https://doi.org/10.5194/bg-2020-63
Preprint. Discussion started: 17 March 2020

Biogeosciences Discussions
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Interactions between biogeochemical and management factors explain soil organic carbon in Pyrenean grasslands

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https://doi.org/10.5194/bg-2020-63
Preprint. Discussion started: 17 March 2020

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Author contributions

Antonio Rodríguez designed the statistical procedure, carried out the statistical analyses and wrote the original draft.

Rosa M Canals was responsible from field monitoring, lab analyses and acquisition of information for the data base implementation in the Western Pyrenees (Navarra). She has reviewed the draft.

Elena Albanell designed NIRS study and reviewed the draft.

Haifa Debouk sampled and processed some of the data in the PASTUS Database and reviewed the draft.

Jordi García-Pausas processed some of the data in the PASTUS Database and reviewed the draft.

Josefina Plaixats carried out the chemical analisys of herbage samples for NIR calibration and validation equations and reviewed the original draft.

Leticia San Emeterio designed methodology and data collection, performed soil and vegetation sampling. She has reviewed the draft.

Juan José Jiménez collaborated in the fieldwork and reviewed the draft.

M.-Teresa Sebastià contributed to the conception, design and development of the PASTUS database. In addition, she ensured funding and coordinated the projects whose

https://doi.org/10.5194/bg-2020-63
Preprint. Discussion started: 17 March 2020

data are included in PASTUS. Finally, she contributed to initial modelling, supervised the development of the paper, and read and reviewed the drafts.

Abstract

Grasslands are one of the major sinks of terrestrial soil organic carbon (SOC). Understanding how environmental and management factors drive SOC is challenging because they are scale-dependent, with large scale drivers affecting SOC both directly and through drivers working at detailed spatial scales. Here we addressed how regional, landscape and grazing management, soil properties and nutrients and herbage quality factors affect SOC in mountain grasslands in the Pyrenees. Taking advantage of the high variety of environmental heterogeneity in the Pyrenees, we fit a set of models with explicative purposes using data that comprise a wide range of environmental and management conditions. We found that temperature seasonality (TSIS) was the most important geophysical driver of SOC in our study. TSIS was positively related to SOC but only under certain local conditions: exposed hillsides, steep slopes and relatively highly grazed areas. High TSIS conditions probably are more favourable for plant biomass production, but landscape and grazing management factors buffer the accumulation of this biomass into SOC. Concerning biochemical SOC predictors, we obtained some surprising, interactive effects between grazer type, soil nutrients and herbage quality. Soil N was a crucial factor modulating effects of livestock species and neutral detergent fibre content of plant biomass and herbage recalcitrance effects varied depending on grazer species. These results highlight the gaps in the knowledge about SOC drivers in grassland under different environmental and management conditions, and they may serve to generate testable hypothesis in latter studies directed to climate change mitigation policies.

Keywords

SOC, semi-natural grasslands, grazing management, climate change, soil nutrients

Introduction

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Soil organic carbon (SOC) plays key roles in the terrestrial ecosystems (Lal, 2004a). SOC enhances soil and water quality and biomass productivity, and has an important role in relation to climate change (Lal, 2004b). Although grasslands have small aboveground biomass compared to other ecosystems, their SOC stocks can be comparable to those in forest ecosystems (Berninger et al., 2015). This is due to their high root biomass and residues, which are a substantial carbon source and can contribute to water retention in soil. This creates favourable conditions for the accumulation of organic matter (Von Haden and Dornbush, 2014; Yang et al., 2018). These attributes, together with the high extent of grassland global cover, make grasslands store around 34% of the terrestrial carbon, mostly in their soils (White et al., 2000).

SOC accumulation results from a complex equilibrium between primary production and organic matter decomposition which depends on multiple environmental factors such as climate, soil texture and nutrients or land management (Jenny, 1941; Schlesinger, 1977). Understanding how these environmental factors drive SOC is challenging because they are scale-dependent and are disposed on a hierarchy of controls over SOC, so large scale drivers affect also those working at fine spatial scales (Fig. 1; Manning et al., 2015). Climate is known to be the main SOC driver at broad (global and regional) scales; mean annual precipitation (MAP) and mean temperature (MAT) being the most frequent climate indicators (Wiesmeier et al., 2019). However, climate seasonality variables are be commonly neglected drivers affecting SOC in broad-scale models, in spite of being some important factors for plant primary production or enzymatic activity of soil microorganisms (Fernández-Alonso et al., 2018; Garcia-Pausas et al., 2007; Puissant et al., 2018). Other regional and

https://doi.org/10.5194/bg-2020-63
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landscape factors like bedrock or topography are also considered to be at the top of the hierarchy because they influence multiple geophysical and biochemical factors affecting SOC, including soil texture or water flow paths (Gray et al., 2015; Hobley et al., 2015). Next in the hierarchy after regional and landscape factors, are several soil geophysical properties, like pH and texture, which are controlled by climate, bedrock, and which affect SOC through both plant primary production and microbial activity and the capacity to stabilise the SOC (Deng et al., 2016; Xu et al., 2016a). Soil macro and micronutrients are in the next level of the hierarchy, as their abundance is determined by multiple factors, including climate, soil pH, water content or clay content (Hook and Burke, 2000; de Vries et al., 2012). They play an essential role in primary production and herbage quality, and act as resources for microbes to mineralise SOC (Aerts and Chapin, 1999; Vitousek and Howarth, 1991). However, these variables are commonly omitted in the broad-scale SOC studies, especially if those focus on predictive models instead of explicative ones (Gray et al., 2015; Manning et al., 2015; Zhang et al., 2018). This kind of variables are less frequently available and more difficult to measure than the other indicators used for SOC modelling (Manning et al., 2015). Moreover, the use of soil nutrients as SOC predictors in linear models can be challenging, as they are often so linked to SOC dynamics that their effect can mask the effect of other predictors at higher levels (Bing et al., 2016; Cleveland and Liptzin, 2007; Tipping et al., 2016). Vegetation represents another group of SOC predictors, affected by climate, topography and soil properties and nutrients (Fernández-Martínez et al., 2014; de Vries et al., 2012; Zhu et al., 2019). Plant biomass is the main input of organic carbon into the soil (Shipley and Parent, 1991). However, plant litter quality can determine decomposition rates and

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patterns, and hence soil carbon sequestration (Ottoy et al., 2017; Yan et al., 2018, 2019).

Apart from these factors, management effects on grassland SOC is a noteworthy issue since they are poorly understood (Wiesmeier et al., 2019). It is known that herbivores can affect SOC through different paths, such as regulating the quantity and quality of organic matter returned to soil (Bardgett and Wardle, 2003), or affecting soil respiration and nutrients by animal trampling or soil microbiota alteration (Lu et al., 2017). However, most of the studies investigating grazing effects on SOC focus on grazing intensity, in spite of evidence pointing to a greater role of grazer species in determining vegetation and SOC (Chang et al., 2018; Sebastia et al., 2008). Moreover, several studies describing interactions of grazing with other SOC predictors at diverse scales have been published (Abdalla et al., 2018; Eze et al., 2018; Lu et al., 2015, 2017; Zhou et al., 2017). Hence, grazing management on grasslands may be considered a unique SOC driver, because it has effects at multiple levels of the driver hierarchy (Fig. 1).

