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Biotic and Abiotic Drivers of Topsoil Organic Carbon Concentration in Drylands Have Similar Effects at Regional and Global Scales

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ABSTRACT

Drylands contain 25% of the world's soil organic carbon (SOC), which is controlled by many factors, both abiotic and biotic. Thus, understanding how these factors control SOC concentration can help to design more sustainable land-use practices in drylands aiming to foster and preserve SOC storage, something particularly important to fight ongoing global warming. We use two independent, large-scale databases with contrasting geographic coverage (236 sites in global drylands and 185 sites in Patagonia, Argentina) to evaluate the relative importance of abiotic (precipitation, temperature and soil texture) and biotic (primary productivity) factors as drivers of SOC concentration in drylands at global and regional scales. We found that biotic and abiotic factors had similar effects on SOC concentration across regional and global scales: Maximum temperature and sand content had negative effects, while precipitation and plant productivity exerted positive effects. Our findings provide empirical evidence that increases in temperature and reductions in rainfall, as forecasted by climatic models in many drylands worldwide, promote declines in SOC both directly and indirectly via the reduction in plant productivity. This has important implications for the conservation of drylands under climate change; land management

should seek to enhance plant productivity as a tool to offset the negative impact of climate change on SOC storage and on associated ecosystem services.

INTRODUCTION

Arid, semi-arid and dry sub-humid ecosystems (drylands hereafter) cover about 45% of Earth's land surface (Prăvălie 2016) and provide habitat and ecosystem services to 38% of the global population, yet they are highly sensitive to climate change and desertification (MEA 2005; Reynolds and others 2007; Maestre and others 2012a). Climatic models for the second half of this century forecast average warming between 3.2 and 3.7 °C, widespread increases in aridity and changes in rainfall amounts and patterns in drylands worldwide (Christensen and others 2007; Huang and others 2016; Lin and others 2015). These changes will expand the global area occupied by drylands by up to 23% by 2100 (Huang and others 2016) and will have profound effects on multiple aspects of the structure and functioning of their ecosystems. These include reductions in aboveground net primary productivity and plant cover (Anadón and others 2014; Gherardi and Sala 2015), which will lead to reduced soil organic carbon (SOC) sequestration and content (Jenkinson and others 1991; Schimel and others 1994; Kirschbaum 1995). The world's dryland soils contain about 470 Pg of SOC in the top 1 m, which is about 32% of total world's SOC (Plaza and others 2018). This represents ∼ 42 times more carbon than that added into the atmosphere through anthropogenic activities, estimated at 11.2 Pg C/year in 2015 (Le Quéré and others 2016). According to Li and others (2015), SOC storage in drylands is highly sensitive to climate changes, as even small variations in rainfall and temperature can lead to increased soil respiration and CO_2 efflux (Vicca and others 2014). This could have an impact on the global atmospheric C budget because soil CO_2 efflux, on a global scale, is an order of magnitude larger than the amount of CO_2 released from burning fossil fuels and land-use change combined (Luo and Zhou 2006). In addition to storage of C as a vital ecosystem service, SOC influences the physical, chemical and biological properties of the soil and contributes to processes such as the biogeochemical cycling of several nutrients (McGill and Cole 1981) and the formation and stabilization of soil aggregates (Tisdall and Oades 1982). Therefore, SOC has been proposed as a main indicator of soil quality in drylands (Manley and others 1995, Herrick and Wander 1997) and is routinely used when monitoring land degradation and desertification processes in these areas (FAO 2011; Oliva and others 2011).

