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1 **Contribution of biological crust to soil CO_2 efflux in a Mediterranean shrubland ecosystem**

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11 **Abstract**

12   In Mediterranean ecosystems, the soil biological crust (hereafter biocrust) plays a crucial

13 role in maintaining ecosystem functioning. In these ecosystems, soil water content can often be a

14 stronger driver of soil CO_2 efflux than soil temperature, or at least comparable. However, little is

15 known on the contribution of the biocrust to soil CO_2 efflux or how the respiration of the biocrust

16 responds to soil water content and temperature. A manipulative experiment was performed in a

17 Mediterranean shrubland ecosystem in Sardinia (Italy) to assess the contribution of the bicocrust to

18 soil CO_2 efflux and to identify the main environmental drivers of the CO_2 efflux. For 19 months, *in

19 situ* soil CO_2 efflux was measured over two different surfaces: soil deprived of biocrust (hereafter

20 *Soil*) and intact soil (hereafter *Soil+BC*), and estimated by subtraction in a third surface: biocrust

21 (hereafter *BC*). CO_2 efflux emitted by *Soil*, *BC* and *Soil+BC* were uniquely driven by soil moisture

22 and temperature: *BC* respiration was mainly controlled by soil moisture at 5 cm depth, whereas both

23 soil temperature and water content at 20 cm depth determined *Soil* CO_2 efflux. Soil temperature and

24 water content at 5 cm depth drove *Soil+BC* respiration. We also found that biocrusts can contribute

25 substantially (up to 60%) to the total soil respiration depending on its moisture content. This

26 contribution persists even in periods in which deeper soil layers are inactive, as small water pulses

27 can activate the metabolism of carbon in soils through lichens, mosses and cyanobacteria associated

28 with the biocrust, while deeper soil layers remain dormant. The important differences observed in

29 CO_2 efflux between *Soil* and *Soil+BC* suggest that carbon models and budgets may underestimate

30 soil CO_2 efflux in spatially heterogeneous Mediterranean areas. Our results highlight the importance

31 of accounting for the biocrust contribution to soil respiration and its response to environmental

32 drivers. We provide an accurate estimation of this key component of the carbon cycle at the

33 ecosystem level in water limited ecosystems.

34 **Keywords:** Soil temperature; Soil moisture; Semiarid ecosystems; Soil respiration; Spatial and

35 temporal heterogeneity; Carbon cycling

1. **Introduction**

Soil CO_2 efflux is the sum of autotrophic respiration by plant roots, heterotrophic respiration by decomposition of organic carbon (C) substrates operated by soil microbes, catabolic processes of mycorrhizas, respiration by arthropods, soil worms and other animals occupying different trophic niches (Hanson et al., 2000) and carbonate weathering (Rey, 2015). Soil CO_2 efflux is an important component of the C cycle (Fernandez et al., 2006) and is estimated to account for over 25% of global CO_2 emissions (Bouwmann and Germon, 1998). Despite its relevance and the determined efforts to studying this process, present knowledge still lacks reliable field data to enable better estimates of soil-atmosphere fluxes. Importantly, such knowledge gaps hinder our potential to accurately predict the effects of global environmental change such as rising atmospheric CO_2 and climate change on the C cycle.

The uncertainty surrounding the response of soil CO_2 efflux to environmental factors is greater for water-limited environments such as Mediterranean ecosystems. There are relatively fewer articles where CO_2 efflux has been quantified and the controlling factors established in dry areas compared to more humid environments (Castillo-Monroy et al., 2011). Mediterranean ecosystems are often characterized by complex spatial vegetation patterns, with patches devoid of vegetation that vary in size and shape depending on water availability and role of engineering plants (Gilad et al., 2007). Differences in the distribution of soil organic matter content (Reynolds et al., 2007), biological activity (Stubbs and Pyke, 2005) and microbial abundance (Gallardo and Schlesinger, 1992), are typically found between plant patches and bare soils and are largely responsible for the high spatial variation in soil respiration (R_s) in these areas (Maestre and Cortina 2003). Despite its recognized relevance for ecosystem functioning, the effects of this small-scale spatial variation in CO_2 efflux remain scarcely understood.

59   One key aspect of the spatial heterogeneity in Mediterranean ecosystems is the presence of

60   the biological soil crusts (hereafter biocrust), which can encompass up to 70% of the cover in

61   absence of vascular plants (Belnap and Lange, 2003). Biocrusts are specialized communities that

62   cover the first millimeters of the soil surface in water-limited ecosystems worldwide. Such

63   communities are composed of cyanobacteria, lichens, liverworts, fungi, eukaryotic algae and

64   mosses in various proportions (Belnap and Lange, 2001; Eldridge and Greene 1994). They largely

65   affect the ecosystem functioning by influencing soil nutrient cycling (Castillo-Monroy et al. 2010;

66   Morillas and Gallardo, 2015), soil stability and water infiltration (Eldridge et al., 2010; Kidron,

67   2014; Reynolds et al. 2001), local hydrological cycle (Belnap et al., 2005), nitrogen fixation and

68   transformations (Belnap, 2002; Evans and Lange, 2003; Hu et al., 2015), and C cycling (Maestre

69   and Cortina, 2003; Thomas and Hoon, 2010; Zhao et al., 2014). Thus, the need to improve our

70   estimation of soil-atmosphere fluxes is more acute in crusted soils due to the increased spatial

71   heterogeneity of fluxes.