In this study, our goal was to identify the main drivers of SOC stocks in semi-natural grasslands of the Pyrenees, asses the interactions between them and describe their relative importance. Mountain grasslands comprise a wide range of climatic, topographic, management and edaphic conditions that make carbon stocks highly variable (Garcia-Pausas et al., 2007, 2017). For this reason data analysed here comprise a wide range of environmental conditions, comparable to studies on SOC developed at continental or even worldwide scales (Table 1). Additionally, we consider an exceptionally broad compilation of predictors (Table 1). In particular, the specific questions of this study are 1) how are the effects of the geophysical, widely used predictors located at the top of the hierarchy of

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controls on SOC? 2) how are the effects of the biochemical, unfrequently used (soil nutrient and herbage), predictors on SOC? 3) Can grazing management regulate the effects of other SOC drivers located at different levels of the hierarchy of controls?

Material & methods

2.1 Location and sampling design

The set of data used in this study has been extracted from the PASTUS Database (http://ecofun.ctfc.cat/?p=3538), which was compiled by the Laboratory of Functional Ecology and Global Change (ECOFUN) of the Forest Sciences Centre of Catalonia (CTFC) and the University of Lleida (UdL). We sourced a wealth of data of 128 grassland patches distributed across the Pyrenees (Fig.S1), and including topographical, climatological, soil, herbage and management variables. The sampled area encompasses a wide variety of temperate and cold-temperate climates, with different precipitation conditions, depending on altitude and geographical location from Mediterranean to Continental and Boreo-Alpine (de Lamo & Sebastià, 2006; Rodríguez et al., 2018; Table 1).

Sampling in the PASTUS database was designed according to a stratified random scheme, where samples were selected at random within strata. This process was done using the software ArcMap 10 (ESRI, Redlands, CA, USA). The basis for randomization was the map of habitats of Catalonia 1:50000 (Carreras and Diego, 2006) for the Eastern and Central sectors, the map of habitats of Madres-Coronat 1:10000 (Penin, 1997) for the North-Eastern sector and the land use map of Navarra 1:25000 (Gobierno de Navarra, 2003) for the Western sectors. Four variables were initially considered for sampling stratification within each sector: altitude (< 1800 m; 1800-2300 m; > 2300 m), slope (0-20º; 20-30º; > 30º), macrotopography (mountain top/southern-facing slope; valley bottom/northern-facing slope) and grazing management (sheep grazing; cattle

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grazing; mixed grazing). Accordingly, we determined a set of homogeneous grassland patches by crossing the stratification variable layers. Grassland patches were then listed by type and arranged within each list randomly to determine sampling priority. At least one to two replicates of each patch type were sampled.

In each sampled grassland patch, a 10 x 10 m^2 plot was systematically placed in the middle of each homogeneous grassland patch, including a particular plant community. Soils and vegetation were sampled inside this 100 m^2 plot, and environmental variables assessed (see Rodríguez et al., (2018) for additional details about sampling design). Local variables were assessed inside the 100 m^2 plots. Aboveground biomass was estimated from herbage cut at ground level in four 50 x 50 cm^2 quadrats placed in a 2 x 2 m^2 subplot inside the 100 m^2 plot. Herbage from two of the four quadrats were dried and sent to the laboratory for duplicated chemico-bromatological analysis. In addition, in each quadrat, a 20-cm depth soil core was extracted with a 5 x 5 cm probe after herbage was removed. The soil sample in the probe was separated into two soil layers: 0-10 and 10-20 cm.

2.2 Regional and landscape environmental drivers

In order to investigate the relationship between soil organic carbon (SOC) and potential environmental drivers, 29 independent environmental variables were initially considered (Table S1). These variables were grouped into five sets: Regional, landscape: livestock management, soil nutrient stocks and herbage variables.

Regional variables included climate variables and bedrock. Climate variables were determined from Worldclim 2.0 (Fick and Hijmans, 2017). We selected Mean Annual Temperature (MAT), Mean Annual Precipitation (MAP) and Mean Summer Precipitation (MSP). The difference between mean annual and mean summer temperature emerged as a relevant explanatory factor of soil organic carbon stocks during previous modelling efforts by one of the co-authors (MTS). Latter attempts to improve models by substituting this variable by other temperature indices in climatic databases (Fick and Hijmans, 2017) showed that, for the PASTUS database, this variable provided higher explanatory power than other temperature seasonality indices. Thus, we decided to keep it and here we name it Temperature Seasonality Index of Sebastià (TSIS from now on).

Bedrock type was determined in the field and confirmed by the geographical maps mentioned above. Bedrock was categorized into three categories: basic (marls and calcareous rocks), acidic (mostly sandstones and slates) and heterogeneous.

Landscape variables included topography and soil type variables. Topography variables included Slope, Aspect, Macrotopography and Microtopography. Slope and Aspect were determined in the field by clinometer and compass respectively. Macrotopography and Microtopography were determined visually in the field. Macrotopography differenciated exposed from protected positions. Mountain top and south-facing slopes were identified as exposed positions and valley bottoms and north-facing slopes as protected positions. Microtopography considered three positions: convexities, concavities and smooth areas. Soil type variables are described in section 2.4.

2.3 Livestock management variables

Regarding livestock management variables, detailed surveys were carried out among farmers, shepherds and land managers. Two management variables were considered: Grazing intensity and Grazer type. Grazing intensity was determined estimating livestock stocking rates measured as livestock units ha^{-1} (LU ha^{-1}), and treated as a semi-quantitative variable with three categories (Sebastià et al. 2008): low (1; lower than 0.2 LU ha^{-1}), medium (2; between 0.2-0.4 LU ha^{-1}) and high (3; above 0.4 LU ha^{-1}). Grazer type was categorized into three main types: sheep grazing, cattle grazing and mixed grazing. Mixed grazing included associations comprising small and big livestock species, mainly sheep and cattle, and more rarely horses. Sheep flocks always included some goats.

2.4 Soil sampling and physicochemical analysis

Soil samples were air-dried and weighted. Each sample was sieved to 2 mm to separate stones and gravels from the fine earth fraction; the fine fraction was sent to the laboratory for physicochemical analysis. Standard physicochemical soil analyses were performed in the upper 0-10 cm soil layer of all grasslands. Some analyses were also performed on samples from the 10-20 cm soil layer, including: soil organic carbon, total nitrogen. For those variables, we later calculated values for the whole top 20 cm soil layer.