Given the potential feedbacks to climate of reductions in SOC associated with climate change (Schlesinger and Andrews 2000), the extent of drylands worldwide and the important role they play in the global C cycle, it is crucial to improve our understanding of the relative importance of biotic and abiotic factors affecting SOC concentration in these ecosystems. It is also critical that the world's dryland soils are managed efficiently and sustainably to mitigate against the potentially negative effects of changing climate (Lal 2004; Deb and others 2015). There has been significant progress in understanding controls on regional patterns of SOC, which have been derived mostly from correlative analyses across natural environmental gradients focusing on bivariate relationships between variables such as SOC and primary productivity and climatic features (Parton and others 1987; Oades 1988; Burke and others 1989; Wu and others 2003; He and others 2014). These studies have revealed that a large proportion of the variation in SOC can be accounted for by its relationship with abiotic factors such as precipitation, temperature and soil texture. However, abiotic factors covary with biotic attributes such as species richness or aboveground net primary productivity (ANPP; Ma and others 2010; Gaitán and others 2014), and it is often difficult to disentangle their independent effects. As SOC storage is largely controlled by the balance of C inputs from plant production and outputs through mineralization (Jenny 1941), biotic attributes such as ANPP are key factors controlling SOC concentration (Jobbágy and Jackson 2000). Despite the growing recognition of biotic attributes as a major driver of ecosystem functioning in drylands (Maestre and others 2012b, 2016; Jing and others 2015; Delgado-Baquerizo and others 2016), there are few studies that attempt to evaluate how biotic factors modulate the effects of climate on SOC concentration and dynamics (see, for example, Luo and others 2017 for cropping systems from Australia).

Abiotic and biotic factors work together to control SOC concentration and dynamics; therefore, correlative bivariate analyses focusing on single effects of these factors to predict SOC would lead to some interpretation errors as the observed effect of

a particular factor may be due to the combined consequences of its direct and indirect (modulated by another factor) effects on SOC (Luo and others 2017). In addition, there is some evidence showing that the main factors controlling SOC concentration differ between regions (Dai and Huang 2006; Evans and others 2011; Wang and others 2013) or are scale dependent (Qin and others 2016). To produce more reliable future predictions about SOC concentration and dynamics in drylands under climate change we must elucidate how abiotic and biotic drivers work together to directly and/or indirectly regulate SOC (Luo and others 2017), and test the scale dependency of these drivers. We aimed to do so by evaluating the relative importance of abiotic (precipitation, temperature and soil texture) and biotic (ANPP) factors as drivers of SOC concentration in drylands at regional and global scales. To do this, we used data from two large-scale and unique surveys, a global study including 236 drylands from all continents except Antarctica (''Global'' hereafter; Maestre and others 2012b; Ochoa-Hueso and others 2018) and a regional network of long-term monitoring of drylands including 185 sites in Argentinian Patagonia (''Patagonia'' hereafter; Gaitán and others 2014). Our central hypothesis is that biotic and abiotic factors play a different role in regulating SOC concentration in drylands at regional and global scales.

METHODS

Study Sites and Field Data Collection

Global

We used data from a global network of 236 dryland sites located in 19 countries from all continents except Antarctica (Ochoa-Hueso and others 2018, Figure 1). All the sites were surveyed between February 2006 and November 2013 according to a standardized sampling protocol (see Maestre and others 2012b for details). At each site, four parallel 30-m transects, spaced 8 m apart and oriented downslope, were established. The cover of perennial vegetation was measured in each transect using the line-intercept method (Tongway and Hindley 2004). Using a stratified sampling design, we sampled the top 7.5 cm of the soil from up to three different microsites per site, depending on the dominant growth forms present. These microsites always included a location with bare soil (that is, devoid of vascular plants), as well as microsites under woody (trees or shrubs) and/or under grassy patches. Five samples were collected from each microsite, yielding between 10 and 15 samples per site. After field collection, soil samples were taken to the laboratory, where they were air-dried, sieved (with 2-mm mesh) and stored awaiting laboratory analyses. Soil organic carbon was determined by colorimetry after oxidation with a mixture of potassium dichromate and sulfuric acid (Anderson and Ingramm 1993). Soil texture was quantified using a modified version of the pipette method (Kettler and others 2001). This is a simple and rapid quantitative method in which particles are dispersed using 3% hexametaphosphate ($(NaPO3)n$), and then a combination of sieving and sedimentation is used to determine the grain size distribution. The data obtained with this approach and with the pipette method are highly correlated (Kettler and others 2001).

Patagonia

We used a subset of 185 sites from the more than 300 sites comprising the MARAS (Spanish acronym for ''Environmental Monitoring for Arid and Semi-Arid Regions'') network (Gaitán and others 2014) for which we were able to obtain soil data (Figure 1). All the sites were surveyed between February 2007 and February 2013. At each site, three parallel 50-m transects, spaced 6.5 m apart and oriented downslope, were established. The cover of perennial vegetation was measured in one of these transects using the line-intercept method (Tongway and Hindley 2004). Soil samples (0–10 cm) were collected and stored using the same procedure described above. Soil organic carbon and texture were determined by the Walkley–Black (Nelson and Sommers 1996) and pipette (Gee and Or 2002) methods, respectively.