72   In Mediterranean ecosystems, the metabolic activity of microbes and roots is restricted by

73   low temperatures in the humid winter and limited soil moisture during the warm summer (de Dato

74   et al., 2010; Morillas et al., 2013). Thomas et al. (2008) showed that R_s does not respond to a large

75   range of temperatures unless moisture levels are above a critical threshold, whereas temperature

76   responses are much greater when moisture is sufficient to allow microbial respiration of organic

77   matter. These findings highlight the pivotal role played by the interaction between temperature,

78   moisture and CO_2 efflux in Mediterranean ecosystems. Indeed soil CO_2 efflux models for water

79   limited environments must account for the exponential effect of soil temperature (T_s) on the

80   metabolism of soil organisms and roots, and the limiting effects of soil moisture (de Dato et al.,

81   2010; Lloyd and Taylor, 1994; Reichstein, 2002; Vargas et al., 2011). Although the importance of

82   the biocrust for the ecosystems biogeochemistry is widely recognized (Belnap, 2006, 2003; Belnap

83   and Lange, 2003), its contribution to soil CO_2 efflux dynamics, which could be decoupled from the

84 respiration of the deeper soil layers, has been neglected. Indeed, biocrust organisms can be activated

85 by dew formation (Herrnstadt and Kidron, 2005; Kidron et al., 2002; Veste et al., 2008) that does

86 not affect the deeper soil layers, and this can occur at any time of the year (Moro et al., 2007). There

87 are a number of unique and subtle processes affecting soil CO_2 efflux in crusted soils, such as

88 changes in diffusion gradients of CO_2 in soil pore spaces due to the biocrust cover (Belnap et al.,

89 2003; Thomas et al., 2008), or CO_2 uptake by autotrophic biocrust components, which increases the

90 complexity of assessing the biocrust role on soil CO_2 efflux.

91   In these circumstances, soil CO_2 efflux models may lose accuracy and neglect the

92 contribution of the biocrust to this flux. Recently, some research efforts have been made to bridge

93 this gap. Zhang et al. (2013) reported that the biocrust contributed up to 2/3 to total R_s in a

94 temperate desert. Accordingly, Castillo-Monrroy et al. (2011) found that biocrust-dominated areas

95 are the main contributor to the total R_s in a semiarid ecosystem. On the other hand, Wilske et al.

96 (2008) reported that the highest biocrust-related net CO_2 uptake occurred during the wet winter,

97 whereas low soil water content (SWC) resulted in low uptake rates which can hardly compensate

98 for biocrust respiration. As this contribution depends on the biocrust cover and type (Zhao et al.,

99 2014), it is of paramount importance to collect data from a broad range of environments. Therefore,

100 understanding the biocrust contribution to soil CO_2 efflux in water-limited environments is crucial

101 to better comprehend the functioning of these ecosystems and improve prognostic modeling.

102   In this article, we present the results of a manipulative experiment in a Mediterranean shrubland

103 ecosystem in Sardinia, Italy. The objectives were to quantify the biocrust contribution to R_s and

104 identify the main environmental factors affecting it. The objectives were addressed by measuring *in*

105 *situ* soil CO_2 efflux over two different surfaces: soil deprived of biocrust (hereafter *Soil*), and intact

106 soil (hereafter *Soil+BC*), and estimating by subtraction the CO_2 efflux associated with the biocrust

107 (hereafter *BC*). Three hypothesis were tested: (i) the contribution of the biocrust to soil CO_2 efflux

108 varies over the seasons being minimum during the dry months due to its large dependence on

109   superficial moisture, (ii) CO_2 efflux of the studied surfaces (*Soil, BC* and *Soil+BC*) would respond

110   differently to SWC and T_s as a consequence of the very different exposure to environmental factors

111   regimes experienced by the biocrust and deep soil layers, (iii) since SWC is a main driver for

112   respiration and since small rain pulses can increase the moisture content of the upper soil layers but

113   have a minor effect on the soil moisture of the deeper layers, a two layer model would disentangle

114   how the biocrust contribution to R_s occurs in periods when deeper soil layers are inactive and

115   estimate its contribution on an annual base.

2. Materials and methods

2.1.   Study site

This study was carried out in a maquis shrubland coastal ecosystem at the National reserve Portoconte – Capo Caccia in northwestern Sardinia (40° 36' 18" N, 08° 09' 07" E; mean altitude 74 m asl), located 326 m from a deep sea cliff. The climate is sub-humid Mediterranean, with mild winter season and warm dry summer (usually from May to September). Strong predominant north-west (Mistral) and south-west winds blow in this area. Average annual air temperature (1970-2012) is 16.5 ± 5.0 °C ranging from a minimum of 6.2 ± 4.9 °C to a maximum of 32.7 ± 5.6 °C. The coldest month is February with an average temperature of 10.4 ± 1.1 °C, whereas the hottest month is August with an average temperature of 23.8 ± 1.5 °C. Spring and autumn are the rainy seasons, and mean annual rainfall is 494 ± 153 mm.

The underlying substrate is a Mesozoic limestone, and the main soil types are Lithic Xerorthent and Typic Rhodoxerarfs (USDA 1993). Soil texture is a clay-silt, with 55 – 60 % clay, 20 – 30 % silt and 10 – 25 % sand. Soil depth is 30 cm – 40 cm and because of its texture is highly erodible (Spano et al., 2009). Soil water holding capacity is 24 % and total Leaf Area Index ranges between 2.7 – 3.0 m^2 m^{-2} (Marras et al., 2011). Maximum canopy height is around 3 m, and the discontinuous vascular vegetation cover is 80 % on average. In this area, Mediterranean maquis appears as a shrubland of different species, mainly *Juniperus phoenicea* L. (53 % of total cover) but also *Pistacia lentiscus* L., *Phyllirea angustifolia* L., *Smilax aspera* L. and *Chamerops humilis* L. (27 % of total cover). The remaining 20 % are the inter spaces between shrubs, colonized by a well-developed lichen-dominated biocrust with a depth of about 0.5 cm. The dominant lichens are *Cladonia* sp. (23.8 % of the inter spaces between shrubs), *Squamarina cartilaginea, Diploschistes* sp. and *Collema* sp. (10.4 % all together). Green mosses cover 14.4 %, whereas litter accumulation and bare soil areas cover 26.3 and 10.0 % of these patches, respectively.

2.2.   Sampling design, field measurements and laboratory analyses

141   In April 2012, 16 permanent polyvinyl chloride (PVC) collars of 20 cm diameter were

142   installed on the soil surface covered by biocrust (*Soil+BC*). In March 2013, eight additional PCV

143   collars were installed in areas where the biocrust was physically removed using a spatula i.e. the

144   *Soil* surface. All the 24 collars were placed at random within eight inter spaces between shrubs:

145   patches were between 10 m and 50 m from each other and collars within each patch were at a

146   minimum of 2 m distance. Soil CO_2 efflux was measured from June 2013 to January 2015.

147   Measurements did not have a specific frequency, but they were rather performed in order to

148   measure over the widest range of combinations of T_s and SWC. All measurements were taken at

149   least three days after the last precipitation event to avoid measuring at moments when the SWC was

150   above its maximum field condition. In doing so, we attempted to minimize the disturbance

151   generated in our long-term experimental site by trampling into the plots while soil was muddy.

