ORIGINAL PAPER

N₂-fixing Shrubs as Nature-based Solutions to Store Soil Nutrients in Grazed Post-mining Pastures of Northern Spain

Elena Muñoz-Cerro[1] · Juan García-Duro[1] · Carolina Martínez-Ruiz[1] · Daphne López-Marcos[2]

Abstract

Grazing can adversely affect soil physicochemical properties and, despite its potential benefits on restored areas, may ultimately lead to the ecosystem degradation. Given that shrubs can partially buffer these effects, we investigate their potential as a Nature-based Solution to enhance soil nutrient storage in grazed, post-mining pastures. We assessed the combined influence of legume shrubs (plots with vs. without shrubs) and grazing (plots with vs. without a fence to prevent browsing and trampling) on soil C: N:P stoichiometry, as well as on C-N-P and exchangeable cations' stocks in a rehabilitated coal mine. The natural colonization of legume shrubs in post-mining Mediterranean pastures maintained C: N:P stoichiometry and nutrient stocks at levels comparable to those in ungrazed areas. Specifically, the presence of shrubs increased total soil organic carbon, nitrogen, and phosphorus stocks by approximately 15%, 18%, and 12%, respectively, compared to grazed areas without shrubs. In addition, exchangeable potassium (K^+) and magnesium (Mg^{+2}) stocks increased by approximately 20% and 16%, respectively, under shrub canopies. In contrast, exchangeable calcium (Ca^{+2}) and sodium (Na^+) stocks exhibited divergent trends. In Mediterranean post-mining grasslands with low grazing pressure, native leguminous shrubs can effectively replicate the benefits of grazing exclusion by significantly enhancing soil nutrient storage. Variations in soil organic matter and structural properties accounted for 75% and 76% of the variability in nutrient stocks, respectively, underscoring their key mediating roles. These findings highlight the importance of integrating shrub management with grazing practices to support nutrient cycling and soil restoration in degraded grassland ecosystems.

Highlights

- Legume shrubs have the same effect as livestock exclusion in storing soil nutrients.
- Shrubs and grazing influence soil nutrients via soil organic matter and structure.
- Shrubs as NbS in grazed post-mining pastures to increase soil nutrient storage.
- Grazing and shrub management joint strategies for soil nutrient storage in pastures.
- Shrubs in post-mining pastures with moderate grazing balance soil nutrient storage.

✉ Elena Muñoz-Cerro
  elena.munoz.cerro@uva.es

  Juan García-Duro
  juan.garcia.duro@uva.es

  Carolina Martínez-Ruiz
  carolina.martinez.ruiz@uva.es

  Daphne López-Marcos
  daphne.lopez@uva.es

1 Área de Ecología, Dpto. Ciencias Agroforestales, Instituto Universitario en Gestión Forestal Sostenible (iuFOR), E.T.S. de Ingenierías Agrarias,, Universidad de Valladolid, Campus La Yutera, Avda. Madrid 50, Palencia 34071, Spain

2 Área de Edafología y Química Agrícola, Dpto. Ciencias Agroforestales, Instituto Universitario en Gestión Forestal Sostenible (iuFOR), E.T.S. de Ingenierías Agrarias, Universidad de Valladolid, Campus La Yutera, Avda. Madrid 50, Palencia 34071, Spain

