 cm) containing mixed substrate (75% vegetal substrate, 15% sand and 10% perlite) and moistened. The composition of the soil seed bank (<4 mm) was determined using the seedling emergence method over an 8-month period in a greenhouse (University of Cordoba). The trays remained in darkness until the germination of the seeds, at which time the trays were moved into a growth chamber under a photoperiod of 16 hr light and 8 hr of darkness, at a temperature of 22°C (±2°C) and a humidity of 32% (±5%), and were watered every 2 days by spraying the substrate. Seedlings were counted and removed from the trays once they were sufficiently large to be identified from other species. Representative seedlings were transplanted into 10 cm pots and grown until they were identified (Romero-Zarco, 2015; Valdés, Talavera, & Fernández-Galiano, 1987). Plants not in flower were identified by comparing their physical features with those of species that were currently flowering on the corresponding field site in 2014 and 2015.

2.4 Diversity landscape indexes

Several weed species are very sensitive to the distance from the edge (species dispersed by wind) (Cubiña & Aide, 2001). The diversity of the surrounding landscape may also affect the diversity of the seed bank as remnants of natural vegetation act as a plant refuge and a seed source, hosting the highest plant diversity (Barrio, Bueno, Villafuerte, & Tortosa, 2013; Dalton, Carpenter, Boutin, & Allison, 2017). Landscape diversity was measured by using two diversity variables at the site level: (a) the Shannon index and (b) the edge density of the landscape, which were obtained using FRAGSTATS4<<Query: Please provide manufacturer name of 'FRAGSTATS4.1', 'InfoStats software' and 'Primer, version 6'. Ans: McGarigal, K., SA Cushman, and E Ene. 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: http://www.umass.edu/landeco/research/fragstats/fragstats.html
Di Rienzo, J. A., Casanoves, F., Balzarini, M. G., González, L., Tablada, M., & Robledo, Y. C. (2011). InfoStat versión 2011. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina. URL http://www. infostat. com. ar, 8, 195-199.
Clarke, K. R., & Gorley, R. N. (2006). PRIMER ver. 6. User Manual/Tutorial. PRIMER-E, Plymouth, UK.>>.1 software. The landscape diversity index and edge density were calculated in a 500-m radius buffer around the center of the sampling site. The different land cover classes (urban land uses, rivers and natural streams, arable crops, olive groves, vineyards, irrigated crops, citrus and dense scrub) were recorded for each buffer. Information concerning land cover classes was obtained from aerial photographs (Junta de Andalucía, 2003).

2.5 Statistical analysis

In order to determine the relationships between olive grove type (conventional tillage; no-tillage, with the mowing of spontaneous weedy vegetation; and no-tillage, with the mowing of planted cover crops) and seed species richness (Model 1) and total seed abundance (Model 2), two generalized linear mixed models (GLMMs) were developed. In both models, the Shannon index of the landscape, percentage of cover and edge density were included as a covariable, whereas management (three levels) was added as fixed factors. In these models, the experimental unit was the soil core (n = 200). In both models, a Poisson distribution and the log-link function were used.

With regard to aboveground flora, three GLMMs were developed in order to determine the relationships among each type of olive grove and (a) plant richness (Model 3), (b) abundance of individuals (Model 4) and (c) percentage of coverage (Model 5). In all the models, the Shannon index of the landscape and edge density were included as a covariable, whereas management (three levels) and year (two levels) were added as fixed factors. The sampling plots (five levels) were considered a random factor in all the models, such that transect was nested in the plot (n = 2), and a Poisson distribution and log-link function were used for Models 1 and 2, whereas a normal distribution and identity-link function were used for Model 3. In these models, the experimental unit was sampling point (n = 600).

Fisher's least significant difference test for comparisons of the estimated means within a mixed analysis was developed to check the differences among the level of olive grove management systems and to illustrate the interactions. The selection of the most plausible models was carried out by comparing Akaike's information criterion (AIC) in the models following a backward procedure. These statistical analyses were performed using InfoStats software.

