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# Contribution of biological crust to soil $CO_2$ efflux in a Mediterranean shrubland ecosystem

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## Abstract

In Mediterranean ecosystems, the soil biological crust (hereafter biocrust) plays a crucial role in maintaining ecosystem functioning. In these ecosystems, soil water content can often be a stronger driver of soil $CO_2$ efflux than soil temperature, or at least comparable. However, little is known on the contribution of the biocrust to soil $CO_2$ efflux or how the respiration of the biocrust responds to soil water content and temperature. A manipulative experiment was performed in a Mediterranean shrubland ecosystem in Sardinia (Italy) to assess the contribution of the bicocrust to soil $CO_2$ efflux and to identify the main environmental drivers of the $CO_2$ efflux. For 19 months, *in situ* soil $CO_2$ efflux was measured over two different surfaces: soil deprived of biocrust (hereafter *Soil*) and intact soil (hereafter *Soil+BC*), and estimated by subtraction in a third surface: biocrust (hereafter *BC*). $CO_2$ efflux emitted by *Soil*, *BC* and *Soil+BC* were uniquely driven by soil moisture and temperature: *BC* respiration was mainly controlled by soil moisture at 5 cm depth, whereas both soil temperature and water content at 20 cm depth determined *Soil* $CO_2$ efflux. Soil temperature and water content at 5 cm depth drove *Soil+BC* respiration. We also found that biocrusts can contribute substantially (up to 60%) to the total soil respiration depending on its moisture content. This contribution persists even in periods in which deeper soil layers are inactive, as small water pulses can activate the metabolism of carbon in soils through lichens, mosses and cyanobacteria associated with the biocrust, while deeper soil layers remain dormant. The important differences observed in $CO_2$ efflux between *Soil* and *Soil+BC* suggest that carbon models and budgets may underestimate soil $CO_2$ efflux in spatially heterogeneous Mediterranean areas. Our results highlight the importance of accounting for the biocrust contribution to soil respiration and its response to environmental drivers. We provide an accurate estimation of this key component of the carbon cycle at the ecosystem level in water limited ecosystems.

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

One key aspect of the spatial heterogeneity in Mediterranean ecosystems is the presence of the biological soil crusts (hereafter biocrust), which can encompass up to 70% of the cover in absence of vascular plants (Belnap and Lange, 2003). Biocrusts are specialized communities that cover the first millimeters of the soil surface in water-limited ecosystems worldwide. Such communities are composed of cyanobacteria, lichens, liverworts, fungi, eukaryotic algae and mosses in various proportions (Belnap and Lange, 2001; Eldridge and Greene 1994). They largely affect the ecosystem functioning by influencing soil nutrient cycling (Castillo-Monroy et al. 2010; Morillas and Gallardo, 2015), soil stability and water infiltration (Eldridge et al., 2010; Kidron, 2014; Reynolds et al. 2001), local hydrological cycle (Belnap et al., 2005), nitrogen fixation and transformations (Belnap, 2002; Evans and Lange, 2003; Hu et al., 2015), and C cycling (Maestre and Cortina, 2003; Thomas and Hoon, 2010; Zhao et al., 2014). Thus, the need to improve our estimation of soil-atmosphere fluxes is more acute in crusted soils due to the increased spatial heterogeneity of fluxes.