Graphical abstract
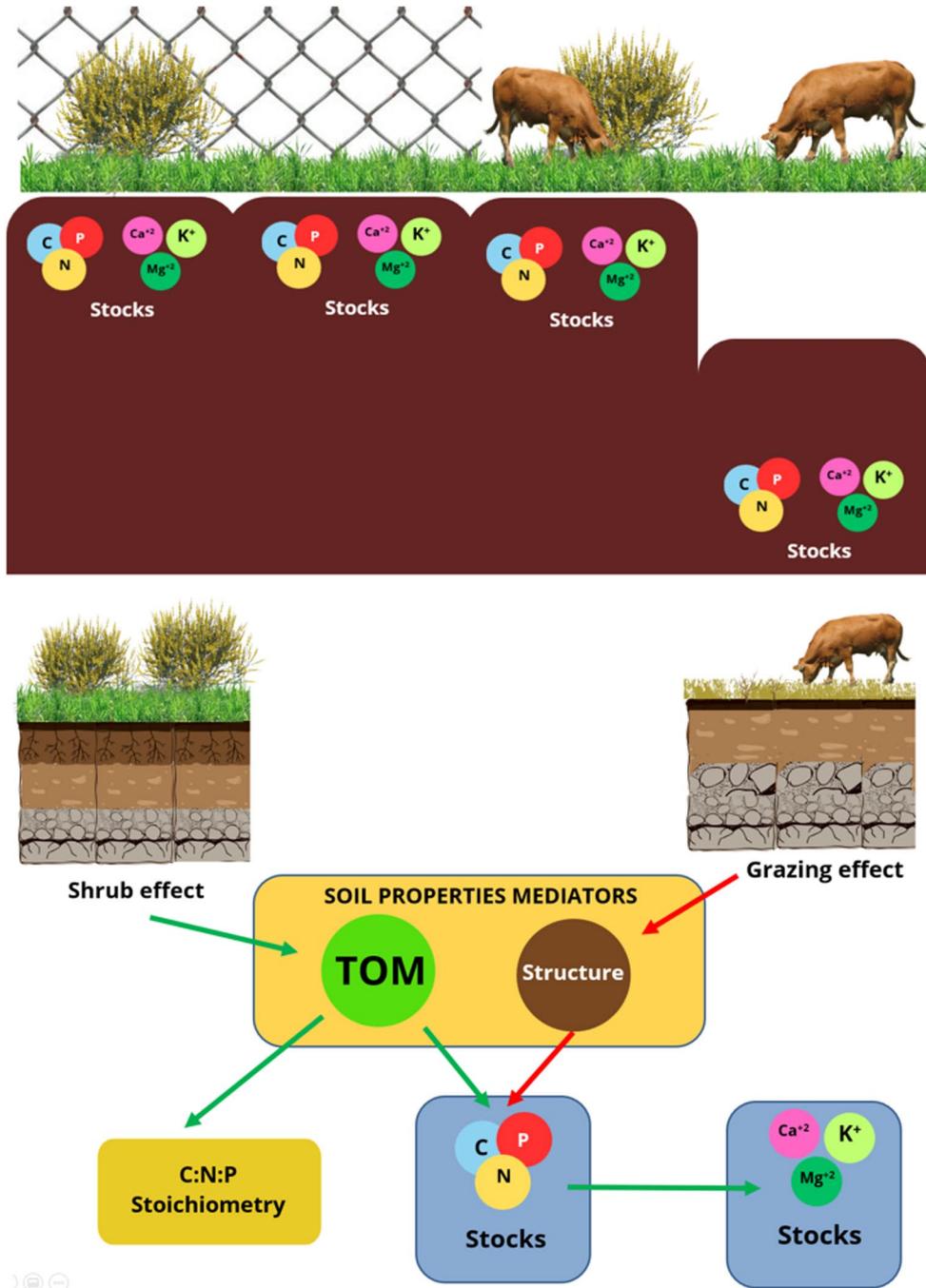
1 Introduction

In Spain, the progressive decline of coal mining since the 1990s (IEA 2019) has profoundly transformed local economies, leading many rural communities to adopt agriculture and extensive livestock farming as alternative livelihoods after mining (Sigcha et al. 2018). However, the long history of mining has left persistent impacts, critically impairing soil properties and their ecological functions (Bell and Donnelly 2006). Post-mining landscapes often exhibit severely degraded soil conditions —low nutrient availability, poor structure, altered

groundwater regimes, and reduced biological activity— that hinder natural regeneration and ecosystem recovery (Bell and Donnelly 2006; Misebo et al. 2022). Consequently, restoring soil health has become a central objective in ecosystem reclamation, aiming to enhance soil fertility, nutrient cycling, biodiversity, and overall ecosystem productivity (Vitousek et al. 1997; Lal 2004; Alday et al. 2011).

Livestock grazing is a common management practice in rehabilitated pastures following mining, providing both economic support and continuity of land use for local communities. Nevertheless, the effects of grazing on soil characteristics are highly variable and context dependent. Although grazing often increases the availability of nutrients such as nitrogen and phosphorus, its impacts on soil organic carbon stocks vary widely depending on grazing intensity, management regimes, and site-specific ecological conditions (Hassan et al. 2021). Under intensive grazing, soil compaction and erosion caused by trampling can exacerbate degradation and reduce long-term productivity (Eldridge et al. 2015; Liu et al. 2022).

Within these grazing systems, the presence of scattered native legume shrubs is increasingly recognized for its ecological benefits (Alday et al. 2014; Manso-Arribas et al. 2024). Legume shrubs enhance soil fertility primarily through nitrogen fixation and decomposition of nutrient-rich litter, increasing soil organic carbon and improving overall soil nutrient dynamics (Costa et al. 2017; Mushinski et al. 2024). Moreover, shrubs mitigate grazing-induced impacts such as compaction and erosion by providing protective cover and stabilizing soil structure through their root systems (Eldridge et al. 2015; Muñoz-Cerro et al. 2023). Integrating shrubs into grazed pastures, therefore, represents a promising ecological strategy that reconciles productive land use with restoration objectives.