All soil physicochemical analyses were performed on the fine earth, according to standard soil analysis methods. Textural classes were determined by the Bouyoucos method (Bouyoucos, 1936). Soil pH (measured in water), total organic carbon (TOC) total nitrogen (TN), Calcium content (Ca), Extractable phosphorus (P), magnesium (Mg) and potassium (K) were measured on air dried samples (Schöning et al., 2013; Solly et al., 2014). Soil carbonates were determined using the Bernard calcimeter. Total carbon and nitrogen (N) contents of the fine earth was determined by elemental auto-analyser. The organic C fraction was determined by subtracting inorganic C in the carbonates from the total C. Soil organic carbon (SOC) stocks in the upper 20 cm soil layer were then estimated taking into account the organic C concentration in the sample and its bulk density, and subtracting the coarse particle (> 2 mm) content, following García-Pausas et al. (2007). Available phosphorus (P) was extracted by the Olsen method (Olsen, 1954) Ca, Mg and K were extracted by ammonium acetate (Simard, 1993) and measured by flame Atomic absorption Spectroscopy (AAS) (David, 1960)).

2.5 Herbage chemical and bromatological analysis

A total of two hundred samples were chemical and bromatological analysed by NIRS (near infrared reflectance spectroscopy). All four herbage samples of each plot were oven-dried at 60ºC to constant weight. Two of the samples was sent to the laboratory. Dried samples were ground to pass a 1 mm stainless steel screen (Cyclotec 1093

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Sample mill, Tecator, Sweden) and stored at 4ºC until it was needed for use. To develop NIRS equations (see below) subsamples were analysed in duplicate. Procedures described by AOAC were used to determine dry matter (DM) and ash content or mineral matter (MM). Crude protein (CP) was determined by the Kjeldhal procedure (N x 6.25) using a Kjeltec Auto 1030 Analyser (Tecator, Sweden). Samples were analysed sequentially for neutral detergent fibre (NDF), acid detergent fibre (ADF) and acid detergent lignin (ADL) in accordance with the method described Van Soest et al. (1991) using the Ankom 200 Fibre Analyser incubator (Ankom, USA). The fibre analysis were determined on an ash-free basis and without alpha amylase. We calculated two additional herbage quality indexes often used in the bibliography: NDF/CP and ADL/HN (Stockmann et al., 2013). For each subsample the C and N content were determined by the Dumas dry combustion method, using an Elemental Analyzer EA1108 (Carlo Erba, Milan, Italy).

2.6 NIRS analysis

NIRS data were recorded from 1,100 to 2,500 nm using a FOSS NIRSystem 5000 scanning monochromator (Hillerød, Denmark). Separate calibration equations were generated for grassland samples. Reflectance (R) data were collected in duplicate every 2 nm. A WinISI III (v. 1.6) software (FOSS, Denmark) was employed for spectra data analysis and development of chemometric models. Prior to calibration, log 1/R spectra were corrected for the effects of scatter using the standard normal variate (SNV), detrend (DT) and multiple scatter correction (MSC) and transformed into first or second derivative using different gap size (nm) and smoothing interval. For each sample, the mean of the spectra from the two lectures were used. Modified partial least square (MPLS) was the regression method used for calibration development and cross validation was undertaken using the standard methodology in the NIRS software program. The performance

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of the model was determined by the following statistical tools: standard error of calibration (SEC), standard error of cross validation (SECV); coefficient of determination for calibration (R^2) and cross validation (r_{cv}^2); the ratio of performance to deviation (RPD) described as the ratio of standard deviation for the validation samples to the standard error of cross validation (RPD=SD/SECV) should ideally be at least three; and the range error ratio (RER=Range/SECV) described as the ratio of the range in the reference data to the SECV should be at least 10 (Williams and Sobering, 1996; Williams et al., 2014).

2.7 Statistical analyses

We applied two different modelling procedures, Boosted Regression Trees (BTR) and General Linear Models (GLM). All the statistical analyses were performed with the software R ver. 3.4.3 (R Core Team, 2017), at 95% significance level when appropriate.

Boosted regression trees global model

We fitted a model with BRT to identify the most important variables affecting SOC. BRT uses two algorithms: regression trees are from the classification and regression tree (decision tree) group of models, and boosting builds and combines a collection of models (Elith et al., 2008). We chose this method because BRT can handle multiple variables better than other techniques as GLM, and can detect automatically curvilinear relationships and interactions, ignoring non-informative ones. We used the gbm and dismo packages (Greenwell et al., 2019; Hijmans et al., 2017), which provide several functions to fit these models.

First, we fitted a model with all the predictors (Table S1), configured with 15 folds, a Gaussian distribution of the error, a tree complexity of 5, a learning.rate of 0.005, a bag.fraction of 0.666, and 5 minimum observations by node. Secondly, we reduced the number of predictors by the method described in Elith et al., (2008). We estimated the

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change in the model´s predictive deviance dropping one by one each predictor (supporting information), and re-fitted the model with the set of variables which actually improved model performance Fig. S2). We checked the relative importance of the predictors and the shape and size of the effects by partial effect plots.

General linear models

We designed and executed a modelling procedure based on general linear models (Legendre and Legendre, 1998) and a hierarchy of controls over function (Diaz et al., 2007; de Vries et al., 2012). We log-transformed SOC using natural logarithm to prevent a breach of the normality assumption by the residuals of the models. We built two models (Fig. S4), one model only based on geophysical predictors and grazing management (Geophysical Model), and another model by adding to the former the biochemical predictors: soil nutrients and herbage quality predictors (Combined Model). We considered that the geophysical factors that potentially affect SOC were regional and landscape (topography and soil type predictors), as they have been widely used in previous studies to model and predict SOC from landscape to continental scales (Manning et al., 2015; Wiesmeier et al., 2019). In addition to soil nutrients and herbage variables, we included again the livestock management variables in the Combined Model and looked for interactions involving these variables and biochemical predictors of SOC.

For model building (Fig. S4A), we added predictor groups following a sequential order. For fitting the geophysical model, we started adding regional, landscape and grazing management predictors, and subsequently included soil properties. Afterwards, we sequentially included soil nutrients and herbage predictors to obtain the Full Model. We added Management variables from the beginning of the modelling process and re-included the discarded ones in each step to guarantee the detection of interactions between Management variables and the rest of the predictors. Each time we added a set of predictors, we first considered their main effects and some quadratic terms which

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were found by preliminary analyses with the scatterplot.matrix function in the R package car (Fox et al., 2018); afterwards we included possible level 2 interactions between all the selected predictors.

At every step we selected several candidate terms by a semi-automatic procedure (Fig. S4C) using a genetic algorithm included in the R package glmulti (Calcagno, 2015). We used SOC as response variable at the first step, and the residuals of the previous model in the remaining steps (Fig. S4B). This semi-automatic process began by obtaining a best subset of models using the corrected Akaike information criterion (AICc), appropriate when n/k is less than 40, being the sample size and k the number of parameters in the most complex model (Symonds and Moussalli, 2011). We selected the best model and its equivalents obtained by the genetic algorithm, which were those within 2 Akaike information criterion-corrected (ΔAICc) values of the best model, as a ΔAICc < 2 indicates that the candidate model is almost as good as the best model (Burnham and Anderson, 2002).

