Species identity improves soil respiration predictions in a semiarid scrubland

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ABSTRACT

Soil respiration accounts for ca. three quarters of total ecosystem respiration and is sensitive to temperature and moisture. Plants can influence soil CO$_2$ emissions through specific effects on soil humidity, soil temperature and soil microbial communities. These plant-soil effects mostly come via litter production and root exudates, enhancing soil autotrophic and heterotrophic respiration. We explored how plant species affected soil CO$_2$ emissions in an arid environment. We altered soil temperature in bare soil and under the canopy of four plant species differing in functional type, and measured monthly fluxes to establish seasonal patterns of CO$_2$ release along a 20-month period. We found that soil temperature explained 69% of the annual soil respiration (SR) variance, while soil water content explained 71% of SR variance. When we included plant species identity in the model, soil temperature and soil water content explained 76% and 81% of SR variance, respectively, exemplifying how plant species modulate SR responses as a function of temperature and water availability. Our results demonstrate that plant species influence soil carbon balance and emphasize that species identity matters in dry ecosystems. SR dynamics in dry ecosystems can be accurately modelled with soil water and temperature as predictors, but models are more efficient if plant species identity is considered.

1. Introduction

Soil respiration (SR) is the second largest flux of CO$_2$ between the ecosystem and the atmosphere, just after photosynthesis (Davidson et al., 2002). Soils can store up to 260 Pg of organic carbon (OC) in drylands (Serrano-Ortiz et al., 2012), making them critical actors in the global C budget. Future scenarios for drylands predict an increase in temperature and changes in precipitation patterns, which will become more unpredictable (IPCC, 2014). Such changes may enhance water scarcity and constrain respiration responses to temperature (Bahn et al., 2010; Rey et al., 2011) increasing the complexity of modeling C fluxes from soil. SR is the sum of autotrophic respiration (roots and mycorrhiza) and heterotrophic respiration (bacteria, archaea, free living fungi, and microfauna) (i.e., Heinemeyer et al., 2007; Heinemeyer et al., 2012). Both temperature and humidity affect SR i) through their effects on soil microbial activity (e.g., Davidson et al., 2012; Sierra, 2012); ii) by their indirect effect on the rhizosphere via plant activity (Bond Lamberty et al., 2004); and iii) by affecting substrate diffusion (e.g., Davidson and Janssens, 2006). Overall, an increase in soil temperature and/or humidity will enhance soluble substrate diffusion in soils, boosting resource availability and affecting SR rate. However, SR responses to temperature and humidity are not well understood, since both factors interact with each other (e.g., Davidson et al., 2012). An increase in temperature could modify the temporal dynamics of SR in semiarid soils; for instance, an increase in temperature reduces SR when soil moisture is limited by drought (Almagro et al., 2009) as shown with manipulative experiments (Carey et al., 2016). This is common in dry environments, where temperature and rainfall are often decoupled and high temperatures reduce water availability through evaporation, resulting in an added difficulty to predict SR responses.

But understanding SR in drylands is also complicated by the heterogeneous and patchy structure of plant communities (Aguiar and Sala, 1999). Such as semi-arid plant communities in south east Spain, where some perennial species create 'islands of fertility' that modify

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both above- and below-ground conditions (Lozano et al., 2019; Pugnaire et al., 2004) influencing the structure of understory plant and soil communities (Aguilera et al., 2016; Hortal et al., 2015; Macek et al., 2016; Martínez-García et al., 2011; Rodríguez-Echeverría et al., 2013). Plants modify environmental variables under their canopies (e.g., soil temperature, water availability, or organic matter; Pugnaire et al., 2011), host different rhizosphere communities (Heinemeyer et al., 2007) and differ in their capacity to retain water under the canopy (Prieto et al., 2012) ultimately modulating SR (Bond Lamberty et al., 2004; Estruch et al., 2018; Fóti et al., 2014; Metcalfe et al., 2011). Plant species differ in their effects on the above-mentioned environmental variables and on how they alter the quality and quantity of carbon (C) compounds released into the soil. Thus, while some species provide easily decomposable materials, others produce more recalcitrant compounds, slowing organic matter decomposition and contributing to a decrease in SR (García Palacios et al., 2013; Hasibeder et al., 2015). Even though some plant effects on SR are clear (e.g., the amount of root biomass; Hopkins et al., 2013), SR seems to be regulated by plant traits. For example, Curiel Yuste et al. (2004) found that leaf phenology influences SR, as in evergreen forests SR showed less seasonal variation than in deciduous forests.

Several authors have emphasized the importance of environmental heterogeneity, reporting differences in SR linked to plant species identity (Castillo-Monroy et al., 2011; Estruch et al., 2018; Maestre and Cortina, 2003; Oyonarte et al., 2012). Most reports evidence the need for better approaches to fine-tune SR estimates as a function of the plant species present in a patch. By isolating the role of plant species on SR processes we should be able to improve predictions of SR under future scenarios of global change.

Here we report a field experiment in which we manipulated soil temperature in bare soil and in soils under the influence of the most representative plant species in an arid community in a Mediterranean dryland in South-East Spain. To account for the variety of plant types in the system, we selected four dominant plant species and recorded SR in bare soil and in plant understories over a 20-month period. We wanted to examine SR responses to soil temperature (experimentally manipulated) and its responses to seasonal changes in soil temperature and water availability under different plant types. We hypothesized that i) SR under different plants species will respond differently to changes in soil temperature and humidity; therefore ii) accounting for plant species identity will improve our capacity to model CO_2 emissions. We built an empirical model taking into account seasonal responses to changes in water availability, plant identity, and their interaction with temperature.