Grazing-shrub interactions can strongly influence soil C: N:P stoichiometry, a key indicator of soil fertility and biogeochemical cycling (Wang et al. 2022). Soil ratios such as C: N, C: P, and N: P are fundamental for understanding nutrient availability, decomposition rates, and overall soil health (Hu et al. 2022; Mushinski et al. 2024). Despite their recognized importance, the specific interactions between grazing intensity and shrub presence remain poorly understood and highly variable across environmental contexts (He et al. 2019). Comprehensive assessments of soil nutrient stocks —including total organic carbon, nitrogen, and phosphorus, and exchangeable cations such as calcium, magnesium, potassium, and sodium— are therefore essential for maintaining ecosystem functions and productivity in restored post-mining landscapes (Olde Venterink et al. 2003; Sardans and Peñuelas 2021; Tränkner et al. 2018). These nutrients directly support plant growth (Lal 2004), sustain ecosystem productivity (Vitousek et al. 1997), and enhance resilience to environmental stresses (Bell and Donnelly 2006). Hence, evaluating the influence of shrub-grazing interactions on soil nutrient storage provides critical insights for sustainable management of post-mining lands.

Our previous research highlights shrubs' significant positive impacts on soil nutrient status and fertility in coal mines restored to pastures in northern Spain (Alday et al. 2014; Muñoz-Cerro et al. 2023). These studies revealed that shrubs increase soil nutrient contents beneath their canopies —particularly organic carbon, nitrogen, and essential cations— thereby improving soil structure and nutrient cycling processes (Costa et al. 2017; Mushinski et al. 2024). Enhanced soil organic matter under shrub canopies also promotes soil aggregation, stability, and carbon sequestration for ecosystem sustainability (Pugnaire et al. 2004; Aramrak et al. 2021).

Legume shrubs, through their nitrogen-fixing capacity, provide additional ecological benefits by enriching soils with biologically available nitrogen, directly supporting plant productivity and ecosystem recovery (Jobbágy and Jackson 2001; Eldridge et al. 2015). Consequently, integrating shrubs into post-mining pasture systems can increase soil fertility while reducing dependence on external nutrient inputs, offering a cost-effective, nature-based solution to the environmental challenges on former mining sites (IUCN 2020; Hudson et al. 2023).

Based on previous evidence that legume shrubs can buffer the negative effects of grazing on soil structure and fertility, we hypothesized that (1) leguminous shrubs canopies mitigate grazing-induced degradation and enhance soil quality and nutrient storage in Mediterranean post-mining pastures, and (2) there is a cascade effect of the main factors (shrubs, and grazing), on the C: N:P stoichiometry and nutrient stocks through secondary factors, such as soil total organic matter and structure. Specifically, our specific objectives were: (1) to quantify the single and combined effects of shrub and grazing presence on soil C: N:P stoichiometry and soil nutrient stocks, including total organic carbon, nitrogen and phosphorus, and key exchangeable cations; (2) to evaluate the relative contribution of shrubs and grazing to soil nutrient dynamics; and (3) to assess the potential feedback mechanisms among shrubs, grazing, soil stoichiometry, and nutrient storage. Insights from this study aim to inform management strategies that integrate productive agricultural practices with ecological restoration goals, thereby supporting the long-term sustainability and resilience of Mediterranean post-mining ecosystems.

2 Materials and Methods

2.1 Study Site

This study was carried out in the central Cantabrian range (Northern Spain), within a 17-ha opencast coal mine rehabilitated to pasture in Guardo (42°48′ N, 4°52′ W; ca. 1200 m a.s.l.; Fig. 1A). The climate is Oceanic Mediterranean (Csb) according to the Köppen classification for the Iberian Peninsula (Nafría-García et al. 2013), characterized by an average annual precipitation of 977 mm, with rainy periods in autumn and spring, and acute summer drought in July and August, when only 8% of the annual rainfall occurs (Milder et al. 2013). The mean annual temperature is 9.3 °C, the mean minimum temperature of the coldest month (January) is -2.7 °C, and the mean maximum temperature of the warmest month (August) is 25.9 °C (Milder et al. 2013). The mine is surrounded by deciduous broadleaved forests dominated by *Quercus pyrenaica* Willd., with the presence of *Quercus petraea* (Matt.) Liebl., and a diverse understorey (e.g., *Crataegus monogyna* Jacq., *Sorbus* spp., *Cytisus scoparius* (L.) Link, and *Genista florida* L.; see Milder et al. 2013). The natural soils are mainly Inceptisols (*sensu* Soil-Survey-Staff 2022) with a udic soil moisture regime and mesic soil temperature regime (López-Marcos et al. 2020). The dominant soil class surrounding this mine is a Typic Dystroudept (*sensu* Soil Survey Staff 2022), with a sandy clay loam texture, acid pH ($4.3-4.8$), electrical conductivity of 0.0082 S m^{-1}, without evidence of carbonates, high soil organic matter content, and low available phosphorous content (López-Marcos et al. 2020).