152   Thus, we avoided the CO_2 pulses that typically follow wetting of dry soils (Birch effect; Birch,

153   1964) and the physical displacement of CO_2-enriched pore space gases by water during rainfall, as

154   we were interested in the effect of T_s and SWC on R_s rather than on the effect of rewetting on R_s. In

155   any case, preliminary results showed that R_s was inhibited within 24 hours after a rain event in this

156   study site, most likely due to the impeded diffusion of gas through the saturated clay soil. Direct

157   measurements were collected on *Soil+BC* and *Soil* surfaces, whereas the CO_2 efflux emitted by *BC*

158   surface was estimated by subtracting the soil CO_2 efflux of *Soil* surfaces from that of *Soil+BC*.

159   Soil CO_2 efflux was measured *in situ* using a portable LI-COR 8100 (Lincoln, Nebraska –

160   USA) containing an infrared gas analyser system equipped with a flow-through closed chamber LI-

161   COR 8100-103 connected to the central unit. The chamber of 20 cm of diameter was inserted 5 cm

162   into the collar, and measurements were preformed in a dark condition. Measurements took 105 s per

163   collar, and were performed between 8:00 and 9:00 a.m. (local time, GMT + 1) to avoid direct

164   radiation from reaching the collars, which ensures minimization of variability in T_s within the

165 sampling day. However, this experimental design could have underestimated daily efflux as a result

166 of the time lags involved in diurnal variations in T_s, i.e. the soil surface will heat very quickly and

167 there will be a short time lag between peak air and soil temperatures, whereas at deeper depths this

168 lag could be of several hours. The offset of each collar was measured and taken into account to

169 calculate the headspace of each collar and quantify the CO_2 emission. Soil temperature at 3 cm

170 depth adjacent to the collars was measured at the same time as CO_2 efflux measurements using a

171 probe connected to the LI-COR 8100.

172 Since 2004, a meteorological and radiometric station (2 m and 3.5 m above the ground,

173 respectively) are located within the experimental site. Air temperature and relative humidity were

174 measured hourly using a HMP45C probe (Campbell Scientific Inc., USA) and an aerodynamic rain

175 gauge (ARG100, Environmental Measurements Limited, UK) was used to record precipitation data

176 every hour. SWC was monitored at 20 cm depth using two Time-Domain Reflectometry (TDR)

177 probes (Model CS616-L, Campbell Scientific Inc., Logan, UT, USA). In January 2012, two

178 additional T_s and SWC sensors (EC-5, Decagon Devices Inc., Pullman, WA, USA) were placed at 5

179 cm depth. All sensors acquired data every minute and were stored as half-hourly averages.

180 In April 2014, 8 soil cores (2 cm in diameter) between 0 cm and 5 cm depth and between 5

181 cm and 10 cm depth below the mineral soil were collected. The samples were dried at 40 °C for 72

182 h and sieved using a < 2 mm mesh. Sieved samples were ground using Brinkmann Retsch Mortar

183 Grinder (Model: RMO Polished), then 0.15 g analysed with an Elemental analyser (CHN 628, Leco,

184 St. Joseph, USA), to determinate the total C and nitrogen (N) soil content. Soil pH was determined

185 in a water slurry (1:5 w/v in H_2O). The effective cation concentration, Ca, Mg and Na, was

186 extracted by cationic exchange capacity method, in solution of $BaCl_2$ according to ISO 11260, then

187 concentration was determined by atomic absorption spectroscopy analyser (Analyst 200, Perkin

188 Elmer, Waltham, USA). Available phosphorus (P_2O_5) was extracted as in Olsen et al. (1954) and

189   quantified by spectrophotometric analysis (Cary 60 UV-Vis, Agilent, Santa Clara, USA). Calcium

190   carbonate ($CaCO_3$) was quantified using a "Dietrich-Fruhling" calcimeter.

191   *2.3.   Statistical analyses*

192   ANOVA for repeated measurements was used to test for differences among *Soil+BC, Soil,*

193   and *BC* in soil CO_2 efflux measurements. Prior to ANOVA analysis, data were tested for

194   assumptions of normality and homogeneity of variances, and were log-transformed when necessary.

195   Partial correlations were performed to account for collinearity and thus to test the effects of T_s on

196   soil CO_2 efflux of *Soil+BC, Soil* and *BC* while controlling for SWC at 5 cm and 20 cm depth

197   (SWC_{-5cm} and SWC_{-20cm}, respectively) and *vice versa.* All statistical analyses were performed by

198   using the IBM SPSS 15.0 (SPSS Inc., Chicago, IL, USA).

199   Different functions can be used to simulate soil CO_2 efflux response to environmental

200   conditions. In this study, the dependency of R_s on T_s and SWC was investigated for the three

201   studied surfaces (*Soil+BC, Soil* and *BC*). Three different approaches were used: a simple linear

202   regression accounting for both T_s, and SWC_{-5cm} and SWC_{-20cm}, a multi-linear equation to account

203   for the combined effect of these variables, and a modified version of the most common used Lloyd

204   and Taylor (LLT) model (Lloyd and Taylor, 1994). The LLT function is an Arrhenius type equation

205   which is temperature-driven and given by:

206
$$R_{s_{LLT}} = R_{ref} \cdot exp\left[E_0 \cdot \left(\frac{1}{T_{ref}-T_0} - \frac{1}{T_s-T_0}\right)\right] \tag{1}$$

207   where R_s is soil respiration, R_{ref} is the ecosystem respiration rate at a reference temperature (T_{ref})

208   and E_0 is an activation energy parameter that determines the temperature sensitivity. In the original

209   study (Lloyd and Taylor, 1994), T_{ref} and T_0 are set to 10°C and -46°C respectively, and T_s is used as

210   predictor. Although the Lloyd and Taylor equation fits well to the experimental data during

211   standard water availability conditions, in semi-arid ecosystems the dependence of ecosystem

212   respiration on SWC must also be considered. Here we used the modified Lloyd and Taylor equation

213   (LLT$_{mod}$) proposed by Reichstein et al. (2002), which multiplies the original temperature-driven

214   model (equation 1) by a moisture function:

215     $$R_s = R_{s_{LLT}} \cdot \frac{SWC - SWC_0}{(SWC_{1/2} - SWC_0) + (SWC - SWC_0)}$$ (2)

216   where SWC$_0$ is the residual SWC at which respiration is absent, and SWC$_{1/2}$ is the SWC at 50% of

217   the maximal respiration (Reichstein et al., 2002). Equation 2 is the third approach used in this study

218   to simulate R$_s$ as function of T$_s$ and SWC$_{-5cm}$ and SWC$_{-20cm}$. Models performances were evaluated

219   using the following statistical indices: the Pearson's correlation coefficient (r), the root mean square

220   error (RMSE), the index of agreement (d) and the Akaike's information criterion (AIC test, Akaike,

221   1974).

