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

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20 **Abstract**

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

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

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48 **Highlights**

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

55

56 **Introduction**

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

66 In many parts of the world, human activities and their dependence on natural resources, especially  
67 forests, have caused land use changes and destruction of forests (e.g. Cai et al. 2018; Kepfer-Rojas  
68 et al. 2019; Heydari et al. 2019). These disturbances have led to the loss of ecological niches of  
69 many species, to reduced biodiversity (Isbell et al. 2017; Heydari et al. 2017 a; Miedema et al.  
70 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

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

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

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

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

116 above- ground biomass in forest systems have been largely studied (Zuo et al. 2018; Fayiah et al.  
117 2019), but have been less investigated for soil-based ecosystem functions (e.g., carbon  
118 sequestration and basal respiration) (Rey Benayas et al. 2007). This was particularly proven in  
119 Mediterranean forests established on previous agricultural lands such as the Zagros oak forest in  
120 western Iran.

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

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

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

135 We hypothesize that:

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

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

141

## 142 **Methods**

### 143 **Site description**

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

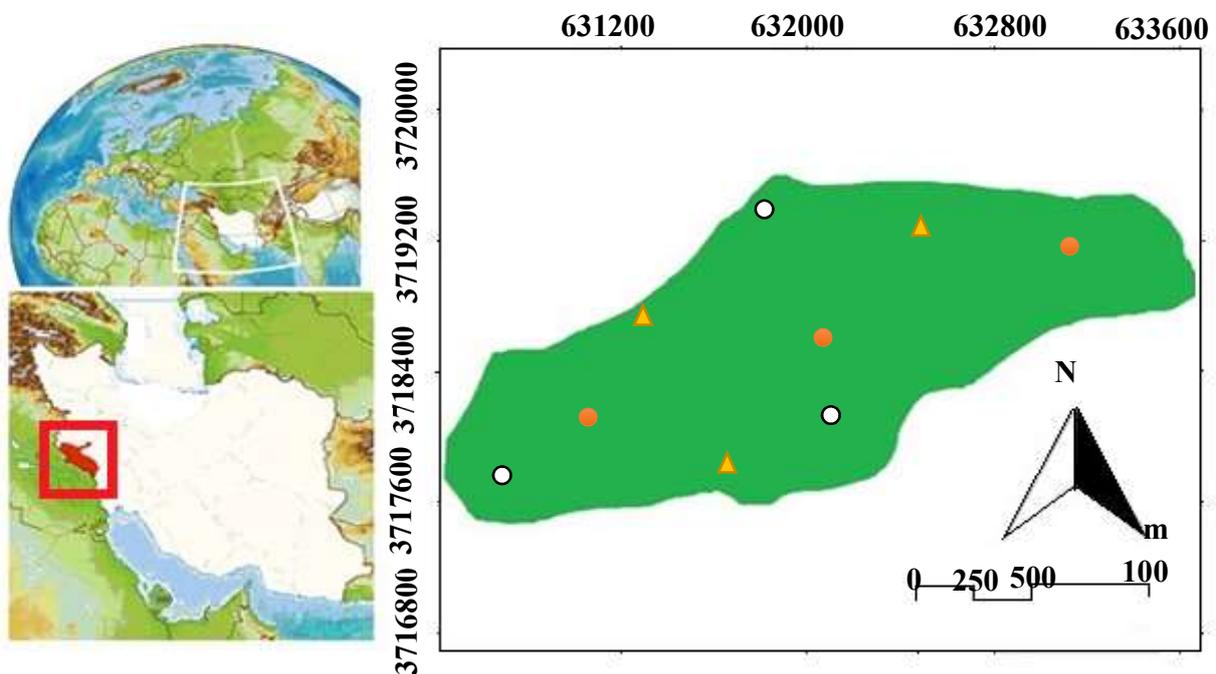
152 (i) The forest stage ("FOR") which represents the terminal stage of the succession. Field evidences  
153 suggest that this stage was previously used by agroforestry, which was abandoned several decades  
154 ago (~ 40-60 years) although a precise date of abandonment cannot be given. It is composed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

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

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

162 The climate of the area is of a Mediterranean type (Fathizadeh et al. 2017) characterized by a dry  
163 period of 5-6 months (May-October). The mean annual rainfall and temperature are 621.3 mm and  
164 17°C, respectively (Ilam weather station, 1999-2015). The soil is classified as Inceptisol (Soil  
165 Survey Staff, 2014). It is a calcareous soil, rich in organic matter with a clay loamy texture and a  
166 mean depth of 30-40 cm (Heydari et al. 2017).