Productivity and Climate

We used mean annual NDVI (NDVImean hereafter) as a surrogate of ANPP in both datasets. Several studies have shown that mean NDVI is a good estimator of ANPP (Tucker and others 1983; Prince 1991; Paruelo and others 1997). We used Google Earth Engine (https://earthengine.google.com) and extracted the mean value of NDVI for each site for the period from May 1, 2007, to April 30, 2012, from the collection LANDSAT/LT05/C01/T1_SR. This collection is the atmospherically corrected surface reflectance dataset from the Landsat 5 ETM sensor (pixel size of 30×30 m). Data on mean annual precipitation (MAP) and mean temperature maxima (T_{max}) for each site were obtained using the Worldclim global database (http://www.worldclim.org/, Hijmans and others 2005).
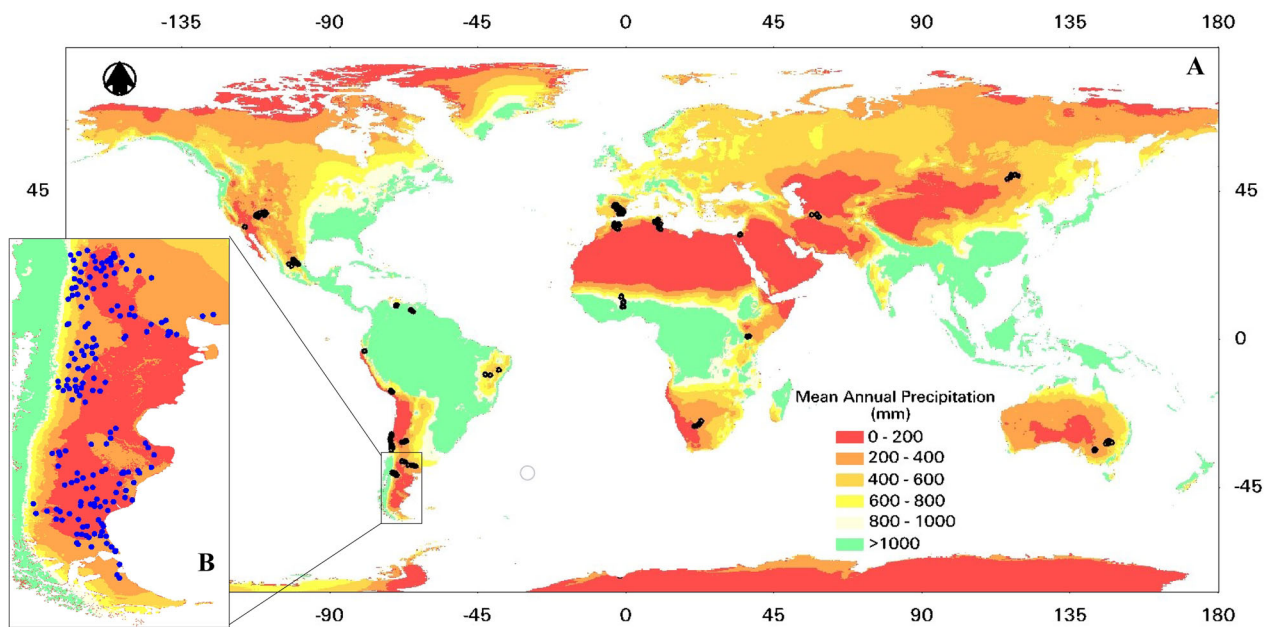
Figure 1. Location of the sampling sites in the Global (dots in **A**) and Patagonia (dots in **B**) datasets. Precipitation data from Worldclim global database (http://www.worldclim.org/, Hijmans and others 2005).

