Biotic and abiotic drivers of topsoil organic carbon concentration in drylands have similar effects at regional and global scales

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35   **Authors contribution**

36   J.J.G. and F.T.M. developed the original idea. J.J.G. conducted statistical analyses. F.T.M.,

37   D.E.B., G.G.B., A.J.D., G.G.M., D.F., R.T.G., A.L., V.M., A.D.T. and G.E.O. collected and

38   provided the data used. J.J.G. wrote the first draft of the article, and all authors contributed to the

39   final versions of the manuscript.

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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 preserver 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 the 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 of 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.

Key words: climate change, precipitation, temperature, soil texture, ecosystem services, aboveground net primary productivity

Introduction

Arid, semi-arid and dry-subhumid 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 °C 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 385 Pg of SOC in the top 1 m (Jobbágy and

Jackson 2000, Safriel and Adeel 2005), which is about one quarter of total world's SOC (Batjes

1996, Jobbágy and Jackson 2000). This represents ~35 times more carbon than that added into

the atmosphere through anthropogenic activities, estimated at 11.2 Pg C/y 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

95 physical, chemical and biological properties of the soil, and contributes to processes such as the

96 biogeochemical cycling of several nutrients (McGill and Cole 1981) and the formation and

97 stabilization of soil aggregates (Tisdall and Oades 1982). Therefore, SOC has been proposed as a

98 main indicator of soil quality in drylands (Manley and others 1995, Herrick and Wander 1997),

99 and is routinely used when monitoring land degradation and desertification processes in these

100 areas (FAO 2011, Oliva and others 2011).

101   Given the potential feedbacks to climate of reductions in SOC associated with climate

102 change (Schlesinger and Andrews 2000), the extent of drylands worldwide and the important

103 role they play in the global C cycle, it is crucial to improve our understanding of the relative

104 importance of biotic and abiotic factors affecting SOC concentration in these ecosystems. It is

105 also critical that the world's dryland soils are managed efficiently and sustainably to mitigate

106 against the potentially negative effects of changing climate (Lal 2004, Deb and others 2015).

107 There has been significant progress in understanding controls on regional patterns of SOC, which

108 have been derived mostly from correlative analyses across natural environmental gradients

109 focusing on bivariate relationships between variables such as SOC and primary productivity and

110 climatic features (Parton and others 1987, Oades 1988, Burke and others 1989, Wu and others

111 2003, He and others 2014). These studies have revealed that a large proportion of the variation in

112 SOC can be accounted by its relationship with abiotic factors such as precipitation, temperature

113 and soil texture. However, abiotic factors covary with biotic attributes such as species richness or

114 aboveground net primary productivity (ANPP; Ma and others 2010, Gaitán and others 2014), and

115 it is often difficult to disentangle their independent effects. As SOC storage is largely controlled

116 by the balance of C inputs from plant production and outputs through mineralization (Jenny

117 1941), biotic attributes such as ANPP are key factors controlling SOC concentration (Jobbágy

118 and Jackson 2000). Despite the growing recognition of biotic attributes as a major driver of

119 ecosystem functioning in drylands (Maestre and others 2012b, Jin and others 2015, Delgado-

120 Baquerizo and others 2016), there are few studies that attempt to evaluate how biotic factors

121 modulate the effects of climate on SOC concentration and dynamics (see for example Luo and

122 others 2017 for cropping systems from Australia). Abiotic and biotic factors work together to

123 control SOC concentration and dynamics; therefore, correlative bivariate analyses focusing on

124 single effects of these factors to predict SOC would lead to some interpretation errors as the

125 observed effect of a particular factor may be due to the combined consequences of its direct and

126 indirect (modulated by another factor) effects on SOC (Luo and others 2017). In addition, there

127 is some evidence showing that the main factors controlling SOC concentration are different

128 between regions (Dai and Huang 2006, Evans and others 2011, Wang and others 2013) or are

129 scale-dependent (Quin and others 2016). To produce more reliable future predictions about SOC

130 concentration and dynamics in drylands under climate change there is a need to elucidate how

131 abiotic and biotic drivers work together to directly and/or indirectly regulate SOC (Luo and

132 others 2017), and to test the scale dependency of these drivers. We aimed to do so by evaluating

133 the relative importance of abiotic (precipitation, temperature and soil texture) and biotic (ANPP)

134 factors as drivers of SOC concentration in drylands at the regional and global scales. To do this,

135 we utilised data from two large scale and unique surveys, a global study including 236 drylands

136 from all continents except Antarctica ("Global" hereafter; Maestre and others 2012b; Ochoa-

137 Hueso and others 2018) and a regional network of long-term monitoring drylands including 185

138 sites in Argentinian Patagonia ("Patagonia" hereafter; Gaitán and others 2014). Our central

139 hypothesis is that biotic and abiotic factors play a different role in regulating SOC concentration

140 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, Fig. 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 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 (i.e. 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 are used to determine the grain size distribution. The data obtained with this approach and with the pipette method are highly correlated (Kettler et al., 2001).

