Impact of climate and land degradation on soil carbon fluxes in dry semiarid grasslands in SE Spain

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Keywords: soil CO_2 efflux, biological soil crust, Mediterranean dry grasslands, seasonality, degraded grasslands, abiotic drivers, climate change, precipitation, temporal autocorrelation.

Abstract

Aims. This study investigates how precipitation, temperature and seasonality (as a proxy of plant productivity) affect the temporal and spatial variability of soil CO_2 efflux in two dry semiarid grasslands with different degrees of land degradation.

Methods. We measured soil CO_2 efflux over four years under plant, biological soil crust and bare soil patches and estimated annual soil carbon losses in both, a natural and a degraded grassland, by means of generalised additive mixed models considering temporal autocorrelation in the data.

Results. Soil CO_2 efflux ranged from 0.08 to 3.70 and from 0.10 to 3.01 μmol CO_2 m^{-2} s^{-1} in the natural and degraded grasslands, respectively. Daily soil CO_2 efflux was mostly affected by moisture in the degraded grassland (25.4%), while in the natural grassland was affected jointly by seasonality, temperature and moisture (27.5%). Overall, the highest soil carbon fluxes were measured in soils covered by biological soil crusts (1.24 ± 0.02 and 1.10 ± 0.02) and the lowest in bare soils (1.11 ± 0.02 and 0.82 ± 0.02 μmol CO_2 $^{-2}$ s^{-1}) in the natural and degraded sites, respectively. Cumulative soil carbon fluxes were mainly driven by temperature and previous precipitation (over three months). The highest soil carbon losses were estimated in the driest year (2009) and the lowest in the wettest (2010) with almost twice the amount of rainfall. The main difference between these years was the timing of the events that mostly occurred in the moments of maximum plant activity with optimum temperatures in spring in the dry year.

Conclusions. Changes in precipitation patterns will affect soil carbon fluxes more than rainfall amount, particularly in degraded grasslands. Therefore, considering all climate drivers together with plant activity is essential to predict how climate change will affect soil biological processes in drylands.

Abbreviations

VEG: under plant cover BS: bare soil BSC: biological soil crust SR: soil CO_2 efflux

Introduction

Soil CO_2 efflux is the largest flux of CO_2 from terrestrial ecosystems with 68-98 Pg C released to the atmosphere annually (Bond-Lamberty & Thomson 2010; Zhao et al. 2017), and the second largest amount in the global carbon balance after that released by oceans (IPCC 2014). Furthermore, soils constitute the largest terrestrial carbon pool with global estimates of *ca.* 2456 Pg (Scharlemann et al. 2014). Despite intensive research over the last two decades (see Bond-Lamberty & Thomson, 2010; Vargas et al. 2011; Rey 2015), we still have a limited understanding of the controlling factors determining the temporal variability of soil CO_2 effluxes across ecosystems (Reichstein & Beer 2008; Huang et al. 2020), particularly drylands. Drylands (arid and semi-arid ecosystems) occupy more than 40% of the surface of the Earth (Schimel 2010) and are responsible for the inter-annual variability in the terrestrial carbon sink (Ahlström et al. 2015). These regions are characterised by scarce and highly variable temporal distribution of rainfall. Thus, water availability is an essential factor driving biological activity in these ecosystems. Rainfall patterns (i.e. frequency, magnitude and timing of events) determine the temporal variability of soil moisture and in turn, the biological activity in soils. Since most of the carbon in semiarid grasslands resides in soils (Burke et al. 2008), predicted changes in precipitation patterns could result in further soil carbon losses and land degradation (Smith 2011).

Some studies have quantified the relative contribution of rain driven carbon fluxes for the ecosystem carbon balance demonstrating that they can be important in determining the high inter-annual variability in the carbon sink capacity of these ecosystems (e.g. Jarvis et al. 2007; López-Ballesteros et al. 2015). Over the last few decades, this phenomenon has prompted increasing interest since climate change predictions for these regions include changes in precipitation patterns with prolonged drought periods and more intense rainfall

events and climate extremes (Smith 2011; Greve et al. 2014). However, results on the impact of intra-annual variation of precipitation distribution on soil carbon fluxes are still inconclusive (Knapp et al. 2008; Fay 2009; Liu et al. 2019). Precipitation interacts with temperature and in turn, with plant activity. Since the factors controlling soil CO_2 efflux are often correlated, only apparent relationships can be obtained in field studies. Experimental studies often manipulate environmental conditions in order to assess individual factors such as precipitation or temperature (e.g. Rey et al. 2017; Arredondo et al. 2018; Zhang et al. 2019; Manzoni et al. 2020). Another approach is to assess individual effects by using ad hoc statistical approaches that take into account these correlations.

Besides high temporal variability in biological activity, these ecosystems are also characterised by large spatial variability, with the presence of sparse vegetation patches, biological soil crust and bare soil (Maestre et al. 2013). Vegetation patches represent islands of nutrient availability, high root density and carbon pools. Moreover, plants modify the energy and water balances as well as the amount and quality of soil organic matter. The translation of rainfall into soil moisture, with subsequent impacts on soil activity, is likely to be affected by ecosystem properties such as vegetation cover, presence of biological soil crusts, and soil texture (Cable et al. 2008; Zhang et al. 2008). Biological soil crusts are globally widespread communities (cyanobacteria, green algae, lichens and mosses) that may constitute a large proportion of the living cover in drylands (Belnap & Lange 2003). These communities play an important role preventing soil erosion, improving soil stability and fertility, and contributing to carbon uptake and nitrogen fixation (Li et al. 2018). Castillo-Monroy et al. (2011) found that biological soil crusts accounted for 43% of the total carbon released via soil respiration in a semiarid steppe in Spain. As biological soil crusts live on the soil surface, they get activated even by small precipitation events and high relative humidity (Li et al. 2018). Thus, factors determining soil CO_2 efflux from

111 different ground covers are likely to differ and may respond differently to rainfall events
112 and environmental variables, which may have potential consequences for soil and
113 ecosystem functioning (Borken & Matzner 2009). The high spatial heterogeneity of
114 vegetation and soil properties in drylands makes soil CO_2 efflux particularly difficult to
115 quantify.

116 Despite the recognised importance of precipitation and temperature as main abiotic drivers
117 of biological activity, a proper characterisation of other factors controlling soil carbon
118 fluxes, considering the spatial variability of soil CO_2 efflux characteristic of drylands and
119 the importance of plant activity, is still lacking (Leon et al. 2014; Nielsen & Ball 2015).
120 While the effect of single precipitation events on soil CO_2 efflux has been fairly well
121 studied (e.g. Cable et al. 2008; Chen et al. 2008; Aanderud et al. 2011; Rey et al. 2017),
122 few studies have examined long-term responses of soil carbon fluxes over several years to
123 precipitation in the field. Moreover, most of the published studies have been carried out in
124 ecosystems with mean annual precipitation above 300 mm (e.g. Correia et al. 2012), but
125 studies examining the response of ecosystems located in more extreme climates are very
126 scarce (e.g. Zhang et al. 2010). Therefore, it is crucial to understand the impact of rainfall
127 amount, timing and distribution and temperature on soil carbon fluxes in more extreme dry
128 environments considering the spatial variability that characterise these ecosystems (Sitch et
129 al. 2008).

130 Furthermore, land degradation is threatening semiarid ecosystems, with more than 20% of
131 semiarid lands prone to desertification potentially affecting soil carbon dynamics (Reed et
132 al. 2012; Feng & Fu 2013). Land-cover change and land degradation greatly affect soil
133 CO_2 efflux by changing vegetation structure, local microclimate and soil properties
134 (Alekseev et al. 2018; Thomas et al. 2018). As soil carbon and nutrient availability, the
135 substrates of soil microbes, ultimately depend on photosynthate supply (Mitra et al. 2019),

136 it is important to consider plant productivity as another relevant factor influencing soil CO_2
137 efflux in these ecosystems. So far, few studies have considered how both climate and land-
138 cover change as a result of land degradation affect the spatial and temporal variability of
139 soil carbon losses (Huang et al. 2020). Thus, in order to predict how dryland carbon
140 dynamics will be affected by climate change, it is necessary to understand how changes in
141 vegetation and biocrust cover and soil impoverishment as a result of land degradation will
142 affect soil carbon fluxes in these regions.
143 In this study, we measured soil CO_2 efflux over almost four years in two nearby sites with
144 different degree of land degradation as a result of distinct land use history (see Rey et al.
145 2011) and in three representative soil covers: under vegetated areas, biological soil crust,
146 and bare soil patches. The overall aim of this study was to characterise the temporal and
147 spatial variability of soil CO_2 efflux rates. We used a statistical approach that allowed us to
148 disentangle the individual effects of environmental factors incorporating seasonality as a
149 proxy of plant productivity. Specific objectives were: (1) to examine the temporal
150 variability of soil CO_2 efflux in two dry semiarid grasslands with different degrees of land
151 degradation, (2) to investigate the spatial variability of soil CO_2 efflux by exploring how
152 the response to environmental variables is modulated by different soil covers, (3) to assess
153 the impact of land degradation on soil CO_2 efflux and soil carbon losses since it can affect
154 biocrust cover and composition and, (4) to understand to what extent rainfall and
155 temperature determine inter-annual variability of soil carbon fluxes, taking into
156 consideration seasonality as a proxy for plant productivity. The final aim is to understand
157 how changes in precipitation patterns and increasing temperatures will affect soil carbon
158 losses via soil CO_2 efflux in these dry ecosystems, including degraded lands. We
159 hypothesised that in these semiarid dry ecosystems: (1) the temporal variability in soil CO_2
160 efflux rates will be very large and mediated by plant productivity since the translation of

rainfall into soil moisture will depend on plant activity, (2) since moisture is the main limiting factor in these ecosystems, we expect the highest soil CO_2 fluxes from biological soil crusts given that they get activated by small to large rainfall events and high relative humidity, (3) since land degradation leads to lower vegetation cover, changes in biocrust cover and composition and large percentage of bare soil patches, we also expect further carbon losses from soils in the degraded grassland, (4) although we expect that precipitation will be the main factor controlling biological activity in these ecosystems, the combination of precipitation, temperature and productivity will determine how precipitation converts into soil moisture and thus will determine soil CO_2 effluxes in these dry semiarid grasslands.