Data Analysis

Soil data obtained in bare soil and vegetated patches were scaled up to obtain site-level estimates following the equation:

$$\text{Soil}_{\text{site}} = \left(\text{Soil}_{\text{bare}} \times \%\text{BSC} \times 100^{-1}\right)$$
$$+ \left(\text{Soil}_{\text{woody}} \times \%\text{WC} \times 100^{-1}\right)$$
$$+ \left(\text{Soil}_{\text{grass}} \times \%\text{GC} \times 100^{-1}\right)$$

where $\text{Soil}_{\text{site}}$, $\text{Soil}_{\text{bare}}$, $\text{Soil}_{\text{woody}}$ and $\text{Soil}_{\text{grass}}$ are the content of a given soil variable (SOC, clay, silt or sand, in %) for the whole site, bare soil patches, woody vegetation patches and grass vegetation patches, respectively. %BSC, %WC and %GC are the percentages of cover of bare soil, woody vegetation and grass vegetation at a given site, respectively. Sand content was negatively correlated with both clay and silt contents (Spearman $\rho_{\text{sand-silt}} = -0.966$ and -0.956; Spearman $\rho_{\text{sand-clay}} = -0.562$ and -0.825; in the Global and Patagonia datasets, respectively; $P < 0.001$ in all cases). Thus, we selected sand content for further analyses, as this variable is known to play a key role in controlling water availability, community structure and biogeochemical processes in drylands (Mills and others 2009).

We used structural equation modeling (SEM, Grace 2006) to evaluate the relative importance and direct/indirect effects of climatic variables and NDVImean as drivers of variations in SOC concentration. The first step in SEM requires estab-

lishing an a priori model based on the known effects and relationships among the drivers of SOC (Supplementary Material Figure S1). We tested the fit of this model to our data using the Chi-square test (χ^2; the model has a good fit when $\chi^2 \sim \leq 2$ and P is high [typically > 0.05]), the root-mean-square error of approximation (RMSEA; the model has a good fit when RMSEA is $\sim \leq 0.05$]) and the normed fit index (NIF; the model has a good fit when NIF is $\sim > 0.90$). Path coefficient estimates were obtained using the maximum likelihood estimation technique; they are equivalent to standardized partial regression coefficients and are interpreted as relative effects of one variable upon another (Grace 2006).

To account for potential effects caused by the spatial structure of the data, we tested the spatial autocorrelation in our data by conducting a semivariogram analysis of the residuals of the SEM models. As can be shown in these semivariograms (Supplementary Material Figure R1), we did not find any relationship between the semivariance explained and the distance between sites. This result indicates the absence of spatial autocorrelation in the residuals and, therefore, suggests that spatial autocorrelation is not an issue in our datasets.

All analyses were done independently for the Global and Patagonia datasets using AMOS 18.0 (SPSS Inc., Chicago, IL, USA) for SEM analyses and GS$^+$ version 9 (Gamma Design Software) for autocorrelation analyses. The data reported in this

article have been deposited in figshare (Gaitán and others 2018).

RESULTS

The two datasets span a broad range of climatic, soil and NDVImean conditions, although the range of variation was greater in the Global than in the Patagonia datasets (Table 1). The bivariate analyses showed a positive relationship between MAP and NDVImean with SOC, and a negative relationship between SOC and sand content in both the Patagonia and Global datasets. In contrast, maximum temperature had a negative relationship with SOC in Patagonia that was not found in the Global dataset (Figure 2). Our a priori SEM model was consistent with our data in both cases, as indicated by the goodness-of-fit statistics (Figure 3). The model explained about 60% and about 75% of the variation in SOC in the Global and Patagonia datasets, respectively. Additionally, our SEM models explained about 45% and about 25% of the variation found in NDVImean in the Global and Patagonia datasets, respectively.

In both datasets, maximum temperature and sand content had negative effects on SOC, while ANPP and precipitation had a positive effect on this variable (Figure 4C). The most important factor controlling SOC was sand content and NDVImean in the Global and Patagonia datasets, respectively (Figure 4C). In both datasets, the negative total effect of sand content was mainly direct (about 90%), and the rest was indirect and mediated by its negative relationship with plant productivity. By contrast, only 10–20% of the positive total effect of precipitation was direct; the rest was indirect and mediated by its positive relationship with plant productivity. In Patagonia, the total negative effect of maximum temperature on SOC was half direct and half indirect (mediated by the negative rela-tionship between temperature and plant productivity), while in the Global dataset maximum temperature had a negative effect on SOC which was 100% direct (Figure 3A, B and Figure 4A–C).