163   Patagonia. We used a subset of 185 sites from the > 300 sites comprising the MARAS (Spanish

164   acronym for "Environmental Monitoring for Arid and Semi-Arid Regions") network (Gaitán and

165   others 2014) for which we were able to obtain soil data (Fig. 1). All the sites were surveyed

166   between February 2007 and February 2013. At each site, three parallel 50 m transects, spaced 6.5

167   m apart orientated downslope, were established. The cover of perennial vegetation was measured

168   in one of these transects using the line-intercept method (Tongway and Hindley 2004). Soil

169   samples (0-10 cm) were collected and stored using the same procedure described above. Soil

170   organic carbon and texture were determined by the Walkley-Black (Nelson and Sommers 1996)

171   and pipette (Gee and Or 2002) methods, respectively.

172   **Productivity and climate**

173   We used mean annual NDVI (NDVImean hereafter) as a surrogate of ANPP in both datasets.

174   Several studies have shown that mean NDVI is a good estimator of ANPP (Tucker and others

175   1983, Prince 1991, Paruelo and others 1997). We used Google Earth Engine

176   (https://earthengine.google.com) and extracted the mean value of NDVI for each site for the

177   period 1st May 2007 to 30th April 2012 from the collection LANDSAT/LT05/C01/T1_SR. This

178   collection is the atmospherically corrected surface reflectance dataset from the Landsat 5 ETM

179   sensor (pixel size of 30 × 30 m). Data on mean annual precipitation (MAP) and mean

180   temperature maxima (Tmax) for each site were obtained using the Worldclim global database

181   (http://www.worldclim.org/, Hijmans and others 2005).

182   **Data analysis**

183   Soil data obtained in bare soil and vegetated patches were scaled up to obtain site-level estimates

184   following this equation:

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

186   where, $Soil_{site}$, $Soil_{bare}$, $Soil_{woody}$, $Soil_{grass}$ are the content of a given soil variable (SOC, clay, silt

187   or sand, in %) for the whole site, bare soil patches, woody vegetation patches and grass

188   vegetation patches, respectively. %BSC, %WC, %GC are the percentages of cover of bare soil,

189   woody vegetation and grass vegetation at a given site, respectively. Sand content was negatively

190   correlated with both clay and silt contents (Spearman $\rho_{sand-silt}$ = -0.966 and -0.956; Spearman

191    $\rho_{sand-clay}$ = -0.562 and -0.825; in the Global and Patagonia datasets, respectively; $P < 0.001$ in all

192   cases). Thus, we selected sand content for further analyses, as this variable is known to play a

193   key role in controlling water availability, community structure and biogeochemical processes in

194   drylands (Mills and others 2009).

195   We used Structural Equation Modelling (SEM, Grace 2006) to evaluate the relative

196   importance and direct/indirect effects of climatic variables and NDVImean as drivers of

197   variations in SOC concentration. The first step in SEM requires establishing an a priori model

198   based on the known effects and relationships among the drivers of SOC (Appendix I). We tested

199   the fit of this model to our data using the Chi-square test (χ^2; the model has a good fit when $\chi^2 \sim$

200   ≤ 2 and P is high [typically >0.05]), the root mean square error of approximation (RMSEA; the

201   model has a good fit when RMSEA is $\sim \leq 0.05$]) and the Normed Fit Index (NIF; the model has a

202   good fit when NIF is $\sim$ >0.90). Path coefficients estimates were obtained using the maximum

203   likelihood estimation technique; they are equivalent to standardized partial regression

204   coefficients, and are interpreted as relative effects of one variable upon another (Grace 2006).

205   To account for potential effects caused by the spatial structure of the data, we tested the

206   spatial autocorrelation in our data by conducting a semi-variogram analysis of the residuals of

207   the SEM models. As can be shown in these semi-variograms (Appendix II), we did not find any

208   relationship between the semivariance explained and the distance between sites. This result

209 indicates the absence of spatial autocorrelation in the residuals and, therefore, suggests that

210 spatial autocorrelation is not an issue in our datasets.

211   All analyses were done independently for the Global and Patagonia datasets using AMOS

212 18.0 (SPSS Inc. Chicago, IL, USA) for SEM analyses and GS^+ Version 9 (Gamma Software

213 Design) for autocorrelation analyses. The data reported in this article have been deposited in

214 figshare (Gaitán and others 2018).