In Mediterranean ecosystems, the metabolic activity of microbes and roots is restricted by low temperatures in the humid winter and limited soil moisture during the warm summer (de Dato et al., 2010; Morillas et al., 2013). Thomas et al. (2008) showed that $R_s$ does not respond to a large range of temperatures unless moisture levels are above a critical threshold, whereas temperature responses are much greater when moisture is sufficient to allow microbial respiration of organic matter. These findings highlight the pivotal role played by the interaction between temperature, moisture and $CO_2$ efflux in Mediterranean ecosystems. Indeed soil $CO_2$ efflux models for water limited environments must account for the exponential effect of soil temperature ($T_s$) on the metabolism of soil organisms and roots, and the limiting effects of soil moisture (de Dato et al., 2010; Lloyd and Taylor, 1994; Reichstein, 2002; Vargas et al., 2011). Although the importance of the biocrust for the ecosystems biogeochemistry is widely recognized (Belnap, 2006, 2003; Belnap and Lange, 2003), its contribution to soil $CO_2$ efflux dynamics, which could be decoupled from the respiration of the deeper soil layers, has been neglected. Indeed, biocrust organisms can be activated by dew formation (Herrnstadt and Kidron, 2005; Kidron et al., 2002; Veste et al., 2008) that does not affect the deeper soil layers, and this can occur at any time of the year (Moro et al., 2007). There are a number of unique and subtle processes affecting soil $CO_2$ efflux in crusted soils, such as changes in diffusion gradients of $CO_2$ in soil pore spaces due to the biocrust cover (Belnap et al., 2003; Thomas et al., 2008), or $CO_2$ uptake by autotrophic biocrust components, which increases the complexity of assessing the biocrust role on soil $CO_2$ efflux.

In these circumstances, soil $CO_2$ efflux models may lose accuracy and neglect the contribution of the biocrust to this flux. Recently, some research efforts have been made to bridge this gap. Zhang et al. (2013) reported that the biocrust contributed up to 2/3 to total $R_s$ in a temperate desert. Accordingly, Castillo-Monrroy et al. (2011) found that biocrust-dominated areas are the main contributor to the total $R_s$ in a semiarid ecosystem. On the other hand, Wilske et al. (2008) reported that the highest biocrust-related net $CO_2$ uptake occurred during the wet winter, whereas low soil water content (SWC) resulted in low uptake rates which can hardly compensate for biocrust respiration. As this contribution depends on the biocrust cover and type (Zhao et al., 2014), it is of paramount importance to collect data from a broad range of environments. Therefore, understanding the biocrust contribution to soil $CO_2$ efflux in water-limited environments is crucial to better comprehend the functioning of these ecosystems and improve prognostic modeling.

In this article, we present the results of a manipulative experiment in a Mediterranean shrubland ecosystem in Sardinia, Italy. The objectives were to quantify the biocrust contribution to $R_s$ and identify the main environmental factors affecting it. The objectives were addressed by measuring *in situ* soil $CO_2$ efflux over two different surfaces: soil deprived of biocrust (hereafter *Soil*), and intact soil (hereafter *Soil+BC*), and estimating by subtraction the $CO_2$ efflux associated with the biocrust (hereafter *BC*). Three hypothesis were tested: (i) the contribution of the biocrust to soil $CO_2$ efflux varies over the seasons being minimum during the dry months due to its large dependence on superficial moisture, (ii) $CO_2$ efflux of the studied surfaces (*Soil*, *BC* and *Soil+BC*) would respond differently to SWC and $T_s$ as a consequence of the very different exposure to environmental factors regimes experienced by the biocrust and deep soil layers, (iii) since SWC is a main driver for respiration and since small rain pulses can increase the moisture content of the upper soil layers but have a minor effect on the soil moisture of the deeper layers, a two layer model would disentangle how the biocrust contribution to $R_s$ occurs in periods when deeper soil layers are inactive and 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*

In April 2012, 16 permanent polyvinyl chloride (PVC) collars of 20 cm diameter were installed on the soil surface covered by biocrust (*Soil+BC)*. In March 2013, eight additional PCV collars were installed in areas where the biocrust was physically removed using a spatula i.e. the *Soil* surface. All the 24 collars were placed at random within eight inter spaces between shrubs: patches were between 10 m and 50 m from each other and collars within each patch were at a minimum of 2 m distance. Soil $CO_2$ efflux was measured from June 2013 to January 2015. Measurements did not have a specific frequency, but they were rather performed in order to measure over the widest range of combinations of $T_s$ and SWC. All measurements were taken at least three days after the last precipitation event to avoid measuring at moments when the SWC was above its maximum field condition. In doing so, we attempted to minimize the disturbance generated in our long-term experimental site by trampling into the plots while soil was muddy. Thus, we avoided the $CO_2$ pulses that typically follow wetting of dry soils (Birch effect; Birch, 1964) and the physical displacement of $CO_2$-enriched pore space gases by water during rainfall, as 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 any case, preliminary results showed that $R_s$ was inhibited within 24 hours after a rain event in this study site, most likely due to the impeded diffusion of gas through the saturated clay soil. Direct measurements were collected on *Soil+BC* and *Soil* surfaces, whereas the $CO_2$ efflux emitted by *BC* surface was estimated by subtracting the soil $CO_2$ efflux of *Soil* surfaces from that of *Soil+BC*.