222   To calculate the contribution of *BC* to R$_s$, the best models were run at a 30 minute timestep for

223   two years (2013-2014) thus accounting for the variations of both T$_s$ and SWC. Daily amounts of *BC*

224   and *Soil* CO$_2$ efflux were first computed separately and then summed to obtain *Soil+BC* respiration

225   rate. *BC* contribution to *Soil+BC* respiration rate was thus calculated as the ratio of the daily *BC*

226   and the estimated *Soil+BC* respiration rates.

227

3. Results

Average annual rainfall during the study period was 430 mm, slightly under the 42-year average (494 mm), while annual mean T_{air} was 16.8 °C (Figure 1). SWC_{-20cm} was generally higher than SWC_{-5cm} during the entire study period, ranging from 19.0 % to 43.1 % for SWC_{-20cm}, and from 12.2 % to 33.6 % for SWC_{-5cm} (Figure 2a). At both depths, SWC followed the same overall pattern of seasonal changes showing higher values in spring, autumn, and winter (average values of 26.9 % and 17.7 % for SWC_{-20cm} and SWC_{-5cm} respectively, Figure 2a) and lower during summer (20.6 % and 13.3 % for SWC_{-20cm} and SWC_{-5cm} respectively, Figure 2a). Daily averages of T_s followed a sinusoidal pattern with maximum daily values of 33.3 °C and 31.1 °C recorded between June and August 2013 and 2014 respectively, and minimum values of 5.2 °C and 3.6 °C recorded during the cold season of 2013 and 2014, respectively (Figure 2b). We did not find any significant differences in soil chemical properties between 5 cm and 10 cm depth (Table 1).

Significant differences in CO_2 efflux were found among *Soil*, *BC* and *Soil+BC* (Figure 3a, b, c, Repeated Measures [RM] ANOVA; F = 1916, df = 2, P <0.001). Respiration rates for *Soil* ranged from 0.80 to 2.17 µmol CO_2 m^{-2} s^{-1} whereas that for *Soil+BC* ranged from 1.36 to 2.59 µmol CO_2 m^{-2} s^{-1} (Figure 3), which was always significantly higher than that of *Soil* (RM ANOVA; P <0.001). Soil respiration rates estimated for *BC* ranged from -0.12 to 1.32 µmol CO_2 m^{-2} s^{-1}, and were lower than *Soil* (RM ANOVA; P <0.001) except for one event in autumn 2014. The *BC* contribution to *Soil+BC* respiration rate was on average 6.9 %, ranging from -16.5 % in the driest and hottest period to a peak of 60.1 % recorded in autumn 2014 (Figure 3b). This event took place when the soil was rewetted after the rainless summer period. The minimum *BC* contribution to *Soil+BC* respiration (-1.6 to -16.5 %) was found during the dry months (i.e. July, August and September) in both 2013 and 2014, whereas higher values of contribution (-0.3 to 60.1 %) were found during the rest of the year (Figure 3b).

252   Partial correlations revealed a significant effect of T_s, SWC_{-5cm} and SWC_{-20cm} on the *Soil*

253   CO_2 efflux (Table 2). The CO_2 efflux of *Soil+BC* was significantly correlated with SWC_{-5cm}

254   (p<0.001) and SWC_{-20cm} (p=0.005), but not with T_s, although the probability level was almost

255   significant (p_{5cm}=0.059; p_{20cm}=0.056, Table 2). Finally, the respiration rate of *BC* was only

256   significantly correlated with SWC_{-5cm} (p=0.001, Table 2).

257   When simulating *Soil* CO_2 efflux, the Lloyd and Taylor (1994) model modified according to

258   Reichstein et al. (2002) to also account for SWC_{-20cm}, outperformed the other models as it is shown

259   by r (0.81, p<0.001), RMSE (0.13 $\mu mol\ m^{-2}\ s^{-1}$), d (0.89),and the lowest AIC test value (=-8.1)

260   (Table 3). The simple linear model which uses SWC_{-5cm} as independent variable, was the best

261   model predicting estimated *BC* respiration rates according to all the statistical indexes (r=0.75,

262   p=0.002, RMSE=0.15 $\mu mol\ m^{-2}\ s^{-1}$, d=0.84, AIC= -7.00). Also the multilinear model with T_s and

263   SWC_{-5cm} showed good performances with a slightly higher AIC test result (AIC=-5.5) (Table 3).

264   *Soil+BC* CO_2 efflux was best explained by the multilinear model accounting for both T_s and

265   SWC_{-5cm} (r=0.75, p=0.002, RMSE=0.19, d=0.85, AIC=1.7). However, the modified Lloyd and

266   Taylor model accounting for SWC_{-20cm}, and the linear model using SWC_{-5cm} as independent

267   variable, performed similarly but showed higher AIC test results (AIC>3.6) (Table 3). In agreement

268   with these models, the CO_2 efflux of all the three surfaces increased with soil moisture (Figures 2

269   and 3). For *Soil* and *Soil+BC*, T_s and CO_2 efflux were positively correlated until the soil dried (see

270   Figures 2 and 3) whereas for *BC* the metrics suggests that respiration was mainly controlled by

271   SWC_{-5cm} with a seasonal pattern decoupled from that of *Soil* or *Soil+BC* (Figure 3).

272   Table 4 reports the coefficients of the best performing models for *BC, Soil* and *Soil+BC*.

273   The daily respiration rate for the two layer model ranged from 89.8 to 406.7 mol $CO_2\ m^{-2}\ d^{-1}$, with

274   the daily modeled values for the *Soil* layer ranged from 87.0 to 181.1 mol $CO_2\ m^{-2}\ d^{-1}$ for *Soil*, and

275   those for the *BC* layer between 0.2 and 193.2 mol $CO_2\ m^{-2}\ d^{-1}$ (Figure 4a). Modeled respiration rates

276   showed the greater temporal variability found in *BC* CO_2 efflux compared to *Soil* (Figure 4a),

277   highlighting the key role of the biocrust in *Soil+BC* respiration rates through the seasons. The

278   modeled *BC* contribution to *Soil+BC* respiration rate was on average 23.6 %, ranging from 0.1 % in

279   June 2012 to a peak of 61.9 % in February 2012 (Figure 4b). Following the trend found in estimated

280   *BC* contribution to *Soil+BC* respiration, modeled *BC* contribution was minimum during the rainless

281   season and became a relevant CO_2 source in the wet months (Figure 4b).