2.2 Post-mining Restoration and Land Use

The opencast coal mine was rehabilitated in October 2000. The open pit was filled up with coal mining wastes from nearby mines to regrade the mine gap to the original contour (Martínez-Ruiz et al. 2021). Then, wastes were covered with fine-textured materials amended with cattle manure (30 t ha^{-1}) and fertilizer (8 N:1P:15 K; 150 kg ha^{-1}). The fine-textured materials were a mixture of topsoil and mine tailings from deeper parts of the nearest opencast pits (Martínez-Ruiz et al. 2021) with a very poor seed bank (González-Alday et al. 2009), clay loam texture, pH of 6.5, electrical conductivity of 0.0114 S m-1, easily oxidizable carbon of 1.98%, available phosphorus of 9.7 mg kg^{-1}, and effective depth of 10–15 cm (López-Marcos et al. 2020). The mine soils after the rehabilitation process were Lithic Udorthents (Soil Survey Staff 2022), and they had a very low water holding capacity compared to the natural soil in the forest (2.27±0.36 vs. 19.87±1.52 g cm^{-2}; López-Marcos et al. 2020). After topsoiling, the mine was hydroseeded with a commercial seed mixture (300 kg ha^{-1}) of mostly perennial grasses and legume herbs (74:26 by weight; Muñoz-Cerro et al. 2023) to contribute to the establishment of a permanent plant cover (Alday et al. 2011).
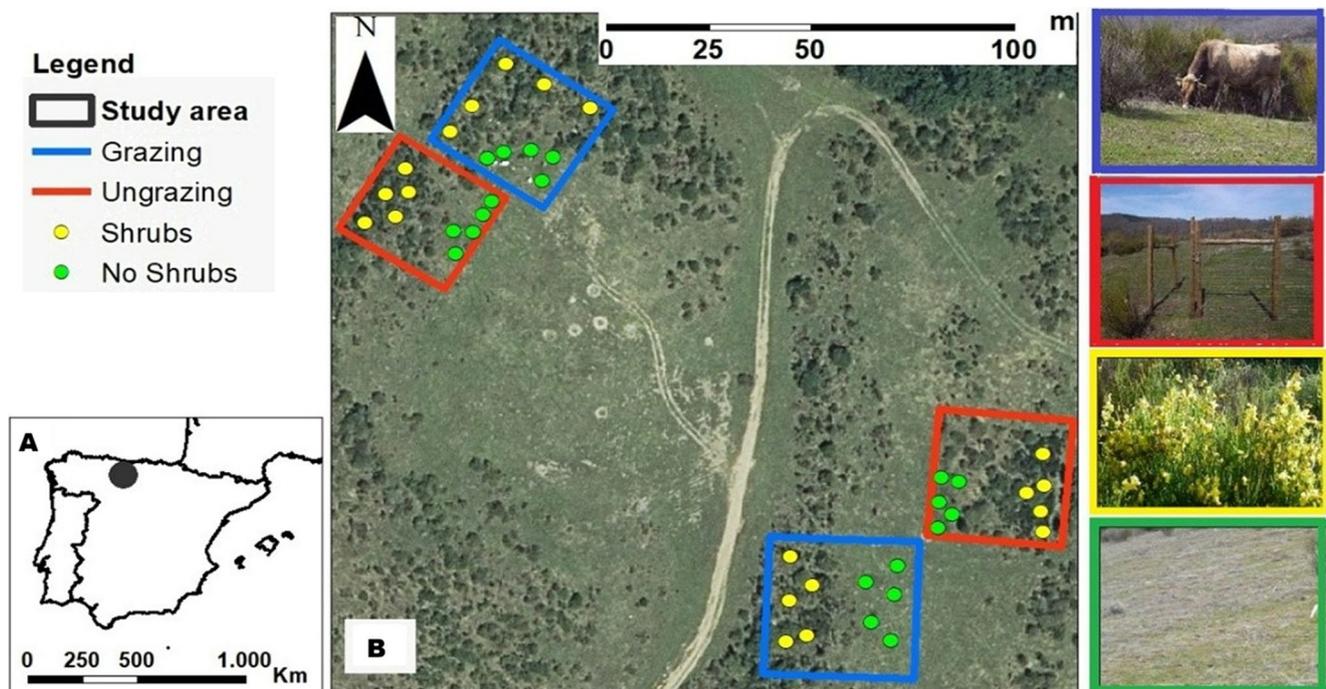

Fig. 1 (**A**) Location of the study area in northern Spain and (**B**) scheme of the experimental device in a current orthophotograph

After mine rehabilitation, wild ungulates (e.g., deer, roe deer, and wild boar) and cattle livestock (light stocking rate < 10 AU 100 ha^{-1}, AU= animal unit; Teague et al. 2011) freely feed on the vegetation established in the study area (Milder et al. 2013). Native herb species from neighbouring areas gradually replaced hydroseeded ones (López-Marcos et al. 2020), and native shrub species, mainly *Cytisus scoparius* and *Genista florida*, also colonized the rehabilitated mine (Muñoz-Cerro et al. 2023).

