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Linkage between plant species diversity and soil-based functions along a post-agricultural succession are influenced by the vegetative forms

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Abstract

There is a growing body of knowledge that ecosystem functions, in particular soil-based ecosystem functions, are related to biodiversity. However, how plant species diversity influences soil-based functions along post-agricultural secondary succession is still a largely ignored question in Mediterranean semi-arid conditions. Therefore, we used the plant functional group approach to investigate the relationships between plant species diversity indices and soil-based functions including microbial biomass carbon (MBC), basal respiration (BR) and carbon sequestration (CS) across three different stages of the vegetation succession corresponding to ~ five years after agricultural abandonment, ~ 15 years after abandonment, and oak forests which represent the terminal stage. We also tested if these relationships are supported by the niche complementarity and selection effect hypotheses. The results showed that soil-based functions significantly increased with time since abandonment as BR, MBC and CS increased respectively by 1.7, 1.5 and 2.7 times across the three successional stages. We also found strong correlations between the diversity indices and the soil-based functions BR, MBC and CS which were positive for richness (R^2 values: 0.75, 0.74 and 0.75) and Shannon diversity (R^2 values: 0.61, 0.58 and 0.61) but negative for evenness (R^2 values: 0.38, 0.38 and 0.36 for, respectively). Similarly, richness and Shannon diversity of the different plant functional groups positively correlated with soil-based functions. However, contrasted results were found for evenness which positively correlated with soil-based functions for perennial grass only. We suggested that increasing the diversity of plant species and facilitating dominant species would be needed to improve the soil-based ecosystem functions after abandonment of degraded soils. This study also revealed that the mechanisms behind the relationships between biodiversity and ecosystems functions were influenced by the vegetative forms.

Keywords Carbon sequestration . Cropland abandonment . Land use change . Richness . Semi-arid forest

Highlights

- Species diversity and soil-based functions improve along the successional stages after land abandonment
- The relationships between plant diversity and soil-based functions are influenced by the plant functional groups. .
- Niche complementarity plays a more vital role in soil-based ecosystem functions than the selection effect.

Introduction

Biodiversity is one of the most important concepts in ecology and is essential for the preservation and maintenance of ecological services and functions in any ecosystem. The dependence of services and functions (i.e., water balancing, mitigation of the microclimate, limitation of erosion, carbon sequestration and soil fertility restoration), in each ecosystem on biodiversity on the one hand, and on the other hand, the accelerating trend of biodiversity reduction in recent decades (e.g. Verdura et al. 2019) has raised concerns about the decline of sustainable ecosystem services and functions (Deng 2012). In this regard, ecologists have been focusing on the impact of diversity on ecosystem functions and services over the past two decades (Tilman et al. 1997; Grime 1997; Naeem et al. 2009; Isbell et al. 2015).

In many parts of the world, human activities and their dependence on natural resources, especially forests, have caused land use changes and destruction of forests (e.g. Cai et al. 2018; Kepfer-Rojas et al. 2019; Heydari et al. 2019). These disturbances have led to the loss of ecological niches of many species, to reduced biodiversity (Isbell et al. 2017; Heydari et al. 2017 a; Miedema et al. 2019) and to the disruptions of various ecosystem services for instance in terms of food production,

71 pest and disease control, carbon sequestration (Cardinale et al. 2007; Poorter et al. 2015). Under
72 such circumstances, awareness of the relationship between diversity and ecosystem services is not
73 only important for the conscious management of forest areas but also valuable for the preservation
74 of biodiversity itself (Forrester and Bauhus 2016).

75 In many areas, in particular in the Mediterranean region, forests result from the secondary
76 succession leading abandoned agricultural lands to woodlands. Forest vegetation diversity was
77 shaped by this process as the successional pathways increased the complexity of forest structure
78 influencing species richness, species composition and variations of taxonomic and functional traits
79 (Lebrija-Trejos et al. 2010; Cadotte et al. 2011).

80 In addition, the development of a forest structure was accompanied by a profound modification of
81 the environmental factors such as changes in nutrients and light availability resulting in the gradual
82 replacement of pioneer species with permanent species more effective in increasing biomass
83 accumulation (e.g. Pinho et al. 2017). The increase in the presence of such species is directly
84 related to the production of the ecosystem and its ecological services such as carbon storage (Beer
85 et al. 2010).

86 In general, in examining the relationship between biodiversity and ecosystem functions, two main
87 hypotheses are mentioned including the concepts of ‘selection effects’ (species with specific traits
88 are dominant) (Tilman et al. 1997; Loreau et al. 2001) and ‘complementarity effect’ (niche
89 differentiation) (Loreau et al. 2001), which have shown contrasted results for different regions and
90 ecosystems. Some studies in forest ecosystems support the hypothesis of selection effects (Prado-
91 junior et al. 2016) while some support niche complementary (Mensah et al. 2018). These
92 contradictory results indicate that the mechanisms driving the diversity of ecosystem-service

relationships depend on various factors such as environmental factors, habitat heterogeneity, temporal and spatial scale, as well as changes of plant communities during succession.

The evaluation of various functions of the ecosystem is an effective way to highlight the relative importance of the selection effects versus the niche complementary hypotheses. For example, Finke and Snyder (2008) emphasized the importance of diversity in increasing the use of available resources (due to niche complementary) leading to a higher production of biomass and carbon storage. In contrast, Tahmasebi et al. (2017) put forward the central role played by the dominant ecosystem species (selection effects) while they found no evidence to support the niche complementary hypothesis. These contrasted studies illustrate that changes in environmental conditions can cause differences in the mechanisms that determine the relationships between biodiversity and ecosystem functioning (Mokany et al. 2015).