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

181

### 182 **Experimental design and vegetation measurements**

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

187 subplots of 1m<sup>2</sup> were regularly distributed along the transects (3 plots in each transect and 1 plot  
188 where transects met) (Tárrega et al. 2009). All vascular species were recorded on each subplot and  
189 each species was named according to the available literature and given of cover percentage. Each  
190 species was then distributed in one of the four functional groups based on plant life form  
191 (forb/grass) and plant life span (annual/perennial): annual forbs, annual grasses, perennial forbs  
192 and perennial grasses. These two plant traits were commonly used in previous studies because they  
193 are elucidative on species morphology, phenology, competitive competition potential and  
194 taxonomy (e.g. Verma et al. 2014).

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

197

198  $SR = S$

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

200  $E = H' / \ln(S)$  (Pielou 1966)

201

202 Where *S* = total number of species and *p<sub>i</sub>* = proportion of cover of species 'i'. All diversity indices  
203 were calculated using the Ecological Methodology software.

204

### 205 **Soil sampling and analysis**

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

209 dichromate oxidation according to the Walkley-Black method (Nelson and Sommers 1982). The  
210 second subsample was kept at field moisture and stored at 4 °C for subsequent measurements of  
211 soil microbial activity. Microbial biomass carbon (MBC) was measured by determining the  
212 organic carbon in chloroform-fumigated and non-fumigated samples by dichromate oxidation, as  
213 described by Vance et al. (1987). Soil basal respiration (BR) was measured by trapping (in 1 M  
214 NaOH traps) and quantifying CO<sub>2</sub> that was emitted from soil samples over a five-day period (Alef  
215 and Nannipieri 1995).

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

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

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

220

## 221 **Statistical analysis**

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

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

234

235 **Results**

236 **Plant functional diversity among different stages of succession**

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

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

Variables	<i>P-value</i>	<i>MS</i>	FOR	LONG	SHORT
<b>Total species</b>					
Richness	<b>&lt;0.001</b>	2160.33	28.76 $\pm$ 0.46 a	24.71 $\pm$ 0.84 b	9.50 $\pm$ 0.45 c
Evenness	<b>&lt;0.001</b>	5.89	0.69 $\pm$ 0.01 b	00.70 $\pm$ 0.02 b	0.80 $\pm$ 0.01 a
Shannon	<b>&lt;0.001</b>	0.08	2.98 $\pm$ 0.02 a	2.84 $\pm$ 0.05 a	2.00 $\pm$ 0.07 b
<b>Annual forb</b>					
Richness	<b>&lt;0.001</b>	592.11	17.66 $\pm$ 0.44 a	16.28 $\pm$ 0.74 a	7.85 $\pm$ 0.37 b
Evenness	<b>&lt;0.001</b>	0.10	0.69 $\pm$ 0.01 b	0.70 $\pm$ 0.01 b	0.82 $\pm$ 0.01 a
Shannon	<b>&lt;0.001</b>	2.802	2.49 $\pm$ 0.02 a	2.41 $\pm$ 0.06 a	1.82 $\pm$ 0.06 b
<b>Perennial forb</b>					

Richness	<b>&lt;0.001</b>	267.57	7.00± 0.27 a	4.71± 0.23 b	0 c
Evenness	<b>&lt;0.001</b>	4.94	0.81± 0.03 a	0.86± 0.02 a	0 b
Shannon	<b>&lt;0.001</b>	1.71	1.71± 0.07 a	1.34± 0.05 b	0 c
<hr/>					
Annual grass					
Richness	<b>0.001</b>	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	<b>0.001</b>	0.004	0.66± 0.09 a	0.83± 0.08 a	0.36± 0.07 b
<hr/>					
Perennial grass					
Richness	<b>&lt;0.001</b>	16.20	1.71± 0.15 a	1.19± 0.08 b	0 c
Evenness	<b>&lt;0.001</b>	6.31	0.92± 0.02 b	0.97± 0.01 a	0 c
Shannon	<b>&lt;0.001</b>	0.74	0.36± 0.07 a	0.10± 0.04 b	0 b

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

#### 249 **Soil-based functions along abandonment gradient**

250 The three soil-based functions were significantly influenced by land abandonment i.e., BR (F-  
251 value= 181.03; P-value <0.001), MBC (F-value= 193.36 P-value <0.001) and CS (F-value=  
252 122.21; P-value <0.001) which showed significant differences among the three stages of the  
253 secondary succession (Fig. 2 a, b, c).