Material and Methods

Site description

We selected two sites in the Cabo de Gata Natural Park, in the province of Almería (Andalucía) in the SE of Spain (N 36º 56' 26.0'', W 2º 01' 58.8''). The climate in this area is semiarid with a mean annual precipitation of 200 mm and a mean annual temperature of approximately 18ºC (nearby meteorological station, Níjar). The area is characterised by prolonged summer droughts (from May to September) and strong inter-annual variation and random patterns of precipitation, which mostly occur in spring and autumn. Geologically, the region is a series of alluvial fans (glacis) with gentle slopes (2 to 8%) with petrocalcic horizons. The dominant soils are classified as Lithic leptosols (calcaric) (WRB 2006), and are thin (on average 10 cm), alkaline (pH above 8), with a sandy loam texture in both sites, saturated in carbonates with a moderate stone content and with common rock outcrops, particularly at the degraded site (Supplementary material S1, S2). The vegetation of these sites is dominated by *Stipa tenacissima*, but there are a large

number of other shorter grass species with low ground coverage (Supplementary material S2), such as: *Chamaerops humilis, Rhamnus lycioides, Asparagus horridus*, *Olea europea* var. *sylvestris*, *Pistacia lentiscus,* and *Rubia peregrina*.

The two sites are located approximately 15 km apart on a flat area. The natural grassland is called Balsablanca and is located over a flat terrain 200 m a.s.l.; whereas the other site, Amoladeras, is located at 50 m a.s.l, with less vegetation cover and shallower soils (see Supplementary material S1 and S2).

Based on a previous hierarchical classification of the ecosystems present in the Cabo de Gata Natural Park (see Escribano, 2002), we selected the two sites as representative of two distinctive degradation stages as a result of distinctive land use history (Rey et al. 2011) making sure that both sites were comparable with the same geology, topography, vegetation type, climate, etc., and consistent with a soil cartography map (CMA, 1999). This analysis indicated that soils in the degraded grassland (Amoladeras) have characteristics typical of degradation processes as a result of past overgrazing, in comparison to soils in the natural grassland (Balsablanca) that remains unmanaged. Other degradation indicators such as the percentage of vegetation cover, rock outcrops, and surface coarse fragments were also used (Cammeraat 1996; Dregne 2002). Thus, even though the sites are 15 km apart, they represent different degrees of ecosystem degradation.

Experimental design

In December 2006, we selected six permanent replicated plots at both sites within a 100 m fetch of the eddy covariance tower. Plots measured 10 m by 10 m and were at least 5 m apart. Vegetation was mainly patchy, with different percentage of plant cover at each site (Supplementary material S1). In each plot, we selected three representative soil covers and

placed three soil collars (15 cm in diameter and 7 cm in height) inserted 3.5 cm into the soil at three different locations: *under plant cover* (VEG), at 40-50 cm from the plants on *bare soil* (BS), and over *biological soil crust* (BSC). The plant cover is *Stipa* spp., the dominant grass species (63% and 23% cover in the natural and degraded sites, respectively). The experimental design is defined by 36 replicated sampling collars representing three soil types in two areas differing in land degradation.

Soil CO_2 efflux and environmental measurements

We measured soil CO_2 efflux (SR) from January 2007 until August 2010 at a frequency of approximately one to two weeks, depending upon the time of year (more frequent in spring and autumn). In order to capture the short-term response to rainfall, we tried to measure soil CO_2 efflux after each rainfall event over the whole duration of the experiment, thus, also under changing humidity conditions. After placing the soil collars and during the entire duration of the study, small plants, litter, insects, and grasses were regularly and carefully removed from each soil collar. To avoid strong diurnal fluctuations, measurements were made between 10:00 and 14:00 h at both sites on alternative consecutive days. We measured diurnal courses of soil CO_2 efflux at different times of the year representative of four seasons in order to adjust the measurements to average diurnal values (Supplementary material S3). Plots were measured in random order on each date to avoid biased estimates. A portable, closed chamber, soil respiration system (EGM-4, PP-systems, MA, USA) was used to measure soil CO_2 efflux rates *in situ*. The chamber covered an area of 78 cm^2 and had a volume of 1170 cm^3. Because of the low rates of soil CO_2 efflux, each measurement period was 90 s to ensure reliable measurements. Given the presence of thin soils, we measured soil temperature and soil water content at 3.5 cm at

235 each measuring time with a soil thermistor and a portable soil moisture sensor (Field Scout
236 TDR 300 Soil Moisture Meter, Spectrum Technologies, Inc., Illinois, USA), respectively.

237

238 *Statistical analyses*

239 Generalised additive mixed models (GAMM hereafter; Wood 2006) were used to analyse
240 the variation of soil CO_2 efflux throughout the study years. GAMMs are based on
241 smoothing techniques aimed to identify non-linear trends in data without adopting strong
242 assumptions about the specific nature of these relationships (e.g., linearity). As soil CO_2
243 efflux was measured on 90 different days not evenly spaced throughout time, we used a
244 continuous-time first-order autoregressive correlation structure (corCAR1) to account for
245 the non-independence temporal serial data, using date as a continuous time covariate. The
246 effect of the time covariate was nested within each sampling point, thus not assuming a
247 common temporal pattern across the 36 sampling collars. In order to account for the
248 seasonality effect in temporal data, we converted the 365 days of the year to 360 degrees
249 (Zar 1999), considering that 0º and 360º correspond to winter solstice (21st December),
250 180º relates to summer solstice (21st June), and 90º and 270º define the spring and autumn
251 equinoxes, respectively. Once time position within an annual cycle was established (i.e.,
252 angular date), the cosine and sine of that angular transformation were obtained (cosine and
253 sine are perfectly orthogonal). As soil CO_2 efflux was measured in each collar throughout
254 the study years, these 36 sampling collars establish the random effect. Soil water content,
255 soil temperature, the cosine and sine of the angular transformation of date, rainfall amount
256 and rainless duration were included in the GAMMs as fixed covariates, while land
257 degradation (two levels) and soil cover (three levels) were considered as fixed factors. We
258 used penalised thin plate regression splines with the individual predictors in the GAMMs,
259 setting the maximum complexity dimension of the smooth (k) to four. A tensor product

smoothing term (i.e., additive regression plane) was used for the seasonal terms cosine and sine of the angular transformation of date, setting the maximum complexity dimension of the smooth (k*k) to seven (maximum of 7*7=49). The relatively low maximum complexity dimension k was established in order to reduce over-fitting of the splines to the data (thus avoiding over-parametrisation in response to local minima/maxima), without much degradation in prediction error performance. The final model of interest was obtained using restricted maximum likelihood estimation (REML).

GAMMs were run using the gamm command of the {mgcv} package in R (Wood 2017), assuming a Gaussian distribution of errors (link function: identity). We checked for normality and the lack of heteroscedasticity in the residuals of the final GAMM. To accomplish these criteria, soil CO_2 efflux was log transformed prior to data analyses.

Since the effects of predictors may change across sites (degraded vs. natural), two different GAMM models were built for soil CO_2 efflux: one for both sites together, and another analysing the effect of soil temperature and soil water content nested within site. Both models were compared using ML estimation and the sample-size corrected version of the Akaike criterion (AICc).

Partial residual plots were obtained to show the effect of each predictor in the GAMM on the response while taking into consideration the influence of the remaining predictors. Finally, we built several reduced models from the full GAMM model to partition the variance in the response variable and to decompose the explanatory capacity of predictors into independent and shared components through variation partitioning (Legendre & Legendre 1998). Significance of post-hoc Student t-tests comparing partial residuals of soil CO_2 efflux rates among soil covers (derived from the corresponding GAMM) were obtained using the false discovery rate adjustment method of the p.adjust function in R

(i.e., controlling the rejection of the null hypothesis when it is false). All analyses were carried out with the statistical program R version 3.5.0 (R Core Team 2018).

Annual estimates of carbon fluxes from soils

In order to estimate annual carbon losses via soil CO_2 efflux as well as the factors controlling the seasonal variability in soil carbon fluxes, we calculated the amount of carbon released (g C m^{-2}) every fortnight from each soil cover at each site by interpolating measurements between sampling dates over the study period. Given the high frequency of measurements, the estimates can be considered fairly robust and comparable between sites. For each study site, we estimated the weighted average of soil carbon loss of all replicates considering the soil cover area of each soil cover type (Supplementary material S1 and S3). This interpolation was carried out using GAMMs where the only predictor was the thin plate spline of sequential date beginning on January 1st 2007 and ending on June 30th 2010 (using k=87 as the dimension of the basis used to represent the smooth term). The same approach was repeated to obtain interpolations of the soil temperature and soil water content every day throughout the study period. All models accounted for an extremely high proportion of deviance (always > 70% for the six combinations of two sites and three soil covers). The predicted-interpolated soil carbon loss was estimated by means of the summation of the interpolated rates over the 15 days. The predicted-interpolated soil temperature and soil water content were estimated by means of the average of the interpolated rates over the 15 days (Supplementary material S4). Although manual measurements done periodically may miss some temporal variability, the frequency in this study was high enough to characterise the temporal variability in soil CO_2 efflux. Daily predicted values for each variable were averaged (soil water content and soil temperature)

or summed up (precipitation and soil carbon loss) over fortnights. Thus, the sampling units are the fortnight values in the analyses accounting for the seasonal rainfall patterns.

Data for soil carbon losses were corrected to obtain mean daily totals based on measurements done between 10 am and 2 pm, according to diurnal measurements made in each soil cover in four seasons (see Supplementary material S3). This correction is needed because soil CO_2 efflux rates at midday were considerably higher (winter) or lower (summer) than that measured for a whole day. In other words, predicted-interpolated data for midday soil CO_2 efflux rates in each soil cover were divided by proper correction indexes in order to scale up for the whole 24 h. Correction figures (i.e., divisors of 10-14 h soil CO_2 efflux rates) ranged between 1.41 and 2.57, depending upon soil cover and season. Although this correction is only an approximation which may have caused some under/overestimation, the comparison between sites and correlation with different predictor variables should be valid.

We applied a GAMM model assuming a Gaussian distribution of errors (link function: identity) to analyse the seasonal variation in soil carbon loss using the fortnight as the sample unit (N=80), grassland degradation (site) as a fixed factor, and the mean *soil temperature* and *precipitation* as continuous predictor variables. We also used temporal autoregressive correlation structure to account for the non-independence temporal serial data, using the fortnight as a continuous time covariate. We tested several time lags for accumulated rainfall (fortnight, 1, 2, 3 and 4 months) using ML estimation. The most parsimonious model (i.e. lower AICc) was the one including the accumulated amount of rainfall over the previous three months. The final model was carried out using REML estimation.

Results

Temporal dynamics of environmental variables and soil CO_2 efflux

Environmental variables showed strong seasonality with warm and dry long summers and wetter and colder winter periods (Figure 1). Environmental conditions significantly differed ($P < 0.01$ in all cases) between both sites with warmer and drier conditions in the degraded than in the natural grassland (Supplementary material S1, Figure 1). Soil temperature ranged from 6.4 to 42.7ºC with an average of 22.3ºC, and from 8.4 to 43.5ºC with an average of 24.0ºC for the natural and degraded grasslands, respectively. Soil water content ranged from 0.7 to 52.6% (average of 15.3%) and from 0.3 to 41.0% (average of 11.7%) for natural and degraded grasslands, respectively.