Soil, as an essential component of terrestrial ecosystem, provides various functions, including carbon storage and support vegetation establishment and growth and activity of various organisms (Binkley and Fisher 2013). Although, many studies have explored the relationships between biodiversity and aboveground biomass (Morandi et al. 2018; Wekesa et al. 2019), especially in forests, the relationships between species diversity indices and soil-based functions have received much less attention. Similarly, the negative impact of land use change on diversity and ecosystem functions was largely investigated (Paudyal et al. 2017; Newbold et al. 2019), while studies on the relationships between plant species diversity and soil-based functions during the secondary succession from abandoned agricultural lands to forests were less frequent.

Moreover, an approach based on plant functional groups could increase our insights related to the effect of diversity of different plants groups on ecosystem functions (Hevia et al. 2016; Biswas et al. 2019). In fact, the relationships between the diversity of different functional groups and the

above- ground biomass in forest systems have been largely studied (Zuo et al. 2018; Fayiah et al. 2019), but have been less investigated for soil-based ecosystem functions (e.g., carbon sequestration and basal respiration) (Rey Benayas et al. 2007). This was particularly proven in Mediterranean forests established on previous agricultural lands such as the Zagros oak forest in western Iran.

In this area, there is a long history of disturbances over the last half-century including grazing (Erfanzadeh et al. 2015; Hashemi et al. 2019) and fires (Heydari et al. 2020), linked to the high dependence of people's livelihood on oak forest services and functions and to the conversion of most of these forests into arable lands or agroforestry systems (Henareh Khalyani et al. 2013). These disturbances were shown to be major factors in the degradation of the physical, chemical and biological properties of the soil (Heydari et al. 2017 a; Hashemi et al. 2019). Afterward, some of these lands were abandoned as a result of conservation management by the office of the natural resources or due to a significant decline of soil fertility and were then gradually colonized by a forest vegetation.

The present study seeks to investigate the relationships between plant species diversity indices of functional groups and soil-based functions of this ecosystem according to three different stages of the vegetation succession corresponding to ~ five years after abandonment, ~ fifteen years after abandonment, and oak forests, which represent the 'climax' stage of the vegetation succession.

In this study, the functional groups are defined according to species growth form and lifespan.

We hypothesize that:

- i) Soil-based functions and diversity indices improve across the successional stages.
- ii) There is a positive relationship between species diversity and soil based functions supporting the niche complementary hypothesis.

iii) The functional groups differentially influence the relationships between diversity and ecosystem functions.

Methods

Site description

The forest cover of the study area (383 ha) was originally dominated by the Brant's oak (*Quercus brantii* Lindl.) and was partly cleared for agricultural needs. The study area is characterized by homogeneous physiographic conditions: a global flat topography (slope < 10 %) and a mean elevation of about 1450 m a.s.l. Forests were converted into an agroforestry system consisting in cultivating cereals between oak trees and shrubs (wheat/oak farming system). Due to rural-to-urban migration and to a loss of productivity after soil erosion, a part of these fields were abandoned at different time periods and progressively colonized by a woody vegetation. We selected three stages of the succession from abandoned areas to forests (Fig. 1):

(i) The forest stage ("FOR") which represents the terminal stage of the succession. Field evidences suggest that this stage was previously used by agroforestry, which was abandoned several decades ago (~ 40-60 years) although a precise date of abandonment cannot be given. It is composed of sparse overstory of Persian oak trees (density = 85 n/ha, mean height = 7.6 m) and an understory dominated by shrubs such as *Daphne mucronata* Royle and *Crataegus pontica* C. Koch. This formation is run as simple coppice mainly for the production of firewood.

(ii) The wheat/oak farming system after 15 years of abandonment from 1999-2014 ("LONG": long-term abandonment) and,

(iii) The wheat/oak farming system after 5 years of abandonment from 2009-2014 ("SHORT": short-term abandonment').

The climate of the area is of a Mediterranean type (Fathizadeh et al. 2017) characterized by a dry period of 5-6 months (May-October). The mean annual rainfall and temperature are 621.3 mm and 17°C, respectively (Ilam weather station, 1999-2015). The soil is classified as Inceptisol (Soil Survey Staff, 2014). It is a calcareous soil, rich in organic matter with a clay loamy texture and a mean depth of 30-40 cm (Heydari et al. 2017).