Dissimilarities in the composition of the plant communities according to the type of soil management and seed bank species composition, along with the 2015 aboveground flora community, were tested using the permutational multivariate analysis of variance (PERMANOVA). The PERMANOVA was performed by using management (three levels: conventional tillage; no-tillage, with the mowing of spontaneous weedy vegetation; and no-tillage, with the mowing of planted cover crops) and plant community (two levels; soil seed bank in 2014 and aboveground flora in the year 2015) as fixed factors. Type I Sum of Squares was used, and 9,999 permutations were performed to derive an empirical p-value for the F statistic. Differences in plant communities (seed bank and aboveground flora) according to the olive soil management systems were visualized by means of nonmetric multidimensional scaling (NMDS) using the Bray–Curtis dissimilarity index.

The distance-based linear model (DistLM) is analogous to linear multiple regression and was used to identify the relationship between predictor variables (in this case, seed species) and the Bray–Curtis dissimilarity matrix performed on the 2015 aboveground flora samples. Two DistLM analyses were<<Query: Please confirm if the edits made to the sentence ‘Two DistLM analyses were...’ are fine. Ans: ok>> used to identify the relationship between the seed bank species from the year 2014 and aboveground flora. The first DistLM was performed with a forward procedure, 9,999 permutations and R^2 as criteria. The sequential test obtained in this analysis made it possible to select those seed species that had a significant effect on the variability observed in the 2015 aboveground flora ($p < .05$). These seed species were included in the second DistLM, which was also performed with 9,999 permutations, while an AICc (AIC corrected for small number of samples) was used as a selection criterion (owing to the low ratio of samples/predictor variables), and “best” was used as the selection procedure. Finally, a distance-based redundancy analysis (dbRDA) was used to visualize the DistLM results as principal components. These multivariate analyses were performed using Primer, version 6, including the PERMANOVA+ add-on package (Anderson, Gorley, & Clarke, 2008).

3 RESULTS

3.1 Comparison of soil seed bank and ground flora in the olive groves

A total of 148 plant species were identified, including 45 species in the soil seed bank and 135 in the aboveground vegetation of the olive groves, of which 32 were present in both communities. The most common species of aboveground flora, occurring in at least 80% of the transects, were *Anagallis arvensis*, *B. rubens* and *Bromus hordeaceus*, while in the case of the seed banks, they were *A. arvensis*, *Campanula erinus*, *Galium murale*, *Heliotropium europaeum*, *Lamium amplexicaule*, *Poa infirma* and *Stellaria media*. The complete list of species is provided in Table S1 (plants) and Table S2 (seed). A total of 531 seedlings germinated and were identified from the soil seed bank. The average (±*SD*) seed density per site was 106 ± 88 seedlings/m^2 (ranging from 39 to 259 seedlings/m^2).

3.2 Effects of soil management systems on vegetation and soil seed richness and abundance

With regard to seed richness (Model 1), the best model showed a significant effect of olive grove management and a positive effect of the edge density (Table 1). The results showed significant differences between no-tillage, with the mowing of spontaneous weedy vegetation and no-tillage, with the mowing of planted cover crops versus conventional tillage but not between both mowing managements (Figure 3a). With regard to total seed abundance (Model 2), the best model showed a significant effect of olive grove management, the landscape diversity index, edge density and the percentage of cover (Table 1). The post-hoc test showed that the abundance in mowing of spontaneous weedy vegetation was significantly higher than conventional tillage and in mowing of planted cover crops (Figure 3b).

Table 1 F-values and coefficients of the variables included in the best models to explain seed species richness (Model 1) and total seed abundance (Model 2)

Variables	**F-value**	**Coefficient ± *SE***
Seed richness (Model 1)		
Intercept	6.6**	−1.64 ± 0.34
Management	4.46**	Bare ground = −0.90 ± 0.25
		Monospecific cover crop = −0.28 ± 0.26
Edge density	23.44***	0.06 ± 0.01
Total seed abundance (Model 2)		
Intercept	15.3***	−1.96 ± 0.40
Management	14.9***	Bare ground = −1.59 ± 0.25
		Monospecific cover crop = −1.13 ± 0.33
Edge density	16.49***	0.05 ± 0.01
Shannon index of the landscape	5.39*	1.03 ± 0.44
Percentage of cover	16.7***	0.03 ± 0.01

Note: Coefficients for the level of fixed factor were calculated using reference value of "Natural cover cro p" in the variable "management".