Temporal variability in soil CO_2 efflux showed strong seasonality ranging from 0.08 to 3.70 μmol CO_2 m^{-2} s^{-1} (average value of 1.19) and from 0.10 to 3.01 μmol CO_2 m^{-2} s^{-1} (average value of 0.95) in the natural and degraded grasslands, respectively (Figure 1). Soil CO_2 efflux rates varied similarly in all soil covers following temporal variation in environmental variables (Pearson correlation between 0.83 and 0.95). However, temporal fluctuations in soil CO_2 efflux were much larger than those observed for soil water content and soil temperature.

Precipitation showed strong intra- and inter-annual variation. The year 2009 was the driest (166 mm) and 2010 the wettest (364 mm) year. On average across all years, it rained 10% of the days of the year. Although just 11% of the events were larger than 15 mm, these events accounted for between 36% and 52% of total annual precipitation (Table 1). Apart from very dry summers with practically no rain, rainfall varied among seasons from year to year. Therefore, the study years differed considerably in rainfall amount and distribution (Table 1).

Factors controlling soil CO_2 efflux

A model for soil CO_2 efflux including the effects of *soil water content* and *soil temperature* nested within soil degradation attained a higher strength of evidence (according to the lowest AICc value: -1224) than the model that generalised their effects without distinguishing between levels of soil degradation (AICc = -1046; see Supplementary material S5). Soil CO_2 efflux was a predictable and highly explainable phenomenon (Table 2; likelihood ratio test: $Chi^2 = 1867$, df = 16, $P << 0.001$; $R^2 = 53.2\%$). All effects in the model were highly significant ($P << 0.001$). An alternative model including the two rainfall predictors (*rainfall amount* and *rainless duration*), instead of *soil water content*, had a considerably lower strength of evidence than the previous model (AICc = -254, ΔAICc = 971; see Supplementary material S5), and accounted for a lower proportion of variability in soil CO_2 efflux ($R^2 = 37.6\%$).

Variation partitioning of soil CO_2 efflux showed that the relative importance of the factors determining soil CO_2 efflux differed between sites (Figure 2). *Soil water content* was the main factor controlling soil CO_2 efflux in the degraded grassland (25.4%), while the combined, correlated effect of *soil water content, soil temperature* and *seasonality* exerted the largest control in the natural grassland (27.5%). Indeed, both *soil temperature* and *seasonality* exerted much larger control on soil CO_2 efflux in the natural (19.1%) than in the degraded grassland (9.4%).

Soil CO_2 efflux increased markedly with soil temperature up to 22ºC almost linearly at both sites. Above this value, soil CO_2 efflux remained constant in the degraded grassland, and gently decreased in the natural grassland (Figure 3a). Soil CO_2 efflux increased with soil water content at a higher rate up to *ca.* 15% in the degraded grassland and remained significantly lower above 20% in the natural grassland. That is, high soil moisture values

382 (above 20%) led to higher soil CO_2 efflux rates in the degraded grassland than in the
383 natural grassland (Figure 3b).

384 Soil CO_2 efflux showed a striking seasonal pattern, all other factors being equal: it reached
385 the lowest levels around winter solstice, with the highest recorded values from spring
386 equinox to summer solstice, when the activity of vegetation and biocrust was in its peak in
387 the study area (see the smoothing seasonal pattern in Figure 3c). Finally, Figure 4 shows
388 how soil CO_2 efflux was influenced by soil moisture and soil temperature at both sites.
389 Maximum soil CO_2 efflux rates were measured in both areas at soil temperatures *ca*. 40 ºC
390 and soil water content *ca*. 40%. The influence of soil temperature was more marked (i.e.,
391 higher slopes) in the natural than in the degraded grassland, while the influence of soil
392 water content was more marked in the degraded grassland.

393

394 *Spatial variability in soil CO_2 efflux*

395 **Site** and **soil cover** had a very significant influence on soil CO_2 efflux other effects held
396 constant (see Table 2 and Figure 5). The interaction term **soil cover*site** was also
397 significant, indicating that the differences among the three soil covers changed between
398 sites. The highest soil CO_2 efflux rates were measured in the biological soil crust (mean ±
399 SE: 1.24 ± 0.02 and 1.10 ± 0.02 μmol CO_2 m^{-2} s^{-1} in the natural and degraded sites,
400 respectively) and the lowest in bare soil (1.11 ± 0.02 and 0.82 ± 0.02 μmol CO_2 m^{-2} s^{-1} in
401 the natural and degraded sites, respectively) at both sites, but differences were more
402 pronounced in the degraded grassland (Figure 5a). Differences among soil covers, although
403 highly significant ($P << 0.001$), accounted for only 4.6% of explained variation in the
404 previous model. Adjusted soil CO_2 efflux (that is, controlling for the difference in soil
405 temperature and soil water content among soil covers and sites) was higher in soils covered
406 by biological soil crust and in bare soils in the natural than in the degraded grassland,

407 although this difference was larger in the bare soil cover (Figure 5b). Differences between
408 sites disappeared (F = 0.76, P = 0.385) when soil CO_2 efflux rates were expressed on a soil
409 carbon basis (mg C g C^{-1} day^{-1}, Figure 5c). Nevertheless, soil cover remained significant (F
410 = 19.30, P << 0.001). When soil CO_2 efflux was expressed on a carbon basis, the
411 interaction term **soil cover*site** was not significant (F = 1.04, P = 0.355).

412

413 *Annual estimates of carbon losses from soils*

414 Soil carbon losses on a 15 days basis were significantly predicted by a GAMM including
415 grassland degradation as a fixed factor, and accumulated rainfall during the three previous
416 months and average soil temperature as fixed covariates nested within degraded and
417 natural grasslands (likelihood ratio test: Chi^2 = 142.6, df = 13, P << 0.001, R^2=65.3%;
418 Table 3). A model including the accumulated rainfall during the three previous months was
419 considerably better (AICc = 768.6) than one including the average soil water content for
420 the fortnight (AICc = 793.5; see Supplementary material S5). Accumulated rainfall during
421 the three previous months positively and significantly influenced soil carbon losses at both
422 sites, with a steeper slope in the degraded grassland (Figure 6). Soil carbon loss was also
423 significantly affected in a quadratic-like manner by average soil temperature, particularly
424 in the natural grassland. Soil carbon losses were higher in the natural than in the degraded
425 grassland at average fortnight temperatures that maximise soil CO_2 efflux rates (i.e.,
426 around 20-23 ºC), and lower at temperatures above 30 ºC.

427 Differences among sites were highly significant (P = <0.001), with soil carbon fluxes
428 larger in the natural (adjusted mean: 9.9 g C m^{-2} 15 $days^{-1}$) than in the degraded (7.2 g C m^{-2}
429 15 $days^{-1}$) grassland. The total soil carbon loss per year in 2008 and 2009, when we
430 sampled the whole annual cycle, ranged between 228.7-239.1 g C m^{-2} $year^{-1}$ in the natural
431 and 146.2-173.6 g C m^{-2} $year^{-1}$ in degraded grasslands (see Table 1). The very different

total rainfall in these two years (32.2% lower in 2008 than in 2009; Table 1) contrasts with the very similar total carbon loss estimated (higher in the driest year 2009 than in 2008: 4.5% higher in the natural and 18.7% in the degraded grassland), in spite of the above-mentioned positive relationship between carbon loss and accumulated rainfall during the last three months. This counterintuitive result can be easily explained considering the seasonal rainfall pattern in both years: 42.5% of annual rainfall in the driest year 2009 occurred in spring (70.5 mm) while this amount was 19.7% (48.2 mm) in 2008.

Repeating the previous GAMM separately for the two study sites, 67.8% of variance in soil carbon loss was explained by soil temperature and accumulated rainfall over the last three months in the natural grassland, and 57.2% in the degraded grassland. The exclusive partial effect of soil temperature was larger in the natural (36.3%) than in the degraded grassland (13.8%), while relatively similar amounts of variance were observed for rainfall (16.7% in natural and 22.6% in the degraded grassland).

Discussion

Factors controlling the temporal dynamics of soil CO_2 efflux in dry semiarid grasslands: Impact of land degradation

Our study showed that in these dry grassland ecosystems the seasonal pattern of soil CO_2 efflux followed mostly environmental variables, but its temporal variability was much larger than changes in soil moisture and soil temperature alone, suggesting that other factors modulate this flux. The observed values are lower than in mesic ecosystems and similar to those reported in other similar ecosystems (e.g. Chen et al. 2008; Zhao et al. 2014; Arredondo et al. 2018). Overall, soil CO_2 efflux rates were consistently larger in the natural than in the degraded grassland, mostly as a result of larger vegetation cover and plant activity and consequently, soil activity (Rey et al. 2012). Indeed, soil moisture was

457 the main controlling factor of soil CO_2 efflux in the degraded site (25.4%) whereas the
458 combined effect of soil moisture, soil temperature and seasonality, was the main driver in
459 the natural grassland (27.5% of variation accounted for). The strong combined effect of
460 soil temperature and soil moisture on soil CO_2 efflux has already been observed in similar
461 semiarid ecosystems (i.e. Arredondo et al. 2018; Barron-Gafford et al. 2011; Liu et al.
462 2018).

463 At both sites, soil CO_2 efflux responded positively to soil moisture values up to ca. 20%
464 and then remained practically constant or even decreased. Similar or even lower threshold
465 values have been observed in other semiarid grasslands (e.g. Oyonarte et al. 2012;
466 Arredondo et al. 2018). Above this soil moisture value, soil CO_2 efflux rates were larger in
467 the degraded than in the natural grassland. Thus, soil biological activity in the degraded
468 grassland was much more limited by water availability than in the natural site which agrees
469 with previous studies at these sites (Rey et al. 2011). Greater sensitivity of biological
470 activity to soil moisture in drier sites has been observed elsewhere (Averill et al. 2016).
471 Soil microbes may adapt to dry conditions and water pulses in several ways. Local
472 variation in the response of microbes to soil moisture may include legacy effects (Hawkes
473 & Keitt 2015), adaptation or microbial species to rainfall regime optimising enzyme
474 production (Collins et al. 2008; Hawkes et al. 2011), and persistence of enzymes in
475 drought periods allowing for accumulation of soluble substrates that are available upon
476 rewetting (Manzoni et al. 2012). This is supported by manipulative studies where rainfall is
477 reduced showing that soil enzyme activities are more sensitive to changes in soil moisture
478 (Alster et al. 2013).