215

216 **Results**

217 The two datasets span a broad range of climatic, soil and NDVImean conditions, although the

218 range of variation was greater in the Global than in the Patagonia datasets (Table 1). The

219 bivariate analysis showed a positive relationship between MAP and NDVImean with SOC, and a

220 negative relationship between SOC and sand content in both the Patagonia and Global datasets.

221 In contrast, maximum temperature had a negative relationship with SOC in Patagonia that was

222 not found in the Global dataset (Fig. 1). Our a priori SEM model was consistent with our data in

223 both cases, as indicated by the goodness-of-fit statistics (Fig. 2). The model explained ~60% and

224 ~75% of the variation in SOC in the Global and Patagonia datasets, respectively. Additionally,

225 our SEM models explained ~45% and ~25% of the variation found in NDVImean in the Global

226 and Patagonia datasets, respectively.

227   In both datasets, maximum temperature and sand content had negative effects on SOC,

228 while ANPP and precipitation had a positive effect on this variable (Fig. 3c). The most important

229 factor controlling SOC was sand content and NDVImean in the Global and Patagonia datasets,

230 respectively (Fig. 3c). In both datasets, the negative total effect of sand content was mainly direct

231 (about 90%), and the rest was indirect and mediated by its negative relationship with plant

232   productivity. By contrast, only 10-20% of the positive total effect of precipitation was direct; the

233   rest was indirect and mediated by its positive relationship with plant productivity. In Patagonia,

234   the total negative effect of maximum temperature on SOC was half direct and half indirect

235   (mediated by the negative relationship between temperature and plant productivity); while in the

236   Global dataset maximum temperature had a negative effect on SOC which was 100% direct (Fig.

237   2a,b and Fig. 3a,b,c).

238

239   **Discussion**

240   In this study we applied a SEM approach and an a priori model based on sound theory and

241   previous findings from two large-scale and unique observational datasets collected at regional

242   and global scales in drylands. By doing so, we could separate the direct and indirect (via plant

243   productivity) effects of climate and soil texture on SOC concentration. These drivers explained a

244   high portion of the variability in SOC concentration (~75% in Patagonia and ~60% in Global)

245   and, contrary to our hypothesis, had very similar effects on SOC at regional and global scales:

246   maximum temperature and the content of sand had negative effects on SOC, while precipitation

247   and plant productivity exerted positive effects on this variable. Our findings provide new insights

248   about how climate, soil texture and plant productivity control SOC in drylands.

249   Our results are consistent with previous studies that have shown, in climatically similar

250   regions, relationships between SOC and its environmental controls are similar, independent of

251   the evolutionary history of the region (Paruelo and others 1998). The amount of SOC results

252   from the balance of C inputs from primary productivity and the return of C to the atmosphere

253   through mineralization of organic matter (Jenny 1941). Water availability largely controls

254   ecosystem processes in drylands, affecting carbon fixation and decomposition (Whitford 2002).

255   We found a positive relationship between mean annual precipitation and NDVImean (a surrogate

256   of aboveground net primary productivity), as found in previous studies across regional and

257   global scales (Sala and others 1988, Paruelo and others 1999, Bai and others 2008).

258   Mineralization of organic matter also increases with increasing soil moisture in drylands

259   (Amundson and others 1989, Raich and Schlesinger 1992, Conant and others 2000); however,

260   we did not find significant relationships between mean annual precipitation and SOC in either

261   the Global or the Patagonia datasets. This is probably due to the fact that mineralization responds

262   to precipitation pulses at fine temporal scales (hours or days) that are not captured by annual

263   precipitation (Schwinning and Sala, 2004). We found a positive effect of precipitation on SOC,

264   which was mainly indirect (mediated by NDVImean), this result agrees with findings from

265   previous studies conducted across regional natural environmental gradients showing a positive

266   relationship between precipitation and SOC (e.g. Parton and others 1987, Burke and others 1989,

267   He and others 2014).

268   The direct negative effect of maximum temperature on SOC observed in both datasets is

269   supported by other studies showing soil organic matter contents decrease with increasing

270   temperature (He and others 2014) as a result of increased mineralization rates (McDaniel and

271   Munn 1985, Raich and Schlesinger 1992, Kirchbaum 1995). Additionally, temperature increases

272   are associated with higher incident solar radiation and C output through photo-degradation

273   (Austin and Vivanco 2006, Almagro and others 2015). In Patagonia, we found that about 50% of

274   the total negative effect of temperature on SOC was indirect via its effect on plant productivity.

275   We found a negative relationship between maximum temperature and NDVImean in Patagonia,

276   which was not found when analysing the data from the Global dataset. This could be due to the

277   soil evaporation and vegetation drought stress increase as temperature increases (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 Global, the maximum temperature does not seem to affect the 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 1997, Burke and others 1989, Buschiazzo and others 1991, He and others 2014). A large proportion (~85%) of this total 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 favour the loss of SOC due to leaching below the root zone but this was not evaluated in this study. SOC storage at depth 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). In this study, we evaluated the concentration of shallow SOC (0 to 10 cm in Patagonia and 0 to 7.5 cm in Global); 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.