Soil $CO_2$ efflux was measured *in situ* using a portable LI-COR 8100 (Lincoln, Nebraska – USA) containing an infrared gas analyser system equipped with a flow-through closed chamber LI-COR 8100-103 connected to the central unit. The chamber of 20 cm of diameter was inserted 5 cm into the collar, and measurements were preformed in a dark condition. Measurements took 105 s per collar, and were performed between 8:00 and 9:00 a.m. (local time, GMT + 1) to avoid direct radiation from reaching the collars, which ensures minimization of variability in $T_s$ within the sampling day. However, this experimental design could have underestimated daily efflux as a result of the time lags involved in diurnal variations in $T_s$, i.e. the soil surface will heat very quickly and there will be a short time lag between peak air and soil temperatures, whereas at deeper depths this lag could be of several hours. The offset of each collar was measured and taken into account to calculate the headspace of each collar and quantify the $CO_2$ emission. Soil temperature at 3 cm depth adjacent to the collars was measured at the same time as $CO_2$ efflux measurements using a probe connected to the LI-COR 8100.

Since 2004, a meteorological and radiometric station (2 m and 3.5 m above the ground, respectively) are located within the experimental site. Air temperature and relative humidity were measured hourly using a HMP45C probe (Campbell Scientific Inc., USA) and an aerodynamic rain gauge (ARG100, Environmental Measurements Limited, UK) was used to record precipitation data every hour. SWC was monitored at 20 cm depth using two Time-Domain Reflectometry (TDR) probes (Model CS616-L, Campbell Scientific Inc., Logan, UT, USA). In January 2012, two additional $T_s$ and SWC sensors (EC-5, Decagon Devices Inc., Pullman, WA, USA) were placed at 5 cm depth. All sensors acquired data every minute and were stored as half-hourly averages.

In April 2014, 8 soil cores (2 cm in diameter) between 0 cm and 5 cm depth and between 5 cm and 10 cm depth below the mineral soil were collected. The samples were dried at 40 °C for 72 h and sieved using a < 2 mm mesh. Sieved samples were ground using Brinkmann Retsch Mortar Grinder (Model: RMO Polished), then 0.15 g analysed with an Elemental analyser (CHN 628, Leco, St. Joseph, USA), to determinate the total C and nitrogen (N) soil content. Soil pH was determined in a water slurry (1:5 w/v in $H_2O$). The effective cation concentration, Ca, Mg and Na, was extracted by cationic exchange capacity method, in solution of $BaCl_2$ according to ISO 11260, then concentration was determined by atomic absorption spectroscopy analyser (Analyst 200, Perkin Elmer, Waltham, USA). Available phosphorus ($P_2O_5$) was extracted as in Olsen et al. (1954) and quantified by spectrophotometric analysis (Cary 60 UV-Vis, Agilent, Santa Clara, USA). Calcium carbonate ($CaCO_3$) was quantified using a "Dietrich-Fruhling" calcimeter.

### *2.3. Statistical analyses*

ANOVA for repeated measurements was used to test for differences among *Soil+BC, Soil*, and *BC* in soil $CO_2$ efflux measurements. Prior to ANOVA analysis, data were tested for assumptions of normality and homogeneity of variances, and were log-transformed when necessary. Partial correlations were performed to account for collinearity and thus to test the effects of $T_s$ on soil $CO_2$ efflux of *Soil+BC, Soil* and *BC* while controlling for SWC at 5 cm and 20 cm depth ($SWC_{-5cm}$ and $SWC_{-20cm}$, respectively) and *vice versa.* All statistical analyses were performed by using the IBM SPSS 15.0 (SPSS Inc., Chicago, IL, USA).