479 In agreement with previous studies (e.g. Cable et al. 2008), this study found that a
480 significant amount of variation in soil CO_2 efflux can be attributed to unknown temporal
481 effects (between 44 and 52%). In order to explain other factors controlling the temporal

variability in soil CO_2 efflux, we showed that the inclusion of seasonality as a proxy of plant activity and soil water effects into a model significantly improved explained variance. Recent studies have included day of the year as a predictor to model soil CO_2 efflux (Acosta et al. 2018). The importance of incorporating other factors into models have been highlighted by recent studies showing the potential importance of photosynthetic carbon inputs for understanding the magnitude of soil CO_2 efflux (Vargas et al. 2011) or even microbial activity and community composition (Liu et al. 2018). Thus, this study supports that plant productivity is an important factor controlling soil CO_2 effluxes that should be take into account in order to accurately predict the temporal variability of this flux in these semiarid grasslands (Roby et al. 2019). Consequently, the loss of plant cover resulting from land degradation will affect soil carbon losses.

Spatial variability in soil CO_2 efflux

We aimed to characterise the large spatial variability in soil CO_2 efflux typical of these dry ecosystems by analysing the response of different soil covers to environmental variables. Since soil carbon and soil microclimate differed among soil covers, we expected different contribution to soil carbon losses. Although small, differences between soil CO_2 efflux rates among soil covers was highly significant. Vegetation cover alters soil properties not only by reducing solar radiation (Zou et al. 2007), but also by increasing root density, soil nutrients and soil organic matter (Jackson et al. 2000). This results in changes in soil structure underneath plants with fine-textured soils that have high water-holding capacity (Jobbagy & Jackson, 2000), increasing the availability of water in surface layers where most microbes are found (Rey et al. 2008). Thus, changes in soil structure as a result of plant cover may have also contributed to the observed differences in the spatial variation in

506 soil CO_2 efflux, but we expect that the contribution was small given that most roots are
507 also found underneath plants (Rey et al. 2011).
508 Our statistical approach allowed us to compare soil CO_2 efflux rates removing the different
509 environmental conditions under vegetated areas, biological soil crusts and bare soil. The
510 analysis revealed that soil CO_2 efflux rates differed between soil covers beyond
511 environmental conditions, with highest rates under biological soil crusts at both sites and
512 lowest under bare soil which agrees with previous studies (Li et al. 2018). Some of the
513 observed differences were caused by higher soil organic matter concentration underneath
514 plants (Leon et al. 2014; Rey et al. 2017) so that when we expressed soil carbon fluxes on
515 a carbon basis, differences between soil covers and sites differed from soil CO_2 efflux rates
516 on an area basis. Soil CO_2 efflux rates measured under vegetated areas were lowest while
517 larger amounts of soil carbon losses were measured under bare soil. These results indicate
518 that for the same environmental conditions, and despite higher soil organic matter and
519 carbon concentrations under plants, a larger proportion of carbon is lost from bare soils
520 compared with soils under vegetated areas. Since heterotrophic respiration is more
521 sensitive to changes in soil moisture than autotrophic respiration (Carbone et al. 2008),
522 higher sensitivity to soil moisture under bare soils can be expected. However, in a previous
523 study, Rey et al. (2017) found that substrate availability limits the response of soil CO_2
524 efflux from bare soils to larger rainfall events, so soils under biological soil crusts lost
525 more carbon than the other two soil covers.
526 In a previous study investigating the immediate response of soil CO_2 efflux to rainfall
527 amount and timing at the same study sites, Rey et al. (2017) showed that soils covered by
528 biological soil crust were most responsive to precipitation, responding even to small
529 rainfall events, more than vegetated and bare soil patches. This agrees with other studies
530 showing that biological soil crusts respond more than plants and microbes to small rainfall

531 events (i.e. Cable & Huxman 2004; Bowling et al. 2011; Rey et al. 2017). Soil moisture at
532 3.5 cm may not reflect small changes in surface moisture capable of activating biological
533 soil crusts communities as recently shown (Tucker et al. 2017). Indeed, previous studies
534 have shown that biocrusts gain similar amounts of water as vascular plants (Zhang et al.
535 2008; Berdugo et al. 2014). In this study, soils covered by biological soil crusts respired
536 more than vegetated and bare soils over the study years, which agrees with previous
537 studies in similar areas (Castillo-Monroy et al. 2011; Ouyang & Hu 2017; Tucker et al.
538 2017; Li et al. 2018). Besides changes in soil physical conditions, changes in microbial
539 communities and soil carbon and nitrogen substrates underneath biological soil crusts
540 could also explain higher soil carbon fluxes (Zhao et al. 2014; Fisher et al. 2020).
541 However, biological soil crusts get activated by small precipitation events and high relative
542 humidity favoring CO_2 uptake as previously observed at the same site (Rey et al. 2012)
543 and in other studies (Tucker et al. 2017; Li et al. 2018). The net carbon balance of these
544 soils covered by biological soil crusts are beyond the scope of this study. Since most of the
545 rainfall events were small (between 47 and 70% of less than 5 mm), soils covered by
546 biological soil crusts also contributed the most to soil carbon losses in these ecosystems.
547 Thus, as suggested in this study, changes in precipitation patterns may alter the respiratory
548 contribution from different components of the ecosystem, thereby altering the carbon
549 budget of dryland ecosystems (Li et al. 2018).
550
551 *Impact of precipitation on soil carbon fluxes*
552 Precipitation in this semiarid area is very low (averaging 200 mm) falling in few events
553 (around 10% of the days) and is characterised by large temporal variability. Over the study
554 years, rainfall ranged from 165 mm in 2009 to 364 mm in 2010, so the study period
555 covered dry, intermediate and wet years. Although only 10% of the events were larger than

15 mm, they constituted between 36 and 52% of total annual precipitation. Thus, most rain occurs in few extreme events in the year as it is often the case in drylands (Knapp et al. 2015). Apart from consistent dry summers, timing was highly variable with rainfall falling in autumn, spring and winter. Precipitation was a much better factor explaining seasonal soil carbon fluxes than soil moisture. In particular, we found that cumulative rainfall over three months was the best predictor of soil carbon losses over two weeks. The effect of precipitation was larger for the degraded grassland, particularly for accumulated rainfall larger than 60 mm, suggesting that degraded ecosystems are more strongly limited by soil moisture. This agrees with other studies (Liu et al. 2016), suggesting that ecosystem sensitivity to precipitation increases with aridity. As previously observed (Arredondo et al. 2018), plants dampened the sensitivity to moisture while increasing the sensitivity to temperature. Our study supports these findings as the natural grassland was less responsive to precipitation and more sensitive to temperature than the degraded one with much less vegetation cover. As highlighted by Knapp et al. (2015) and Liu et al. (2016), experiments should therefore focus on manipulating not only the amount of rain but the timing and number of extreme events, as timing seems to be more important for soil biological activity than rainfall amount.

Maximum soil CO_2 efflux rates also coincide with the peak of maximum photosynthesis in spring for Mediterranean ecosystems (Jarvis et al. 2007) with adequate microclimatic conditions for soil microbial decomposition. In agreement with previous studies (Robertson et al. 2009; Bell et al. 2014; Averill et al. 2016), this study supports that soil biological activity can be more responsive to seasonal availability of precipitation than to the amount of annual precipitation. Indeed, the highest soil carbon losses were estimated in the driest year (2009) and the lowest in the wettest with almost doubled the amount of rainfall (2010). The main difference between these years was the timing of the events that

581 mostly occurred in the moments of maximum plant and biocrust activity with optimum
582 temperatures in spring in the driest year.

583 This study also highlights the important interaction between precipitation and land
584 degradation. Land degradation affects more than 20% of semiarid lands and is expected to
585 increase with climate change (Reed et al. 2012). As a result, plant and soil cover are lost
586 and in turn, biochemical and biophysical processes. The loss of vegetation cover and
587 concomitant productivity reduction alters the ecosystem energy balance, hydrological
588 budget, and productivity (Barron-Gafford et al. 2014; Ghezzehei et al. 2019). Larger
589 interspace patches with rock and bare soil cover, as well as lower soil organic matter
590 content in the degraded site, resulted in larger evaporative losses and lower soil moisture
591 contents than in the natural grassland, and thus, lower soil carbon fluxes for the same
592 precipitation amount, but more sensitive to increases in rainfall amount. This greater
593 sensitivity might be related to comparatively greater extensions of plant interspaces in the
594 degraded grassland, which then translates into greater exposure to radiation, and
595 accelerated cycles of desiccation, higher temperatures, sensible heat fluxes and rewetting.
596 As a consequence, precipitation caused larger carbon fluxes, particularly for intense
597 rainfall events. Previous studies (Fei et al. 2018) have attributed soil carbon losses to
598 changes in soil properties resulting from land degradation.

599 Current models predict rainfall reduction, increased drought periods and increased extreme
600 rainfall events (Groisman et al. 2005; Huntington 2006; IPCC 2014). Expected changes in
601 rainfall patterns will alter soil moisture dynamics, affecting multiple ecosystem processes
602 in drylands (Greve et al. 2014). This study supports that both, changes in rainfall amount
603 and rainfall patterns, will affect belowground activity and soil carbon fluxes, particularly in
604 degraded grasslands. Furthermore, since most of the rain falls in few extreme rainfall
605 events, in agreement with previous work (Fay et al. 2008), this study also suggests that an

606 increase in extreme events will likely lead to further soil carbon losses via soil carbon
607 fluxes, aggravating land degradation.

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832

Figure legends

Figure 1

Seasonal variability in: (a) soil temperature (^{o}C) and (b) soil volumetric water content (%) measured at 3.5 cm depth, (c) mean (for the three soil covers) soil CO_2 efflux rates (μmol CO_2 m^{-2} s^{-1}) for each site (natural and degraded grasslands), and (d) precipitation (mm) spanning the study period (January 2007-July 2010). Symbols represent the mean ± 1SE (*n* = 6 soil covers).

Figure 2

Conceptual model with variance partitioning of the factors controlling soil CO_2 efflux (μmol m^{-2} s^{-1}) at both sites (natural –upper figures– and degraded –lower figures– grasslands): *soil temperature* (^{o}C), *soil water content* (%) and *seasonality*. The *Combined Effect* refers to the shared variance among predictors, as opposed to their partial exclusive effects.

Figure 3

Partial residual plots of: (a) *soil temperature* (^{o}C), (b) *soil water content* (%) and (c) *seasonality* on soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}). Shaded areas represent 95% confidence intervals.

Figure 4

Modelled response of soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) to soil temperature (^{o}C) and soil moisture (%) in the natural (a) and degraded (b) grasslands.