C. scoparius and *G. florida* are two common native shrub species that often colonize degraded sites (Milder et al. 2013), forming mixed patches. Both species are non-thorny leguminous shrubs that share most of their structural and functional characteristics (e.g., structure, leaf-related traits, phenology, and atmospheric N-fixation; Talavera and Castroviejo 1999). In addition, both species' populations within the rehabilitated mine also had very similar ages and sizes (height mean ± SE: 2.22 ± 0.066 m), and the number of individuals per species was balanced so they were not differentiated in the experiment (Muñoz-Cerro et al. 2023).

2.3 Experimental Set-up

To assess the independent and combined influence of nurse shrubs and grazing upon C: N:P stoichiometry, and nutrient and cation stocks, we implemented a split-plot experimental design combining two factors: shrub presence (with shrub vs. without shrub) and grazing regime (grazing vs. no-grazing). For that the experimental set-up consisted of four permanent plots (30 m x 30 m) established in a flat area of the mine in February 2011 (i.e., 11 years after rehabilitation): two of them surrounded by 2-m-height fences (5 cm x 15 cm mesh hole) for the exclusion of wild ungulates and livestock, and another two non-fenced plots in their proximity (Fig. 1B). Within each plot, ten permanent subplots (five with shrubs and five without shrubs) were allocated randomly ca. 4 m apart from each other; shrub presence or absence was not manipulated for the experiment. Each subplot measured ca. 2 m x 2 m, and the subplots with shrubs included 2–3 mature, naturally recruited shrub plants of *C. scoparius* and *G. florida* (Torroba-Balmori et al. 2015; Muñoz-Cerro et al. 2026). The four combinations to be tested were: (a) grazing with shrubs, (b) grazing without shrubs, (c) no-grazing with shrubs, and (d) no-grazing without shrubs.

2.4 Soil Sampling and Analysis

Soil sampling was conducted in spring 2019 (i.e., 9 years after grazing exclusion, and 19 years after mine rehabilitation). In each of the 40 subplots, soil was collected from the first mineral horizon. Two samples were

obtained per subplot: One undisturbed and another disturbed. The 40 undisturbed samples, collected with a 5 cm-depth cylinder (251.33 cm^3), oven-dried at 105 °C for 24 h and weighed (± 0.001 g), were used to determine the bulk density (BD). For the 40 disturbed samples, all the topsoil in a 25 cm x 25 cm quadrant up to the coal wastes was collected, thus varying the thickness of this first mineral horizon (TH) in each subplot (15 cm maximum depth, see Muñoz-Cerro et al. 2023). These were air-dried and sieved (2 mm mesh) to determine the fine-earth fraction (< 2 mm; %EF). With this fraction, we measured the texture (sand, silt, and clay) by the Bouyoucos method (Day 1965); real density (RD) by the pycnometer method (MAPA 1994); total organic carbon (TOC) by the Van Bemmelen factor (1.724; Van Bemmelen 1890) from total organic matter (TOM) measured by the redox volumetric method (Walkley and Black 1934); total N by the Kjeldahl method (Bremner and Mulvaney 1982); total P, extracted by microwave digestion (ETHOS EASY Milestone Microwave) with a 9:1 concentrated Nitric: Hydrogen Peroxide solution, and measured by optical ICP (Spectro Genesis); pH and electrical conductivity (EC) determined by 1:2.5 soil: deionized-water slurry (Allen 1989); cation exchange capacity (CEC) by Rhoades (1982) method with barium chloride and triethanolamine at pH = 8.1; and exchangeable cations (calcium [Ca^{+2}], potassium [K^+], magnesium [Mg^{+2}], sodium [Na^+]) by atomic emission spectroscopy (Schollengberger and Simon 1945) in 1 M ammonium acetate (pH 7).