DISCUSSION

In this study we applied a SEM approach and an a priori model based on sound theory and previous findings from two large-scale and unique observational datasets collected at regional and global scales in drylands. By doing so, we were able to separate the direct and indirect (via plant productivity) effects of climate and soil texture on SOC concentration. These drivers explained a high portion of the variability in SOC concentration (~ 75% in Patagonia and ~ 60% in Global) and, contrary to our hypothesis, had very similar effects on SOC at regional and global scales: Maximum temperature and the content of sand had negative effects on SOC, while precipitation and plant productivity exerted positive effects on this variable. Our findings provide new insights into how climate, soil texture and plant productivity control SOC in drylands.

Our results are consistent with previous studies showing that, in climatically similar regions, relationships between SOC and its environmental controls are similar regardless of the evolutionary history of the region (Paruelo and others 1998). The amount of SOC results from the balance of C inputs from primary productivity and the return of C to the atmosphere through mineralization of organic matter (Jenny 1941). Water availability largely controls ecosystem processes in drylands, affecting carbon fixation and decomposition (Whitford 2002). We found a positive relationship between mean annual precipitation and NDVImean (a surrogate of aboveground net primary productivity), as found in previous studies across

Table 1. Mean, Standard Deviation, Minimum and Maximum for Mean Annual Precipitation (MAP), Mean Annual Temperature Maxima (T_{max}), Soil Sand Content (SAND), Mean Annual of the Normalized Difference Vegetation Index (NDVImean) and Soil Organic Carbon (SOC) for Global (G) and Patagonia (P) Datasets

Variable	Mean		SD		Minimum		Maximum	
	G	P	G	P	G	P	G	P
MAP (mm year^{-1})	425.40	232.80	238.80	110.30	66.00	138.00	1219.0	801.00
T_{max} (°C)	22.40	15.40	5.40	3.30	4.90	9.40	34.90	23.00
SAND (%)	65.00	71.80	18.10	15.00	6.90	13.40	98.40	97.00
NDVImean (unitless)	6.88	5.25	2.64	1.91	1.58	2.33	14.57	12.87
SOC (%)	1.54	1.03	1.05	0.87	0.10	0.09	5.40	4.82

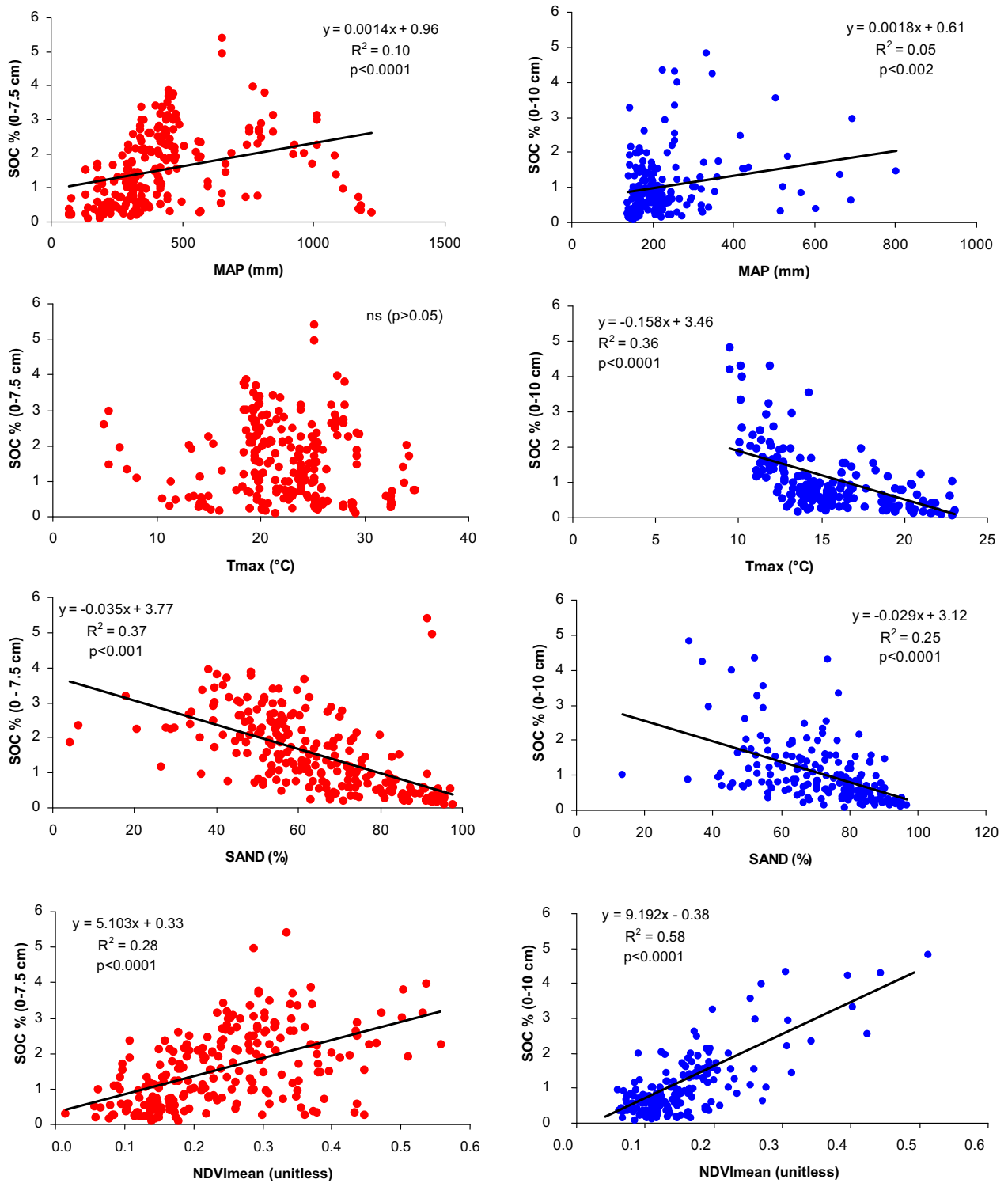*N = 236 and 185 in Global and Patagonia datasets, respectively.*