* $p < .05$.

** $p < .01$.

*** $p < .001$.

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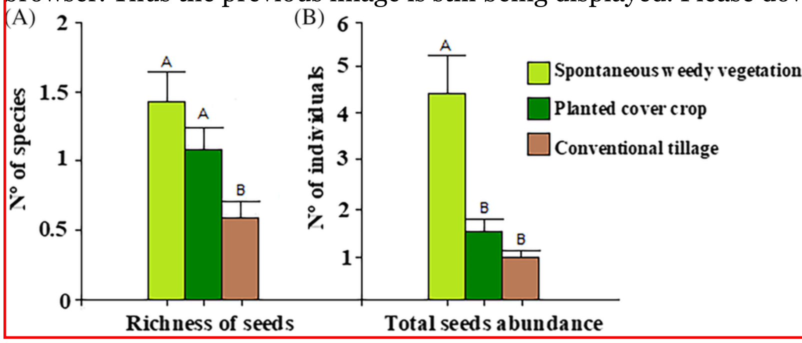

Figure 3 Predicted mean values (±*SE*) of richness of seeds (a) and abundance of seeds (b) in different olive grove management <<Query: The supplied figures 3, 4 are in poor text quality. Kindly provide us the better version. Please refer to http://media.wiley.com/assets/7323/92/electronic_artwork_guidelines.pdf for the guidelines on how to produce good figures. Ans: Text quality was improved>>systems. Capital letters indicate significant differences ($p < .05$) among management according to Fisher's least significant difference tests

In relation to aboveground flora (Model 3), the best model showed a significant effect of sampling year, the landscape diversity index and edge density (Table 2). In addition, the best model of abundance of individuals (Model 4) showed a significant effect of olive grove management, the landscape diversity index, the sampling year and the edge density (Table 2). The post-hoc test showed significant differences in abundance among the three soil management systems (Figure 4a). Finally, the percentage of coverage (Model 5) was significantly affected by type of management and sampling year (Table 2). The post-hoc test showed significant differences in abundance among the three soil management systems (Figure 4b). In both models (4 and 5), the mowing of spontaneous weedy vegetation had the highest values (for abundance and coverage), followed by the mowing of plated cover crops and, finally, the conventional tillage.

Table 2 F-values and coefficients of the variables included in the best models to explain plant aboveground flora (Model 3), abundance of individuals (Model 4) and percentage of coverage (Model 5)

Variables	F-value	Coefficient ± *SE*
Aboveground flora (Model 3)		
Intercept	6.22**	1.1 ± 0.11
Shannon index of the landscape	21.52***	0.67 ± 0.06
Year	62.22***	2015 = −0.49 ± 0.06
Edge density	57.57***	0.03 ± 0.0044

Variables	F-value	Coefficient ± *SE*
Abundance of individuals (Model 4)		
Intercept	55.3^{***}	3.07 ± 0.07
Management	146.6^{***}	
		Bare ground = −0.45 ± 0.06
		Monospecific cover crop = −0.16 ± 0.06
Year	151.59^{***}	2015 = −0.18 ± 0.01
Shannon index of the landscape	56.39^{***}	1.94 ± 0.08
Edge density	80.7^{***}	0.08 ± 0.002
Percentage of coverage (Model 5)		
Intercept	6.6^{*}	3.85 ± 0.14
Year	5.42^{*}	2015 = −0.05 ± 0.02
Management	49.31^{***}	
		Bare ground = −0.67 ± 0.17
		Monospecific cover crop = −0.35 ± 0.13

Note: Coefficients for the level of fixed factors were calculated using reference values of “Natural cover crop” in the variable “management” and “2014” in the variable “year”.

$^{*}p < .05$.

$^{**}p < .01$.

$^{***}p < .001$.