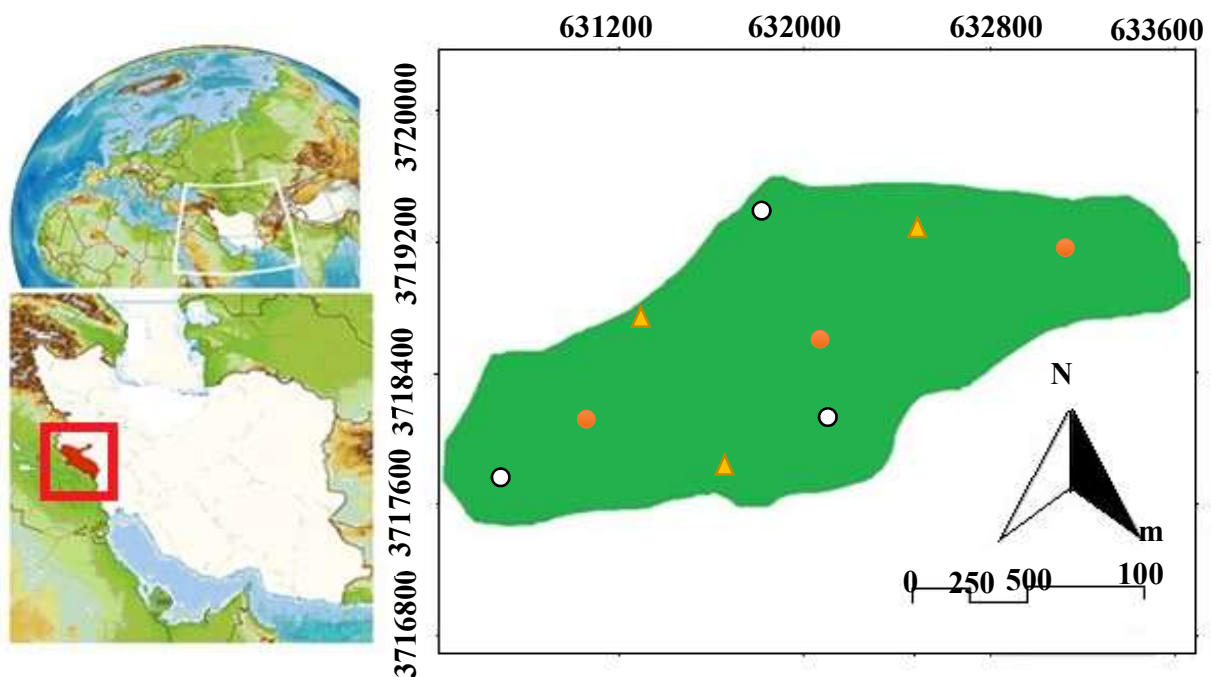


Fig 1. The location of the study area in Iran and Ilam province, ● : Forest, ▲ : Long- term abandonment and ○ : Short- term abandonment

Experimental design and vegetation measurements

Three areas, each of 2-4 ha, were selected for each stage of the succession (i.e. nine areas). Areas were selected in similar site conditions, in particular a same altitude (1450 m a.s.l.) and a comparable slope (<10%), and separated by a distance of 800 m to 1600 m. In each area, two randomly perpendicular transects of 30m length were set up. Seven plots composed of two

subplots of 1m² were regularly distributed along the transects (3 plots in each transect and 1 plot where transects met) (Tárrega et al. 2009). All vascular species were recorded on each subplot and each species was named according to the available literature and given of cover percentage. Each species was then distributed in one of the four functional groups based on plant life form (forb/grass) and plant life span (annual/perennial): annual forbs, annual grasses, perennial forbs and perennial grasses. These two plant traits were commonly used in previous studies because they are elucidative on species morphology, phenology, competitive competition potential and taxonomy (e.g. Verma et al. 2014).

We then computed at plot level three diversity indices: The species richness (*SR*), diversity (*H'*) and evenness (*J'*) using the following equations:

$$SR = S$$

$$H' = -\sum_{i=1}^S p_i \ln p_i \quad (\text{Shannon and Weaver 1949})$$

$$E = H' / \ln (S) \quad (\text{Pielou 1966})$$

Where *S* = total number of species and *p_i* = proportion of cover of species 'i'. All diversity indices were calculated using the Ecological Methodology software.

Soil sampling and analysis

Around each plot, three soil subsamples were collected at 20 cm depth and then combined (1 sample/plot). Soils were immediately sieved through a 2 mm sieve and divided into two subsamples. The first subsample was air dried and used to measure soil organic carbon (SOC) by

dichromate oxidation according to the Walkley-Black method (Nelson and Sommers 1982). The second subsample was kept at field moisture and stored at 4 °C for subsequent measurements of soil microbial activity. Microbial biomass carbon (MBC) was measured by determining the organic carbon in chloroform-fumigated and non-fumigated samples by dichromate oxidation, as described by Vance et al. (1987). Soil basal respiration (BR) was measured by trapping (in 1 M NaOH traps) and quantifying CO₂ that was emitted from soil samples over a five-day period (Alef and Nannipieri 1995).

The following equations was used for estimating carbon sequestration (CS):

$$CS (T.ha^{-1}) = 100 \times OC (\%) \times BD (g.cm^{-3}) \times \text{Soil depth (cm)}$$
 where OC is the organic carbon content and BD is the bulk density.

Also, undisturbed soil samples were also taken to determine bulk density (Blake and Hartge 1986).

Statistical analysis

First, the normality and homogeneity of variance of the data assessed by means of the Kolmogorov–Smirnov test and Levene's test, respectively, and the necessary conversions made when needed. The differences in diversity, richness and evenness indices of all species as well as different vegetative forms (annual forb, perennial forb, annual grass and perennial grass) among different stages of the succession were tested by one-way analysis of variance (ANOVA) followed by Duncan's multiple range test. Linear regressions were used to investigate the relationships between species diversity, richness and evenness indices of total species and soil-based functions: Microbial Biomass Carbon (MBC), Basal Respiration (BR) and Carbon Sequestration (CS). Pearson's correlation coefficient analysis was also used to determine the relationships between diversity, richness and evenness indices of different plant functional groups (annual forb, perennial

forb, annual grass and perennial grass) with soil-based functions including MBC, BR and CS. This analysis was performed using "ggplot2" package in R var. 3.6.0 (R Core Team 2019).

Results

Plant functional diversity among different stages of succession

Diversity, richness and evenness indices of total species and different functional groups based on growth form and lifespan were significantly different ($P < 0.01$) between successional stages (except evenness of annual grasses: $P=0.819$). The highest values of Shannon diversity and richness indices were observed in FOR, except for the annual grass group (maximum in LONG), while the lowest values were recorded in SHORT. Evenness showed a different pattern: it decreased from SHORT to FOR in all groups but Perennial forb and Perennial grass where values were the lowest in SHORT (Table 1).

Table 1 Mean values (mean \pm standard error) of plant diversity indices across the three stages of the secondary succession following land abandonment. Different letters indicate significant differences between three stages of the secondary succession: FOR: forest, SHORT: short-term abandonment and LONG: long-term abandonment.