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

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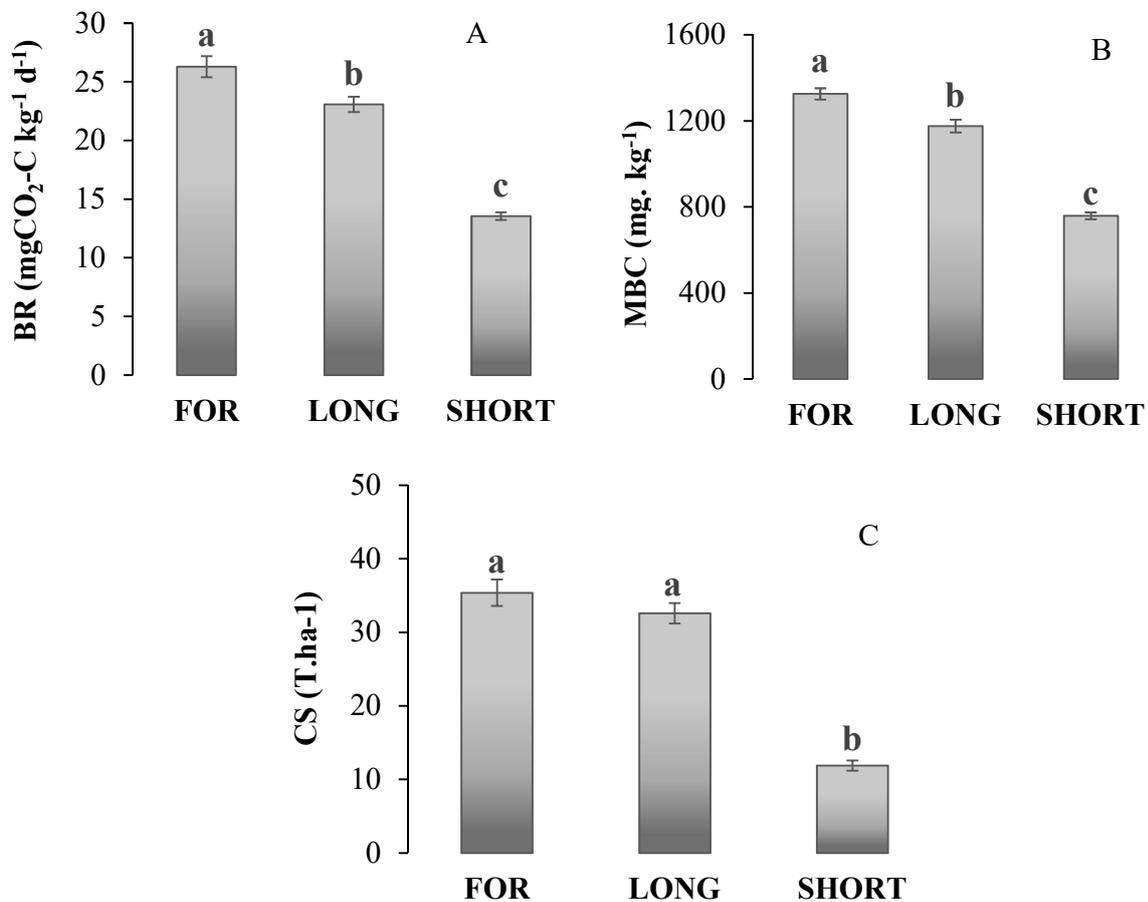
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267 **Fig 2.** Comparison of the soil-based functions (mean ± SE) between the three stages of the  
268 secondary succession. Different letters indicate significant differences among the treatments  
269 (Duncan's multiple range test). Basal respiration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