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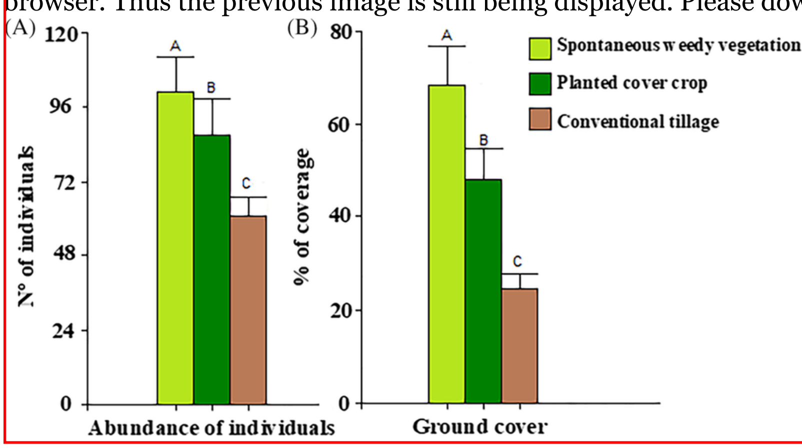

Figure 4 Predicted mean values (±*SE*) of abundance of plants (a) and percentage of coverage (b) in different olive grove management systems. Capital letters indicate significant differences ($p < .05$) among management according to Fisher's least significant difference tests

3.3 Effects of soil management on aboveground flora and soil seed bank community composition

The PERMANOVA results indicated that the seed bank in 2014 and the subsequent aboveground flora recorded in 2015 were different (Table 3), attaining a dissimilarity of 73.77%. In addition, the communities sampled under different management types were also significantly different (Table 3).

Table 3 Permutational multivariate analysis of variance of plant species composition based on plant communities and olive cover crop

Variable		***df***	**M.S.**	**Pseudo-F**
Factors	Plant community	1	59,981	31.26***
	Cover crop	2	25,058	13.06***
	Plant community × cover crop	2	19,466	10.13***
Residuals		194	1919	
Total		199		
Pairwise test: Cover crop		*df*	*t*	Dissimilarity (%)
Bare ground versus monospecific cover		1	3.98***	69.78
Bare ground versus natural cover		1	3.81***	72.17
Monospecific cover versus natural cover		1	2.89***	69.62
Pairwise test: Plant community		*df*	*t*	Dissimilarity (%)
Seed bank versus aboveground plants 2015		1	5.80***	73.77

[*] $p < .05$<<Query: Please cite footnote “*” in Table 3. Ans: These values do not appear in table 3 only ***, so they can be removed from the figure caption.>>.

[**] $p \leq 0.01$<<Query: Please cite footnote “**” in Table 3. Ans: These values do not appear in table 3 only ***, so they can be removed from the figure caption.“**” p < 0.01>>.

[***] $p \leq .001$.

The interaction between both factors (management type and seed bank) also resulted in a significant difference with regard to plant communities. The NMDS (Figure 5) shows that the aboveground plants in natural cover crops collected in 2015 differed from the seed bank communities. It should also be noted that there is a wide distribution in the figure, suggesting high variability in community composition. Furthermore, when conventional tillage occurs, the seed bank samples and aboveground herbaceous plants are located close together in the NMDS, indicating a low dissimilarity between their species composition (Figure 5).