Variables	<i>P-value</i>	<i>MS</i>	FOR	LONG	SHORT
Total species					
Richness	<0.001	2160.33	28.76 \pm 0.46 a	24.71 \pm 0.84 b	9.50 \pm 0.45 c
Evenness	<0.001	5.89	0.69 \pm 0.01 b	0.70 \pm 0.02 b	0.80 \pm 0.01 a
Shannon	<0.001	0.08	2.98 \pm 0.02 a	2.84 \pm 0.05 a	2.00 \pm 0.07 b
Annual forb					
Richness	<0.001	592.11	17.66 \pm 0.44 a	16.28 \pm 0.74 a	7.85 \pm 0.37 b
Evenness	<0.001	0.10	0.69 \pm 0.01 b	0.70 \pm 0.01 b	0.82 \pm 0.01 a
Shannon	<0.001	2.802	2.49 \pm 0.02 a	2.41 \pm 0.06 a	1.82 \pm 0.06 b
Perennial forb					

Richness	<0.001	267.57	7.00± 0.27 a	4.71± 0.23 b	0 c
Evenness	<0.001	4.94	0.81± 0.03 a	0.86± 0.02 a	0 b
Shannon	<0.001	1.71	1.71± 0.07 a	1.34± 0.05 b	0 c
<hr/>					
Annual grass					
Richness	0.001	5.90	2.42± 0.27 a	2.80± 0.23 a	1.76± 0.00 b
Evenness	0.819	1.20	0.88± 0.03	0.87± 0.03	0.90± 0.02
Shannon	0.001	0.004	0.66± 0.09 a	0.83± 0.08 a	0.36± 0.07 b
<hr/>					
Perennial grass					
Richness	<0.001	16.20	1.71± 0.15 a	1.19± 0.08 b	0 c
Evenness	<0.001	6.31	0.92± 0.02 b	0.97± 0.01 a	0 c
Shannon	<0.001	0.74	0.36± 0.07 a	0.10± 0.04 b	0 b

Significant p-values at p<0.05 are indicated in bold.

Soil-based functions along abandonment gradient

The three soil-based functions were significantly influenced by land abandonment i.e., BR (F-value= 181.03; P-value <0.001), MBC (F-value= 193.36 P-value <0.001) and CS (F-value= 122.21; P-value <0.001) which showed significant differences among the three stages of the secondary succession (Fig. 2 a, b, c).

MBC, BR and CS values were the highest in FOR and the lowest in SHORT while values were intermediate in LONG. In other words, long-term abandonment compared to short-term abandonment increased respectively by 1.7, 1.5 and 2.7 times, the basal respiration, the microbial biomass carbon, and the carbon sequestration (Fig. 2 a, b, c).

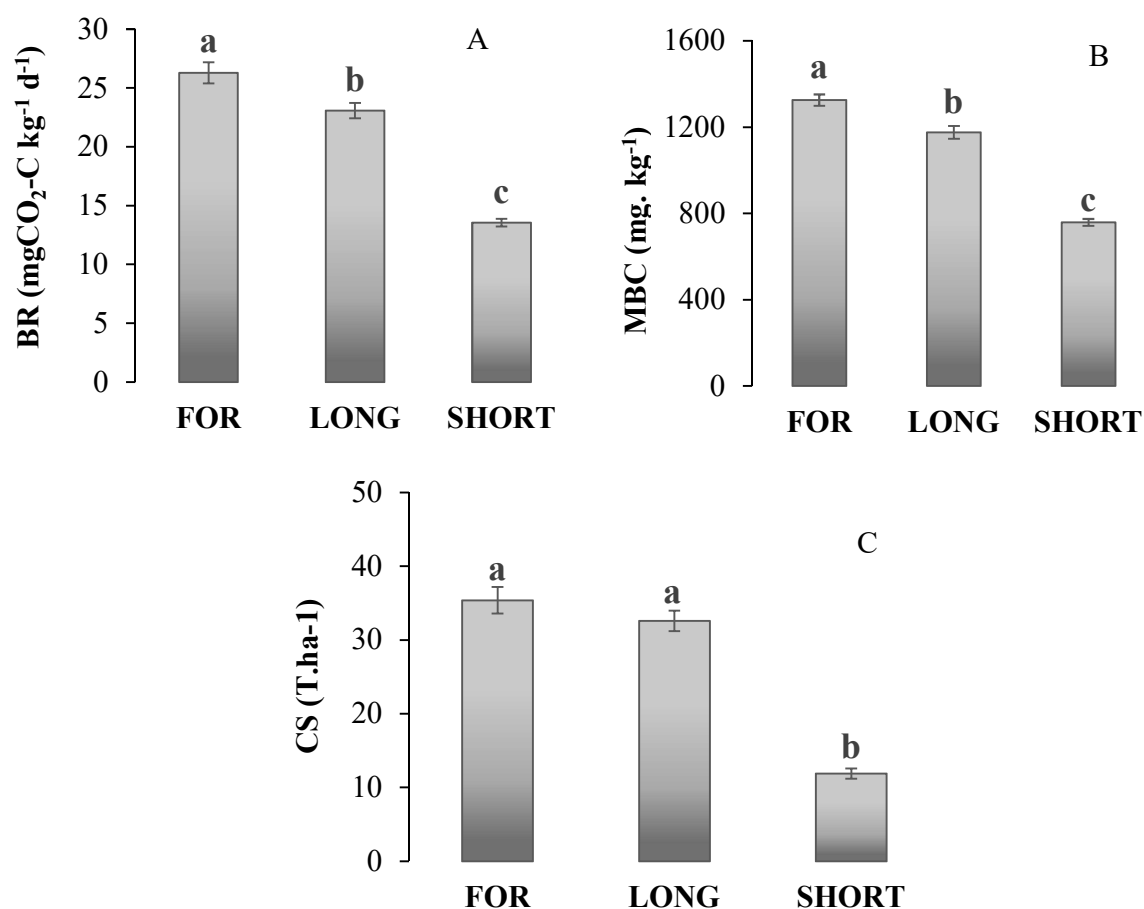


Fig 2. Comparison of the soil-based functions (mean \pm SE) between the three stages of the secondary succession. Different letters indicate significant differences among the treatments (Duncan's multiple range test). Basal respiration (BR) (A), Microbial biomass carbon (MBC) (B) and carbon sequestration (CS) (C)