2.5 Determination of Stoichiometric Ratios and Stocks of Nutrients and Exchangeable Cations

The mineral soil's C: N:P ratios were expressed as mass ratios of TOC, TN, and TP, respectively. The stocks of TOC, TN, TP, and exchangeable cations (K^+, Ca^{+2}, Mg^{+2}, and Na^+) of the soil up to the coal wastes were calculated as in López-Marcos et al. (2018):

$$E_{stock}\ [kg\ ha^{-1}] = E_{cont}\ [g_{ELEMENTAL}\ kg_{EF}^{-1}] \times BD\ [g_{SOIL}\ cm^{-3}] \times EF\ [g_{EF}\ kg_{SOIL}^{-1}] \times TH\ [cm] \quad (1)$$

where E_{stock} is the elemental stock, E_{cont} is the elemental content, BD is the bulk density, EF is the fine-earth fraction, and TH is the thickness up to the coal wastes.

The sum of bases (SB) was calculated as the sum of the concentrations of exchangeable cations (see López-Marcos et al. 2018), and the porosity as in MAPA (1994):

$$Porosity = [1 - (BD\ [g\ cm^{-3}])/RD\ [g\ cm^{-3}]]) \times 100 \quad (2)$$

where BD and RD are bulk and real density, respectively.

2.6 Statistical Analysis

To assess the effects of shrubs and grazing on soil nutrient stocks and C: N:P stoichiometry, we built linear-mixed models (LMM; Pinheiro and Bates 2000), with the fixed effects of shrub and grazing and their interaction on each soil parameter. During the preliminary analysis, all different random effects, nesting structures, heteroscedasticity, and autocorrelation variations were tested to get the most accurate results possible, fitting the models by maximum likelihood (ML; Richards 2005) to get the most accurate results possible. The Akaike information criterion (AIC) was used to select the most parsimonious model (i.e., smaller values of AIC; Pinheiro and Bates 2000), and the ANOVA was applied to test the significant differences among them. No clear evidence of autocorrelation and/or heteroscedasticity was found for any variable, and subplot 40 from treatment 'grazing with shrubs' was considered an outlier and excluded from all analyses because it had special soil conditions. The models selected for testing differences among treatments included the intercepts of the plot and the subplot nested within it as random effects. They were fit by the restricted maximum likelihood method (REML; Richards 2005), and the significance of fixed effects was determined by the analysis of the variance for the terms of the model, and the corresponding p-value significance (Pinheiro and Bates 2000). Finally, working over the model matrix, multiple pairwise comparisons (Pinheiro and Bates 2000) were calculated to test differences between treatments when the interaction between both fixed factor levels had significant effects. The Bonferroni correction was used to adjust the significance level for each t-test, thus preventing Type I error inflation (Sokal and Rohlf 1995).

Variance partitioning was used to determine the proportion of variation in C: N:P stoichiometry, C-N-P stocks, and exchangeable cations' stocks explained individually and collectively by different factors (i.e., main factors and secondary factors). Shrubs and Grazing were considered the main factors, whereas soil TOM and Structure (a latent variable constructed with clay and porosity data) were selected as secondary factors.

Finally, we used Structural Equation Models (SEMs) to explore the relationship between C: N:P stoichiometry, C-N-P stocks, and exchangeable cations' stocks through the effect of shrubs and grazing (main factors) on soil TOM and Structure (secondary factors). Here, we hypothesized that there is a cascade effect of the main factors (shrubs, and grazing), on the C: N:P stoichiometry (C: N, N: P, and C: P), C-N-P stocks (TOCstock, TNstock, and TPstock), and exchangeable cations' stocks (Ca^{+2}stock, Mg^{+2}stock, and K^+stock) through secondary factors, such as soil TOM and Structure; the Na^+stock was not included in the model

because its content in our mining soils is not high enough to cause problems (Muñoz-cerro et al. 2023). SEMs model simplification method was based on the Akaike Information Criterion (AIC), deleting all the non-significant model's path coefficients (Alday et al. 2016; López-Marcos et al. 2021). The model goodness of fit was evaluated with the chi-square statistic, the root mean square error of approximation (RMSEA), and the goodness-of-fit index (GFI). Chi-square values higher than 0.05, RMSEA below 0.08, and a GFI above 0.90 indicate an acceptable fit for the model (Grace 2006; Alday et al. 2016; López-Marcos et al. 2021).

All statistical analyses were implemented in the R software environment (4.1.2; R-Core Team 2021) with the nlme package for fitting linear mixed models (LMM; 3.1–162; Pinheiro et al. 2023), the "varpart" function of the vegan package for variance partitioning analyses (Oksanen et al. 2020), and the lavaan package for SEMs (Rosseel 2012).