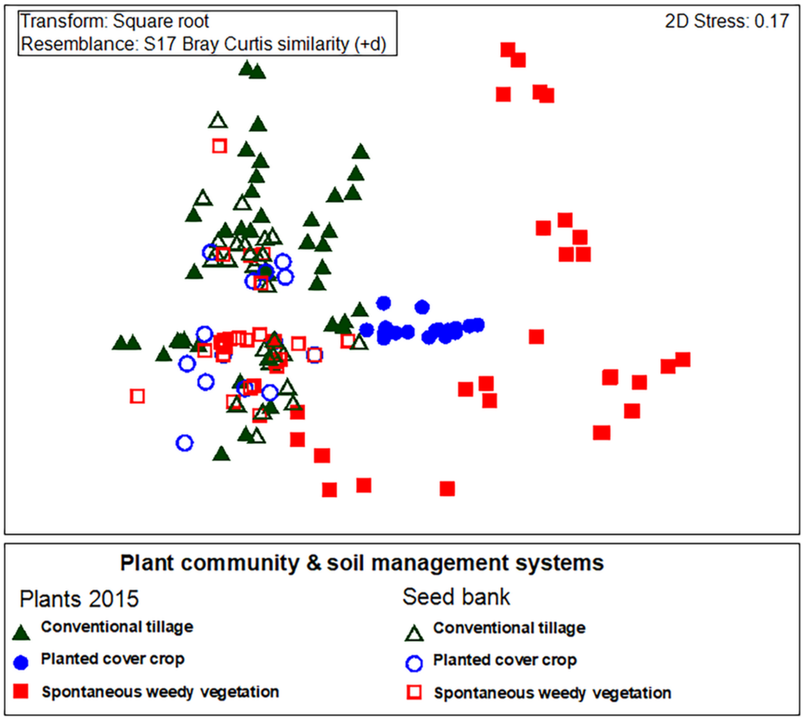

Figure 5 Nonmetric multidimensional scaling ordinations of plant communities for each management system on the basis of Bray–Curtis dissimilarities of square root transformed abundance data

3.4 Relationship between the soil seed bank and ground flora

The sequential test performed by means of the first DistLM indicated that 25 species from the 2014 seed bank had an effect on the structure and composition of the 2015 aboveground flora (Table S3) and that they should, therefore, be included in order to build the best predictive model.

The second DistLM was performed by including only the 25 species mentioned above, and the dbRDA was consequently performed by including vectors corresponding to these species. The model had two axes that explained 55.4% of the fitted variation and 17% of the total variation (Figure 6). In Figure 6, the samples corresponding to olive groves with spontaneous weedy vegetation are distributed along the first axis. Samples from a planted cover crop also have a horizontal distribution but with a narrower range. The samples of herbaceous plants collected in olive crops with conventional tillage are, meanwhile, dispersed along the second axis (Figure 6).

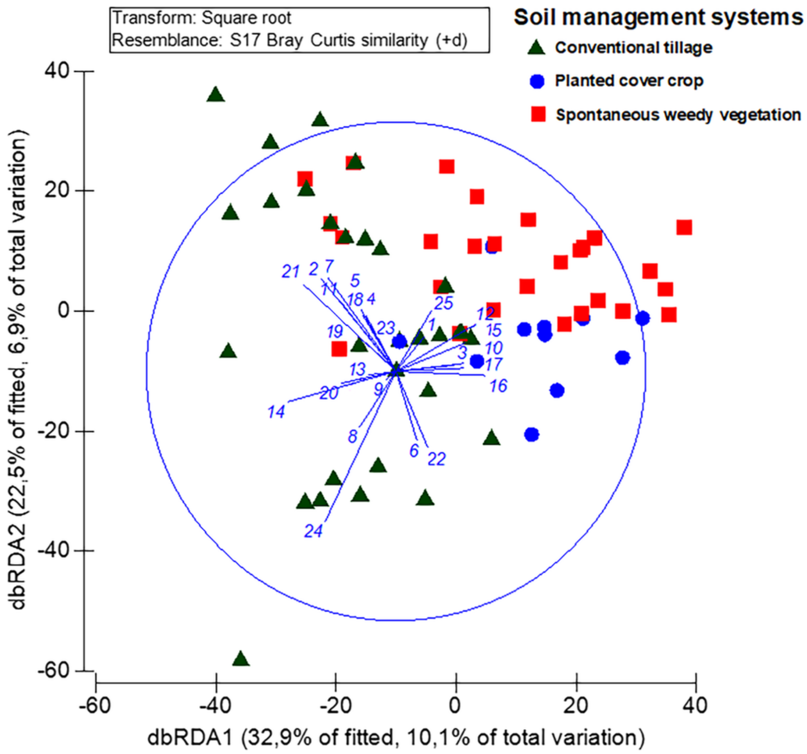

Figure 6 Distance-based redundancy analysis (dbRDA) of plant communities of each management system showing vector overlays of seed bank species included in the best model by distance-based linear model analysis. Species corresponding to each vector are showed in Table S3