For this set of models, we built averaged models using the MUMIn package (Barton, 2015). We calculated partial standardized coefficients, obtained by multiplying the unstandardized coefficient in the model by the partial standard deviation of the variable, which is a function of the standard deviation of the variable, the sample size, the number of variables in the model and the variance inflation factor of the variable (Barton, 2015). We selected all the variables with significant effects (alone or in interaction with each other) in the conditional average model, which was preferred over the full average model because we wanted to avoid excessive shrinkage effects at this moment of the modelling procedure (Grueber et al., 2011).

Then, we added these terms to the consolidated model, and made a selection through a backward forward procedure. We used several methods to compare and determine the final model, including the AICc, the adjusted determination coefficient R^2 (R_{adj}^2) and model comparison techniques with the “anova()” function in R, using Chi-square tests to

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test whether the reduction in the residual sum of squares was statistically significant. Once we had the final model we assessed the significance of each term by removing it and performing an F test. For estimating the significance of the main effects we also removed the interaction terms in which they were involved, to avoid transferring the effects of the main terms to the interaction terms (de Vries et al., 2012). We estimated the variance explained by the models through the adjusted determination coefficient R^2 (R_{adj}^2).

Finally, we estimated the importance of the terms of each model by the lmg method in the relaimpo package (Grömping, 2006), and drew partial effect plots making predictions with the R package emmeans (Lenth et al., 2019).

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Results

SOC stocks of the upper 20 cm layer ranged between 2.6 and 23 kg m^{-2}, with a median and a mean value of 9.1 and 9.6 kg m^{-2} respectively. Minimum, maximum, median and mean values of the continuous predictors are shown in Table S2.

Relative importance of SOC predictors

The final BRT global model achieved a good goodness of fit, with a cross-validated correlation value of 0.52% and an explained deviance of 88.31%. The most important variables explaining SOC stocks (Fig. 2) were soil N (18.3 %), soil C/N (14.4%) and Clay (13 %) although other variables such as Aboveground biomass (7.3%), ADL (6.4%) or Silt (6.1%) were also relevant for explaining SOC storage. Two of the most important variables in the BRT model, Aboveground biomass and Silt, were not selected in the linear models (Tables 2 & 3). Although accounting for a lower importance value than the previous variables (5%), TSIS was the most relevant selected climate predictor. This variable was also relevant in both linear models (Fig. S5), especially in the Geophysical Model, where TSIS was the most important variable, not only as main effect, but in interaction with other variables (Img: 4 – 10%). Soil nutrient and herbage variables were also important according to the Combined linear model (Fig. S6), but in this case we identified that many of these effects occurred in interaction between these two predictors with grazer type.

Geophysical effects on SOC stocks

The Geophysical Model (Table 2) explained 34 % of the total variance (R^2_{Adj}). Overall, SOC stocks increased with TSIS under certain conditions: exposed

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hillsides, high slopes and low stocking rates (Fig. 3A, 3B & 3D). On the other hand, Clay had a positive relationship with SOC under low MAP values (Fig. 3C), which turned into negative at high MAP values (Fig. 6C).

Soil nutrient and herbage effects on SOC

Adding nutrient and herbage predictors in the previous geophysical model to build the Combined model (Table 3) increased the total variance (R^2_{Adj}) up to 61%. Macrotopography and Clay effects described by the Geophysical model were removed by the new model terms included. SOC increased with C/N (Fig 4A). Soil nitrogen modulated the effects of livestock type and NDF on SOC. Cattle grazed grasslands stored more SOC than mixed and sheep grazed grasslands under low soil N conditions, whereas the opposite occurred at high soil N levels (Fig. 3B). NDF had negative effects on SOC at high soil N values but had no effect under low soil N levels Fig. 4C). Finally, herbage ADL/NH had positive effects on SOC under mixed and sheep grazing regimes, but there was no effect under cattle management (Fig. 4D).

Discussion

Regional, landscape, management, soil and herbage factors drove SOC stocks in grasslands of the Pyrenees with multiple interactions. The BRT model identified soil N and C/N, texture and herbage variables as the most important predictor groups (Fig. 2), TSIS being the most important climate variable. Both linear models followed a hierarchy of controls over function approach to ensure a unique effect of each driver on SOC. Hence, some variables selected in the BRT model, like aboveground biomass, silt or soil K were not included in these models (Tables 2 & 3). The geophysical model showed how some climate variables (TSIS

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and MAP) interacted with landscape (macrotopography and slope), soil clay content and grazing intensity (Fig. 3). Whereas, the Combined Model provided information on how herbage quality effects on SOC (NDF and ADL/NH) varied depending on soil N and grazing species, and on how grazer species had different effects depending on soil N content (Fig. 4).

Considerations about the modelling procedure

As a regression tree machine learning technique, the BTR model identified a set of SOC predictors (Fig. 2) avoiding some of the linear model disadvantages, like guarding against the elimination of good predictors correlated to others or automatically modelling non-linear effects (Cutler et al., 2007; Elith et al., 2008). Thus, the BRT model included some SOC predictors, like a positive logarithmic-like effect of aboveground biomass or soil K on SOC (Fig. S7), which could be masked by the effects of other variables in our linear models (Yang et al., 2009). However, most of the variables selected and their effects were generally consistent with those explained by the linear models (Fig. 3, 4, S7). Consequently, we preferred to focus on the results from the linear models because our approximation allowed us to build models under a hierarchy of controls over function hypothesis (Manning et al., 2015). Hence, although we could not establish the causal links between SOC predictors (Grace, 2006; Grace and Bollen, 2005), we guaranteed that geophysical drivers included in the first model were not the single common cause of variation of both biotic factors included in the second model and SOC (de Vries et al., 2012). In that case, soil nutrient and herbage quality predictors could not be added to the model as

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significant terms, as was the case with aboveground biomass. In addition, our modelling approach allowed us to select biologically meaningful interactions (Manning et al., 2015; de Vries et al., 2012), which cannot be done with a fully automatic approach like BRT. Additionally, our sequenced modelling procedure looking for the primary sources of variation, together with the stratified sampling design, lead us to select a set of lowly correlated predictors for our linear models (Table S3).