2. Material and methods

2.1. Field site

The field site is located in the northern foothills of the Sierra Alhamilla range, Almería, Spain (37°01′N, 002°25′W, ~350 m elevation); the climate is Mediterranean semiarid, with 230 mm mean annual precipitation and a dry period between June and September, with mean annual temperature of 17.9 °C. Soils are orthic solonchak with calcic regosol inclusions and high salinity content (Pérez Pujalte, 1987). In the native scrub community we selected four dominant perennial species as target; two tussock grasses, *Stipa tenacissima* L. and *Lygeum spartum* L. (both Poaceae); tussock grasses are perennial, clonal species with slow growth rates and low root-to-shoot ratio; and two shrubs, *Salsola genistoides* Juss. ex Poir. and *Hammada articulata* Mog. (both Chenopodiaceae); these shrub species are evergreen, perennial woody species with a projected canopy area less than 100 cm². All species are hereafter referred to by genus. For a more complete description of our target plant species see Fig. S1 in the Supplementary Material.

2.2. Experimental design

In March 2012 we randomly selected 36 individuals of each of target species and 36 bare soil patches in between, spread within a ~1 ha plot. Individuals and bare soil patches were at least 1 m apart from each other. We inserted 5-cm deep PVC collars, 10.3 cm in diameter, in the eastern aspect of each individual (Fig. S1), and at ~7 cm from the shrub trunk/tussock grass canopy. Each patch was randomly assigned to one of three treatments, with twelve replicates each. In two treatments we manipulated albedo with a thin layer (> 2 mm) of colored sand (black sand Zolux© to increase temperature, further referred to as *increased*; white sand Zolux© to decrease temperature, further referred to as *decreased*), and nothing to the control. Colored sand changed soil texture in similar ways but increased or decreased soil temperature depending on their color (black sand increased temperature, and white sand decreased temperature). To differentiate both effects, in the statistical analyses we included two fixed factors; one considering a temperature treatment with two levels (increased and decreased), and the other considering as fixed factor a texture treatment with two levels (with and without sand application, irrespective of sand color).

We measured SR monthly between May 2012 and November 2013 with a portable EGM-4 infrared gas analyzer connected to an SRC-1 chamber (PP Systems, Amesbury, MA, USA). Measurements were made along three consecutive days per month between 10:00 and 16:00 GMT and results are shown in Fig. 1. Within this time frame, readings were steady as all measurements were carried out on sunny days with similar temperature; the order of plot measurements was randomized to avoid biases.

2.3. Field parameters

We monitored hourly soil temperature and volumetric soil water content (SWC) in bare soil for all three temperature treatments between March 2012 to November 2013 using ECH₂O probes (n = 3; Decagon Devices Pullman, WA, USA) set at a depth of 5 cm. Additionally, soil temperature was recorded manually at each respiration measurement using a thermocouple inserted at 5 cm depth.

We estimated the volume of each target plant at the beginning of the experiment by measuring height and canopy diameter. Soil organic carbon (SOC) was determined by the wet oxidation method (Nelson and Sommers, 1996) in March 2013.

2.4. Soil respiration modeling

We established two periods based on mean air temperature and precipitation (Fig. S2); 1) **wet period**, from October to March, with mild temperatures that included most of the rainy season; and 2) **dry period**, from April to September, predominantly dry and warm.

We considered SR as a function of soil temperature (T) and soil water content (SWC) following Rey et al. (2011):

$$SR = SR(T) \times SR(SWC) \tag{1}$$

We first analyzed the effects of soil temperature on annual SR (Eq. (2)). We used daily mean SR rate and daily mean soil temperature for the different treatments (control, increased, decreased) and species (n = 12). We adjusted the relationship between temperature, plant species and SR for the whole period following a Gaussian distribution (Bauer et al., 2008; O'Connell, 1990), to have a function able to explain the annual SR as a whole:

$$SR(T) = \sum_{i=1}^{N} \left(\alpha e^{-\left(\frac{(T-\beta)^2}{\gamma^2} \right)} \right) \tag{2}$$