With regard to the seed bank, the species *A. arvensis* var. *caerulea*, *Chrozophora tinctoria*, *Diplotaxis catholica*, *L. amplexicaule* and *Leontodon longirostris* (vector numbers: 3, 10, 12, 15 and 16, respectively) have a positive relationship with the first axis and, therefore, with the spontaneous weedy vegetation crop samples (Figure 6). The direction of the *L. longirostris* vector indicates the close relationship of this species with planted cover crop olives (Figure 6). However, the short length of these vectors indicates a weak relationship with the aboveground communities of spontaneous weedy vegetation crop olives. The seed bank species *Cerastium glomeratum*, *Erophila verna* subsp. *praecox*, *G. murale* and *Pulicaria dysenterica* (vector numbers: 9, 13, 14 and 20, respectively) had a negative relationship with the first axis, and the vector of *G. murale* was the longest, suggesting a negative relationship between this species and natural cover crop herbaceous communities (Figure 6).

With regard to the second axis, the species *A. arvensis*, *Arabidopsis thaliana*, *Capsella bursa-pastoris*, *P. infirma*, *Pulicaria paludosa* and *Sagina apetala* (vector numbers: 2, 4, 7, 19, 21 and 23, respectively) had a positive relationship, suggesting a relationship with the conventional tillage communities collected in 2015. The species *C. erinus*, *Centranthus calcitrapae*, *C. glomeratum*, *Rumex scutatus* and *S. media* (vector numbers: 6, 8, 9, 22 and 24, respectively) had a negative relationship with the second axis (Figure 6). However, the direction of these vectors indicates a relationship with the communities of some conventional tillage samples. The *S. media* vector, which was the longest vector, indicates the close relationship between the seeds of this specie and conventional tillage samples (Figure 6).

4 DISCUSSION

We found that soil management systems strongly affected seed species richness and abundance, in addition to the abundance of the aboveground flora and coverage. On the contrary, aboveground richness was unaffected by this factor, suggesting that plant richness is not directly affected by soil management. A similar conclusion was reached by Dalton et al. (2017), who examined the effects of agricultural disturbance on aboveground riparian vegetation, or by Bowers and Boutin (2008), suggesting that aboveground species richness is not a sensitive indicator of these anthropogenic stressors. In this context, it is expected that the communities of seeds and vegetation diverge under either stable conditions with low disturbance or under stressful conditions (e.g., frequent plow or clearing; Bossuyt & Honnay, 2008), as occurs in the study area. The soil seed banks found in this study, in the olive groves, had a lower species richness (average 14.6 species per study plot) compared to that reported for three habitats in 102 European soil seed bank studies (approximately 32, 26 and 24 species for grasslands, forests and marshes, respectively) (see a review in Bossuyt & Honnay, 2008), which indicates the impoverishment of the seed bank biodiversity suffered in olive orchards. Within our study plots, olive groves with spontaneous weedy vegetation had an average of three times more seed species (24.5 species) than those with planted cover crops or conventional tillage (8 species). These results illustrate the impact of the continuous elimination of aboveground vegetation (by means of tillage or herbicides) on the seed bank in the form of a loss of biodiversity. In addition to spontaneous weedy vegetation, landscape diversity and edge density also had a positive effect on the community composition of vegetation and the soil seed bank.

Our results show that the richness of seeds species was positively influenced by vegetation cover crops, regardless of whether it was planted or natural, which is consistent with studies on other crops, such as those of Mirsky, Gallandt, Mortensen, Curran, and Shumway (2010), which demonstrated how differences in seed species composition were mainly related to tillage system and soil disturbance. Our results also suggest that the aboveground flora disturbance (conventional tillage or planted cover crops) may strongly reduce weed seed banks as we found that there was a higher amount of seeds when spontaneous weedy vegetation occurred. These results coincide with those of Cordeau, Guillemin, Reibel, and Chauvel (2015), who found that no-till cropping systems which include cover crops (e.g., ryegrass in the study in question) could lead to important changes in weed communities by decreasing some annual weed populations, thus indicating that annual weeds could be disadvantaged by no-tillage systems using monospecific cover crops. Monospecific cover crops are established during the winter period and can compete with weeds (Yenish, Worsham, & York, 1996). However, in spontaneous weedy vegetation cover, the weed flora is dominated by annual species (Fried, Petit, Dessaint, & Reboud, 2009), and weed population dynamics are strongly influenced by the prevailing cropping systems (Torresen, Skuterud, Tandsaether, & Hagemo, 2003). The edge density had a positive effect on richness and seed abundance as hedges, boundaries and streams may act as a seed dispersal point (Cubiña & Aide, 2001). Finally, the number of seeds was also positively affected by the landscape diversity index and the percentage of cover. Previous studies, such as that of Gabriel, Thies, and Tscharntke (2005), showed that patterns of plant diversity are often related to local site conditions, in which the landscape context may be an important factor for local plant and seed species richness. Seed rain from ruderal source habitats (adjacent crops, hedges or ditches), and disturbed edges may increase the abundance of a seed bank. An increase in the percentage of coverage is, similarly, directly related to an increase in plant biomass and, therefore, in the production of seed quantity (Henderson, Petersen, & Redak, 1988).