Different functions can be used to simulate soil $CO_2$ efflux response to environmental conditions. In this study, the dependency of $R_s$ on $T_s$ and SWC was investigated for the three studied surfaces (*Soil+BC*, *Soil* and *BC*). Three different approaches were used: a simple linear regression accounting for both $T_s$, and $SWC_{-5cm}$ and $SWC_{-20cm}$, a multi-linear equation to account for the combined effect of these variables, and a modified version of the most common used Lloyd and Taylor (LLT) model (Lloyd and Taylor, 1994). The LLT function is an Arrhenius type equation which is temperature-driven and given by:

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

where $R_s$ is soil respiration, $R_{ref}$ is the ecosystem respiration rate at a reference temperature ($T_{ref}$) and $E_0$ is an activation energy parameter that determines the temperature sensitivity. In the original 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 predictor. Although the Lloyd and Taylor equation fits well to the experimental data during standard water availability conditions, in semi-arid ecosystems the dependence of ecosystem respiration on SWC must also be considered. Here we used the modified Lloyd and Taylor equation ($LLT_{mod}$) proposed by Reichstein et al. (2002), which multiplies the original temperature-driven model (equation 1) by a moisture function:

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

where $SWC_0$ is the residual SWC at which respiration is absent, and $SWC_{1/2}$ is the SWC at 50% of the maximal respiration (Reichstein et al., 2002). Equation 2 is the third approach used in this study to simulate $R_s$ as function of $T_s$ and $SWC_{-5cm}$ and $SWC_{-20cm}$. Models performances were evaluated using the following statistical indices: the Pearson's correlation coefficient (r), the root mean square error (RMSE), the index of agreement (d) and the Akaike's information criterion (AIC test, Akaike, 1974).

To calculate the contribution of *BC* to $R_s$, the best models were run at a 30 minute timestep for two years (2013-2014) thus accounting for the variations of both $T_s$ and SWC. Daily amounts of *BC* and *Soil* $CO_2$ efflux were first computed separately and then summed to obtain *Soil+BC* respiration rate. *BC* contribution to *Soil+BC* respiration rate was thus calculated as the ratio of the daily *BC* and the estimated *Soil+BC* respiration rates.

## 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).

Partial correlations revealed a significant effect of $T_s$, $SWC_{-5cm}$ and $SWC_{-20cm}$ on the *Soil* $CO_2$ efflux (Table 2). The $CO_2$ efflux of *Soil+BC* was significantly correlated with $SWC_{-5cm}$ ($p<0.001$) and $SWC_{-20cm}$ ($p=0.005$), but not with $T_s$, although the probability level was almost significant ($p_{5cm}=0.059$; $p_{20cm}=0.056$, Table 2). Finally, the respiration rate of *BC* was only significantly correlated with $SWC_{-5cm}$ ($p=0.001$, Table 2).

When simulating *Soil* $CO_2$ efflux, the Lloyd and Taylor (1994) model modified according to Reichstein et al. (2002) to also account for $SWC_{-20cm}$, outperformed the other models as it is shown by r (0.81, $p<0.001$), RMSE (0.13 μmol $m^{-2}$ $s^{-1}$), d (0.89),and the lowest AIC test value (=-8.1) (Table 3). The simple linear model which uses $SWC_{-5cm}$ as independent variable, was the best model predicting estimated *BC* respiration rates according to all the statistical indexes (r=0.75, p=0.002, RMSE=0.15 μmol $m^{-2}$ $s^{-1}$, d=0.84, AIC= -7.00). Also the multilinear model with $T_s$ and $SWC_{-5cm}$ showed good performances with a slightly higher AIC test result (AIC=-5.5) (Table 3).