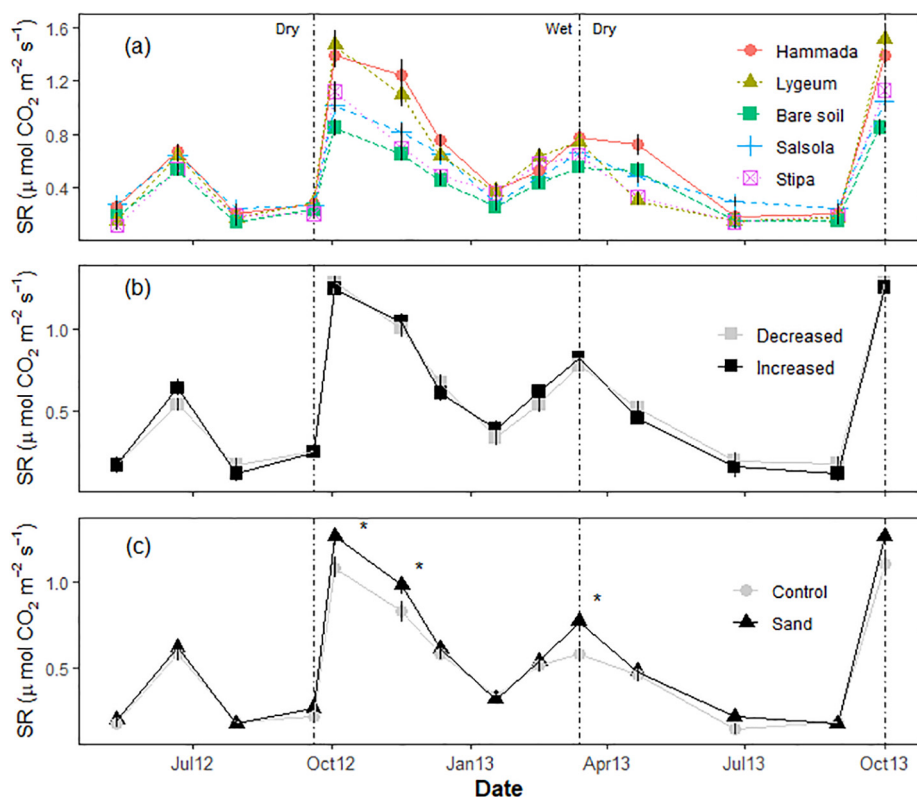where SR(T) is soil respiration as a function of temperature (T) resulting

Fig. 1. Soil respiration (SR) rate under the canopy of the four target plant species and in bare soil along 20 months of measurements (a), in two soil temperature treatments (decreased and increased temperature) (b), and in control and sand addition treatments (i.e., the effect of applying coarse sand to the soil) (c). Asterisks in the last panel indicate significant differences in SR (p < 0.05) between the control and the sand addition treatment. Vertical dotted line represents the transition between our defined dry and wet periods. Symbols and bars represent mean values ± 1 SE; n = 12.
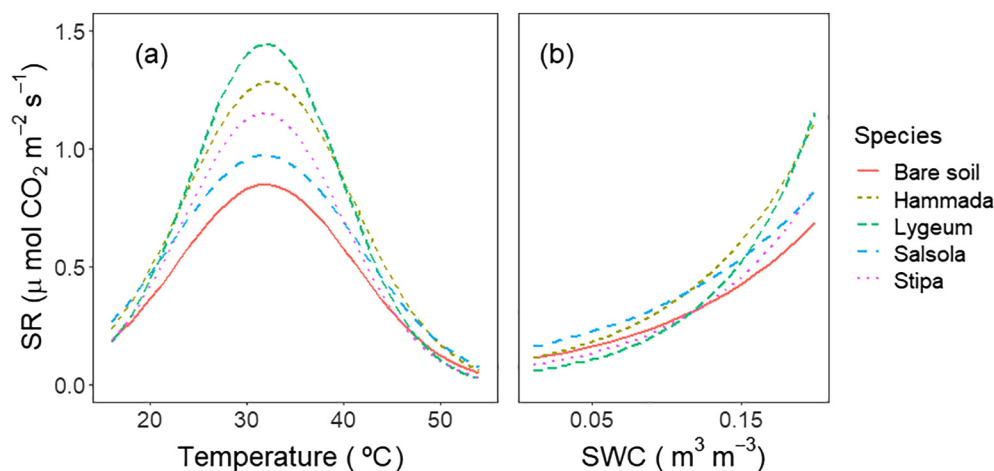

Fig. 2. Soil respiration (SR) rate as a function of soil temperature (a) (from Eq. (2) in the text) modeled across different species and bare soil. We used daily mean values from field measurements in each temperature treatment level (increased and decreased) and the control and for each species (four plant species and bare soil) at each sampling date. SR as a function of volumetric soil water content (SWC) (Eq. (3)) (b). In this case, soil respiration data were those obtained from each plant species and sampling date but only in control plots.

from the contribution of each species; α is the maximum soil respiration, β is temperature at maximum soil respiration and γ is the fitted parameter from the curve, for each species and bare soil (i to N). We present results of these models in Fig. 2a.

We calculated SR as a function of soil moisture for the whole period, using SWC data in bare soil (n = 3) at the time of SR measurements (10:00–16:00 GMT). For soil moisture we used only control plots because we were unable to tease apart the effects of sand application on soil moisture. We fitted SR as a function of SWC considering an exponential curve (Bauer et al., 2008; Moyano et al., 2013; Fig. S3):

$$SR(SWC) = \sum_{i=1}^{N} \left(\sigma \ e^{\lambda swc} \right) \quad (3)$$

where SR(SWC) is soil respiration as a function of soil moisture; SWC is soil volumetric water content (m^3 m^{-3}) and σ and λ are the fitted parameters. Curve fitting was done for each species and bare soil (i to N). We present results of these models in Fig. 2b.