Figure 2. Bivariate relationships between abiotic (*MAP* mean annual precipitation, T_{max} mean maximum temperature and *SAND* soil sand content) and biotic (*NDVImean* mean annual of the normalized difference vegetation index) factors with topsoil organic carbon concentration (SOC) in the Global (right panel) and Patagonia (left panel) datasets.

regional and global scales (Sala and others 1988; Paruelo and others 1999; Bai and others 2008). Mineralization of organic matter also increases

with increasing soil moisture in drylands (Amundson and others 1989; Raich and Schlesinger 1992; Conant and others 2000); however,
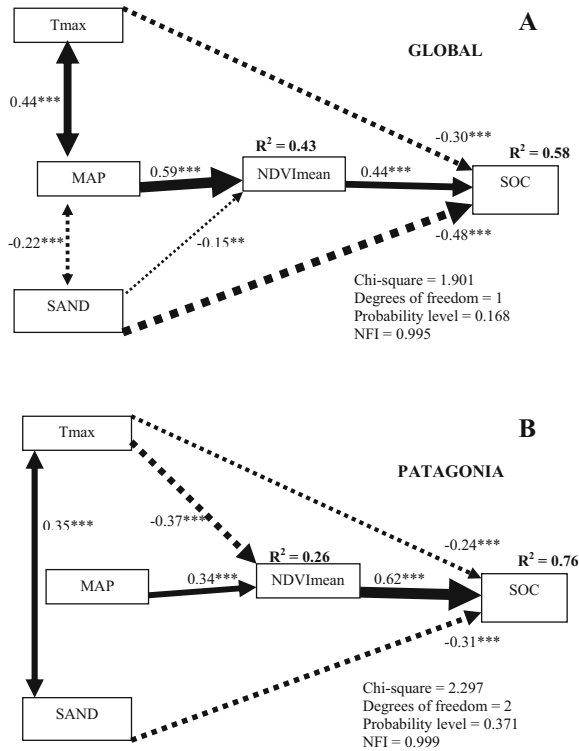
Figure 3. Structural equation models for soil organic carbon (SOC) from the Global (A) and Patagonia (B) datasets. Single-headed arrows indicate a hypothesized causal influence of one variable upon another. Double-headed arrows indicate correlation without causal relationship. The numbers adjacent to arrows are path coefficients; they show the strengths of the effect. The widths of the arrows are proportional to the path coefficients. Full (dotted) arrows indicate positive (negative) relationships. Nonsignificant ($P > 0.05$) paths were eliminated. The R^2 next to response variables indicates the proportion of variance explained. Significance levels as follows: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. Abbreviations are as in Table 1.