282

4. Discussion

The importance of biocrust for ecosystems functions has received increasing attention from the scientific community in recent years (Grote et al. 2010; Ladron de Guevara et al. 2014; Maestre and Cortina 2003; Thomas and Hoon, 2010). However, despite previous attempts to assess CO_2 efflux from biocrust in dryland ecosystems (Castillo-Monroy et al., 2011; Thomas, 2012; Thomas et al., 2008, 2011, 2014; Wilske et al., 2008, 2009; Zhang et al., 2013; Zhao et al., 2014), there is still a large uncertainty on the estimation and controlling factors of biocrust contribution to soil CO_2 efflux.

Wilske et al. (2008) followed an experimental design similar to ours to assess biocrust CO_2 efflux in a Mediterranean shrubland, but measuring net CO_2 exchange instead of R_s. Regardless of this difference, Wilske et al. (2008) also pointed out the key role of biocrust moisture in regulating CO_2 exchange, reporting high net uptake rates under wet conditions and decreased net uptake in rainless periods. Accordingly, Wilske et al. (2009) assessed the annual biocrust net C fluxes in the same study site using a model where SWC had a central role. Zhang et al. (2013) modeled the effect of moisture at different soil depths on both biocrust and rhizosphere respiration in a temperate desert, and they found that the former was determined by superficial water content, whereas the latter was driven by deep SWC. However, the soil depths considered in this study were rather coarse compared to those in our study, as superficial water content accounted from 0 cm to -20 cm soil layer, and deep SWC referred from -30 cm to -210 cm soil layer. Thomas et al. (2014) applied two different techniques to isolate biocrust efflux on a salt pan: by subtraction (same approach applied in this article) and by removing the biocrust and sitting in on a bed of inert substrate. Although both approaches have shortcomings, the second method is very manipulative and consequently, the CO_2 efflux measurements are performed in a highly artificial environment, which may make the subtraction method the most suitable for estimating the biocrust contribution to R_s. In their study, they found that the biocrust was a small contributor to R_s in the dry season and reported

308   a net uptake of CO_2 to the biocrust when following the subtraction method in the wet season. The

309   major short coming of the subtraction method is that the removal of the biocrust from the soil

310   surface as part of the experiment may also have changed the natural soil to air diffusion gradient

311   and may have increased the measured CO_2 efflux, without any biological processes being involved.

312   That is, if by removing the biocrust the natural diffusion gradient between the soil and atmosphere

313   has been increased, the subsoil CO_2 efflux would be enhanced to without any increased respiration,

314   which would lessen the difference between R_s on *Soil+BC* and *Soil*. In this likely situation, the

315   biocrust contribution to R_s would have been even greater than that reported. The relatively small

316   and negative estimated values for *BS* respiration found in summer suggest that the possible increase

317   in CO_2 fluxes due to the biocrust removal was not large and partially attributable also to spatial

318   variation. It is well known that soil CO_2 efflux may change greatly even over short distances and

319   that the relative differences in space also change in time as consequence e.g. of the mosaic pattern

320   of clumps of vegetation and patches of soil typical of Mediterranean ecosystems. In fact, Qi et al.

321   (2010) proved that CO_2 fluxes from the soil under the canopy of shrubs were significantly higher

322   than those from the soil covered with biocrusts and the bare soil in the interplant spaces of a

323   semiarid ecosystem. It is thus likely that our negative values for *BC* are partially due to an artefact

324   created by both the subtraction method and spatial variability. However, these two components are

325   difficult to separate and would require *ad-hoc* experiments to do so.

326   Zhao et al. (2014) and Thomas et al. (2011, 2008) reported that soil moisture was the

327   primary limiting factor to biocrust CO_2 efflux in the Kalahari and Tengger deserts, respectively, but

328   these studies did not estimate the contribution of biocrust to total R_s. In agreement with our results,

329   both Zhang et al. (2013) and Castillo-Monroy et al. (2011) proved that the biocrust respiration is a

330   major player in CO_2 efflux, contributing ca. 66 % and 42 % to total R_s in a temperate desert and a

331   semiarid ecosystem, respectively. In the light of these findings and our own results which show a

332   biocrust contribution of ca. 23.6 % in a sub-humid Mediterranean ecosystem, it could be inferred

that the biocrust contribution to R_s increases with the aridity of the site. A higher contribution of deeper soil layers in the less arid ecosystems can be due to a number of factors promoting both root and microbial respiration such as higher root density, microbial biomass and soil organic C.

It is worth noting that the interpretation of CO_2 efflux data is complex, since it involves several different processes, such as soil microbial, root, arthropods and mycorrhizal respiration, and therefore changes occurring in any of these processes can be masked by opposite changes in other ones (Buyanovsky and Wagner, 1995). Consequently, it has been pointed out that soil CO_2 efflux data are of moderate value in differentiating soil processes (Raich and Tufekcioglu, 2000). However, as we always waited for soil to drain for three days after rainfall before measuring CO_2 efflux to minimize the plot disturbance while soil was muddy and to focus on the effect of T_s and SWC on R_s rather than on the effect of rewetting on R_s, we can exclude the possibility of a contribution from two typically important processes in this type of ecosystems. First, the physical displacement of higher concentrations of CO_2 following rainfall that would be accumulated in pore spaces between rainfall pulses (Huxman et al., 2004). Second, the rewetting of dry soils which frequently produces a R_s peak, also known as Birch effect (Birch, 1964). This process is particularly relevant in Mediterranean ecosystems, as it is known to constitute a large proportion of the total R_s in water limited ecosystems (Jarvis et al., 2007; Unger et al., 2010). On the other hand, our experimental design, which accounted for R_s in dark conditions, was conceived to exclude the contribution of the biocrust autotrophic components because we were interested in assessing R_s instead of soil net CO_2 exchange. Determining the length of the dark period required before the biocrust autotrophic activity stops is a controversial issue. Ladron de Guevara et al. (2014) measured R_s for 120 s leaving no time in dark conditions before measurement in a semiarid ecosystem, whereas Grote et al. (2010) darkened crusted soils for 10 minutes before measuring dark R_s in a desert ecosystem. In general, respiration rate appears to change over time so that CO_2 measurements are in part relative to the protocol used.