301   Our models explained more than 60% of the variation in SOC data, a very high

302   percentage when dealing with large-scale surveys like ours (Burke and others 1989, Yang and

303   others 2008). Other factors not evaluated in this study and that can affect SOC may explain the

304   percentage of unexplained variation observed. For example, grazing is an important factor

305   affecting SOC in drylands (McSherry and Ritchie 2013). Moreover, in this study although we

306   utilized average climate data for a 30 year period from 1970 to 2000 (Fick and Hijmans 2017),

307   SOC formation processes can operate at longer time-scales. Indeed a recent study using our

308   global dataset has highlighted the importance of past climates as drivers of current SOC contents

309   (Delgado-Baquerizo and others 2017), so the climate of the past may be another source of

310   variability not explained by our models.

311   Several studies conducted along natural gradients have reported effects of precipitation,

312   temperature, soil sand content and plant productivity on SOC similar to those in this study

313   (Parton and others 1987, Burke and others 1989, Wu and others 2003, He and others 2014).

314   However, very few studies have simultaneously assessed how multiple biotic and abiotic

315   attributes affect SOC concentration and have quantitatively partitioned its direct and indirect

316   effects (Maestre et al. 2016). Moving beyond bivariate analyses can enhance our mechanistic

317   understanding of the factors controlling SOC because focusing on bivariate relationships can

318   lead to misleading interpretation of some results when testing the effects of multiple independent

319   variables that are not fully independent. This is exemplified with our bivariate analysis, which

320   showed a non-significant relationship between the maximum temperature and SOC in the Global

321   database; however, our SEM analysis revealed a direct negative effect of maximum temperature

322   on SOC. The use of SEM is a powerful approach to study ecological processes and is being

323   increasingly used in ecology to account for the potential effects of co-varying drivers of

324   environmental variables and to separate their direct and indirect effects (e.g. Grace 2006, Grace

and others 2010). Across broad natural gradients, multiple abiotic factors co-vary (e.g. De Frenne and others 2013, Guuroh et al. 2018), as was also found in our study (i.e., positive correlation between precipitation and maximum temperature, and negative 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 co-varying 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 we interpreted as being due to the input of organic matter to the soil. However, SOC influences several physical, chemical and biological properties of the soil (Herrick and Wander 1997), and could therefore affect plant productivity via different pathways.

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 of plant cover and primary productivity (Delgado-Baquerizo and others 2013, Brookshire and Weaver 2015). While 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 non-linear responses in SOC (Burkett and others 2005) - they have important implications for the conservation and management of SOC in drylands under climate change. Because more than 65% of drylands are used for grazing of domestic herbivores (Millennium Ecosystem Assessment 2005), actions aiming to maintain and enhance plant productivity can also offset the

349 negative impacts of climate change on ecosystem services and functions associated with SOC

350 storage. These actions include the appropriate management of the livestock carrying capacity, the

351 use of rotational grazing systems and the use of different aspects of plant diversity (functional vs.

352 taxonomical) to keep rangelands in a productive state or to restore degraded rangelands (García-