Geophysical predictors driving SOC

Considering the difficulties of modelling SOC in a widely heterogeneous mountain environment (Garcia-Pausas et al., 2017), the Geophysical model provided important information about SOC drivers in the Pyrenees. TSIS was a key predictor of SOC with a varying effect depending on macrotopography, slope and grazing intensity (Table 2). This result contrasts with most of the previous studies addressing soil carbon in mountain grasslands, which usually pinpoint mean temperature and precipitation as the most important climate drivers of SOC (Hobley et al., 2015; Manning et al., 2015; Wiesmeier et al., 2019). Overall, the TSIS effect on SOC was positive under certain conditions. Sites characterised by low mean temperatures presented a wider spectrum of TSIS values than warm sites (Fig. S8). Considering that climate regulates large scale patterns of aboveground net primary production (Chapin et al., 1987), a positive effect of TSIS on SOC could be associated with higher biomass accumulation in cold locations with more favourable temperatures during summer, this fact reducing geophysical stress for plants (Garcia-Pausas et al., 2007; Kikvidze et al., 2005).

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This plant biomass accumulation during summer would overcome an eventual increase of soil organic matter decomposition rates due to high temperatures (Sanderman et al., 2003), which could even be diminished if microbial biomass decreases as a result of soil moisture reduction (Puissant et al., 2018).

The interactions of TSIS with macrotopography and slope illustrate the capacity of landscape factors to modulate macroclimate effects on soil (Hook and Burke, 2000). Induced microclimate changes are often the explanation for the effects of topography in SOC (Lozano-García et al., 2016). In our case, SOC stocks increased with temperature seasonality particularly at mountain exposed areas (Fig. 3A; Table 2). In protected sites, located in shady slopes and valley bottoms, the hypothesized positive effect of high TSIS values on productivity could be mitigated due to lower solar radiation, longer snow-covered periods and freezing episodes (Garcia-Pausas et al., 2007; López-Moreno et al., 2013). Conversely, negative effects of low TSIS values on productivity could be compensated thanks to more humid conditions in protected than in exposed sites (Garcia-Pausas et al., 2007). Additionally, it is important to take into account that differences in SOC between exposed and protected sites may also occur through other mechanisms, for instance the alteration of soil physico-chemical properties like pH, soil texture or stoniness (Zhang et al., 2018) or differences in vegetation (Sebastià, 2004). Since we used a hierarchy of controls approach (Manning et al., 2015), these topography indirect effects could be behind the exclusion on the linear models of some predictors selected in the BRT model, like silt or pH (Figs. 2 & 3).

In addition, high TSIS values compensated SOC decrease in steep slopes, probably due to reduced carbon inputs and increased carbon losses induced by high soil erosion (Yuan et al., 2019 and refferences therein). The decrease in

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SOC stocks under low TSIS values were also compensated by grazing pressure increase (Fig 3D). Recent meta-analyses conclude that grazing has a commonly decreasing, but strongly context-specific effect on SOC, depending on other factors like climate, soil type vegetation or grazing intensity (Abdalla et al., 2018; Eze et al., 2018; Mcsherry and Ritchie, 2013). Particularly, light and medium grazing intensities can increase SOC inputs by dung deposition and promoting aboveground and root biomass production (Franzluebbers et al., 2000; Zeng et al., 2015). Considering that in our semi-natural grasslands all grazing intensities are relatively low (see methods), our medium and high stock rates may increase soil carbon inputs in low seasonality locations by enhancing productivity.

Interestingly, clay content and precipitation presented interacting effects on SOC (Fig. 3C; Table 2). Both MAP and clay content are widely assumed to be positively correlated to SOC (Wiesmeier et al., 2019). High MAP would increase SOC inputs by promoting plant productivity (Author et al., 2000; Hobley et al., 2015). Clay positive effects are often attributed to a larger contact surface of soil particles (Kennedy et al., 2002), the absorption of negatively charged organic matter, high soil water retention and the exclusion of decomposer organisms due to their low pore size (Krull et al., 2001). In our study, high water contents may inhibit decomposition if a shortage of oxygen supply occurs (Xu et al., 2016b). However, as MAP values increased, clay effect on SOC became negative. To explain low SOC values at high MAP and high clay content, McSherry and Rithchie (2013) hypothesized that finer texture soils could be waterlogged more frequently, leading to inhibition of root growth and soil C allocation belowground.

Biochemical predictors driving SOC

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Adding soil nutrient and herbage predictors to our modelling procedure implied the substitution of the terms including clay content and macrotopography by the newly added terms (Tables 2 & 3), highlighting the importance of indirect effects of these variables on SOC through other small scale predictors (Leifeld et al., 2015; Xu et al., 2016b; Zhu et al., 2019). In this case, we obtained a complex model with some surprising, less frequently tested effects involving interactions between graze type, soil nutrients and herbage quality variables (Table 3, Fig 4). Although our interpretations have limitations because our models were based on observational data, they can still provide some hints about some of the most complex and unknown relationships between SOC and its drivers. In can also contribute to generate testable hypotheses in latter studies.

As expected, SOC increased with the C/N ratio (Fig 4A), which is an indicator of the difficulty of soil organic matter decomposition by soil microbes, decreasing decomposition rates of SOC with increasing soil C/N (Wanyama et al., 2019; Xu et al., 2016b). Conversely, total soil N conditioned livestock type effect on SOC in a surprising way. Cattle grazed grasslands stored more SOC than mixed and sheep grazed ones under low soil N conditions, whereas the opposite occurred at high soil N content (Fig. 4B). Chang et al. (2018) found that in a N poor semi-arid grassland, sheep decreased SOC content in comparison to cattle due to vegetation changes caused by their feeding preference for highly palatable forbs, promoting less palatable grasses which supported less root biomass. A shift towards higher grass biomass with sheep grazing was also found in the Pyrenees (Sebastia et al., 2008). Conversely, in our study mixed grazing increased SOC, probably through effects on soil environment and decomposition processes. Our results suggested that those processes could vary depending on soil conditions.

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Negative effects of sheep grazing on SOC through their selective feeding could occur mostly in poor N soils (Fig 4B). Under such conditions, palatable plants could produce higher SOC inputs, since plant productivity is more reliant on the ability of fixing atmospheric N of legumes (Van Der Heijden et al., 2008) and the exceptional capacity of forbs to allocate C in roots is especially stimulated (Ågren and Franklin, 2003; Warembourg et al., 2003). However, these processes could be different under different soil N conditions, although the concrete mechanisms are hard to suggest, since livestock type may affect SOC content not only through changes in plant composition, but other differences in certain features of livestock assemblages, like trampling, faeces deposition patterns or effects on plant regrowth, which could promote differences in soil respiration and/or plant productivity (Aldezabal et al., 2019; Chang et al., 2018; Liu et al., 2018), resulting in different SOC levels under different grazers. Grasslands with mixed grazed regimes stored even more SOC than sheep grazed ones under high soil N conditions (Fig. 4B, Table 3). This result emphasises that mixed livestock assemblages deserve particular attention as they can affect plant composition distinctly from single grazing species regimes or alter traveling and trampling behaviours of grazing animals (Chang et al., 2018; Liu et al., 2015).