858

859 **Figure 5**

860 Soil CO_2 efflux values expressed as: (a) measured mean values (μmol m^{-2} s^{-1}), (b) adjusted
861 means (μmol m^{-2} s^{-1}) and (c) mean soil carbon loss (mg C g C^{-1} day^{-1}) for each soil cover:
862 under plant cover (VEG), biological soil crust (BSC) and bare soil (BS) in each site:
863 natural and degraded grassland over the entire study period (January 2007-July 2010). Bars
864 represent the mean (±1SE, n = 6 replicates per soil cover) for the whole duration of the
865 study (90 measured days). Bars with different letters are significantly different ($P < 0.05$)
866 between soil covers within sites (post hoc test).

867

868 **Figure 6**

869 Partial residual plots: (a) *rainfall amount* (accumulated over the last three months) (mm)
870 and (b) *soil temperature* (^{o}C) (mean over the fortnight) on soil carbon losses (g C m^{-2} 15
871 $days^{-1}$) in the natural and degraded grasslands. The range of soil temperature is restricted to
872 the natural variation measured at each study area. Shaded areas represent 95% confidence
873 intervals.

874

Figure 1

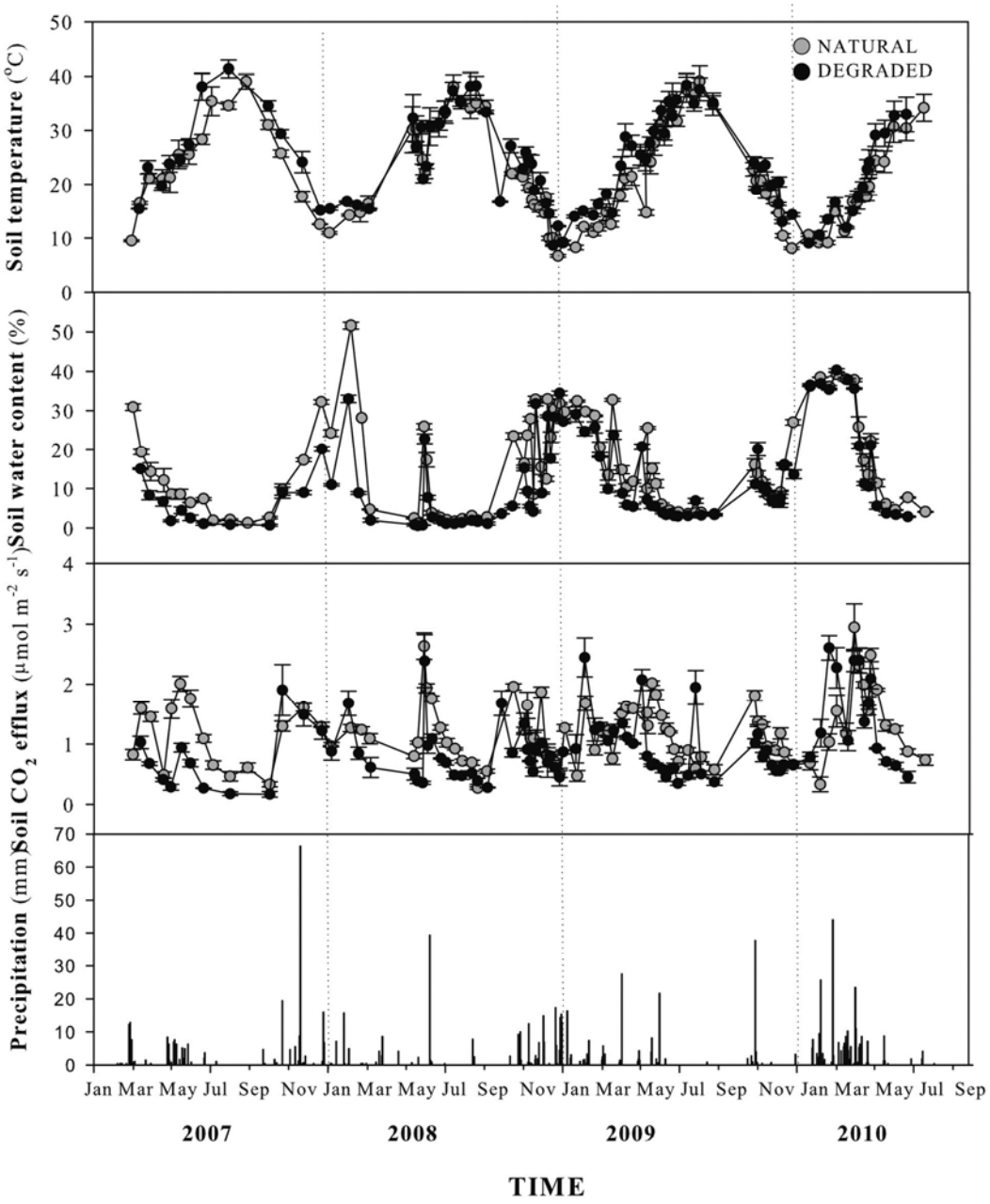

NATURAL
DEGRADED
Soil temperature (°C)
Soil water content (%)
Soil CO2 efflux (µmol m-2 s-1)
Precipitation (mm)
Jan Mar May Jul Sep Nov Jan Mar May Jul Sep Nov Jan Mar May Jul Sep Nov Jan Mar May Jul Sep
2007
2008
2009
2010
TIME

Figure 2

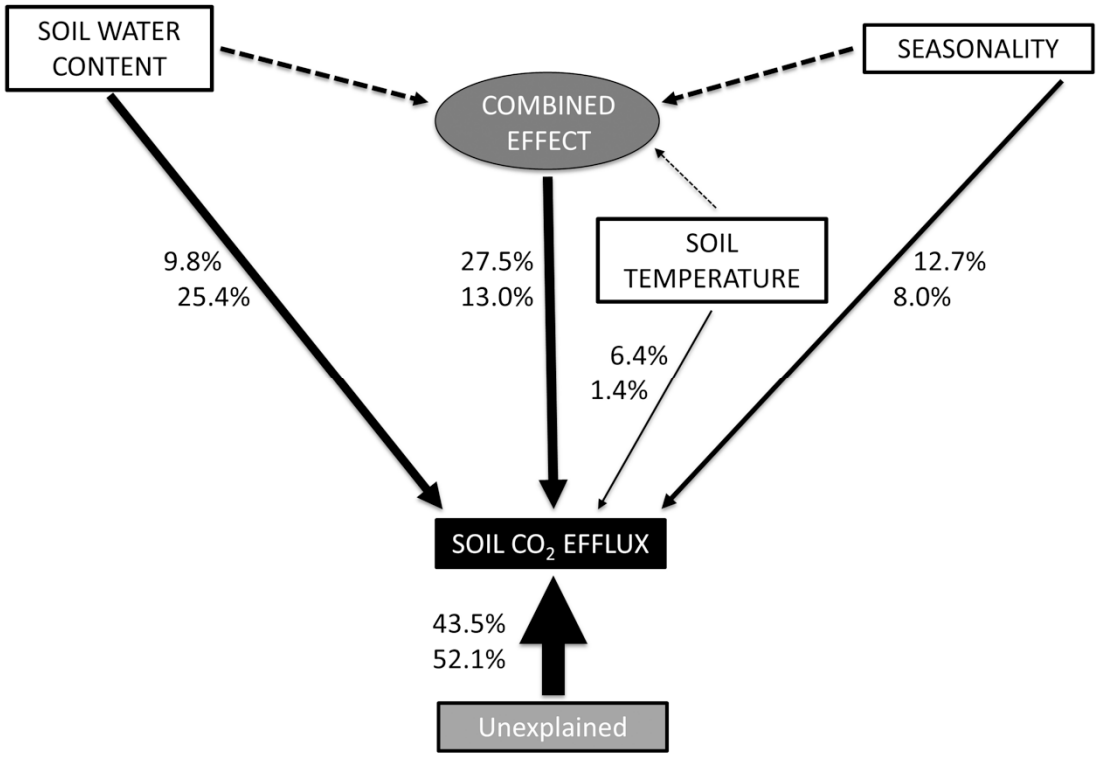

SOIL WATER CONTENT
SEASONALITY
COMBINED EFFECT
SOIL TEMPERATURE
9.8%
25.4%
27.5%
13.0%
6.4%
1.4%
12.7%
8.0%
SOIL CO_2 EFFLUX
43.5%
52.1%
Unexplained

Figure 3

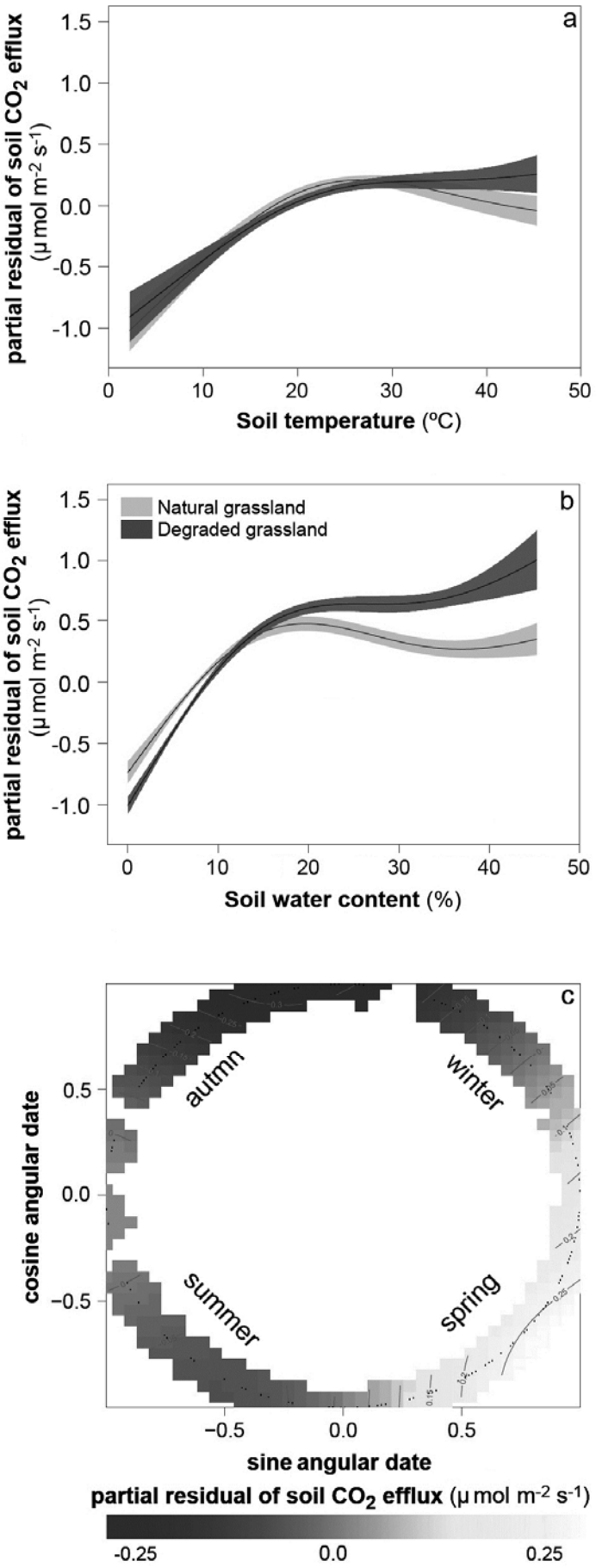

a
partial residual of soil CO_2 efflux (µ mol m^{-2} s^{-1})
1.5
1.0
0.5
0.0
-0.5
-1.0
0
10
20
30
40
50
Soil temperature (ºC)
b
Natural grassland
Degraded grassland
partial residual of soil CO_2 efflux (µ mol m^{-2} s^{-1})
Soil water content (%)
c
autmn
winter
summer
spring
cosine angular date
sine angular date
partial residual of soil CO_2 efflux (µ mol m^{-2} s^{-1})
-0.25
0.0
0.25