Finally, and according to Eq. (1), we calculated SR as a function of

both temperature and SWC in control plots following the equation:

$$SR = \sum_{i=1}^{N} \left(\alpha e^{-\left(\frac{(T-\beta)^2}{\gamma^2} \right)} \right) (\sigma \ e^{\lambda swc}) \quad (4)$$

To test how plant species improved our prediction of SR dynamics, we fitted Eqs. (2), (3) and (4) to our data. First we used equations for the whole SR dataset as if there were no different plant species (i.e., N = 1). Second, we fitted Eqs. (2), (3) and (4) for each plant species and bare soil separately. The value obtained was the sum of the individual response of each of the four plant species and bare soil divided by the total number of cases (total cases, N = 5). We then performed simple linear regression analyses between predicted values, obtained with above equations, and observed values measured in the field. We considered the r^2 value as a measure of the predictive value of the model (Kuppel et al., 2018). To show the deviance of observed and predicted values we made scatter plots that included the line of fit (linear

regression) and the hypothetical best fit (i.e., the y = x line). These results are shown in Fig. 4. SR models as a function of temperature excluded three months from the data set (October 2012, December 2012 and June 2013, Appendix 1). Data from December 2012 and October 2013 were neither used when modelling SR as a function of SWC (Appendix 2); in the latter month the SWC datalogger failed.

We modeled SR with the fitted parameters from each equation, as a function of temperature (Eq. (2)), SWC (Eq. (3)) and both factors (temperature and SWC, Eq. (4)), using field data. We built separated models for each plant species and bare soil, summed the resulting values and divided them by the number of cases (N = 5). These results are shown in Fig. 4.

2.5. Statistical analyses beyond SR modelling

Differences in soil temperature, soil water content, and SR among plant species were analyzed using general linear models (GLM) in a complete factorial design that included repeated-measures (the repeated measured unit being each PVC collar). We first checked the assumptions of normality and homoscedasticity for all variables. To test solely for the effect of adding sand (i.e., excluding the temperature effect), we performed an analysis considering sand addition as fixed factor with two levels, with and without, and used soil temperature as covariate. To test only the effect of plant species (5 levels; 4 plant species and bare soil) and temperature manipulations on SR, we performed a second GLM excluding the control treatment with no sand (i.e., we only included two levels of temperature treatment, both with sand added). Species, temperature treatment, time (of measurement) and their statistical interactions were considered fixed factors. Means were compared using the LSD Fisher post-hoc test (p < 0.05).

In GLMs we used the glm function in R (R-Core Team, 2017) in the InfoStat statistical package (Di Rienzo et al., 2018). All other statistical analyses were performed using R (version 3.4.3, R-Core Team, 2017). Results throughout the text and figures are mean ± 1 SE.

3. Results

3.1. Soil respiration under plant species and experimental treatments

Plant species differed in their effects on SR over time (Table 1, Fig. 1a) and, overall, SR was higher in the wet than in the dry period (0.75 ± 0.01 vs 0.35 ± 0.01 μmol CO_2 m^{-2} s^{-1}, respectively). SR rates were unrelated to plant functional type, since soils under the shrub *Hammada* and the tussock grass *Lygeum* showed the highest SR rates. Thus, SR rates for the whole period were highest under *Hammada* (0.64 ± 0.02 μmol CO_2 m^{-2} s^{-1}) and *Lygeum* (0.60 ± 0.02 μmol CO_2 m^{-2} s^{-1}), followed by soils under *Salsola* (0.53 ± 0.01 μmol CO_2 m^{-2} s^{-1}) and *Stipa* (0.48 ± 0.01 μmol CO_2 m^{-2} s^{-1}), all significantly above bare soil SR rates (0.42 ± 0.01 μmol CO_2 m^{-2} s^{-1}; Fig. S4). If we compare dry and wet period, we see that SR under *Hammada* was the highest all along the measuring period, while SR under *Lygeum* was high only during the wet period (0.85 ± 0.03 μmol CO_2 m^{-2} s^{-1}), remaining low during the dry period (0.37 ± 0.03 μmol CO_2 m^{-2} s^{-1}). Soils under *Stipa* and *Salsola* had overall low respiration rates, with *Stipa* showing very low rates in the dry period (0.31 ± 0.03 μmol CO_2 m^{-2} s^{-1}). SR rate of bare soil remained the lowest for most of the year (0.29 ± 0.03 μmol CO_2 m^{-2} s^{-1}), except in the dry period where in one occasion (April 2013) it was higher than SR below both grass species (Fig. 1). There were no differences in SR between temperature treatments and this lack of differences remained unchanged with time (Table 1, Fig. 1b). Overall, and compared to the control treatment, the addition of sand significantly increased SR during rainy periods but not during dry periods (Table 1, Fig. 1c).

The addition of sand of two different colors on the soil surface affected soil temperature, showing a mean annual difference of 1.90 °C between black sand (23.31 ± 0.01 °C) and white sand

Table 1

Results from general linear models (GLM) with soil respiration rate as the dependent variable. In GLM_1 plant species (Species), sand application (Sand) and time were fixed factors and soil temperature was included as a covariate. In GLM_2 plant species (Species), soil temperature treatment (Temp) and time were fixed factors, and soil temperature was included as a covariate. P-values denoting significant differences across factor levels are highlighted in bold (p > 0.05).

GLM_1	df	F	p-value
Species	4	38.87	**< 0.001**
Sand	1	26.31	**< 0.001**
Time	13	135.71	**< 0.001**
Soil temperature	1	5.92	**0.0151**
Species × Sand	4	1.21	0.3064
Species × Time	52	3.90	**< 0.001**
Sand × Time	13	2.48	**0.0023**
Species × Sand × Time	52	0.87	**0.7330**

GLM_2	df	F	p-value
Species	4	27.47	**< 0.001**
Temp	1	0.02	0.8980
Time	13	103.71	**< 0.001**
Soil temperature	1	7.25	**0.0072**
Species × Temp	4	2.36	0.0512
Species × Time	52	2.70	**< 0.001**
Temp × Time	13	1.48	0.1176
Species × Temp × Time	52	0.75	0.9095

(21.42 ± 0.01 °C) treatments. Canopy size had no effect on the amount of SOC but affected soil temperature; the two plant species with smaller canopies (*Hammada* and *Lygeum*) had higher soil temperatures than the bigger ones (*Salsola* and *Stipa*), surprisingly even higher than bare soil (Fig. S5), and irrespective of adding or not sand to the soil. None of the species differed in SOC content and only in *Lygeum* there were differences in SOC between treatments.