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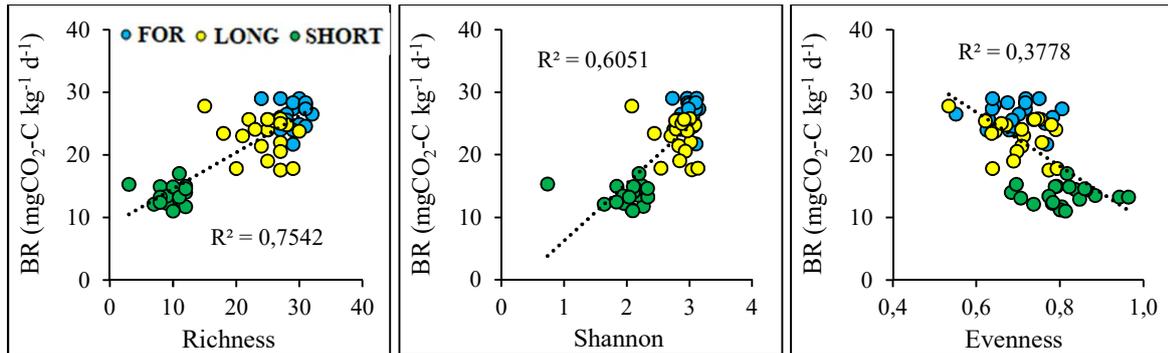
### 272 **The relationships between species diversity indices of total species and soil-based functions**

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

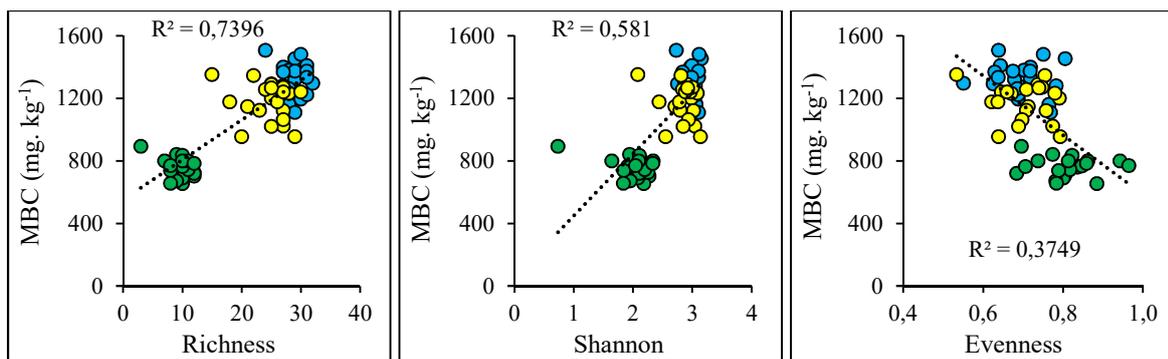
277 indices (Fig. 3). In contrast, negative relationships were found between all soil-based function and  
 278 evenness with similar regression coefficients ( $R^2$  values: 0.38, 0.38 and 0.36 for BR, MBC and  
 279 CS, respectively) (Fig. 3).