Figure 4

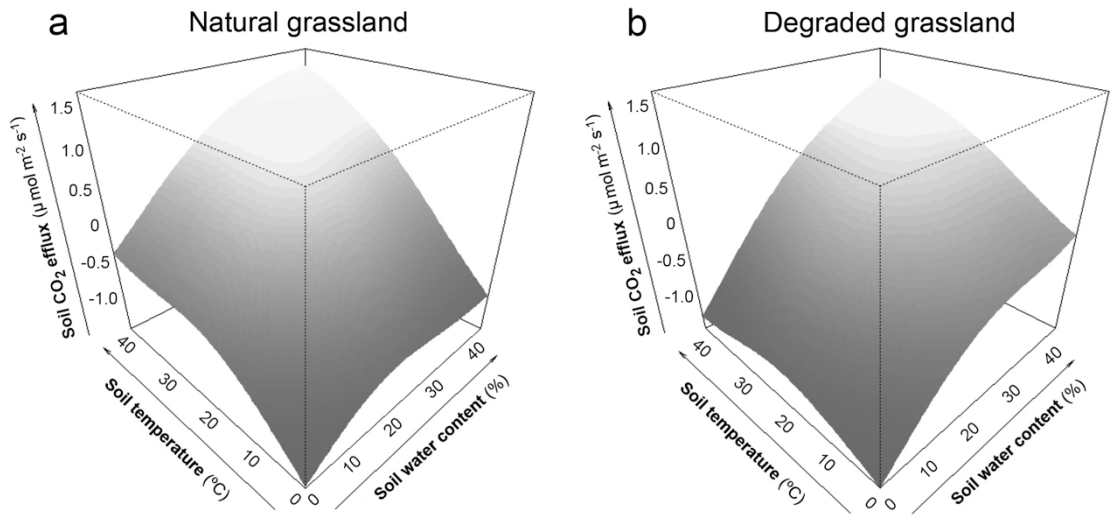

a
Natural grassland
b
Degraded grassland
Soil CO2 efflux (µmol m-2 s-1)
1.5
1.0
0.5
0
-0.5
-1.0
Soil temperature (°C)
0
10
20
30
40
Soil water content (%)
0
10
20
30
40

Figure 5

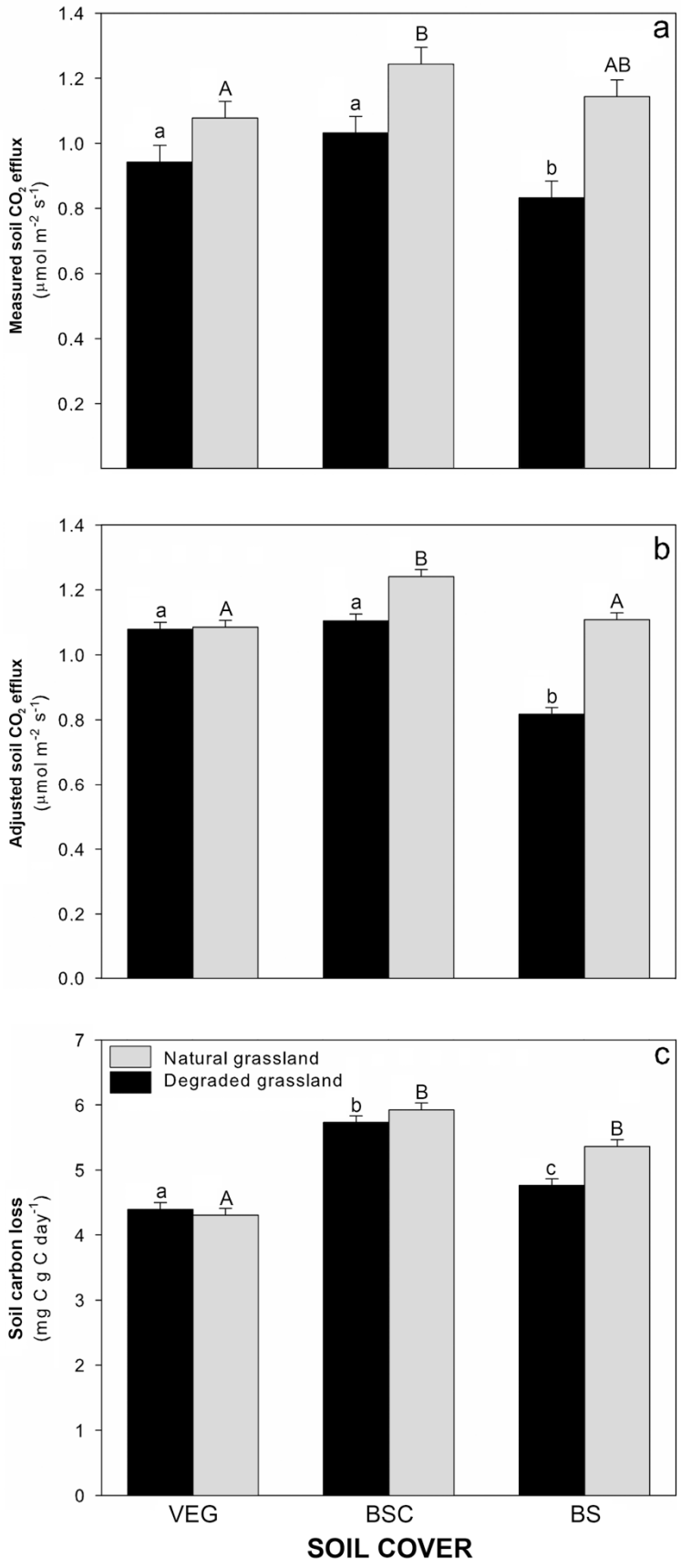

a
Measured soil CO_2 efflux
(µmol m^{-2} s^{-1})
1.4
1.2
1.0
0.8
0.6
0.4
0.2
a
A
a
B
b
AB
b
Adjusted soil CO_2 efflux
(µmol m^{-2} s^{-1})
0.0
a
A
a
B
b
A
c
Natural grassland
Degraded grassland
Soil carbon loss
(mg C g C day^{-1})
7
6
5
4
3
2
1
0
a
A
b
B
c
B
VEG
BSC
BS
SOIL COVER

Figure 6

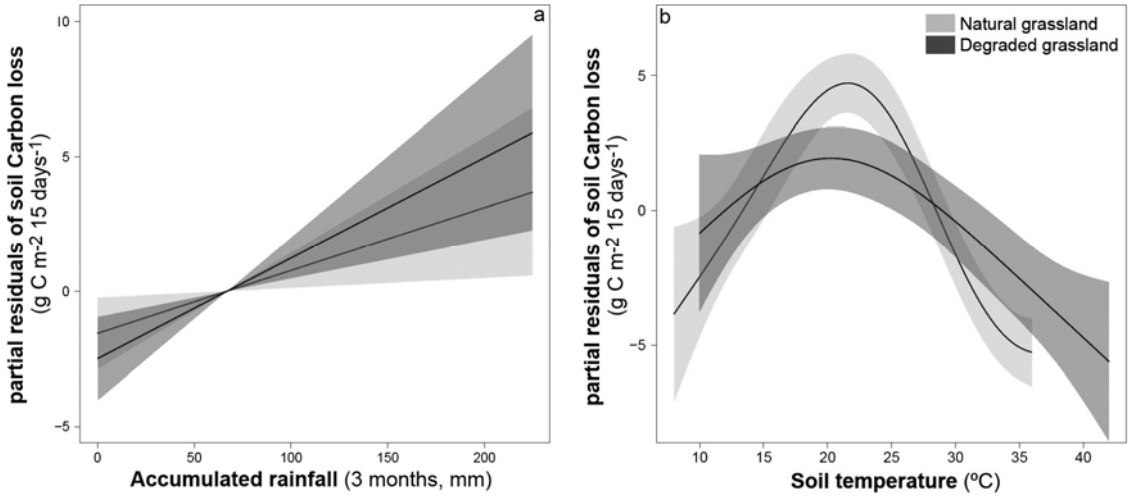

a
b
Natural grassland
Degraded grassland
partial residuals of soil Carbon loss
(g C m-2 15 days-1)
Accumulated rainfall (3 months, mm)
Soil temperature (ºC)

Table 1

Rainfall patterns throughout the study years (2007-2010) in the natural and degraded grasslands according to intensity and timing and soil carbon loss per year (g C m^{-2} yr^{-1}). Events refer to the number of days with rainfall above 1 mm. The total soil carbon loss (g C m^{-2} yr^{-1}) for 2010 is in italic because it refers to half a year only.

	YEAR			
Rainfall amount	**2007**	**2008**	**2009**	**2010**
Total rainfall (mm)	276.6	244.6	165.8	363.8
% of days with rainfall	9.9	9.0	7.4	13.2
Event frequency (%)				
1-5 mm	47.2	54.5	70.4	47.9
5-15 mm	41.7	33.3	18.5	39.6
> 15 mm	11.1	12.1	11.1	12.5
Rainfall distribution (% mm)				
1-5 mm	14.6	19.1	27.1	16.7
5-15 mm	41.9	44.8	20.5	40.4
> 15 mm	42.4	36.1	52.4	42.8
Timing (%)				
Winter	26.4	19.4	26.9	51.3
Spring	24.2	19.7	42.5	21.0
Summer	2.2	4.0	0.5	4.2
Autumn	47.2	57.0	30.1	23.6
Soil C loss (g m^{-2})				
Natural grassland	206.5	228.7	239.1	*148.4*
Degraded grassland	126.9	146.2	173.6	*129.2*

Table 2

Results of the generalised additive mixed model analysing daily soil CO_2 efflux (µmol m^{-2} s^{-1}). edf: estimated degrees of freedom for the model terms. Phenology is defined by a tensor product smoothing term (i.e., additive regression plane) using the cosine and sinus of the angular date transformation.

