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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 biocrust 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* was 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.

## 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.

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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 et al., 2002; Vargas et al., 2011). Although the importance of the biocrust for the ecosystem biogeochemistry is widely recognized (Belnap, 2003, 2006; 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-Monroy 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 hypotheses 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 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, Soil Conservation Service, 1983). 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 soil is highly erodible (Spano et al., 2009). Soil water holding capacity is 24% and total Leaf Area Index ranges between 2.7 and 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 interspaces 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 interspaces 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 interspaces 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