we did not find significant relationships between mean annual precipitation and SOC in either the Global or the Patagonia datasets. This is probably due to the fact that mineralization responds to precipitation pulses at fine temporal scales (hours or days) that are not captured by annual precipitation (Schwinning and Sala, 2004). We found a positive effect of precipitation on SOC, which was mainly indirect (mediated by NDVImean), and this result agrees with the findings from previous studies conducted across regional natural environmental gradients showing a positive relationship between precipitation and SOC (for example, Parton and others 1987; Burke and others 1989; He and others 2014).
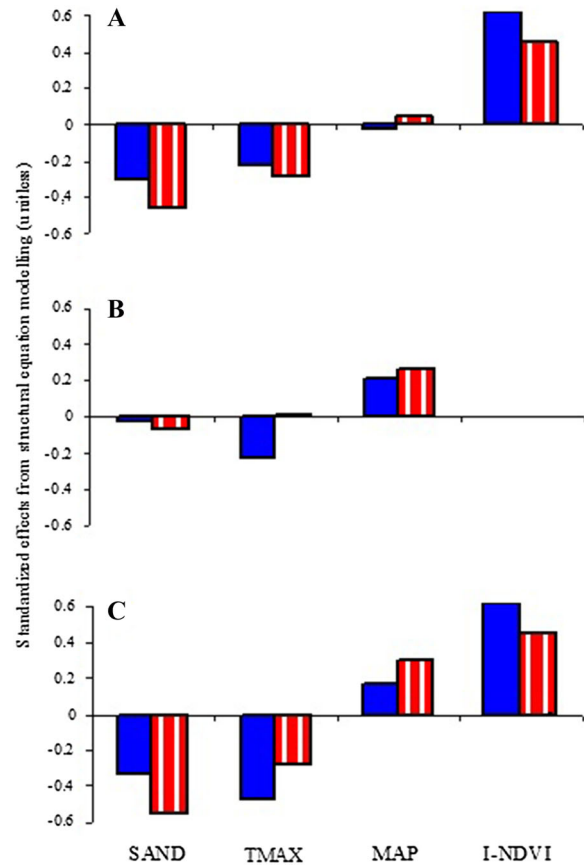

Figure 4. Standardized direct (A), indirect (B) and total effects (C) of soil sand content (SAND), mean annual temperature maxima (T_{max}), mean annual precipitation (MAP) and mean annual of the normalized difference vegetation index (NDVImean) upon soil organic carbon in the Global (solid bars) and Patagonia (striped bars) datasets.

The direct negative effect of maximum temperature on SOC observed in both datasets is supported by other studies showing soil organic matter contents decrease with increasing temperature (He and others 2014) as a result of increased mineralization rates (McDaniel and Munn 1985; Raich and Schlesinger 1992; Kirschbaum 1995). Additionally, temperature increases are associated with higher incident solar radiation and C output through photodegradation (Austin and Vivanco 2006; Almagro and others 2015). In Patagonia, we found that about 50% of the total negative effect of temperature on SOC was indirect via its effect on plant productivity. We found a negative relationship between maximum temperature and NDVImean in Patagonia, which was not found when analyzing the data from the Global dataset. This could be due to augmented vegetation drought stress as soil evaporation and temperature increase

(Epstein and others 1996) in Patagonia, as we found a positive relationship between maximum temperature and aridity (calculated as: 1 − [evapotranspiration/precipitation]; Pearson $r = 0.54$, $P < 0.001$). In contrast, in the Global dataset the maximum temperature did not seem to affect aridity conditions since these variables were uncorrelated (Pearson $r = -0.07$, $P = 0.27$).

We found a negative total effect of soil sand content on SOC, which agrees with previous regional studies conducted in drylands (Parton and others 1987; Burke and others 1989; Buschiazzo and others 1991; He and others 2014). A large proportion (∼ 85%) of this effect was direct and likely caused by the reduction in clay content as the sand fraction increases. Clay has been shown to actively protect organic matter from decomposition by adsorption and aggregation, slowing turnover and increasing SOC residence times (Paul 1984; Schimel and others 1985). About 15% of the total effect of sand content was indirect and mediated by its negative relationship with NDVImean. These effects are likely related to those of texture on soil water availability; increasing sand content decreases the water-holding capacity of soils (Rawls and others 2003; Saxton and Rawls 2006), which can have a negative effect on plant productivity in water-limited ecosystems (Huenneke and Schlesinger 2006). In addition, coarse-textured soils have a greater water infiltration capacity than fine-textured soils (Saxton and others 1986). This could favor the loss of SOC due to leaching below the root zone, albeit this was not evaluated in this study. Our surveys assessed the concentration of shallow SOC (0 to 10 cm in Patagonia and 0 to 7.5 cm in Global), and thus we were not able to explore SOC storage at depth, which is an important component of total soil C stocks. For example, the percentage of SOC in the 20 to 100 cm (relative to the first meter) averaged 67% for deserts (Jobbágy and Jackson 2000). Therefore, the assessment of SOC in deeper soil layers could be a useful next step to have a more complete knowledge of the biotic and abiotic factors controlling total soil C stocks in drylands.