The relationships between species diversity indices of total species and soil-based functions

We found positive significant linear relationships between the soil-based functions and the species richness and diversity indices for all species (all $P < 0.05$). The lowest regression coefficients (R^2) between species richness and diversity were found for MBC (R^2 values: 0.74 and 0.58, respectively), while BR and CS had the highest coefficients with species richness and diversity

indices (Fig. 3). In contrast, negative relationships were found between all soil-based function and evenness with similar regression coefficients (R^2 values: 0.38, 0.38 and 0.36 for BR, MBC and CS, respectively) (Fig. 3).

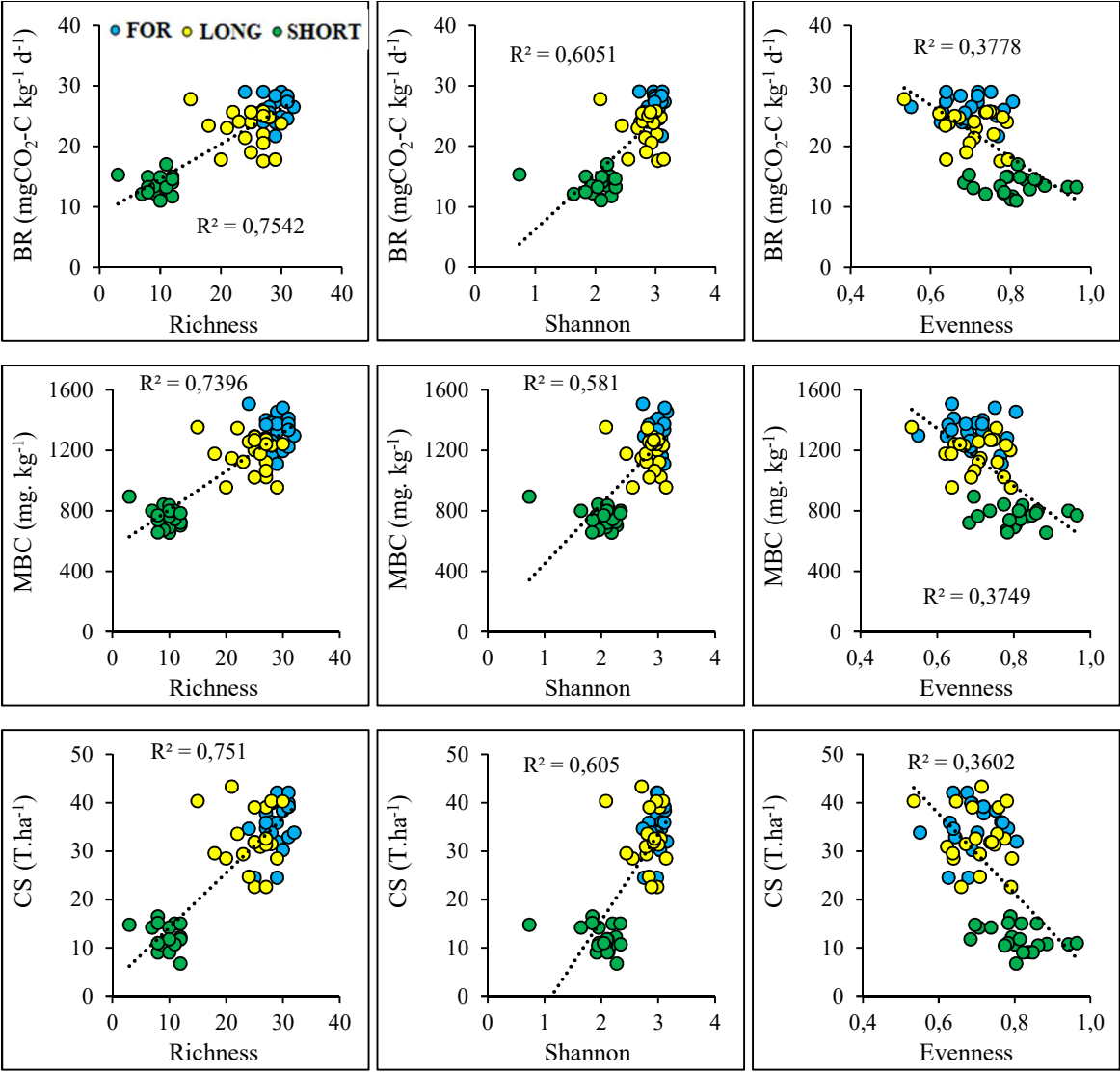


Fig 3. Relationships between species diversity indices of total species and soil-based functions including microbial biomass carbon (MBC), basal respiration (BR) and carbon sequestration (CS) for the three stages of the succession (●: SHORT, ●: LONG and ●: FOR). Linear regressions and regression coefficients are indicated.

Correlation between diversity of plant functional groups and soil- based functions

Species richness and Shannon diversity indices of different functional groups were positively and significantly correlated with all soil-based ecosystem functions (Fig. 4). However, contrasted results were observed for species evenness as a) the correlation was negative for annual and perennial forbs, b) positive for annual grass and c) no significant correlation was found for perennial grass (Fig. 4).