In agreement with other authors, respiration rates of *Soil* decreased as the soil dried (Inglima et al, 2009; Unger et al, 2012) and increased with T_s (de Dato et al., 2010; Poll et al., 2013). These results are in line with those from many previous studies that reported that T_s is a strong predictor of R_s, as rising temperatures increase soil decomposition rates, producing a proportionate increase in CO_2 efflux (Lloyd and Taylor, 1994). The Lloyd and Taylor (1994) model has been reported to give good results for a variety of soil types (Lloyd and Taylor, 1994) and has been successfully used in a number of soil and ecosystem models (Adair et al., 2008; Kucharik et al., 2000; Thornton et al., 2002). However, as proposed by Reichstein et al. (2002), it was necessary to include soil moisture as a predictor to have an improved fit, confirming the importance of the interaction between T_s and SWC for R_s in Mediterranean ecosystems. According to this, the Lloyd and Taylor (1994) model modified by Reichstein (2002) was the best model for *Soil* respiration in our experimental site.

As microbial activity in drylands is limited by the availability of moisture and organic substrates (Zak et al., 1994), increased water content in the subsoil is likely to produce an augmented population and activity of heterotrophs, which is reflected by an increased soil CO_2 efflux. In line with these findings, Conant et al. (2000) found that soil moisture was the main factor determining R_s in three semiarid ecosystems in Arizona. However, although increased soil moisture generally leads to a rise of CO_2 efflux, respiration rates in *Soil* reached its minimum peak under the highest recorded SWC (35%) that was found in November 2014. Decreased respiration under high soil moisture has been previously reported (Grote et al., 2010; Maestre and Cortina, 2003), and is likely driven by the CO_2 affinity for water thus dissolving in soil water during wet periods, or alternatively by impeded diffusion of CO_2 through soil when the pore spaces are filled with water.

According to previous research (Ladron de Guevara et al., 2014; Thomas and Hoon, 2010; Thomas et al., 2011; Wilske et al., 2008), our results reveal that the respiration rate of the *BC* is strongly influenced by its moisture content and less by T_s. The biocrust can contribute to the R_s even in periods in which the deeper soil layers are inactive; consistently respiration rates of *Soil*

383   depend on SWC_{-20cm}, whereas the correlation of respiration of the *BC* with SWC is strongest at 5

384   cm depth. The SWC at 20 cm and 5 cm depths strongly co-vary, however small water pulses can

385   increase the moisture only of the top layer, and the top layer may dry much faster than the deeper

386   ones. Thus, small water pulses can activate lichens, mosses and cyanobacteria associated to the

387   biocrust, and the metabolism of C in soils, while deeper soil layers remain dormant. Likewise,

388   respiration in the deeper soil layers may persist in periods when the biocrust is inactive. In line with

389   these findings, Cable and Huxman (2004) found that the relative contributions of biocrust and deep

390   soil layers to CO_2 efflux in Arizona varied with rainfall magnitude. Using δ13C and CO_2 data, they

391   reported that over 80 % of the respiration originated from biocrust during small rainfall events,

392   whereas 98 % was originated from deep soil layers after-intense rainfall events. Consequently, the

393   proportional contribution of the biocrust changes over the seasons, playing an important role when

394   the soil is wet and being minimum during the dry months (i.e. July, August and September).

395   We found that both the modeled and estimated *BC* contribution to *Soil+BC* respiration rate

396   peaked following the soil rewetting after the rainless summer period. Similar results have been

397   found by Zhao et al. (2014) when studying mixed biocrust (composed of mosses, algae and lichens)

398   and algae-dominated biocrust respiration responding to an extreme rainfall event in a mesocosm

399   experiment. Zhao et al. (2014) reported that CO_2 efflux was inhibited for several days after the

400   rainfall event in both biocrust types, and then it increased. However, less influence of extreme

401   rainfall events on R_s was found for moss-dominated biocrusts. The authors attributed these findings

402   to the increased soil hydrophobicity due to the biocrust extracellular polysaccharide (EPS)

403   secretions (Mager and Thomas, 2011). EPS can block superficial soil pores (Avnimelech and Nevo,

404   1964) leading to water accumulation in the surface of mixed and algae-dominated biocrust after

405   heavy rainfall. As EPS are decomposed by microbes (Fischer 2009), soil pores will reopen

406   producing a burst in CO_2 efflux in mixed and algae-dominated biocrust. In contrast, the higher

407   porosity and infiltration rates that characterizes moss tissue allows water to percolate deep into the

408   soil avoiding water accumulation on the soil surface in moss-dominated biocrusts (Frey and

409   Kürschner, 1991; Chamizo et al., 2012). An alternative explanation for these findings is that a

410   relatively thick film of water for the first days after the rainfall may restrict the exchange of gases,

411   impeding in turn photosynthesis and respiration until water evaporation (Lange et al., 1992). The

412   higher infiltration on moss-dominated biocrust could also be attributed to the low amount of EPS at

413   these crusts due to the fact that mosses do not excrete EPS (Kidron et al., 2003). Given that the soil

414   rewetting dynamics have been proved to affect differently to the contributions of distinct biocrust

415   types to R_s (Zhao et al., 2014), especially after large rainfall pulses (>10 mm), it is crucial to

416   account for the biocrust composition in this type of studies.