Our models explained more than 60% of the variation in SOC data, a very high percentage when dealing with large-scale surveys like ours (Burke and others 1989; Yang and others 2008). Other factors not evaluated in this study and that can affect SOC may explain the percentage of unexplained variation observed. For example, grazing is an important factor affecting SOC in drylands (McSherry and Ritchie 2013). Moreover, in this study although we utilized average climate data for a 30-year period from 1970 to 2000 (Hijmans and others 2005), SOC formation processes can operate at longer timescales. Indeed, a recent study using our Global dataset has highlighted the importance of past climates as drivers of current SOC contents (Delgado-Baquerizo and others 2017), so the climate of the past may be another source of variability not explained by our models.

Several studies conducted along natural gradients have reported the effects of precipitation, temperature, soil sand content and plant productivity on SOC similar to those in this study (Parton and others 1987; Burke and others 1989; Wu and others 2003; He and others 2014). However, very few studies have simultaneously assessed how multiple biotic and abiotic attributes affect SOC concentration and have quantitatively partitioned its direct and indirect effects (Maestre and others 2016). Moving beyond bivariate analyses can enhance our mechanistic understanding of the factors controlling SOC because focusing on bivariate relationships can lead to misleading interpretation of some results when testing the effects of multiple independent variables that are not fully independent. This is exemplified with our bivariate analysis, which showed a nonsignificant relationship between the maximum temperature and SOC in the Global database. However, our SEM analysis revealed a direct negative effect of maximum temperature on SOC. Structural equation modeling is a powerful approach to study ecological processes and is being increasingly used in ecology to account for the potential effects of covarying drivers of environmental variables and to separate their direct and indirect effects (for example, Grace 2006; Grace and others 2010). Across broad natural gradients, multiple abiotic factors covary (for example, De Frenne and others 2013; Guuroh and others 2018), as was also found in our study (that is, positive correlation between precipitation and maximum temperature, and negative correlation between precipitation and sand content in Global and positive correlation between maximum temperature and sand content in Patagonia). To account for the potential effects of covarying drivers of SOC in our study, and to separate the independent effects of controlling factors on the variable of interest, we have included these correlations in our SEM. However, we acknowledge that establishing cause–effect relationships using observational data like ours is always difficult (Grace 2006). For example, we found a positive relationship between plant productivity and SOC, which is likely due to the inputs of organic C into the soil by vegetation. However, SOC also influences several physical,

chemical and biological properties of the soil (Herrick and Wander 1997) that ultimately affect plant productivity.

Our study suggests the existence of an important degree of convergence in how biotic and abiotic factors control SOC at both regional and global scales in drylands, which has important implications in the context of ongoing climate change. Our findings suggest that projected increases in temperature and aridity by the second half of this century (Huang and others 2016) will promote significant declines in SOC both directly and indirectly via the reduction in plant cover and primary productivity (Delgado-Baquerizo and others 2013; Brookshire and Weaver 2015). Although our findings should be interpreted with caution and not be directly projected into the future—climate change can promote changes in vegetation and soil processes that trigger nonlinear responses in SOC (Burkett and others 2005)—they have important implications for the conservation and management of SOC in drylands under climate change.

Actions aiming to maintain and enhance plant productivity can offset the negative impacts of climate change on ecosystem services and functions associated with SOC storage. These actions include the appropriate management of the livestock-carrying capacity—more than 65% of drylands are used for grazing of domestic herbivores (Millennium Ecosystem Assessment 2005)—the use of rotational grazing systems and the use of different aspects of plant diversity (functional vs. taxonomical) to keep rangelands in a productive state or to restore degraded rangelands (García-Palacios and others 2018).

ACKNOWLEDGEMENTS

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