353 Palacios and others 2018, Guuroh et al. 2018).

354 **Acknowledgments**

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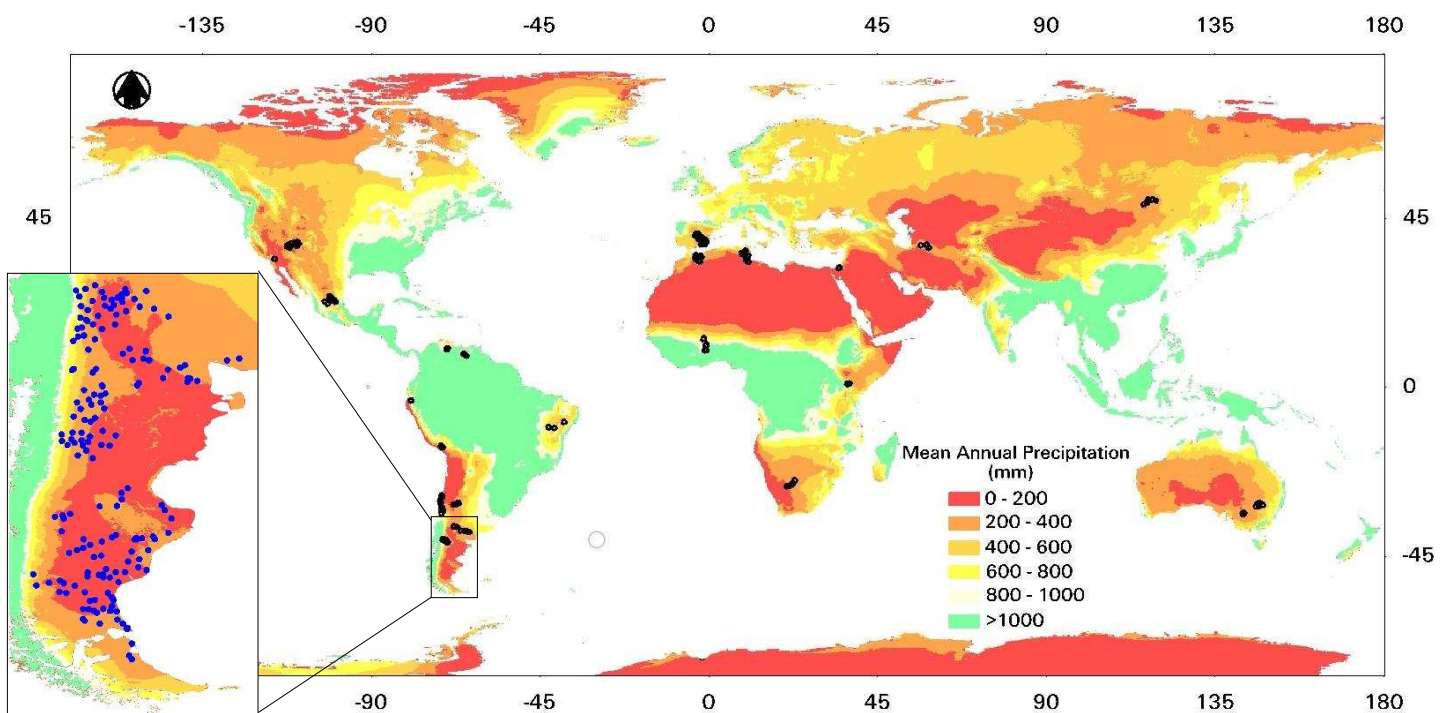
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Table 1.

Variable	Mean		Standard deviation		Minimum		Maximum	
	G	P	G	P	G	P	G	P
MAP (mm.yr^{-1})	425.40	232.80	238.80	110.30	66.00	138.00	1219.0	801.00
Tmax (°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

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Table 1. Mean, standard deviation, minimum and maximum for mean annual precipitation (MAP), mean annual temperature maxima (Tmax), 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. N = 236 and 185 in Global and Patagonia datasets, respectively.

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Mean Annual Precipitation
(mm)

0 - 200
200 - 400
400 - 600
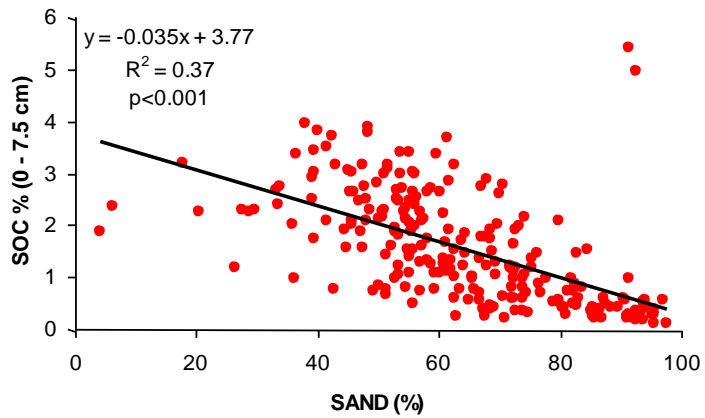600 - 800
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677 **Figure 1.**