Effects	**edf**	**F**	**P**
Site (degradation level)	1	22.76	<<0.001
Soil cover	2	8.46	<<0.001
Site x Soil cover	2	3.97	0.019
Phenology	5.8	49.39	<<0.001
Soil water content (within natural grassland)	3.0	95.34	<<0.001
Soil water content (within degraded grassland)	3.0	350.47	<<0.001
Soil temperature (within natural grassland)	2.9	65.57	<<0.001
Soil temperature (within degraded grassland)	2.7	29.63	<<0.001

Table 3

Results of the generalised additive model analysing cumulative soil carbon loss (g C m^{-2} 15 $days^{-1}$). Sample size is 160 for the four study years and two sites. edf: estimated degrees of freedom for the model terms.

Effects	**edf**	**F**	***P***
Site (degradation level)	1	15.76	<0.001
Accumulated rainfall in 3 months (within natural grassland)	1.0	10.68	0.001
Accumulated rainfall in 3 months (within degraded grassland)	1.0	9.51	0.002
Soil temperature (within natural grassland)	3.6	13.22	<< 0.001
Soil temperature (within degraded grassland)	2.7	5.98	0.006

SUPPLEMENTARY MATERIAL S1

Main characteristics of the study sites

	SITE	
	NATURAL	**DEGRADED**
Variable	**(Balsablanca)**	**(Amoladeras)**
Longitude	2º1'58"W	2º15'1"W
Latitude	36º56'30"N	36º50'5"N
Altitude (m)	208	65
Orientation	NW	SW
Slope (%)	2-6	2-6
Mean annual air temperature (ºC)	18	18
Mean summer air temperature (ºC)	34	36
Average annual rainfall (mm)	200	200
Mean soil temperature at 3.5 cm (ºC)	22.5	24.0
Mean soil water content at 3.5 cm (%)	15.2	11.7
Mean PPFD (µmol mol^{-1})	1549	1549
Mean annual atmospheric pressure (kPa)	99	101
Maximum VPD (kP)	4.3	4.6
Mean annual relative air humidity (%)	69.3	68.7
Vegetation	Steppe alpha grass	Steppe alpha grass
Soil type (Calcaric; WRB, 2006)	Mollic Lithic Leptosol	Lithic Leptosol
Soil texture class	Sandy loam	Sandy loam
Clay (%)	16.1	14.6
Silt (%)	22.8	27.0
Sand (%)	61.1	58.4
Bulk density (g cm^{-3})	1.25	1.11
Maximum soil depth (cm)	20	10
Vegetation cover (%)	63.2	23.1
Biological soil cover (%)	18.2	23.1
Bare soil (%)	0.3	8.1
Other cover (rock, gravel, etc.)	22.3	46.7

SUPPLEMENTARY MATERIAL S2

Spatial variability in soil properties

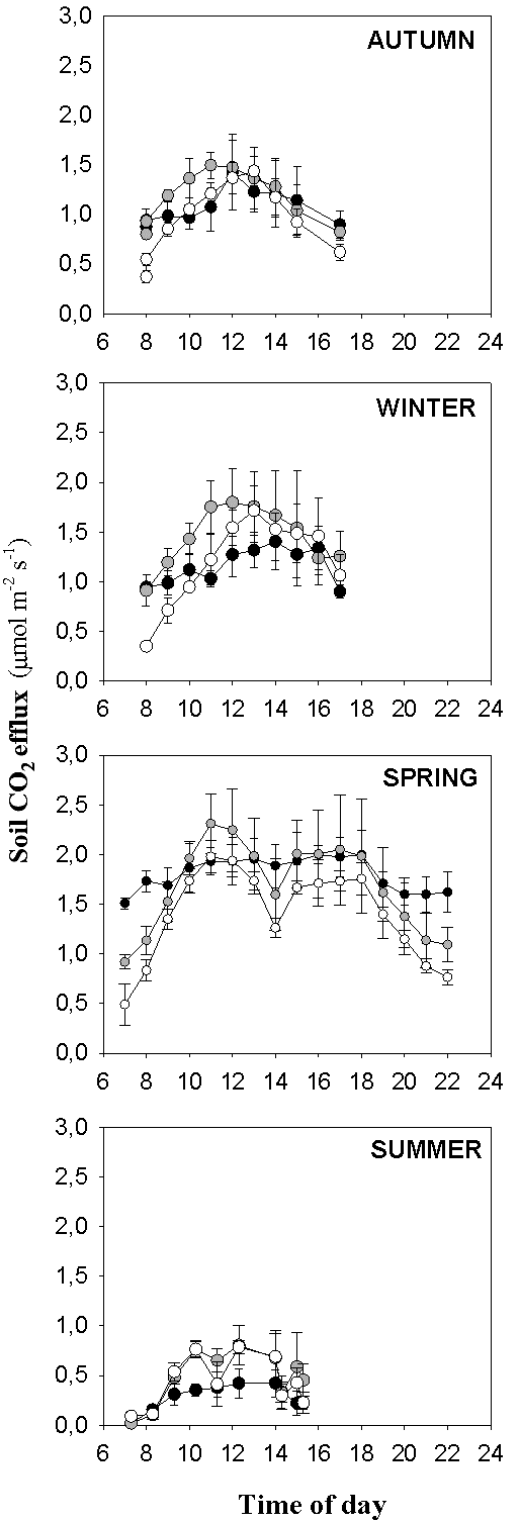
Soil properties under the three soil covers: under vegetation areas (VEG), biological soil crusts (BSC) and bare soils (BS). Values are the mean ± 1SE (n = 10).

SITE	NATURAL GRASSLAND			DEGRADED GRASSLAND		
Soil cover	**VEG**	**BSC**	**BS**	**VEG**	**BSC**	**BS**
Soil organic carbon (%)	2.17(0.14)	1.77(0.14)	1.63(0.14)	2.14 (0.08)	1.46(0.14)	1.33 (0.08)
Total nitrogen (%)	0.19(0.01)	0.15(0.01)	0.16 (0.01)	0.21(0.09)	0.15(0.01)	0.14 (0.01)
Bulk density (g cm^{-3})	1.20(0.03)	1.23(0.04)	1.32(0.04)	1.21(0.02)	1.36(0.02)	1.34(0.02)
Fine root density (mg cm^{-2})	3.30(0.44)	1.99(0.31)	2.03(0.28)	5.91(0.73)	1.30(0.24)	1.01(0.30)

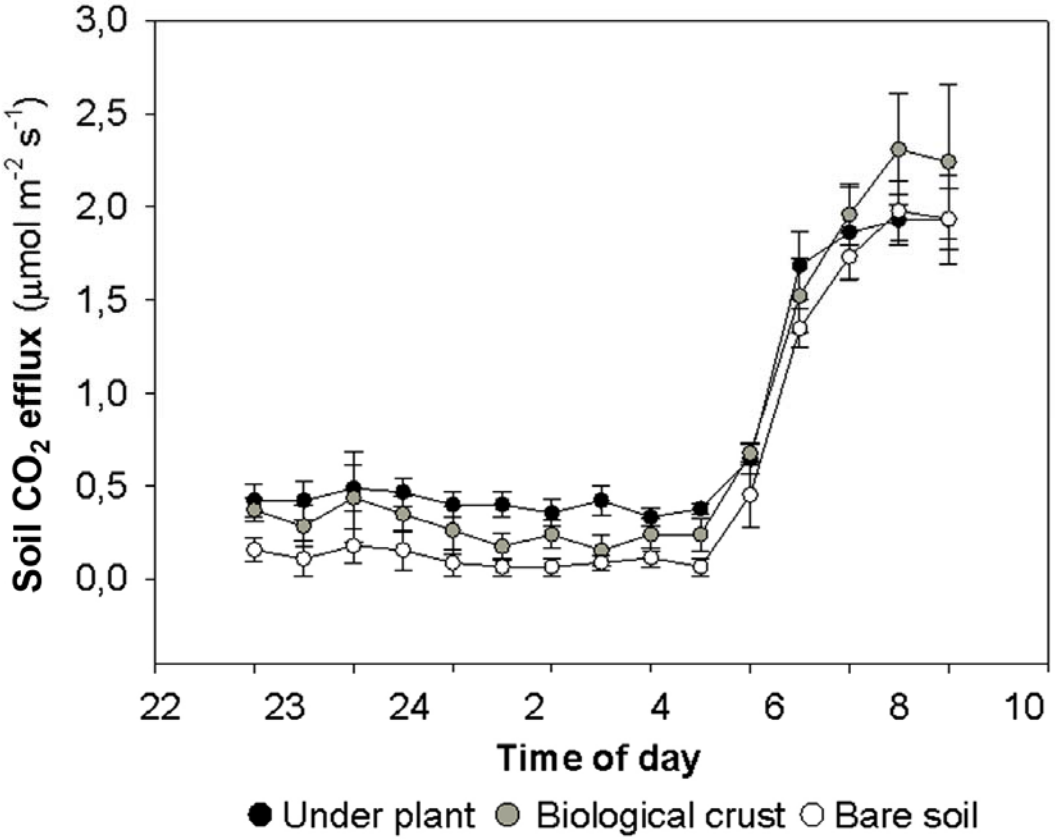
SUPPLEMENTARY MATERIAL S3

Calculation of mean daily soil CO_2 efflux rates

(a) Diurnal course of soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) in four seasons in the three soil covers, under plant, biological soil crust and bare soil (n = 6) measured in the natural grassland. Values are mean ± 1SE.



(b) Nocturnal measurements of soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) made in spring in the three soil covers: under plant, biological soil crust and bare soil (n = 6) in the natural grassland (Balsablanca). Values are mean ± 1SE.