*Soil+BC* $CO_2$ efflux was best explained by the multilinear model accounting for both $T_s$ and $SWC_{-5cm}$ (r=0.75, p=0.002, RMSE=0.19, d=0.85, AIC=1.7). However,  the modified Lloyd and Taylor model accounting for $SWC_{-20cm}$, and the linear model using $SWC_{-5cm}$ as independent variable, performed similarly but showed higher AIC test results (AIC>3.6) (Table 3). In agreement with these models, the $CO_2$ efflux of all the three surfaces increased with soil moisture (Figures 2 and 3). For *Soil* and *Soil+BC*, $T_s$ and $CO_2$ efflux were positively correlated until the soil dried (see Figures 2 and 3) whereas for *BC* the metrics suggests that respiration was mainly controlled by $SWC_{-5cm}$ with a seasonal pattern decoupled from that of *Soil* or *Soil+BC* (Figure 3).

Table 4 reports the coefficients of the best performing models for *BC, Soil* and *Soil+BC*. The daily respiration rate for the two layer model ranged from 89.8 to 406.7 mol $CO_2$ $m^{-2}$ $d^{-1}$ , with 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 those for the *BC* layer between 0.2 and 193.2 mol $CO_2$ $m^{-2}$ $d^{-1}$ (Figure 4a). Modeled respiration rates showed the greater temporal variability found in *BC* $CO_2$ efflux compared to *Soil* (Figure 4a), highlighting the key role of the biocrust in *Soil+BC* respiration rates through the seasons. The modeled *BC* contribution to *Soil+BC* respiration rate was on average 23.6 %, ranging from 0.1 % in June 2012 to a peak of 61.9 % in February 2012 (Figure 4b). Following the trend found in estimated *BC* contribution to *Soil+BC* respiration, modeled *BC* contribution was minimum during the rainless season and became a relevant $CO_2$ source in the wet months (Figure 4b).

# 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 a net uptake of $CO_2$ to the biocrust when following the subtraction method in the wet season. The major short coming of the subtraction method is that the removal of the biocrust from the soil surface as part of the experiment may also have changed the natural soil to air diffusion gradient and may have increased the measured $CO_2$ efflux, without any biological processes being involved. That is, if by removing the biocrust the natural diffusion gradient between the soil and atmosphere has been increased, the subsoil $CO_2$ efflux would be enhanced to without any increased respiration, which would lessen the difference between $R_s$ on *Soil+BC* and *Soil*. In this likely situation, the biocrust contribution to $R_s$ would have been even greater than that reported. The relatively small and negative estimated values for *BS* respiration found in summer suggest that the possible increase in $CO_2$ fluxes due to the biocrust removal was not large and partially attributable also to spatial variation. It is well known that soil $CO_2$ efflux may change greatly even over short distances and that the relative differences in space also change in time as consequence e.g. of the mosaic pattern of clumps of vegetation and patches of soil typical of Mediterranean ecosystems. In fact, Qi et al. (2010) proved that $CO_2$ fluxes from the soil under the canopy of shrubs were significantly higher than those from the soil covered with biocrusts and the bare soil in the interplant spaces of a semiarid ecosystem. It is thus likely that our negative values for *BC* are partially due to an artefact created by both the subtraction method and spatial variability. However, these two components are difficult to separate and would require *ad-hoc* experiments to do so.

Zhao et al. (2014) and Thomas et al. (2011, 2008) reported that soil moisture was the primary limiting factor to biocrust $CO_2$ efflux in the Kalahari and Tengger deserts, respectively, but these studies did not estimate the contribution of biocrust to total $R_s$. In agreement with our results, both Zhang et al. (2013) and Castillo-Monroy et al. (2011) proved that the biocrust respiration is a major player in $CO_2$ efflux, contributing ca. 66 % and 42 % to total $R_s$ in a temperate desert and a semiarid ecosystem, respectively. In the light of these findings and our own results which show a 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* depend on $SWC_{-20cm}$, whereas the correlation of respiration of the *BC* with SWC is strongest at 5 cm depth. The SWC at 20 cm and 5 cm depths strongly co-vary, however small water pulses can increase the moisture only of the top layer, and the top layer may dry much faster than the deeper ones. Thus, small water pulses can activate lichens, mosses and cyanobacteria associated to the biocrust, and the metabolism of C in soils, while deeper soil layers remain dormant. Likewise, respiration in the deeper soil layers may persist in periods when the biocrust is inactive. In line with these findings, Cable and Huxman (2004) found that the relative contributions of biocrust and deep soil layers to $CO_2$ efflux in Arizona varied with rainfall magnitude. Using δ13C and $CO_2$ data, they reported that over 80 % of the respiration originated from biocrust during small rainfall events, whereas 98 % was originated from deep soil layers after-intense rainfall events. Consequently, the proportional contribution of the biocrust changes over the seasons, playing an important role when the soil is wet and being minimum during the dry months (i.e. July, August and September).