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688   **Figure 2.**

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Tmax

GLOBAL

0.44***

MAP   0.59***   NDVImean   0.44***   SOC

R² = 0.43   R² = 0.58

-0.30***

-0.22***   -0.15**   -0.48***

SAND

Chi-square = 1.901
Degrees of freedom = 1
Probability level = 0.168
NFI = 0.995

Tmax

PATAGONIA

0.35***   -0.37***

MAP   0.34***   NDVImean   0.62***   SOC

R² = 0.26   R² = 0.76

-0.24***

-0.31***

SAND

Chi-square = 2.297
Degrees of freedom = 2
Probability level = 0.371
NFI = 0.999
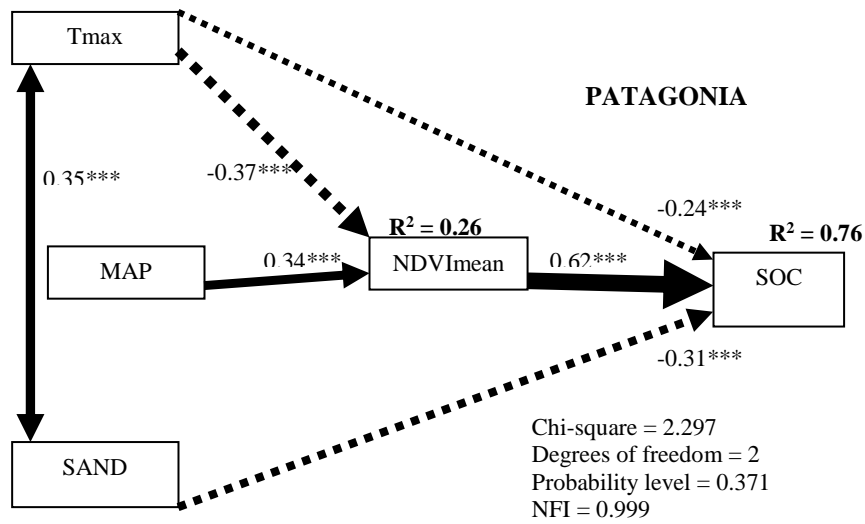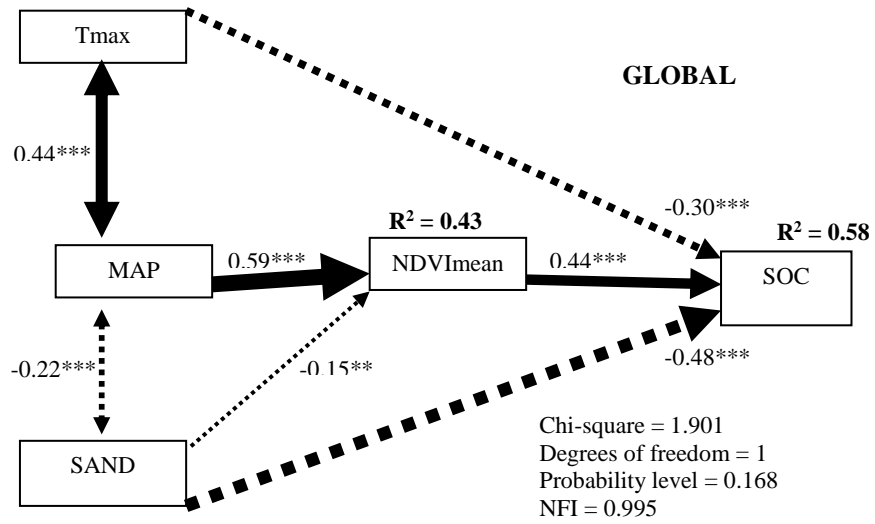
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692   **Figure 3.**