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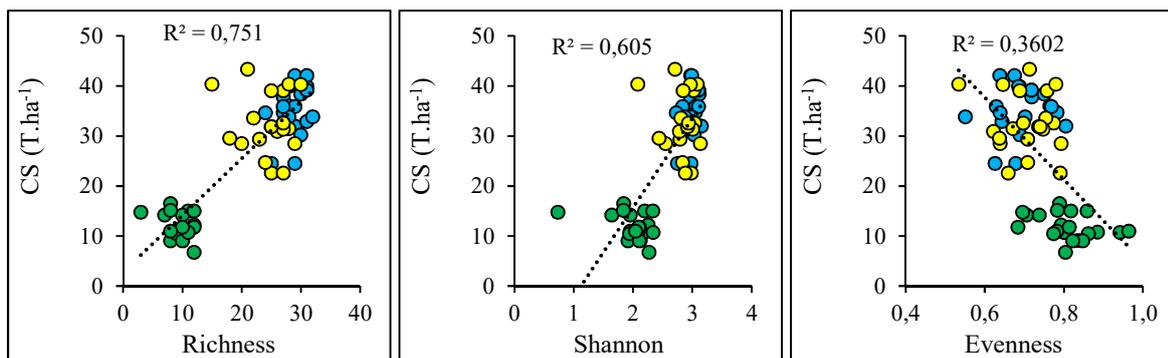
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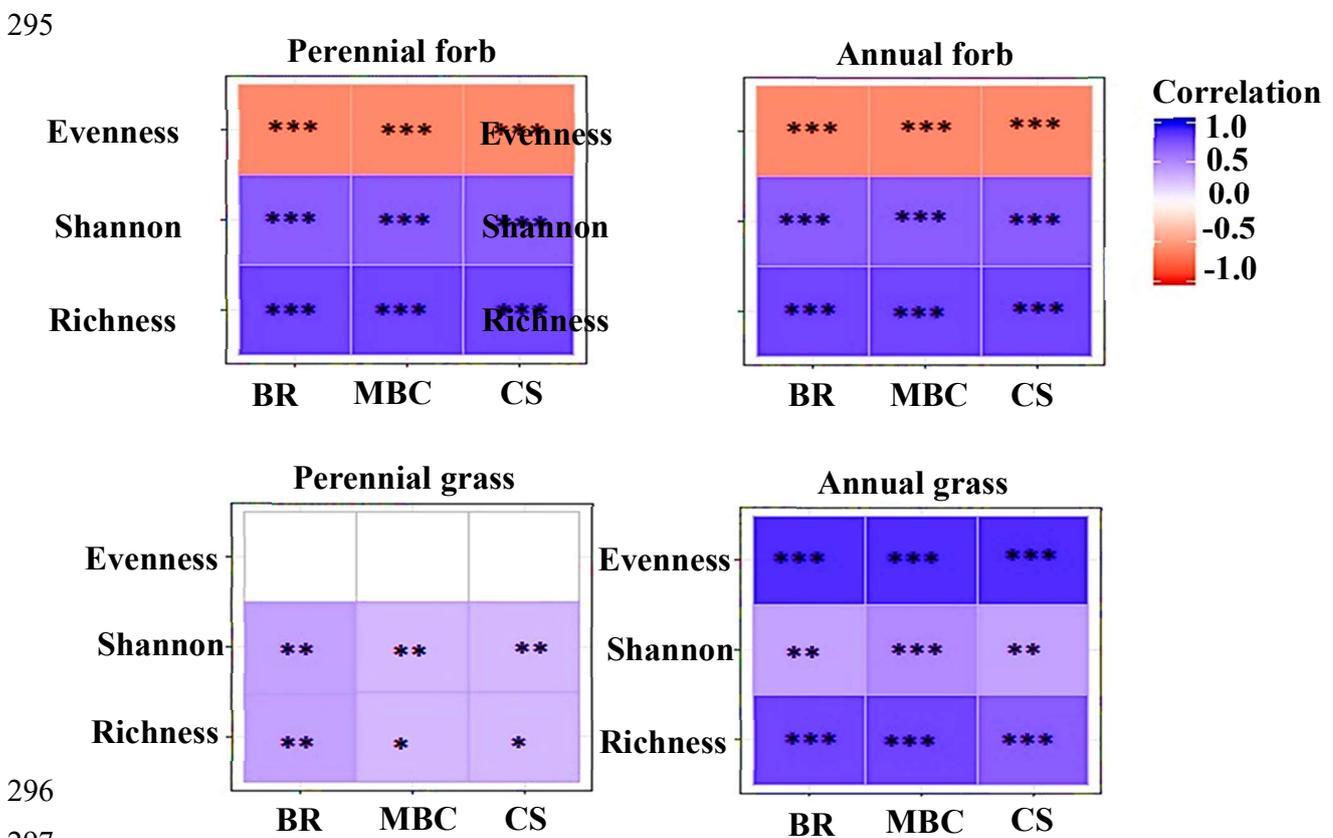


284 **Fig 3.** Relationships between species diversity indices of total species and soil-based functions  
 285 including microbial biomass carbon (MBC), basal respiration (BR) and carbon sequestration (CS)  
 286 for the three stages of the succession (●: SHORT, ●: LONG and ●: FOR). Linear regressions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

288

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

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



296  
 297 **Fig 4.** Pearson's correlation coefficient between diversity of plant functional groups and soil-  
 298 based functions: Microbial biomass carbon (MBC), basal respiration (BR) and carbon  
 299 sequestration (CS). (\*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ ).

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304

## 305 **Discussion**

### 306 **Total species diversity and functional groups diversity after abandonment**

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

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

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

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

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

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

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

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

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

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

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

354

### 355 **Comparison of soil-dependent ecosystem functions between different stages of secondary** 356 **succession**

357 Soil-based functions of the ecosystem improved with the passage of time since the abandonment  
358 from agriculture to the forest stage. In fact, the levels of basal respiration, microbial biomass  
359 carbon and soil carbon sequestration were doubled between the forest stage and the short  
360 abandonment stage. Our results about the increasing of soil respiration in the later stages of  
361 secondary succession (LONG) are consistent with the findings reported by Griffiths and Swanson  
362 (2001), and are related to a higher annual organic matter input to soil surface. Microbial respiration  
363 has a direct relationship with soil organic carbon storage due to the high dependence of soil  
364 microbial activity on substrate carbon availability (Zhang et al. 2014). Therefore, with higher  
365 carbon storage in the later stages of the succession, the basal respiration increases (Soleimani et  
366 al. 2019). Also, higher amount and stability of organic carbon in forests than in arable lands (Gelaw  
367 et al. 2015) increase microbial biomass and microbial derivatives and stimulates decomposition  
368 products and metabolites (Leff et al. 2012).