We found that both the modeled and estimated *BC* contribution to *Soil+BC* respiration rate peaked following the soil rewetting after the rainless summer period. Similar results have been found by Zhao et al. (2014) when studying mixed biocrust (composed of mosses, algae and lichens) and algae-dominated biocrust respiration responding to an extreme rainfall event in a mesocosm experiment. Zhao et al. (2014) reported that $CO_2$ efflux was inhibited for several days after the rainfall event in both biocrust types, and then it increased. However, less influence of extreme rainfall events on $R_s$ was found for moss-dominated biocrusts. The authors attributed these findings to the increased soil hydrophobicity due to the biocrust extracellular polysaccharide (EPS) secretions (Mager and Thomas, 2011). EPS can block superficial soil pores (Avnimelech and Nevo, 1964) leading to water accumulation in the surface of mixed and algae-dominated biocrust after heavy rainfall. As EPS are decomposed by microbes (Fischer 2009), soil pores will reopen producing a burst in $CO_2$ efflux in mixed and algae-dominated biocrust. In contrast, the higher porosity and infiltration rates that characterizes moss tissue allows water to percolate deep into the soil avoiding water accumulation on the soil surface in moss-dominated biocrusts (Frey and Kürschner, 1991; Chamizo et al., 2012). An alternative explanation for these findings is that a relatively thick film of water for the first days after the rainfall may restrict the exchange of gases, impeding in turn photosynthesis and respiration until water evaporation (Lange et al., 1992). The higher infiltration on moss-dominated biocrust could also be attributed to the low amount of EPS at these crusts due to the fact that mosses do not excrete EPS (Kidron et al., 2003). Given that the soil rewetting dynamics have been proved to affect differently to the contributions of distinct biocrust types to $R_s$ (Zhao et al., 2014), especially after large rainfall pulses (>10 mm), it is crucial to account for the biocrust composition in this type of studies.

Dew events in water limited ecosystems are common throughout the year, and typically range from 0.15 mm to 0.30 mm per day (Jacobs et al., 2000; Moro et al., 2007). Previous studies reported that biocrust organisms can utilize the morning dew as a window of opportunity for activating their metabolism (Delgado-Baquerizo et al., 2013; Thomas and Hoon, 2010; Veste et al., 2008). However, other authors have found that while dew can wet rock and stones in a dew desert such as the Negev, its capability to wet the soil is very limited, since the activation threshold of 0.1 mm (Lange et al., 1992) is rarely reached on the soil surface (Agam and Berliner, 2006; Kidron et al., 2002). Our experimental design was focused on understanding the general effect of SWC and $T_s$ and not of rain pulses nor of dew on biocrust respiration or the limiting effect of over saturated soil on diffusion. The estimation of superficial soil moisture is most likely an even stronger predictor for biocrust respiration than $SWC_{-5cm}$. Perhaps, if the superficial SWC had been monitored, an even greater decoupling of *BC* respiration from that of *Soil* would have been reported. However the isolation of superficial moisture from the background soil under field conditions is quite challenging.