3.2. Relationship between soil respiration, temperature and water content

Soil respiration under all species reached maximum SR values around 32 °C, but the magnitude of SR response was different for each plant species. SR under *Lygeum* presented the highest maximum SR rates (1.44 ± 0.07 μmol CO_2 m^{-2} s^{-1}) followed by *Hammada* (1.28 ± 0.10 μmol CO_2 m^{-2} s^{-1}), *Stipa* (1.15 ± 0.07 μmol CO_2 m^{-2} s^{-1}), *Salsola* (0.97 ± 0.08 μmol CO_2 m^{-2} s^{-1}) and bare soil (0.84 ± 0.06 μmol CO_2 m^{-2} s^{-1}) (Table 2, Fig. 2a, and additional information in Appendix 1).

Soil respiration increased exponentially as SWC increased in all understory soils and in bare soil all year round (Fig. 2b). This relationship was different between bare soil and soils under two species, *Hammada* and *Lygeum,* which released more CO_2 with increasing SWC than *Salsola* and *Stipa*. Soils under the two tussock grasses had lower SR values than bare soil under the driest conditions (Table 2, Fig. 2b, more information Appendix 2).

3.3. Seasonal soil respiration patterns

We estimated the annual rate of daytime SR under the different species and in bare soil (10:00–16:00 GMT) as a function of different abiotic factors (soil temperature, SWC and their combination). All models that include plant species identity as a parameter in the model performed better than their only abiotic-parameter counterpart (Fig. 3). However we excluded three months from the models (Appendix 1 and 2), which means that some parameters not measured other than temperature and humidity also affected the temporal SR response.

When we modeled SR using 2012 data including species identity and SWC as predictors (SWC, Fig. 4) we found greater CO_2 emissions during the wet season. It was also noticeable how this model predicted

Table 2
Mean (± 1 SE) values of α, β and γ parameters in the Gaussian curve relating soil respiration and soil temperature (Eq. (2)), and σ and λ parameters in the exponential curve relating soil respiration and SWC (Eq. (3)) in the understory of each species, in bare soil, and when accounting for all species together (All spp.). All coefficient estimations had significant curve fits (p < 0.05). Table S2 includes results from normality tests.

	Species	α	β	γ
Soil Temp	*Hammada*	1.28 ± 0.10	32.17 ± 0.74	0.12 ± 0.01
	Lygeum	1.44 ± 0.07	31.96 ± 0.45	0.13 ± 0.01
	Salsola	0.97 ± 0.08	31.80 ± 0.74	−0.10 ± 0.01
	Stipa	1.15 ± 0.07	31.70 ± 0.49	0.12 ± 0.01
	Bare soil	0.84 ± 0.06	31.92 ± 0.66	0.11 ± 0.01
	All spp.	1.15 ± 0.04	31.90 ± 0.29	−0.11 ± 0.01

	Species	σ	λ	–
SWC	*Hammada*	0.10 ± 0.03	12.16 ± 1.90	
	Lygeum	0.04 ± 0.02	15.97 ± 2.29	
	Salsola	0.14 ± 0.04	8.69 ± 1.92	
	Stipa	0.07 ± 0.02	12.29 ± 1.57	
	Bare soil	0.10 ± 0.03	9.66 ± 1.73	
	All spp.	0.08 ± 0.01	11.81 ± 0.98	

SR responses to rain events, especially during the dry season. The model that included only plant species identity and temperature as predictors (Temperature, Fig. 4) overestimated SR in the dry period while underestimated SR during the wet period. The model with temperature, SWC and plant species as predictors (T_SWC, Fig. 4) improved SR estimations compared to only Temperature; T_SWC model reduced the overestimation of SR in the dry period compared to the model that included only temperature and plant species identity. However, T_SWC model did not improve predictions compared to SWC model.

4. Discussion

Our data evidence how the inclusion of plant species identity contributes to improve predictions of SR responses to soil temperature or SWC in this arid and patchy environment, and reduced uncertainty predicting seasonal patterns of CO_2 emissions. In addition, both temperature and humidity were better predictors of SR when considered separately than together.