Model terms involving herbage predictors could represent both biochemical and physical pathways of litter incorporation to soil organic matter (Cottrufo 2015). In our model, NDF was negatively related to SOC at high N values (Fig 4C). NDF proportion represents the amount of structural compounds on litter, and hence is inversely related to non-structural compounds content (Goering and Van Soest, 1970). The latter are the main source of organic matter formation at the early stages of decomposition, and they are incorporated into microbial biomass in a

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highly efficient way (Cotrufo et al., 2013). However, if microbial necromass is recycled by microbes before its incorporation to mineral-associated organic matter, it could be respired and mineralized instead of stored (Córdova et al., 2018). Thus, our model suggested that incorporation of labile and fast metabolized non-organic compounds to soil organic matter could be a pathway of SOC allocation at high soil N in Pyrenean grasslands. At low soil N conditions, induced changes in microbial composition or priming effects (De Deyn et al., 2008; Fontaine et al., 2007; Wild et al., 2019; Yan et al., 2018) may disable SOC accumulation trough this biochemical pathway.

On the other hand, the ADL/NH ratio was positively related to SOC in sheep and mixed grazed grasslands (Fig. 4D). The ADL/NH ratio is a commonly used indicator for the resistance of litter to degradation, particularly at later stages of decomposition (Taylor et al., 1989). Hence, the increase of SOC with ADL/NH could be related to the physical pathway of soil organic matter incorporation, forming coarse particulate organic matter (Cotrufo et al., 2015). Moreover, our model suggests that this pathway would be inhibited under cattle grazing, presumably because of their less selective diet and higher digestive efficiency than sheep (Rosenthal et al., 2012; Sebastià et al., 2008). Since lignin content is inversely related to plant palatability (Moore and Jung, 2001), plants with high lignin content will be avoided with greater probability under sheep-based management regimes (Wang et al., 2018), and that would promote differences in recalcitrant litter mineralization rates. Additionally, lower diet selectivity and higher digestive efficiency of cattle compared with sheep, can result into less

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recalcitrant faeces (Wang et al., 2018), which could explain also SOC differences between grazer types at high ADL/NH conditions.

Implications of livestock effects on SOC

One key point of our results is that they highlight the need for a deeper research effort in disentangling not only grazing intensity but grazer type effects on grassland soil organic carbon and nutrient cycling under different environmental circumstances. Our results concerning interactions between grazer type and herbage quality provide some evidence of grazing effects not only through alterations of plant communities that were reported by previous studies in the region (Canals and Sebastià, 2000; Sebastià et al., 2008),but also through interactions with them. Although grazing effects were not the most important factors affecting SOC stocks, this is by far the easiest component to manipulate in order to increase or maintain SOC in soils and face climate change (Komac et al., 2014). Despite the need of a precise knowledge on the effects of different land uses on ecosystems for climate change mitigation (Lo et al., 2015) studies addressing grazer type effects on SOC are scarce (i.e. Zhou et al., 2017; Chang et al., 2018). Considering our results, we would suggest to carry out more experiments testing the effects of livestock type on SOC under different soil fertility conditions and plant communities with contrasting herbage quality parameters.

To conclude, we showed how a combination of regional, landscape, management, soil properties, soil nutrients and herbage factors might drive SOC stocks in the Pyrenees. Among all the regional and landscape scale factors, a seasonality variable, TSIS seemed to be the most decisive, although interacting with some topographical drivers and grazing intensity. To our knowledge, this is the first time these factors were combined together with soil nutrients and herbage quality factors to model SOC. Soil N was a crucial factor modulating the effect of livestock species and NDF, and herbage recalcitrance effect on SOC varied depending on grazer species. Our study highlight the need to expand knowledge about grassland SOC drivers under different conditions, specially grazing, as this is the most easily tractable factor affecting SOC and it has other advantages like preventing the accumulation of aboveground C and reducing the risk of forest fires (Nunes and Lourenço, 2017). We provided the basis to generate new testable hypothesis for latter studies that may be useful to design improved policies to palliate climate change.

DATA ACCESSIBILITY

Data are not public as the PASTUS database is currently being used for other research projects. Please contact one of us by e-mail for queries concerning the data used in this study.

Acknowledgements

We would like to express our thanks to the many people who collaborated in fieldwork, sample processing and data analysis over time. Research in this paper is based on the PASTUS database, which was compiled from different funding sources over time, the most relevant being: the EU Interreg III- A Programme (I3A- 4- 147- E) and the POCTEFA Programme/Interreg IV- A (FLUXPYR, EFA 34/08); the Spanish Science Foundation FECYT- MICINN (CARBOPAS: REN2002- 04300- C02- 01; CARBOAGROPAS: CGL2006- 13555- C03- 03 and CAPAS: CGL2010- 22378- C03- 01); the Foundation Catalunya- La Pedrera and the Spanish Institute of Agronomical Research INIA (CARBOCLUS: SUM2006-00029- C02- 0). L. San Emeterio was funded through a Talent Recruitment grant from Obra Social La Caixa - Fundación CAN. ARAID foundation is acknowledged for support to J.J. Jiménez. This work was funded by the Spanish Science Foundation FECYT- MINECO (BIOGEI: GL2013- 49142- C2- 1- R) and the University of Lleida (PhD Fellowship to AR).

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Table captions

Table 1: Considered factors affecting SOC in some recent studies. ✓: the study considers this variable type; ✗: the study does not consider this variable type.

Table 2: Results of the geophysical model for soil organic carbon (R^2_{Adj} = 0.34).

Table 3: Results of the Combined model for soil organic carbon (R^2_{Adj} = 0.61).

Figure captions

Figure 1: Conceptual scheme used in this work to relate potential environmental drivers with SOC. We assume that drivers may affect soil organic carbon (SOC) both directly or hierarchically through other driver. Interactions between factors from different types could also drive SOC. Grazing management has a special location as may act through different paths and interact with factors at different scales.

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Tables

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*Fertilizer effects.
** Only aboveground and/or belowground biomass index