3 Results

3.1 Effects of Shrub and Grazing on Soil C: N:P Stoichiometry

The C: N ratio was influenced by shrubs' and grazing' simple effects (Table 1.a) and reached higher values beneath than outside the shrub canopy (10.8 ± 0.26 vs. 9.6 ± 0.40) and without than with grazing (10.5 ± 0.39 vs. 9.8 ± 0.32). The C: P and N: P ratios were influenced by the combined effect of shrub and grazing (Table 1.a) and reached higher values beneath than outside shrubs in grazed areas but similar values in ungrazed areas (Fig. 2).

Table 1 F-value and significance ($*p < 0.05$; $**p < 0.01$; $***p < 0.001$) of the ANOVA applied to each Linear-Mixed Models (LMM) testing the effect of shrub, grazing, and their interaction on **(a)** C: N:P stoichiometry, **(b)** C-N-P stocks, and **(c)** Exchangeable cations' stocks. TOC: total organic carbon; TN: total nitrogen; TP: total phosphorous; C:N=TOC/TN; N:P=TN/TP; C:P=TOC/TP

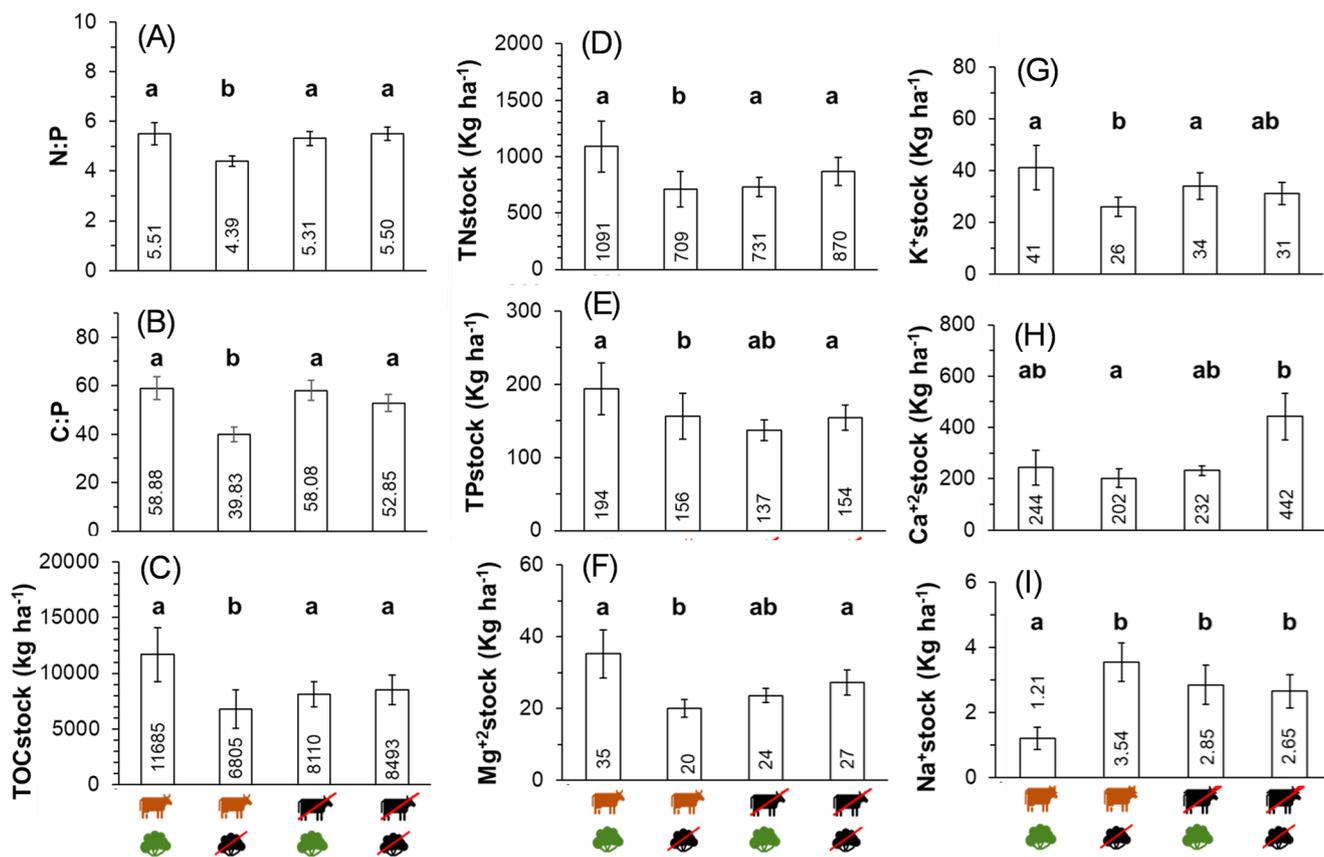|	Shrub	Grazing	Shrub x Grazing
(a) C: *N:P* stoichiometry			
C: N	11.31**	4.81*	2.60
N: P	3.35	7.48**	5.34*
C: P	14.95***	9.82**	5.99*
(b) C-N-P stocks [kg ha^{-1}]			
TOCstock	4.53*	13.39***	10.02**
TNstock	2.99	13.08**	10.09**
TPstock	2.30	7.14*	6.65*
(c) Exchangeable cations' stocks [kg ha^{-1}]			
Ca^{+2}stock	0.004	2.68	4.69*
Mg^{+2}stock	0.99	3.58	6.36*
K^+stock	1.70	3.15	5.07*
Na^+stock	4.98*	4.32*	6.50*