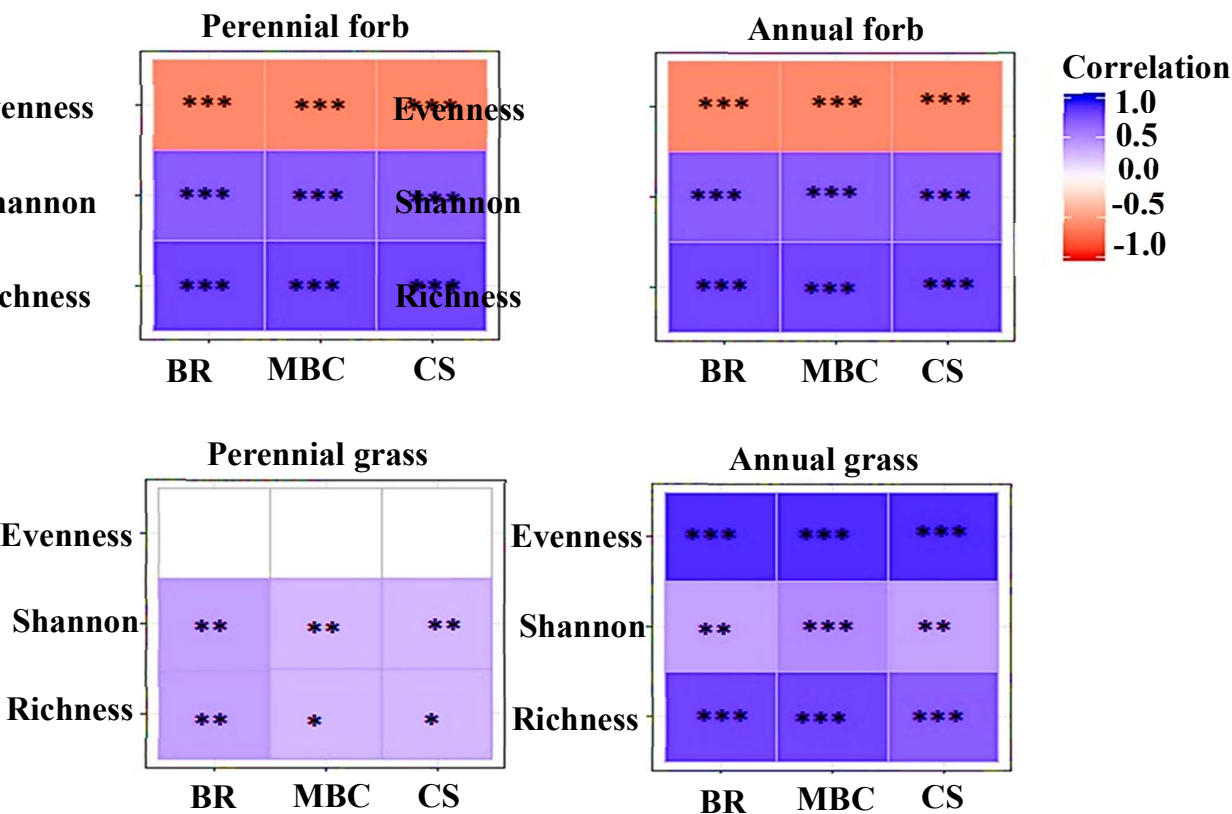


Fig 4. Pearson's correlation coefficient between diversity of plant functional groups and soil-based functions: Microbial biomass carbon (MBC), basal respiration (BR) and carbon sequestration (CS). (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Discussion

Total species diversity and functional groups diversity after abandonment

We found an increase in richness and diversity and a decrease in evenness of total plant species along the successional trajectory from recently abandoned lands to the forest system.

It is well known that land use change from forest to simpler ecosystems such as agroforestry systems and orchards, causes an alteration of main soil properties (Ayala-Orozco et al. 2018; Lizaga et al. 2019) accompanied by a degradation of most vegetation characteristics including plant diversity and composition (Colombaroli et al. 2013; Tinoco, et al. 2018). This profound alteration of the forest structure (Plieninger et al. 2011) and the soil seed bank depletion (Lemenih and Teketay 2006; Weerasinghe et al. 2019) negatively affect richness and diversity of plant species (e.g., Rembold et al. 2017). These changes also reflect the loss of forest-dependent species and the shift from native to alien-dominated plant communities.

On the other hand, with the passage of time from the abandonment of agricultural lands to the terminal forest stage, the rate of seed dispersal and the possibility of establishment of forest-dependent species are likely to increase and the dominance by opportunistic species (invasive) of croplands to decline (Nepstad et al. 1990). In our study, this change was observed and we noted that recovery of species diversity and richness was slow in the early years after abandonment but hastened with time. The main reasons for this slow recovery are the high limitation of seed dispersal (Wijdeven and Kuzee 2000; Cubiña and Aide 2001), intense competition with pioneer species in particular annual grasses (Ortega-Pieck et al. 2011), adverse microclimatic conditions

prevailing in open areas due to excessive solar radiation and extreme temperatures and poor soil conditions due low soil fertility, soil compaction and erosion. These conditions are not favorable for the germination and establishment of incoming seeds (Bassett et al. 2005; Trujillo-Miranda et al. 2018).

We noted that species diversity and richness of all plant functional groups increased along the successional stages. With time, the obstacles to plant species establishment and the intense competition for resources are gradually removed, facilitating the recovery of most annual and perennial functional groups (Meli et al. 2017).

This change also reflects amelioration of the environmental conditions and other studies have also reported the replacement of weedy annual species belonging to the early stages of succession with shade-tolerant and moisture-preferring perennial species at later stages of succession (Holmes et al. 2018).

Basically, after abandonment in degraded sites, the passive landscape restoration (or rewilding) facilitates the restoration of natural ecosystems. However, the time required to achieve this restoration is not same in the different ecosystems depending on the conditions before and after degradation (Meli et al. 2017).