417   Dew events in water limited ecosystems are common throughout the year, and typically

418   range from 0.15 mm to 0.30 mm per day (Jacobs et al., 2000; Moro et al., 2007). Previous studies

419   reported that biocrust organisms can utilize the morning dew as a window of opportunity for

420   activating their metabolism (Delgado-Baquerizo et al., 2013; Thomas and Hoon, 2010; Veste et al.,

421   2008). However, other authors have found that while dew can wet rock and stones in a dew desert

422   such as the Negev, its capability to wet the soil is very limited, since the activation threshold of 0.1

423   mm (Lange et al., 1992) is rarely reached on the soil surface (Agam and Berliner, 2006; Kidron et

424   al., 2002). Our experimental design was focused on understanding the general effect of SWC and T_s

425   and not of rain pulses nor of dew on biocrust respiration or the limiting effect of over saturated soil

426   on diffusion. The estimation of superficial soil moisture is most likely an even stronger predictor for

427   biocrust respiration than SWC_{-5cm}. Perhaps, if the superficial SWC had been monitored, an even

428   greater decoupling of *BC* respiration from that of *Soil* would have been reported. However the

429   isolation of superficial moisture from the background soil under field conditions is quite

430   challenging.

431   This high dependence of *BC* respiration on SWC is not surprising given previous findings

432   that linked SWC to soil microbial biomass (Van Gestel et al. 1992) and to biocrust biomass (Kidron

et al., 2009), biocrust respiration to biocrust biomass (Kidron et al., 2015; Yu et al., 2012), and superficial and deep soil layers moisture to biocrust activity (Kidron and Benenson, 2014). Thus, the biocrust biomass, soil microflora and biocrust type are all shaped by the soil superficial moisture (Kidron et al., 2010). As biocrust respiration is highly dependent on biocrust type, our findings support that lichen-dominated biocrusts performance depends to a large degree on soil moisture conditions, contributing to total R_s mainly during the wet months. These findings complement those of Adebayo and Harris (1971) and Austin et al. (2004), which found that fungal-dominated microbial communities are more desiccation-tolerant than those dominated by cyanobacteria. Interestingly, although mosses generally dry during the dry season ceasing their metabolic activity and regrow in the wet season, Deltoro et al. (1998) found that mosses adapted to xeric conditions can maintain maximal levels of quantum efficiency when drying down to about 5 % soil moisture.

According to both the modeled and estimated *BC* contribution to *Soil+BC* respiration rate, *BC* represents a significant source of CO_2 during humid seasons, showing the highest peaks in autumn and winter coinciding with the maximum values of SWC_{-5cm} and SWC_{-20cm}. On the other hand, although in water limited ecosystems the biocrust is wet and metabolically active less than 10 % of the time (Lange et al., 1994), and high soil moisture likely does not occur regularly, the results of this study reveal the potential for the biocrust respiration rates under a broad range of SWC.

We found no effect of T_s on *BC* respiration, suggesting that in Mediterranean ecosystems T_s is not as an important driver of biocrust respiration as SWC. Johnson et al. (2012) and Zelikova et al. (2012) also found very limited sensitivity of the metabolic activity of biocrust communities dominated by cyanobacteria, cyanolichens, and mosses to T_s. Similar results were reported by Grote et al. (2010) in cyanobacteria- and lichen-dominated biocrust from the Chihuahuan desert and the Colorado Plateau.

456   We found higher R_s rates in *Soil+BC* than in *Soil*. Such difference can be explained by the

457   fact that *Soil* has been devoid of habitats for a dependent foodweb of arthropods, lichens, fungi,

458   bacteria, and other soil organisms typically found in the biocrust (Belnap and Lange, 2003), whose

459   activity significantly contribute to soil CO_2 efflux (Castillo–Monroy et al., 2011). Given the

460   decoupling of the respiration rates of *BC* and *Soil*, it was not possible to identify a model clearly

461   outperforming the others for *Soil+BC*. The resulting model can be seen as a mix of the model for

462   *Soil* and for *BC* as it responds to T_s and to SWC_{-5cm} instead of SWC_{-20cm}. Additionally, the model is

463   multilinear losing the physiological mechanism accounted for by the Lloyd and Taylor model. The

464   highly contrasting seasonal pattern of respiration observed in *Soil* is not visible in *Soil+BC*,

465   suggesting that the biocrust might be masking the seasonal trend showed by deeper soil layers in

466   *Soil+BC*, since the biocrust exhibits an independent dynamic driven by moisture in the first soil

467   centimeters.

468   **5. Conclusions**

469   Our findings show that CO_2 effluxes emitted by *Soil, BC* and *Soil+BC* are differently driven

470   by T_s and SWC: *BC* respiration is mainly controlled by superficial SWC, whereas T_s and SWC_{-20cm}

471   mostly control *Soil* respiration, and T_s and SWC_{-5cm} drive *Soil+BC* respiration. Our results

472   complement those of previous studies highlighting the key role of the biocrust as modulator of R_s in

473   dryland ecosystems, and indicate that the biocrust has the ability to contribute to R_s responding to

474   small water pulses in periods when deeper soil layers are inactive. Thus, our results suggest that

475   accounting for the biocrust contribution to R_s and its responses to environmental drivers is highly

476   relevant in providing accurate estimates of this key component of the C cycle at the ecosystem

477   level. Projections based solely on bare ground and vegetated areas have been used to predict C

478   budgets in semiarid (Rey et al., 2011) and temperate (Kim et al., 1992) grasslands. Nevertheless, the

479   important differences observed in CO_2 efflux between *Soil* and *Soil+BC* suggest that these

480   estimations may underestimate soil CO_2 efflux in spatially heterogeneous Mediterranean

481 ecosystems. Given the large areas covered by biocrust, not only in drylands, but also in temperate,

482 alpine and polar ecosystems (Belnap and Lange 2003), taking into account soil surface covered by

483 biocrust in future modeling studies can significantly contribute to improve our understanding of the

484 global C cycle and our ability to project the effects of global environmental change on soil CO_2

485 efflux.

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730 **Figure 1.** Monthly precipitation and average, minimum, and maximum air temperature at the study

731 site from January 2012 to December 2014.

732 **Figure 2.** (a) Daily sum of precipitation and soil water content (SWC) at 5 and 20 cm at the

733 experimental site. (b) Daily average, minimum, and maximum soil temperature (T_s)

734 measured at 5 cm depth.