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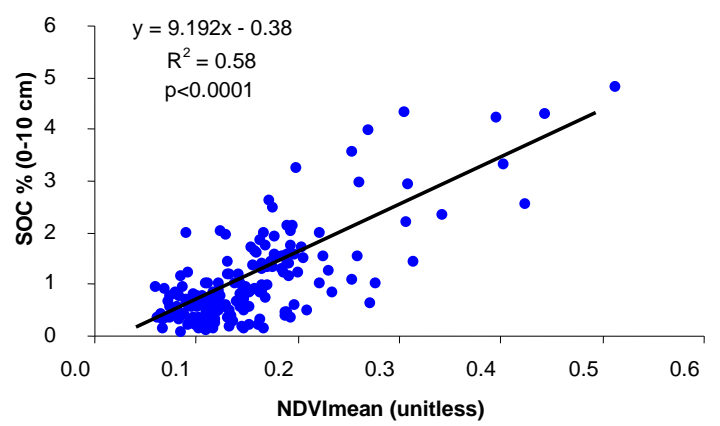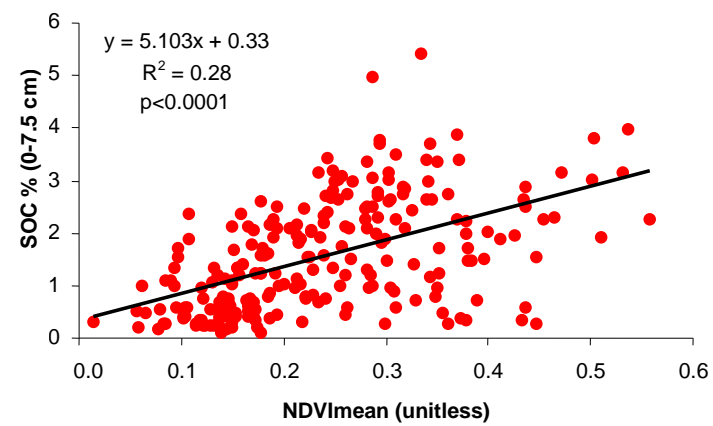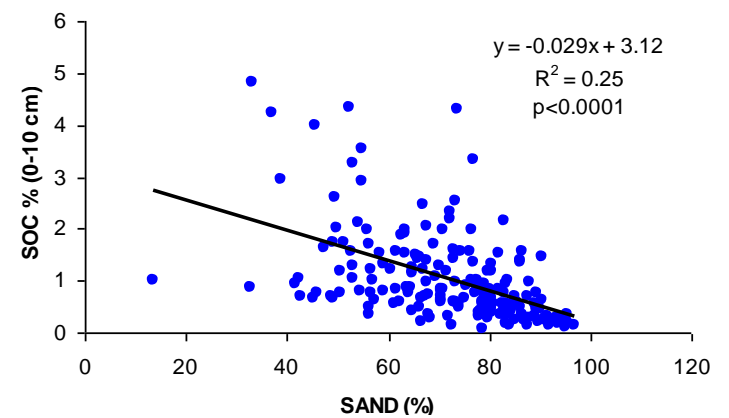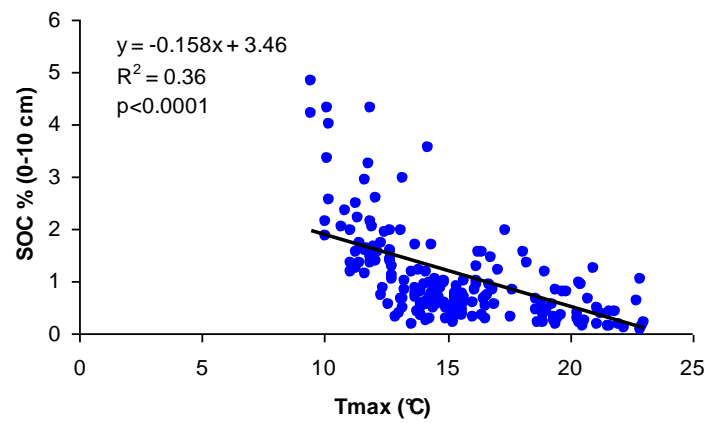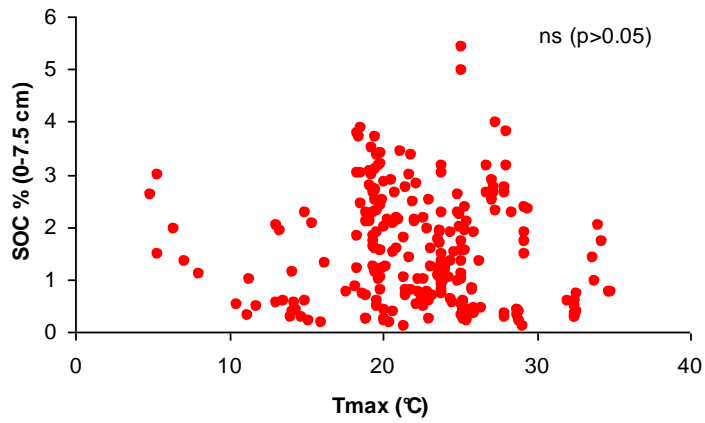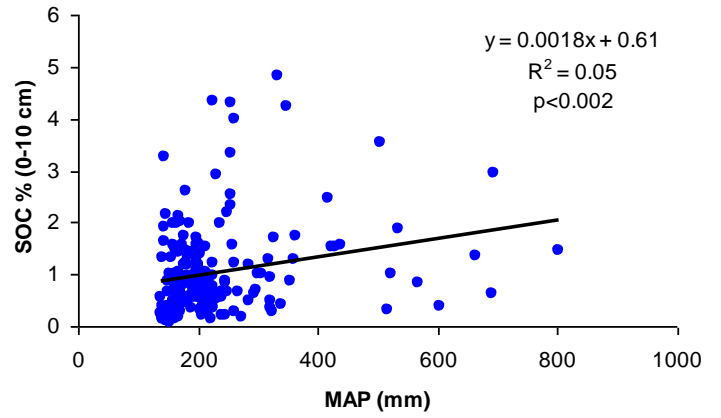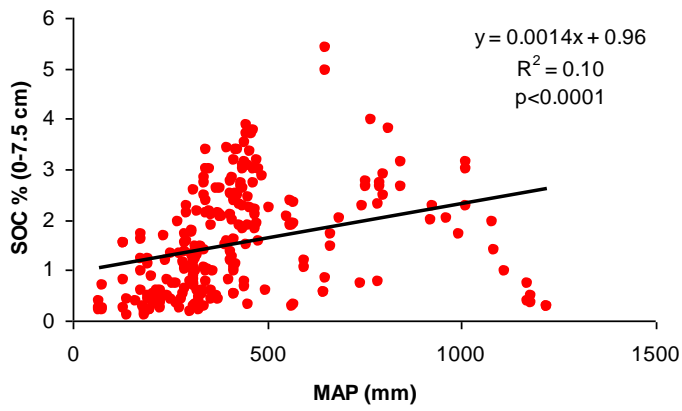
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Figure 4.