4.1. Effects of soil temperature and moisture on soil respiration

Predictions on SR dynamics modelled as a function of SWC alone were more accurate than those taking into account soil temperature alone. In arid and semi-arid environments water is a limiting factor that drives SR (i.e., Almagro et al., 2009; Delgado-Baquerizo et al., 2013). In our system we can consider soil moisture as a limiting factor along the whole period of measurements, since our data always moved in the positive exponential part of the thresholding model suggested by Moyano et al. (2013). The application of sand layer could increase
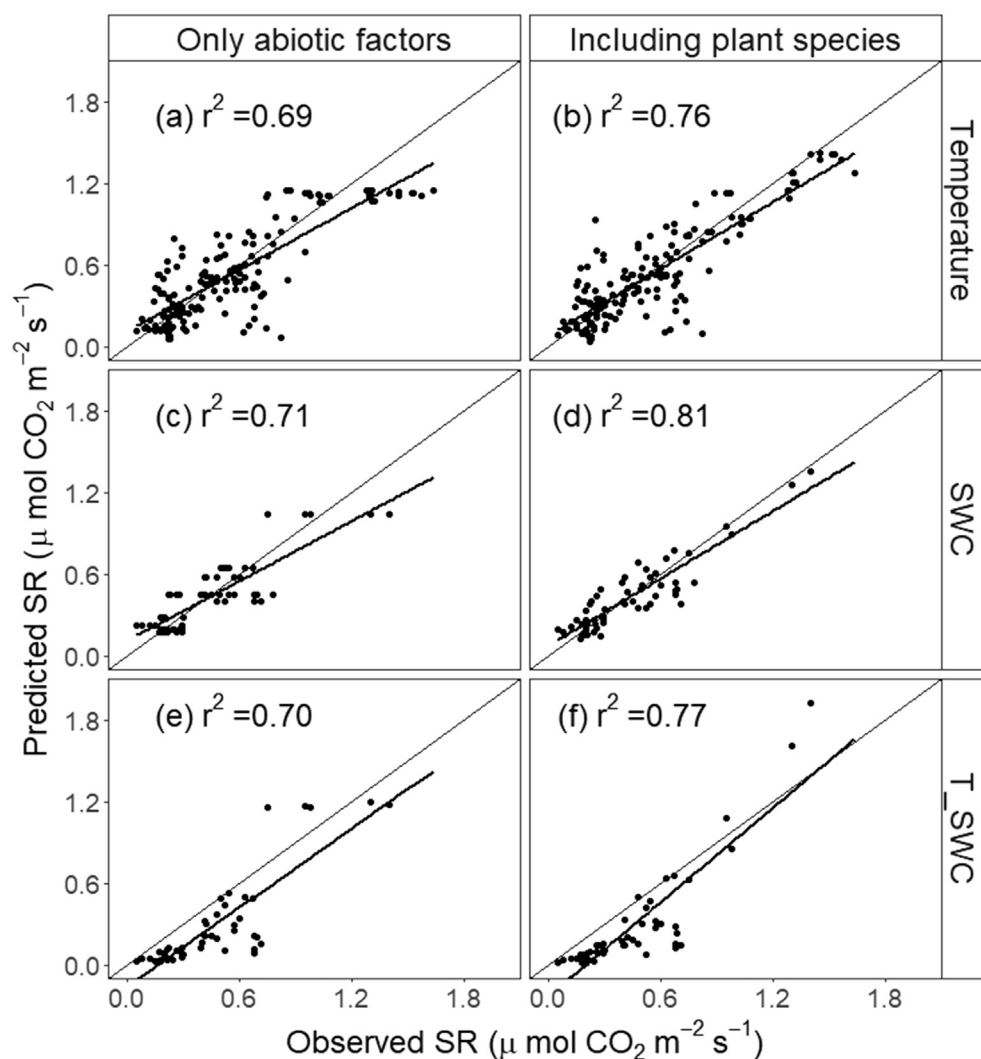

Fig. 3. Predicted (modelled) versus observed (measured in the field) SR values as a function of temperature (a) and including temperature and plant species (b); as a function of SWC (c) and including SWC and plant species (d); as a function of temperature and SWC (e), and including temperature, SWC and plant species (f). (a) and (b) refer to Eq. (2); (c) and (d) refer to Eq. (3); (e) and (f) refer to Eq. (4), all Eqs. in the main text. The r^2 values are results from each linear regression of observed versus predicted values. For temperature we used data from each temperature treatment level (increased and decreased) and the control and for each species (four plant species and bare soil) at each sampling date modeled (3 treatments × 5 species × 11 months, N = 165). For SWC and T_SWC we used data from each species and sampling date modeled in control plots (1 treatment (control) × 5 species × 12 months, N = 60).
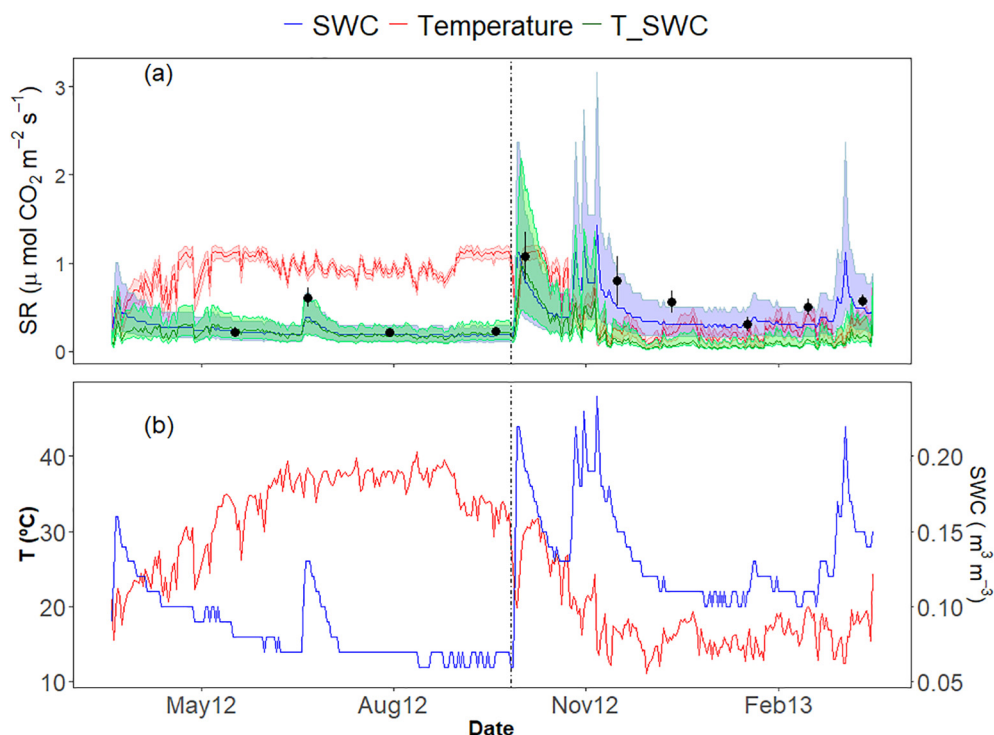
Fig. 4. Modeled soil respiration (SR) rates between March 2012 and March 2013 based on measurements between 10:00 and 16:00 GMT for a period of 3–4 consecutive days each month (a). Modeled values were obtained from the interpolation of α, β, γ from Eq. (2) (soil temperature, red line), the interpolation of α, β, from Eq. (3) (soil water content, SWC, blue line), and their interaction (Eq. (4), T_SWC, green line) for the whole period. Observed SR values are represented as mean values for each field campaign (dots with error bars). Panel b shows daily mean soil temperature and SWC at 5 cm depth in bare soil (10:00–16:00 GMT). Vertical dotted line in both panels represents the transition between our defined dry and wet periods. Lines and areas represent mean values ± 1 SE. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