We found that increasing abandonment history increase the evenness of permanent forbs and decrease the evenness of annual forbs. This result can be explained by the improvement of the environmental conditions along the succession accompanied by the migration and establishment of permanent forms and the decline of opportunistic annual forms such as annual grasses.

As time after abandonment goes by, late-successional perennial species dominate over annual pioneers of early stages after abandonment. These perennial species are dispersed throughout the

area with the same abundance and occupy most of the ecological niches. This trend increases the evenness index of these species in the second decade after abandonment.

Similarly, Paillet et al. (2010) recorded the decrease of the evenness of early-successional shade-intolerant species for the benefit of intermediate-successional species due to the shadier conditions prevailing in the later stages of the succession. In addition, this decline of evenness in annuals species can be explained by the greater dominance of perennial species and shrubs, which are superior competitors for resources (Kouba et al. 2015).

Comparison of soil-dependent ecosystem functions between different stages of secondary succession

Soil-based functions of the ecosystem improved with the passage of time since the abandonment from agriculture to the forest stage. In fact, the levels of basal respiration, microbial biomass carbon and soil carbon sequestration were doubled between the forest stage and the short abandonment stage. Our results about the increasing of soil respiration in the later stages of secondary succession (LONG) are consistent with the findings reported by Griffiths and Swanson (2001), and are related to a higher annual organic matter input to soil surface. Microbial respiration has a direct relationship with soil organic carbon storage due to the high dependence of soil microbial activity on substrate carbon availability (Zhang et al. 2014). Therefore, with higher carbon storage in the later stages of the succession, the basal respiration increases (Soleimani et al. 2019). Also, higher amount and stability of organic carbon in forests than in arable lands (Gelaw et al. 2015) increase microbial biomass and microbial derivatives and stimulates decomposition products and metabolites (Leff et al. 2012).

Our results are also consistent with those of Islam and Weil (2000) who observed a significant reduction of microbial biomass carbon and a decrease in soil quality when forests are turned into agricultural lands. The negative effect of farming operations such as soil compaction, soil disruption, harvesting of crops every year and significant decline in litter input reduce the soil organic matter and the resources availability for microorganisms leading to a general degradation of the amount and quality of the substrate (Niemeyer et al. 2012; Soleimani et al. 2019). These changes negatively influence microorganism's populations and decrease MBC and BR (Van Leeuwen et al. 2017). Also, due to the lack of permanent forest cover following land use change; the soil temperature increases which accelerates the loss of soil carbon (Karmakar et al. 2016). Consistent with our results, Rasouli-Sadaghiani et al. (2018) showed that conversion of forests into agricultural lands significantly reduced carbon sequestration by 68%, and microbial respiration by 50%. Therefore, soil-based functions can be considered as suitable indicators for monitoring changes of soil processes after land abandonment.

Soils with different vegetation have different litter decomposition processes, resulting in the modification of carbon release and storage processes in the soil (Zhang et al. 2013). Therefore, the difference in soil carbon storage between the successional stages could rely for a part in the difference in the type of plant cover (plant functional groups) after abandonment.

Aboveground and belowground biomass of perennial species is higher than the biomass of annuals and there is a direct relationship between biomass and carbon sequestration (McCarty and Ritchie 2002). Recovery of perennial grasses and forbs after long-term abandonment is therefore one of the main factors contributing to higher soil carbon stocks in LONG and FOR than in SHORT.

The basal respiration and microbial biomass carbon increased after long-term abandonment but they remained significantly lower than in the forest stage. In contrast, the gradual increase in soil

carbon sequestration with time did not last after 15 years of abandonment in our study as we found no significant difference between LONG and FOR. Our results indicated that after 15 years of abandonment the soil carbon stock is almost comparable to the pre-land use stock. This time is likely to be vary in different ecosystems. For example, Deng et al. (2013) studying different stages of succession after grassland abandonment in northwest China (1, 7, 13, and 20 years), showed that soil carbon stock in the last stage has not yet reached the pre-land use stock.

Selection Effect vs. Niche Complimentary: response of total and plant functional groups

The results of the present study show that soil-based functions of ecosystem increase simultaneously with increasing richness and diversity of plant species. Many studies have recorded a positive relationship between increased species richness and ecosystem function including soil carbon sequestration (Cardinale et al. 2012; Tahmasebi et al. 2017), microbial respiration (Dias et al. 2010), and microbial biomass carbon (Rawat et al. 2019). A positive relationship was also observed between ecosystem functions and species richness not only in forest ecosystems (Poorter et al. 2015; Sullivan et al. 2017; Liu et al. 2018) but also in other ecosystems such as grasslands (Li et al. 2019) or marine ecosystems (Worm et al. 2006; Burkepile and Hay 2008).

Increase in species richness in various ecosystems (including low- to medium-sized production areas) is likely to enhance the exploitation of existing resources which in turn can stimulate the ecosystem productivity and ecosystem dynamics (Loreau 2010). This positive relationship between species richness and soil-based ecosystem functions provides support to the niche complimentary hypothesis. One of the effective mechanisms in creating complementary use of resources between plants and enhancing the functioning of the ecosystem is resource partitioning (Barry et al. 2018). It implies an increase in productivity due to differences in functional

characteristics (functional divergence) which enhances the functioning of the ecosystem. In line with our results, this mechanism leads to a positive relationship between species richness and ecosystem functions such as carbon sequestration.

As the number of species increases along with a better capture of ecosystem resources, a corresponding increase in ecosystem function will occur. However, the positive effects of this increase in richness depend on the reduction or absence of competition between plants in the use of environmental resources (Grime 2006). In addition, facilitation has also been identified as one of the key drivers of complementary use of resources among plants and has a positive impact on ecosystem functioning (Cardinale et al. 2002; Lambers et al. 2004; Brooker et al. 2016). In the late stages of the secondary succession in our study area, the role of nurse and facilitator species was likely to be reinforced, increasing species diversity and richness and thereby promoting ecosystem function. For example, the higher abundance of woody species such as *Quercus brantii* L., *Crataegus pontica* K. Koch., *Daphne mucronata* Royle. and *Astragalus adscendens* Boiss. in the LONG stage may provide favorable conditions for the establishment of other plants.