735 **Figure 3.** CO_2 efflux emitted by (a) soil deprived of biocrust (*Soil*), (b) biocrust surface (*BC*), and

736 (c) intact soil (*Soil+BC*). The *BC* contribution to *Soil+BC* respiration rate is also shown

737 (gray line). Error bars are ±SE, n = 16 for *BC* and *Soil+BC*, n = 8 for *Soil*.

738 **Figure 4.** (a) Daily values of modeled respiration rates emitted by soil deprived of biocrust (*Soil*),

739 biocrust surface (*BC*), and intact soil (*Soil+BC*). (b) Modeled *BC* contribution to *Soil+BC*

740 respiration rate.

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Table 1. Soil chemical properties in the top 5 and 10 cm of the soil profile at the experimental site.

No significant differences between depths were found. Soil sampling was performed in April 2014.

SE means Standard Error (n = 8).

Soil properties	Soil depth			
	5 cm		10 cm	
	Mean	SE	Mean	SE
pH	7.25	0.12	7.26	0.11
Total C (%)	3.56	0.57	2.77	0.40
Total N (%)	0.194	0.03	0.162	0.02
C/N	19.25	2.34	16.62	1.31
Phosphate (P_2O_5, mg/kg)	1.75	0.45	1.12	0.30
$CaCO_3$ (g/kg)	8.62	2.53	7.37	2.07
Organic matter (g/kg)	61.03	9.44	48.33	6.63
Ca (meq 100 g^{-1})	12.80	3.09	11.77	2.23
Mg (meq 100 g^{-1})	5.88	0.65	6.01	0.51
Na (meq 100 g^{-1})	0.99	0.10	1.11	0.13
K (meq 100 g^{-1})	1.32	0.10	1.53	0.14

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Table 2. Summary of partial correlations among CO_2 efflux, soil temperature (T_s) and soil water content (SWC) at 5 and 20 cm depth respectively for soil deprived of biocrust *(Soil)*, biocrust surface *(BC)* and intact soil *(Soil+BC)*. Statistical differences are indicated as $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***). P values below 0.05 are indicated in bold.

		T_s	SWC_{-5cm}		T_s	SWC_{-20cm}
Soil	CO_2 efflux	**0.594**[*]	**0.546**[*]	CO_2 efflux	**0.632**[**]	**0.563**[*]
	T_s		**-0.589**[*]	T_s		**-0.700**[**]
BC	CO_2 efflux	-0.178	**0.710**[***]	CO_2 efflux	-0.093	0.502
	T_s		-0.111	T_s		-0.396
Soil+BC	CO_2 efflux	0.495	**0.749**[***]	CO_2 efflux	0.499	**0.643**[**]
	T_s		**-0.568**[*]	T_s		**-0.661**[**]

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Table 3. Summary of models simulating CO_2 efflux for soil deprived of biocrust (*Soil),* biocrust surface (*BC*) and intact soil (*Soil+BC*). Soil temperature (T_s) and water content (SWC), at both 5 and 20 cm depth, are used as main predictor in linear, multi-linear, and Lloyd and Taylor (LLT) equations. The best model predicting soil respiration rates for each surface is indicated in bold. Statistical differences are indicated as $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***). The Pearson's correlation coefficient (r), the root mean squared error (RMSE, $\mu mol\ m^{-2}\ s^{-1}$), the index of agreement (d), and the Akaike's information criterion (AIC) test are calculated for each model.

		r	RMSE	d	AIC
Soil	T_s	0.403	0,199	0,534	0.57
	SWC_{-5cm}	0.302	0.208	0.434	1.7
	SWC_{-20cm}	0.218	0.212	0.327	2.4
	T_s+SWC_{-5cm}	0.642*	0.167	0.763	-2.4
	T_s+SWC_{-20cm}	0.654*	0.165	0.769	-2.8
	LLT_{mod} (SWC_{-5cm})	0.440	0.196	0.563	4.0
	LLT_{mod} (SWC_{-20cm})	**0.814***	**0.127**	**0.887**	**-8.1**
BC	T_s	0.367	0.212	0.488	2.3
	SWC_{-5cm}	**0.746***	**0.152**	**0.838**	**-7.0**
	SWC_{-20cm}	0.589*	0.184	0.711	-1.6
	T_s+SWC_{-5cm}	0.755**	0.149	0.847	-5.5
	T_s+SWC_{-20cm}	0.594*	0.183	0.710	0.3
	LLT_{mod} (SWC_{-5cm})	0.616*	0.180	0.726	1.7
	LLT_{mod} (SWC_{-20cm})	NA	NA	NA	NA
Soil+BC	T_s	0.128	0.291	0.189	11.2
	SWC_{-5cm}	0.654*	0.222	0.783	3.6
	SWC_{-20cm}	0.482	0.258	0.631	7.7
	T_s+SWC_{-5cm}	**0.754****	**0.193**	**0.849**	**1.7**
	T_s+SWC_{-20cm}	0.650*	0.223	0.775	5.7
	LLT_{mod} (SWC_{-5cm})	0.267	0.283	0.340	14.4

| LLT $_{mod}$ (SWC$_{-20cm}$) | 0.723[**] | 0.203 | 0.823 | 5.1 |

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765

766 **Table 4.** Summary of the best models simulating CO_2 efflux for soil deprived of biocrust (*Soil*),

767 biocrust surface (*BC*) and intact soil (*Soil+BC*). Statistical differences are indicated as $p < 0.05$ (*),

768 $p < 0.01$ (**), $p < 0.001$ (***). Depending on the model the intercept parameter (a), the T_s slope (b),

769 the SWC slope (c), the ecosystem respiration rate (R_{ref}), the activation energy parameter (E_0), the

770 residual SWC at zero repiration (SWC_0) and SWC at half of maximal respiration rate ($SWC_{1/2}$)

771 were calculated.

	Model	R_{ref}	E_0	SWC_0	$SWC_{1/2}$	a	b	c
Soil	LLT $_{mod}$ (SWC_{-20cm})	1.54 (0.16) ***	84.62 (25.62) **	18.49 (1.01) ***	18.98 (0.54) ***			
BC	SWC_{-5cm}					-1.07 (0.33) **		0.09 (0.02) **
Soil+BC	T_s+SWC_{-5cm}					-0.29 (0.66)	0.02 (0.01) *	0.12 (0.03) **

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