water accumulation in the upper soil layer and/or reduce water evaporation, increasing SR in sand treatments during wetter periods; however, we did not find differences in SWC at 5 cm deep between sand treatments in the control plots. By contrast, temperature was more accurate predicting SR when soil water was above 0.1 m^3 m^{-3}. Almagro et al. (2009) found a similar behavior of SR in other Mediterranean ecosystems with SR being controlled by temperature when SWC was above the 0.1 m^3 m^{-3} threshold. A recent study also concluded that soil temperature was the best factor explaining SR in three Mediterranean ecosystems (González-Ubierna and Lai, 2019). In our case, the relationship between mean daily temperature and SR was well explained by a Gaussian curve, and was positive under a wide range of soil water levels except during droughts and dry spells, as also suggested by Rey et al. (2011).

There were differences in SR related to mean soil temperature. However, SR rates were similar in both temperature treatments irrespective of the period of measurement, suggesting a thermal acclimation to warming treatments (mean difference in soil temperature was ca. 2 °C). Some studies in semiarid environments have reported absence of thermal acclimation on total SR responses to temperature (De Dato et al., 2010; Wang et al., 2014) in the short term, while others studies report than the absence of SR response to temperature is linked to autotrophic respiration (Wang et al., 2014). On the contrary, Carey et al. (2016) found differences in SR between control and warmed plots in deserts and boreal environments. In Mediterranean ecosystems extended warming decreases SR rates and their dependency on water availability (Chang et al., 2014; Rey et al., 2011). However, microbial acclimation processes are usually noticeable only in long-lasting experiments (Romero-Olivares et al., 2017) and might have not played an important role in our study. The response of SR to temperature increases can be ameliorated by microbial acclimation to prolonged warming through species turnover (Luo et al., 2014) or by depleting labile C, which also attenuate the response of SR to temperature increases (Bradford et al., 2008; Romero-Olivares et al., 2017).

4.2. Plant identity affects soil respiration responses to soil temperature and water content

Including plant species in our models reduced uncertainties in the prediction of SR responses to temperature and soil water content. The model that improved the most with the inclusion of plant species as a predictor was the one that modelled SR as a function of SWC; however temperature was a better predictor of SR during the wet period than during the dry period. That is, when water content is not limiting, the importance of temperature as predictor of SR increases (Almagro et al., 2009). All species reported similar optimum temperature around 32 °C, meaning that, although the rate of SR differed under each plant species, soils under every species seemed to share similar metabolic adaptation to temperature. Thus, the differences in SR fluxes found among plant species should be explained by factors other than optimum temperature. Optimum temperature in our site was higher than that reported by Maestre and Cortina (2003), which was in the range of 14–18 °C or Rey et al. (2011) that reported optimum temperatures of 20 °C in environments similar to the one studied here, and lower than in other drylands that found optimum temperatures close to 45 °C (Hamdi et al., 2011; Richardson et al., 2012).

Plant identity also affected seasonal patterns of SR in our field site, as reported elsewhere (Chang et al., 2014). Such effects could be driven by plant effects on understory soil, as individuals produce litter with quite different qualities (Aerts and Chapin, 1999), and shed a huge amount of secondary compounds via root exudates (Bais et al., 2002), that are consumed by soil heterotrophs. In our case, the lack of differences in SOC between species did not explain differences in SR. The fact that we only had one measurement during the growing season limited our interpretation, and more effort should be done it this direction. Root activity and biomass may also differ across species (Han et al., 2014), and they host mycorrhizal symbionts with differing activity and biomass (Heinemeyer et al., 2007). Finally, plants also alter micro-environmental conditions (Moro et al., 1997), and may create 'islands of fertility' (Pugnaire et al., 2004) where soil nutrients, soil humidity and soil temperature are altered. All these changes affect soil microbial and fungal communities under the canopy (Aguilera et al., 2016; Hortal et al., 2013; Hortal et al., 2015; Martínez-García et al., 2011) resulting

in different respiration rates (Estruch et al., 2018; Maestre and Cortina, 2003; Oyonarte et al., 2012).