369 Our results are also consistent with those of Islam and Weil (2000) who observed a significant  
370 reduction of microbial biomass carbon and a decrease in soil quality when forests are turned into  
371 agricultural lands. The negative effect of farming operations such as soil compaction, soil  
372 disruption, harvesting of crops every year and significant decline in litter input reduce the soil  
373 organic matter and the resources availability for microorganisms leading to a general degradation  
374 of the amount and quality of the substrate (Niemeyer et al. 2012; Soleimani et al. 2019). These  
375 changes negatively influence microorganism's populations and decrease MBC and BR (Van  
376 Leeuwen et al. 2017). Also, due to the lack of permanent forest cover following land use change;  
377 the soil temperature increases which accelerates the loss of soil carbon (Karmakar et al. 2016).  
378 Consistent with our results, Rasouli-Sadaghiani et al. (2018) showed that conversion of forests into  
379 agricultural lands significantly reduced carbon sequestration by 68%, and microbial respiration by  
380 50%. Therefore, soil-based functions can be considered as suitable indicators for monitoring  
381 changes of soil processes after land abandonment.

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

386 Aboveground and belowground biomass of perennial species is higher than the biomass of annuals  
387 and there is a direct relationship between biomass and carbon sequestration (McCarty and Ritchie  
388 2002). Recovery of perennial grasses and forbs after long-term abandonment is therefore one of  
389 the main factors contributing to higher soil carbon stocks in LONG and FOR than in SHORT.

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

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

398

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

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

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

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

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

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

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

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

443 We found that the increase of evenness of perennial grasses in the second decade after  
444 abandonment was positively correlated with soil-based ecosystem functions. This result could be  
445 explained by the key role played by some species such as *Poa bulbosa* or *Hordeum bulbosum* as  
446 also reported in other studies in arid and semiarid regions (e.g. Eghdami et al. 2019). Based on  
447 their root systems (tiny dense shallow roots) and the high number of active leaves, these species  
448 can increase soil-based functions, especially carbon sequestration (Barnhart 1985; Kadović et al.  
449 2012; Erfanzadeh et al. 2014). In fact, in the late stages of the succession, the establishment of  
450 oaks and shrubs acting as nurse species, (Heydari et al. 2017) facilitate the installation of a floor  
451 vegetation composed of different vegetative forms, especially perennial grasses and forbs, such as  
452 *Alyssum marginatum* Steud. ex Boiss., *Allium stamineum* Boiss., *Tragopogon bupthalmoides*  
453 (DC.) Boiss., *Trigonella elliptica* Boiss., and *Heterantheum piliferum* (Banks & Soland.) Hochst,  
454 that were not present shortly after abandonment and only established in the late stages. These  
455 changes increase species diversity and could enhance soil carbon capture (Cardinale et al. 2012)  
456 as it is by ~ 2.5 times higher in LONG than SHORT in our study. Consistent with our results, Yang  
457 et al. (2019) found a 178 % increase in annual rates of soil carbon storage after 22 years of  
458 abandonment. This rapid change was attributed to the rapid recovery and increasing richness and  
459 diversity of C3 grasses and legumes, especially perennials species that have higher root: shoot

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

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

469 Therefore, a decreasing richness in plant species has a negative effect on microbial community  
470 activity due to the reduction of temporal and spatial heterogeneity of these resources (Holland and  
471 Coleman 1987). The increase number of species in LONG and FOR with more diverse ecological  
472 traits such as higher nitrogen concentration in roots and leaves (Garnier et al. 1997; Roumet et al.  
473 2006) can explain the positive correlation between plant species diversity and soil-based microbial  
474 functions such as basal respiration and microbial biomass carbon (Yadav 2012; Guillaume et al.  
475 2016).

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

482

## 483 CONCLUSIONS

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

506

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