Article	Location	LAT (º)	LONG (º)	MAP (mm)	MAT (°C)	Topography and bedrock	Grazing Management	Soil properties	Soil nutrients	Herbage
Present study	***Pyrenees***	***42.14 – 43.3***	***-1.22 – 2.26***	***964 – 1586***	***1.1 – 9.9***	✓	✓	✓	✓	✓
Duarte-guardia et al., 2019	Worldwide	-51.72 – 80.23	-163.95 – 158.25	65 – 5115	-21.2 – 30	✓	✗	✓	✗	✓**
Abdalla et al., 2018	Worldwide	-45.85 – 51	-114 – 120.7	150 – 1650	0 – 21	✗	✓	✓	✗	✓
Eze et al., 2018	Worldwide	-44 – 65	-121 – 175	120 – 2000	-4.8 – 26.8	✗	✓	✓	✓*	✓**
Peri et al., 2018	South Patagonia	- 52 – -45	-73.5 – 65.5	139 – 865	4.2 – 11	✓	✓	✗	✗	✓
Zhang et al., 2018	Northern China	103.5 – 124.16	32.5 – 42.5	500 – 1000	8 – 14	✓	✓	✓	✗	✗
Zhao et al., 2017	Mongolia	41.95 – 53.93	108.28- 116.2	150 – 400	-1.3 – 2.1	✗	✓	✓	✗	✓
Zhou et al., 2017	Worldwide	-42.1 – 52.3	-121 – 175	200 – 600	0 – 10	✗	✓	✗	✗	✗
Deng et al., 2016	Eastern China	28.71 – 30.45	120.87 – 122.43	940 – 1720	16.86 – 18.57	✓	✗	✓	✗	✗
Gray et al., 2015	Eastern Australia	-16.7 – -43.5	-31.8 – -28.7	500 – 2000	10 – 30	✓	✗	✗	✗	✓
Lu et al., 2017	Qinghai-Tibetan Plateau	27 – 32	83 – 108	37 – 718	-4.04 – 6.3	✗	✓	✗	✗	✗
Chang et al., 2015	Tibet	Not Reported	Not Reported	397 – 1910	1.7 – 15.5	✓	✗	✗	✗	✓
Manning et al. 2015	England	50.77– 54.58	-4.43 – 0.87	596 – 3191	6.5 – 10.9	✗	✓	✓	✗	✓
McSherry & Ritzie 2013	Worldwide	Not reported	Not reported	180 – 950	Not reported	✗	✓	✓	✗	✓
Garcia-Pausas et al. 2007	Pyrenees	-7 – 2.2	42.5 – 42.9	1416 – 1904	-0.7 – 5	✓	✗	✓	✗	✗

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Table 2: Results of the geophysical model for soil organic carbon (R^2_{Adj} = 0.34).

Model term	Estimate	SE	t-value	P-value	
Intercept	-0.525	1.802	-0.291	0.771	
Climate variables					
MAP	0.003	0.001	4.560	<0.001	***
TSIS	-0.098	0.228	-0.429	0.669	
Topography variables					
Slope	-0.339	0.095	-3.569	0.001	***
Exposed	-3.130	0.936	-3.344	0.001	**
Soil type variables					
Clay	0.121	0.027	4.500	<0.001	***
Management variables					
Low intensity	-5.013	1.196	-4.192	<0.001	***
Medium intensity	2.012	1.168	1.722	0.088	
Interactions between variable types					
TSIS x Exposed	0.417	0.124	3.358	0.001	**
TSIS x Slope	0.044	0.013	3.452	0.001	***
MAP x Clay	0.000	0.000	-4.637	<0.001	***
TSIS x Low intensity	0.655	0.159	4.110	<0.001	***
TSIS x Medium intensity	-0.262	0.156	-1.684	0.095	

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Table 3: Results of the Combined model for soil organic carbon (R^2_{Adj} = 0.61).

Model term	Estimate	SE	t-value	P-value	
Intercept	-0.290	1.458	-0.199	0.843	
Climate variables					
MAP	-0.001	0.000	-2.434	0.017	*
TSIS	-0.004	0.181	-0.022	0.982	
Topography variables					
Slope	-0.225	0.078	-2.868	0.005	**
Management variables					
Cattle	0.487	0.101	4.834	<0.001	***
Mixed	-0.289	0.093	-3.106	0.002	**
Low intensity	-3.249	1.014	-3.204	0.002	**
Medium intensity	1.666	1.073	1.553	0.123	
Soil nutrient variables					
Log(Soil C/N)	0.665	0.076	8.777	<0.001	***
Soil N	3.302	0.617	5.349	<0.001	***
Herbage variables					
NDF	0.014	0.006	2.525	0.013	*
Herbage ADL/NH	0.026	0.009	2.987	0.003	**
Interactions between variable types					
TSIS x Slope	0.030	0.010	2.833	0.006	**
TSIS x Low intensity	0.423	0.136	3.104	0.002	**
TSIS x Medium intensity	-0.214	0.143	-1.495	0.138	
Soil N x Cattle grazing	-0.736	0.168	-4.380	<0.001	***
Soil N x Mixed grazing	0.493	0.175	2.813	0.006	**
Soil N x NDF	-0.039	0.011	-3.505	0.001	***
Cattle x Herbage ADL/NH	-0.030	0.010	-2.872	0.005	**
Mixed x Herbage ADL/NH	0.014	0.011	1.252	0.213	

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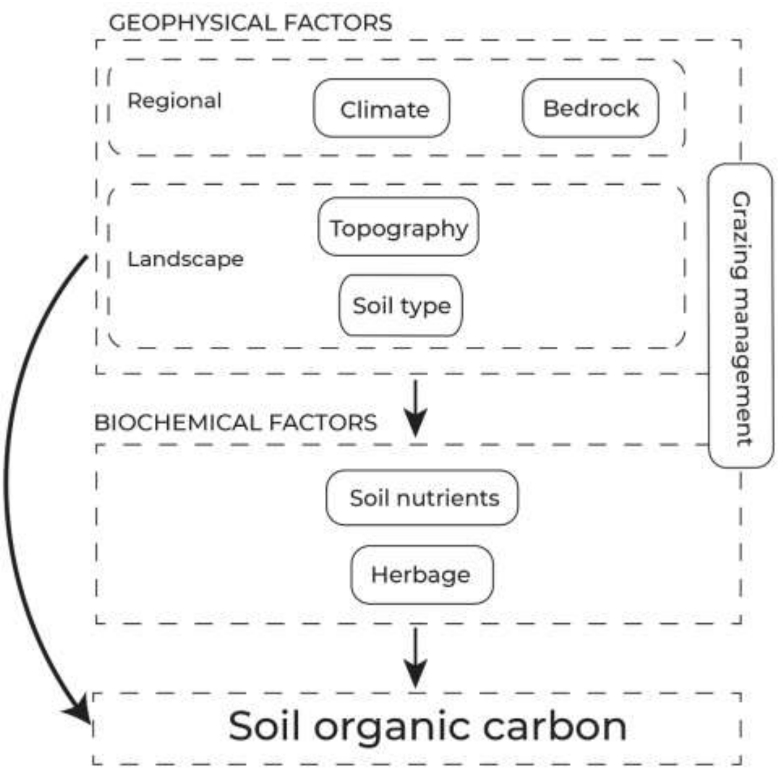
Figures