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

We found higher $R_s$ rates in *Soil+BC* than in *Soil*. Such difference can be explained by the fact that *Soil* has been devoid of habitats for a dependent foodweb of arthropods, lichens, fungi, bacteria, and other soil organisms typically found in the biocrust (Belnap and Lange, 2003), whose activity significantly contribute to soil $CO_2$ efflux (Castillo–Monroy et al., 2011). Given the decoupling of the respiration rates of *BC* and *Soil*, it was not possible to identify a model clearly outperforming the others for *Soil+BC*. The resulting model can be seen as a mix of the model for *Soil* and for *BC* as it responds to $T_s$ and to $SWC_{-5cm}$ instead of $SWC_{-20cm}$. Additionally, the model is multilinear losing the physiological mechanism accounted for by the Lloyd and Taylor model. The highly contrasting seasonal pattern of respiration observed in *Soil* is not visible in *Soil+BC*, suggesting that the biocrust might be masking the seasonal trend showed by deeper soil layers in *Soil+BC*, since the biocrust exhibits an independent dynamic driven by moisture in the first soil centimeters.

## 5. Conclusions

Our findings show that $CO_2$ effluxes emitted by *Soil, BC* and *Soil+BC* are differently driven by $T_s$ and SWC: *BC* respiration is mainly controlled by superficial SWC, whereas $T_s$ and $SWC_{-20cm}$ mostly control *Soil* respiration, and $T_s$ and $SWC_{-5cm}$ drive *Soil+BC* respiration. Our results complement those of previous studies highlighting the key role of the biocrust as modulator of $R_s$ in dryland ecosystems, and indicate that the biocrust has the ability to contribute to $R_s$ responding to small water pulses in periods when deeper soil layers are inactive. Thus, our results suggest that accounting for the biocrust contribution to $R_s$ and its responses to environmental drivers is highly relevant in providing accurate estimates of this key component of the C cycle at the ecosystem level. Projections based solely on bare ground and vegetated areas have been used to predict C budgets in semiarid (Rey et al., 2011) and temperate (Kim et al., 1992) grasslands. Nevertheless, the important differences observed in $CO_2$ efflux between *Soil* and *Soil+BC* suggest that these estimations may underestimate soil $CO_2$ efflux in spatially heterogeneous Mediterranean ecosystems. Given the large areas covered by biocrust, not only in drylands, but also in temperate, alpine and polar ecosystems (Belnap and Lange 2003), taking into account soil surface covered by biocrust in future modeling studies can significantly contribute to improve our understanding of the global C cycle and our ability to project the effects of global environmental change on soil $CO_2$ efflux.

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## Figure captions

**Figure 1.** Monthly precipitation and average, minimum, and maximum air temperature at the study site from January 2012 to December 2014.

**Figure 2.** (a) Daily sum of precipitation and soil water content (SWC) at 5 and 20 cm at the experimental site. (b) Daily average, minimum, and maximum soil temperature ($T_s$) measured at 5 cm depth.

**Figure 3.** $CO_2$ efflux emitted by (a) soil deprived of biocrust (*Soil*), (b) biocrust surface (*BC*), and (c) intact soil (*Soil*+*BC*). The *BC* contribution to *Soil*+*BC* respiration rate is also shown (gray line). Error bars are ±SE, n = 16 for *BC* and *Soil*+*BC,* n = 8 for *Soil*.

**Figure 4.** (a) Daily values of modeled respiration rates emitted by soil deprived of biocrust (*Soil*), biocrust surface (*BC*), and intact soil (*Soil*+*BC*). (b) Modeled *BC* contribution to *Soil*+*BC* respiration rate.

**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 |

**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**$^{**}$ |

**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, µmol $m^{-2}$ $s^{-1}$), 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 |

**Table 4.** Summary of the best models simulating $CO_2$ efflux for soil deprived of biocrust (*Soil*), biocrust surface (*BC*) and intact soil (*Soil+BC*). Statistical differences are indicated as $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***). Depending on the model the intercept parameter (a), the $T_s$ slope (b), the SWC slope (c), the ecosystem respiration rate ($R_{ref}$), the activation energy parameter ($E_0$), the residual SWC at zero repiration ($SWC_0$) and SWC at half of maximal respiration rate ($SWC_{1/2}$) were calculated.

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