According to these daily patterns, the divisors of soil CO_2 efflux rates measured in the field between 10:00 and 14:00 hours used to estimate daily averages were as follows:

	BSC	**VEG**	**BS**
Winter	2.13	1.66	2.41
Spring	1.70	1.41	1.82
Summer	2.21	2.18	2.48
Autumn	2.08	1.65	2.57

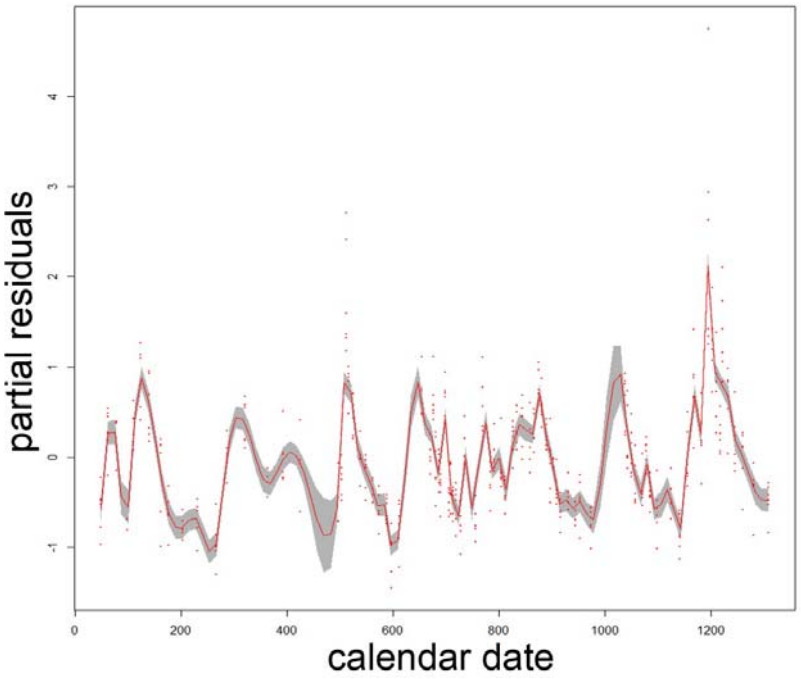
Supplementary Material S4

Interpolation method of daily measurements between sampling dates over the study period

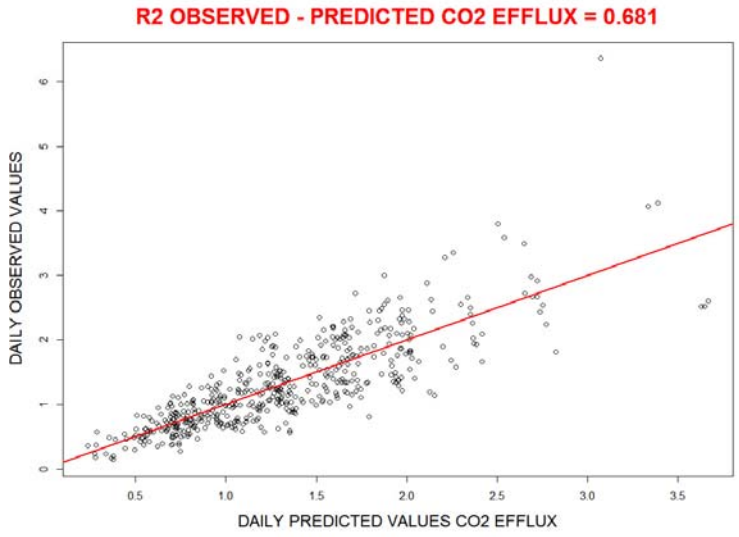
The interpolation of soil CO_2 efflux, soil temperature and soil water content is necessary in order to obtain stable averages when upscaling data to fortnights and estimate annual estimates, in order to gain insights on the role of rainfall amount on soil carbon losses. We measured these three variables intensively enough (i.e., with high frequency) to obtain reliable estimates when interpolating the data between dates. The main sort of variation would be to miss CO_2 peaks after rainfall events, that is exactly why we tried to measure always after each rainfall event as well as on a regular basis.

We applied GAMM with the available data in order to carry out the interpolation. GAMM is applied considering that (1) non-linear relationships may underline predictors-response relationships and (2) there is temporal auto-correlation in consecutive fortnights data. The predictors were *date* and the *rainfall amount of the previous day*, with calendar dates beginning on January 1st 2007 (day 1) and ending on June 30th 2010 (day 1277). The interpolation process employed using GAMMs was very robust according to the predictive power of the six models applied to data for the two sites (degraded and natural grasslands) and three soil covers (vegetation patches, biological soil crust, and bare soil). All models accounted for an extremely high proportion of deviance (always > 75%).

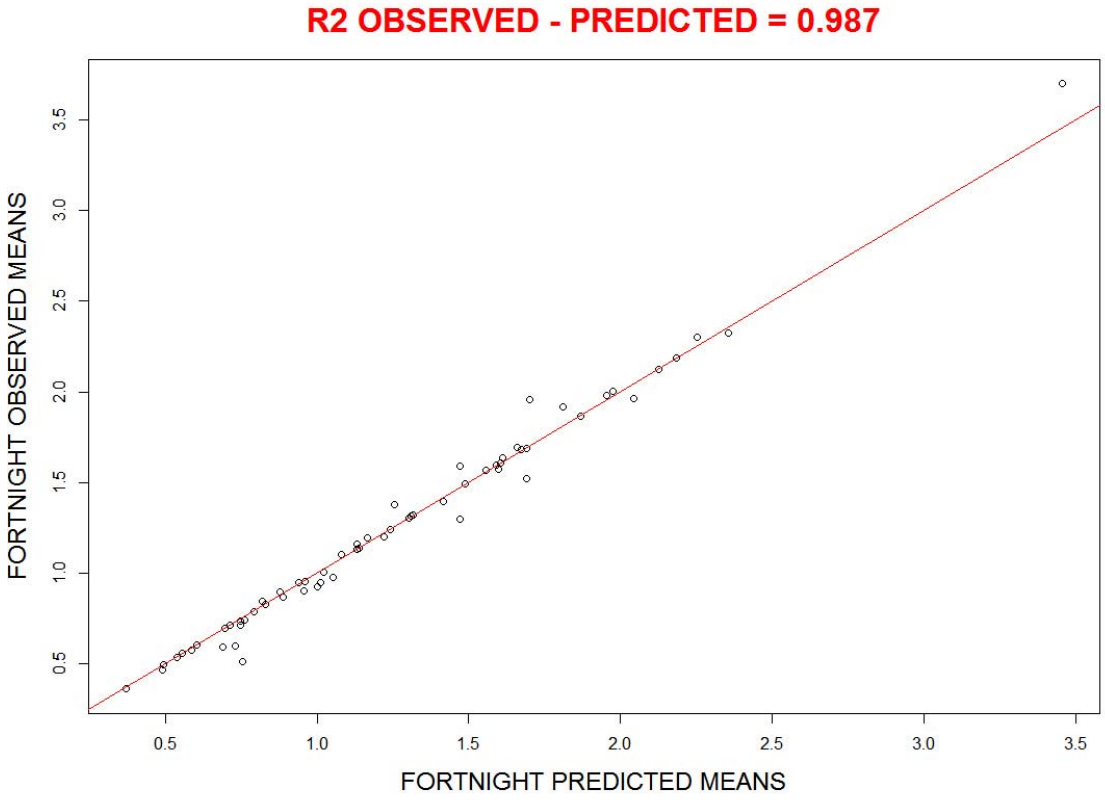
The test of predictive power was carried out by means of jackknifing. Thus, we carried out the GAMMs many times for each site-soil cover not using one particular sample in each model. That sample was predicted by the GAMM that used the remaining samples. This process was repeated as many times as the number of sample units, in such a way that every sample unit is predicted without being used in the modelling process. The following figure shows the result of the "worst" GAMM model applied to the data of Balsablanca (natural grassland), using only the samples of the collars in the vegetation patches. The pseudo-R^2 of the GAMM was 0.746. The little red dots show the residuals for each one of the 516 soil CO_2 efflux measurements of six collars obtained in 86 sampling dates. The R^2 of that model is only 74.6% due to the relatively high sample variance among soil collars within each date, probably related to "microsite" differences between collars regarding vegetation, slope, soil characteristics, insolation related to cardinal position of collars around vegetation patches, etc. Nevertheless, the averages of the six collars for each sampling date follow a tight pattern with only relatively high uncertainty (see the amplitude of the shaded areas) when consecutive sampling dates are more than 20 days apart.



The relationship between the observed (actual) and predicted soil CO_2 efflux estimates for each collar in each sampling date obtained in the jackknife procedure is shown in the next figure.



The R^2 of that relationship (68.1%) is lower than the pseudo-R^2 of the GAMM model, but high enough considering that it is strictly a predictive analysis considering all the variability among soil collars and dates. But this result does not pose any important concern, as our interpolation has been made for fortnights, averaging the predictions of the six collars in the days included in the fortnight. If we consider the sampling days within every fortnight, the averages of the measured rates and the averages of the jackknife-predictions are tightly correlated in the corresponding fortnights. This is clearly shown in the next Figure.


R2 OBSERVED - PREDICTED = 0.987
FORTNIGHT OBSERVED MEANS
FORTNIGHT PREDICTED MEANS
0.5
1.0
1.5
2.0
2.5
3.0
3.5

SUPPLEMENTARY MATERIAL S5

Alternative GAMMs to those presented in Tables 2 and 3

Alternative generalised additive mixed models to that presented in Table 2, regarding daily soil CO_2 efflux (µmol m^{-2} s^{-1}). edf: estimated degrees of freedom for the model terms. Seasonality is defined by a tensor product smoothing term (i.e., additive regression plane) using the cosine and sinus of the angular date transformation.

Soil water content and soil temperature not nested within Sites

Effects	edf	F	P
Site (degradation level)	1	24.41	<<0.001
Soil cover	2	8.41	<<0.001
Site x Soil cover	2	2.97	0.052
Seasonality	5.7	76.58	<<0.001
Soil water content	3.0	422.08	<<0.001
Soil temperature	3.0	76.57	<<0.001

Substitution of soil water content by rainfall amount and rainless duration

Effects	edf	F	P
Site (degradation level)	1	61.67	<<0.001
Soil cover	2	7.09	0.001
Site x Soil cover	2	0.67	0.512
Seasonality	5.8	33.23	<<0.001
Rainfall amount (natural grassland)	1.0	41.91	<<0.001
Rainfall amount (degraded grassland)	2.8	12.42	<<0.001
Rainless duration (natural grassland)	2.9	20.92	<<0.001
Rainless duration (degraded grassland)	2.9	9.33	<<0.001
Soil temperature (natural grassland)	3.0	56.70	<<0.001
Soil temperature (degraded grassland)	2.8	18.07	<<0.001

Alternative generalised additive mixed model to that presented in Table 3, regarding cumulative soil carbon loss (g C m^{-2} 15 $days^{-1}$). Sample size is 160 for the four study years and two sites. edf: estimated degrees of freedom for the model terms.

Substitution of Accumulated rainfall in 3 months by fortnight soil water content

Effects	edf	F	*P*
Site (degradation level)	1	7.87	0.006
Average fortnight soil water content (within natural grassland)	1.1	1.71	0.168
Average fortnight soil water content (within degraded grassland)	1.7	3.93	0.018
Soil temperature (within natural grassland)	3.6	9.32	<< 0.001
Soil temperature (within degraded grassland)	2.6	4.52	0.023