As for the richness and abundance of the aboveground vegetation, both were positively influenced by the landscape diversity index and edge density and differed between the studied years. These results agree with Cubiña and Aide (2001), who showed that plant species richness underwent a dramatic decrease in seedling density and species richness with the distance from the forest edge. The year also had an effect on the abundance, richness of plants and percentage of coverage, with lower values being obtained for the three variables in 2015. This could be explained by the fact that it was a dry year (which might limit the germination and productivity of plants), with an average precipitation throughout the study period of 494 ± 83 mm in 2014 versus 411 ± 37 mm in 2015. Finally, our results show that management systems have a significant impact on the abundance of plants and the percentage of cover. Both abundance and ground cover had higher values when spontaneous weedy vegetation occurred, followed by planted cover crops and, finally, by conventional tillage. These results coincide with those of Teasdale, Hatfield, Buhler, and Stewart (1998), who reported the contribution of cover crops to increasing weeds in sustainable agricultural systems, thus supporting the "diversity begets diversity" hypothesis (Palmer & Maurer, 1997).

The soil seed bank and aboveground vegetation communities clearly differed as only 32 species were present as both plants and seeds. Previous studies have shown that the similarity between seed bank communities and aboveground vegetation is usually low in ecosystems such as wetlands, grasslands and forests (Hopfensperger, 2007). Light intensity and shade tolerance are considered drivers of germinations (Hopfensperger, 2007), and both environmental variables are strongly affected by the presence of vegetation cover in the crop. In addition, the proximity of vegetation structures could work as a source of herbaceous plants by means of the anemochory process. This coincides with our results as 17.5 and 65% of the plant species found were dispersed by means of anemochory and zoochory, respectively.

4.1 Relationship between the soil seed bank and ground flora

The results of DistLM and dbRDA indicated a low relation between seed bank species and herbaceous communities in the three cover crop managements. These results corroborate that the presence of seeds in soil is not the main factor to determine future herbaceous communities, which coincides with the findings of Gabriel et al. (2005), who proposed that the local species richness in arable lands is mainly related to the landscape context and to topographical heterogeneity.

5 CONCLUSIONS

The results of this study confirm that edge density and landscape diversity have a positive effect on both communities (seed bank and aboveground flora), acting as a refuge for the seed bank (Cubiña & Aide, 2001). Moreover, the richness of aboveground flora species is highly related to these vegetation structures as 76% of the flora species (103 of 135 species) are not found in the local seed bank. The presence of cover crops (especially spontaneous weedy vegetation crops) can also help to avoid a drastic reduction in the seed bank and, consequently, in the plant community. However, these results (case of planted cover crops) must be interpreted with caution due to the low number of plots. The results highlight that the seed bank is clearly impoverished in olive groves when compared to the average species richness reported in other habitats on European soil (reviewed in Bossuyt & Honnay, 2008). The intensive long-term applications of herbicides (particularly those of a pre-emergence nature), which are widely used in conventional practices, may explain our results in olive orchards. Ours results lead us to recommend the maintenance of a minimum spatial heterogeneity in order to permit weed biodiversity in the intensive olive orchard landscape. However, due to the strong climate effect on seed bank germination studies, a longer time series combined with a higher number of plots under different soil management types are required to test the long-term effect of soil management on weed diversity and the subsequent loss of ecosystem services of the herbaceous cover.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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