We found negative relationships between plant evenness and the ecosystem soil-based functions, a finding also recorded in other studies (Mulder et al. 2004). In general, the effect of evenness on ecosystem function depends on the contribution and role of dominant species in ecosystem function (Maestre and Reynolds 2006). In areas where the major contribution of ecosystem function is provided by dominant species (e.g. the more important role of woody species than herbaceous species in carbon sequestration), the increase in plant evenness, which reflects a low abundance of dominant species, is likely to have a negative impact on ecosystem functions. Therefore, the negative relationship between evenness and soil-based functions in this study

confirms the hypothesis of selection effect that emphasizes the role played by some dominant species.

The contrasted influence of evenness on ecosystem functions according to the plant functional groups (perennial forbs or grasses, see Figure 3) indicates the positive influence of some dominant forbs on main soil functions, while this effect relies on the contribution of more species for perennial grasses.

We found that the increase of evenness of perennial grasses in the second decade after abandonment was positively correlated with soil-based ecosystem functions. This result could be explained by the key role played by some species such as *Poa bulbosa* or *Hordeum bulbosum* as also reported in other studies in arid and semiarid regions (e.g. Eghdami et al. 2019). Based on their root systems (tiny dense shallow roots) and the high number of active leaves, these species can increase soil-based functions, especially carbon sequestration (Barnhart 1985; Kadović et al. 2012; Erfanzadeh et al. 2014). In fact, in the late stages of the succession, the establishment of oaks and shrubs acting as nurse species, (Heydari et al. 2017) facilitate the installation of a floor vegetation composed of different vegetative forms, especially perennial grasses and forbs, such as *Alyssum marginatum* Steud. ex Boiss., *Allium stamineum* Boiss., *Tragopogon bupthalmoides* (DC.) Boiss., *Trigonella elliptica* Boiss., and *Heteranthelium piliferum* (Banks & Soland.) Hochst, that were not present shortly after abandonment and only established in the late stages. These changes increase species diversity and could enhance soil carbon capture (Cardinale et al. 2012) as it is by ~ 2.5 times higher in LONG than SHORT in our study. Consistent with our results, Yang et al. (2019) found a 178 % increase in annual rates of soil carbon storage after 22 years of abandonment. This rapid change was attributed to the rapid recovery and increasing richness and diversity of C3 grasses and legumes, especially perennials species that have higher root: shoot

ratios, lower decomposition rates of these roots and higher aboveground and belowground production.

The increase in diversity and richness along the successional pathway in addition to carbon sequestration has further enhanced multiple ecological and environmental benefits, including a reduced leaching and a higher production of soil nutrients needed for microbial communities (Tilman et al. 2006; Dijkstra et al. 2007). In contrast, a decrease in plant diversity has a negative effect on the activity of soil heterotrophic organisms: first, by limiting plant biomass production, and the second by producing less diverse mixtures causing a less balanced diet in terms of food quality and a less constant supply in time for microbial activity (Spehn et al. 2000).

Therefore, a decreasing richness in plant species has a negative effect on microbial community activity due to the reduction of temporal and spatial heterogeneity of these resources (Holland and Coleman 1987). The increase number of species in LONG and FOR with more diverse ecological traits such as higher nitrogen concentration in roots and leaves (Garnier et al. 1997; Roumet et al. 2006) can explain the positive correlation between plant species diversity and soil-based microbial functions such as basal respiration and microbial biomass carbon (Yadav 2012; Guillaume et al. 2016).

In this regard, Lange et al. (2015) stated that more carbon inputs to the soil is linked to a greater diversity of plant communities leading to higher activity and abundance of microbial communities. It seems that favorable conditions 15 years after abandonment (such as greater diversity of plant species and higher abundance of perennial species) were effective in increasing microbial activity of this ecosystem and in producing positive relationships between diversity indices and basal respiration and microbial biomass carbon (Zhou et al. 2013).

CONCLUSIONS

Biodiversity is one of the most important determinants of ecosystem functions and a wealth of studies has been conducted to analyze the relationships between diversity indices and ecosystem functions in various types of ecosystems. However, the question of how some diversity indices such as evenness can influence soil-based functions, in the context of agroforestry abandonment in semi-arid Mediterranean areas has received much less attention. The results of this study reveals that species diversity indices and soil-based functions improve with time after land abandonment in accordance with our first hypothesis. Our second hypothesis is also partially confirmed as we found positive relationships between richness and species diversity with soil-based ecosystem functions as predicted by the niche complementarity hypothesis. However, the negative relationships between evenness and soil-based ecosystem functions supports the selection effect hypothesis. These results are in line with many other studies which have emphasized the simultaneous existence and role of both mechanisms and have concluded that these hypotheses are not mutually exclusive (e.g. Conti and Díaz 2013; Tahmasebi et al. 2017). Lastly, as hypothesized, we showed that the functional groups based on plant life form have an influence on the relationships between plant diversity and soil functions. In terms of management, a passive restoration relying on spontaneous recovery of perennial plants (in particular woody species) beneficial to main soil processes can be recommended if the environmental conditions are suitable. In particular, abandoned lands should not be in a too critical stage of degradation impairing the main soil-based functions (e.g. high soil compaction, heavily eroded soils). Therefore, protection measures against major disturbances frequently occurring in semiarid areas submitted to a strong human pressure, such as grazing or fire, are also needed to prevent any regressive vegetation dynamics.

506

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