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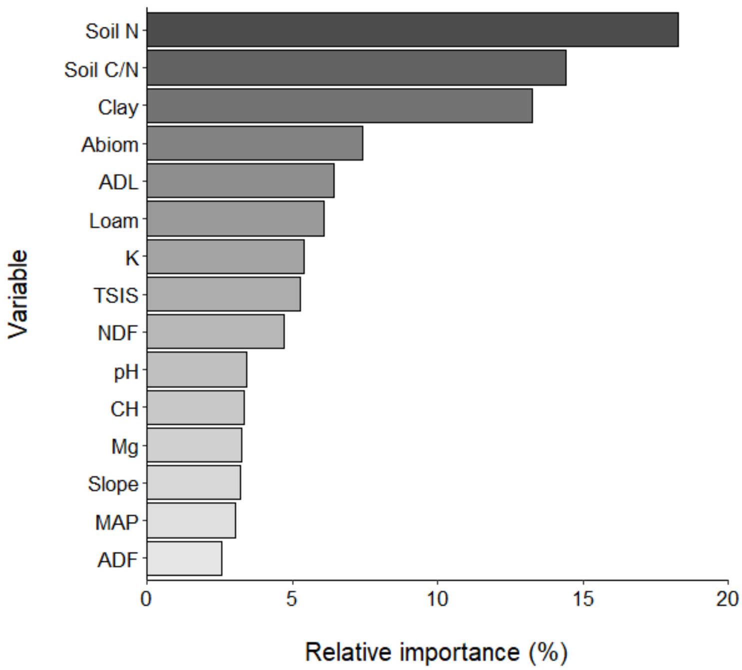

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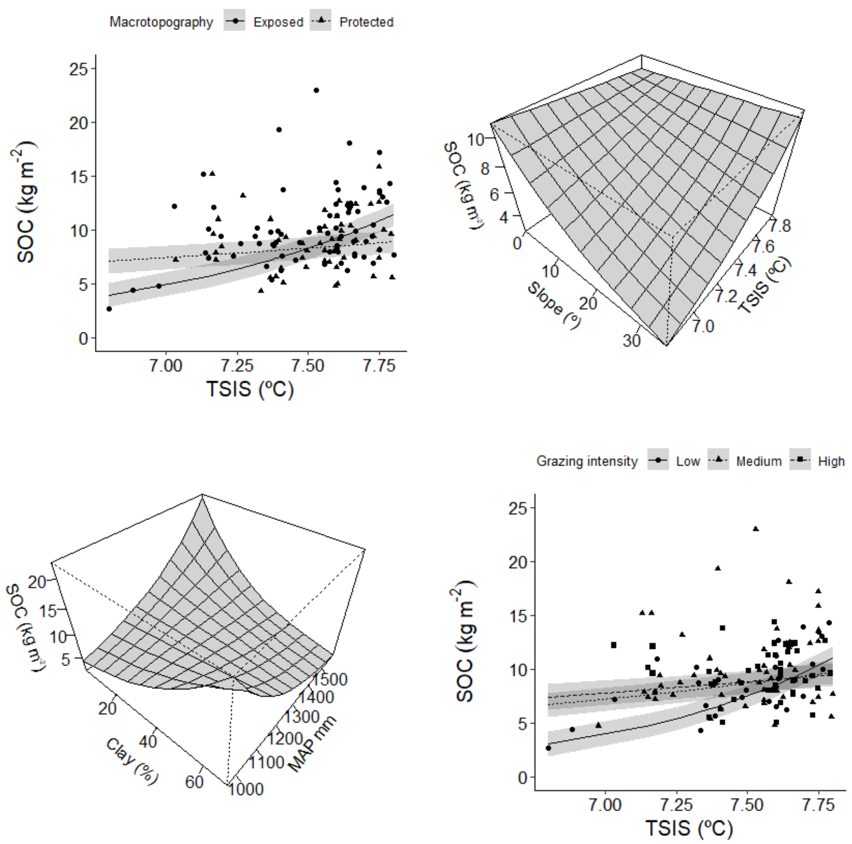

Figure 3. The relationship between SOC and regional and landscape scale factors in the Geophysical model. In A) solid lines and circles represent exposed hillsides, and dotted lines and triangles indicate protected hillsides. In D) solid lines and circles indicate low grazing management intensity, dotted lines and triangles indicate medium grazing management intensity and dashed lines and squares indicate high grazing management intensity. In A-D line and plane values are predictions of the model across the corresponding predictors´ range according to estimate marginal means. Grey areas around regression lines indicate standard errors. In A) and D) points indicate actual values.

https://doi.org/10.5194/bg-2020-63
Preprint. Discussion started: 17 March 2020

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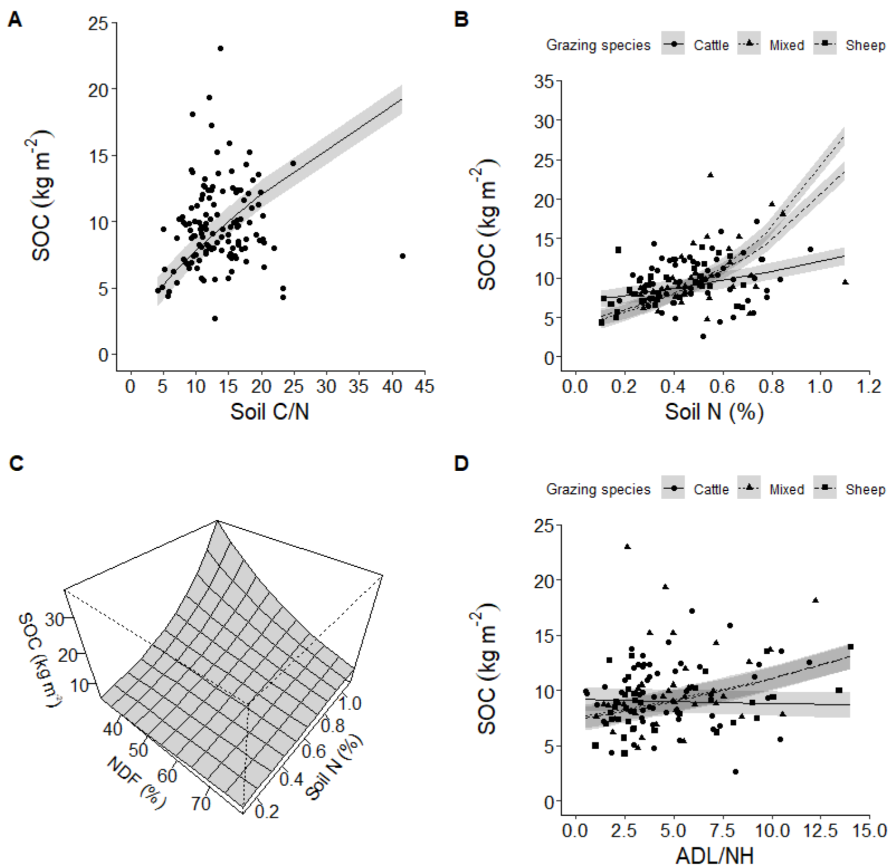

Figure 4. The relationship between SOC and biochemical and herbage factors in the Combined model. In B) and D) solid lines and circle points represent cattle-grazing, dashed lines and square points indicate sheep-grazing and dotted lines and triangle points indicate mixed-grazing. In A-D line and plane values are predictions of the model across the corresponding predictors´ range according to estimate marginal means. In A-D line and plane values are predictions of the model across the corresponding predictors´ range according to estimate marginal means. Grey spectrum indicate 95% confidence intervals. In A) and D) points indicate actual values.