Plant identity can also determine soil humidity in plant understories, which in dry periods can be drier than bare patches (Oyonarte et al., 2012), and differences may depend on the strategy of different species retaining water under their canopies. For instance, some medium-to deep-rooted species in drylands can be engaged in hydraulic lift (Prieto et al., 2012), increasing sub-surface soil water availability and thus affecting SR rates; other species -and the soil activity underneath their canopies- may enter in dormancy during drought periods (Norton et al., 2016). In our study, the shrubs *Salsola* and *Hammada* maintained higher SR rates during the dry period. It is possible that their deeper root system (Martínez-García et al., 2011) had a positive effect on retaining some water near the soil surface, in contrast to tussock grasses, which have dense, more superficial root systems. Unfortunately, we had no SWC data under the different species. But, supporting our results, Oyonarte et al. (2012) reported from a plant community dominated by *Stipa tenacissima* that the CO_2 released to the atmosphere by bare soil during dry spells was higher than that released by soils under *Stipa* tussocks. In fact, our study shows that soils under *Stipa* and *Lygeum* released less CO_2 than bare soil, at least for a short period during the dry season (April 2013). Meanwhile, soils under *Salsola* occasionally equaled bare-soil rates in the dry period, and soils under *Hammada* always released more CO_2 than bare soil, irrespective of the season. We argue that some plant traits might be good predictors of plant effects on SR. Root traits appear to be important decreasing SRrate as i) woody roots contain more recalcitrant components than fine roots (Chapin, 2003), which are harder to mineralize (Zhang et al., 2013); or ii) roots with high tensile strength (like *Salsola* and *Stipa* in our system) have lower SR rates compared to roots with lower tensile strength (De Baets et al., 2008). In fact, *Salsola* and *Stipa* showed the lowest SR rates in our system, whereas *Lygeum,* a species with roots with low tensile strength, showed high SR. These data may suggest that root traits can explain SR fluxes to some extent.

4.3. Implications for CO_2 fluxes

Seasonal variations in SR in this dry ecosystem were satisfactorily predicted by our model using plant identity, soil temperature and soil moisture during almost all the period of study. Moreover, including plant identity increased the accuracy of the model compared to models where only abiotic predictors were included. As a result 24% of the variance in SR remained unexplained in the model that predicts SR as a function of soil temperature, whereas 19% of the SR variance was unexplained when predicting SR as a function of SWC. The combination of both temperature and SWC plus species identity did not reduce uncertainty (23% of variation unexplained), showing that there are still sources of uncertainty that our models could not explain. For example, SR responses to sudden water pulses (short and/or intense rains) are difficult to model, and Cueva et al. (2015) showed that these sudden changes in soil moisture across multiple vegetation types lead to errors in soil CO_2 flux estimations. Water pulses in relatively dry periods can trigger a swift liberation of labile compounds accumulated in the soil during periods of low activity, e.g., during drought (Liu et al., 2016; Meisner et al., 2015; Richardson et al., 2012), which can be up to 40% of the total C released annually in drylands (Ataka et al., 2014; López-Ballesteros et al., 2016). In our case, we were able to predict SR responses to rainfall events based on soil water content, but our models failed to predict SR during the dry period when we used only temperature or a combination of temperature and SWC.

The importance of accounting for plant identity in C emission models has been widely discussed (Cueva et al., 2015; Oyonarte et al., 2012; Reichstein et al., 2003; Rey et al., 2011), particularly in arid environments, where the patchy distribution of species with contrasting strategies can highly increase the spatial heterogeneity of SR emissions in the plant community. A first approach was to classify species by

functional groups, although, in our case differences in SR did not seem to be linked to functional groups. Plant community composition is crucial when analyzing ecosystem responses to environmental drivers, and errors in the estimation of CO_2 fluxes by previous models were partly attributed to plant patchiness (Cueva et al., 2015; Davidson et al., 2006). Previous reports tended to underestimate fluxes at low soil moisture levels (Reichstein et al., 2003), but how water is handled in a model determines its precision to mirror responses observed in natural systems (Rey et al., 2011). In plant communities of arid systems patchiness increases the difficulty in modeling metabolic processes, and the first step to improve models should be to include species identity, with the aim to further refine the output by including their spatial distribution.

5. Conclusions

Our data emphasize the importance of plant species identity in quantifying CO_2 fluxes from dryland soils to the atmosphere, and the complex interactions between plants, soil humidity, and soil temperature in driving SR in an arid patchy plant community. Heterogeneity created by plants affects soil CO_2 fluxes, and small-scale variability in SR rates could explain variability at the whole ecosystem level. Temporal responses of SR to temperature and soil water content were modulated by plant species identity, which significantly decreases uncertainty in the prediction of SR in current models. However, there is still room to improve our understanding of how different plant species affect soil C fluxes to better predict the contribution of drylands to global carbon cycles.

Authors Contribution

CE, PM and FIP designed the study with contributions of CA. CE, PM and NP performed the fieldwork. CE and CA analyzed data. CE wrote the paper with significant contributions from all co-authors.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2019.114153.

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