Standardized effects from structural equation modelling (unitless)

a

b

c

SAND

TMAX

MAP

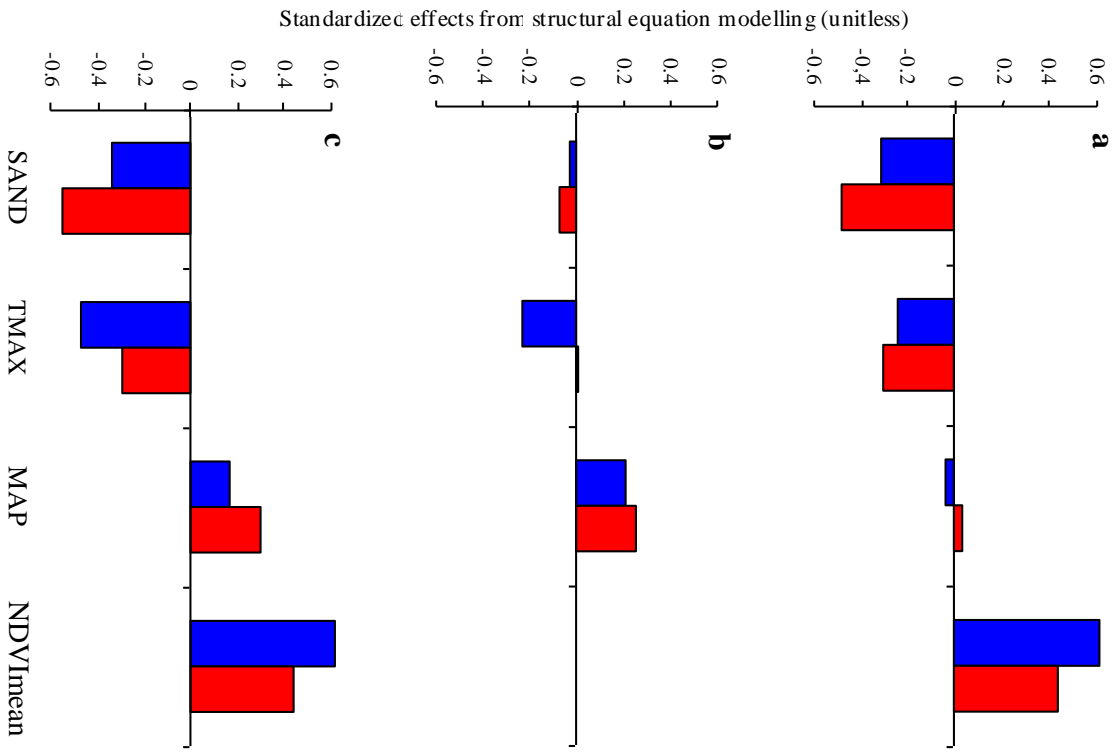NDVImean

719   **Figure 1.** Location of the sampling sites in the Global (black dots) and Patagonia (blue dots)

720   datasets. Precipitation data from Worldclim global database (http://www.worldclim.org/,

721   Hijmans and others 2005).

722

723   **Figure 2.** Bivariate relationships between abiotic (mean annual precipitation -MAP-, mean

724   maximum temperature -Tmax- and soil sand content -SAND-) and biotic (mean annual of the

725   normalized difference vegetation index -NDVImean-) factors with topsoil organic carbon

726   concentration (SOC) in the Global (red dots) and Patagonia (blue dots) datasets.

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728   **Figure 3.** Structural equation models for soil organic carbon (SOC) from the Global and

729   Patagonia datasets. Single headed arrows indicate a hypothesized causal influence of one

730   variable upon another. Double headed arrows indicate correlation without causal relationship.

731   The numbers adjacent to arrows are path coefficients; they show the strengths of the effect. The

732   widths of the arrows are proportional to the path coefficients. Full (dotted) arrows indicate

733   positive (negative) relationships. Non-significant (P>0.05) paths were eliminated. The R^2 next to

734   response variables indicate the proportion of variance explained. Significance levels as follows:

735   *P<0.05; **P<0.01; ***P<0.001. Abbreviations are as in Table 1.

736

737   **Figure 4.** Standardized direct (a), indirect (b) and total effects (c) of soil sand content (SAND),

738   mean annual temperature maxima (TMAX), mean annual precipitation (MAP), and mean annual

739   of the normalized difference vegetation index (NDVImean) upon soil organic carbon in the

740   Global (red bars) and Patagonia (blue bars) datasets.