Fig. 2 Mean value±standard error of soil N: P and C: P stoichiometry (**A**, **B**), C-N-P stocks (**C**, **D**, **E**) and exchangeable cations' stocks (**F**, **G**, **H**, **I**) according to the ANOVA results in Table 1. Different letters indicate significant differences between pair-wise comparisons with Bonferroni's test ($p < 0.05$). Abbreviations as in Table 1

3.2 Effects of Shrub and Grazing on Soil C-N-P Stocks, and Exchangeable Cations' Stocks

Soil C-N-P stocks (Table 1.b) and exchangeable cations' stocks (Table 1.c) were affected by the shrub x grazing interaction effect. They reached significantly higher values beneath the shrub canopy in grazed areas but similar values in ungrazed areas, except for Na$^+$stock, which reached significantly higher values outside than beneath shrubs in grazed areas but similar values in ungrazed areas (Fig. 2).

3.3 Different Factors Explain the Proportion of Variation in Soil C: N:P Stoichiometry, C-P-N Stocks, and Exchangeable Cations' Stocks

Main factors (i.e., Shrubs and Grazing) explained a very low percentage of the variation of C: N:P stoichiometry, C-N-P stocks, and exchangeable cations' stocks (20%, 0%, and 8%, respectively; Table SM1). Nevertheless, secondary factors, such as TOM, and Structure (latent variable constructed by clay and porosity), explained a higher proportion of these variations (75%, 76%, and 13%, respectively; Table SM2),

being the combination of both secondary factors (TOM, and Structure) which explains the greatest variation of C: N:P stoichiometry, C-N-Pstocks, and exchangeable cations' stocks (10%, 32%, and 16%, respectively; Table SM3). In addition, Shrubs explained alone 19% of the TOM variation, and Grazing explained alone 5% of the structure variation (Table SM4). Accordingly, we tested several main and secondary factor combinations to unravel the cascading effect.

The combination of main and secondary factors improved the Exchangeable cations' stocks variance explanation by 24% and reached 37% of the explained variation (Table SM3). Nevertheless, this combination barely improved the explained variation of C: N:P stoichiometry and C-N-P stocks: it increased the explained variation by only 1% in the case of C: N:P stoichiometry (up to 76%; Table SM3) and did not yield any improvement for C–N–P stocks (Table SM3). This suggests that the main factors exert their influence in C: N:P stoichiometry and C-N-P stocks through secondary factors such as the TOM and Structure.

The combination of the secondary factors (i.e., TOM and Structure) plus C: N:P stoichiometry worsened the explained variation of C-N-P stocks by 5% (down to 71%;

Table SM5). In the same way, the combination of the secondary factors plus C: N:P stoichiometry and C-N-P stocks also worsened the explained variation of exchangeable cations' stocks by 25% (down to 12%; Table SM6). That suggests that the C: N:P stoichiometry is an endpoint in the cascade-effects SEM design.

Nevertheless, the combination of the main factors (i.e., Shrubs and Grazing) plus C-N-P stocks improved the explained variation of exchangeable cations' stocks by 25% (up to 47%; Table SM7). In addition, the C-N-P stocks were the factor that alone explained the greatest variation in the exchangeable cations' stocks, in combination with main (33%; Table SM7) or secondary factors (3%; Table SM6). This suggests that the C-N-P stocks are a previous

step to exchangeable cation stocks in the cascade effects SEM design. According to the variance partition analyses, a global Structural Equation Model (SEM) was built.

The SEM showed a 0.75 CFI value, 0.183 SRMR, and 0.263 RMSEA (Fig. 3), relatively close to the acceptable fit convention: CFI > 0.90; SRMR < 0.1; RMSEA < 0.08). The adjustment may not be even greater because there is some intervening factor that we are not controlling. However, the model converged.

Shrubs have a significant direct effect on TOM and a positive, non-significant effect on C: N:P stoichiometry and structure. Grazing has a negative, no significant direct effect on C: N:P stoichiometry, structure, and TOM. TOM has a positive and significant direct effect on C: N:P stoichiometry
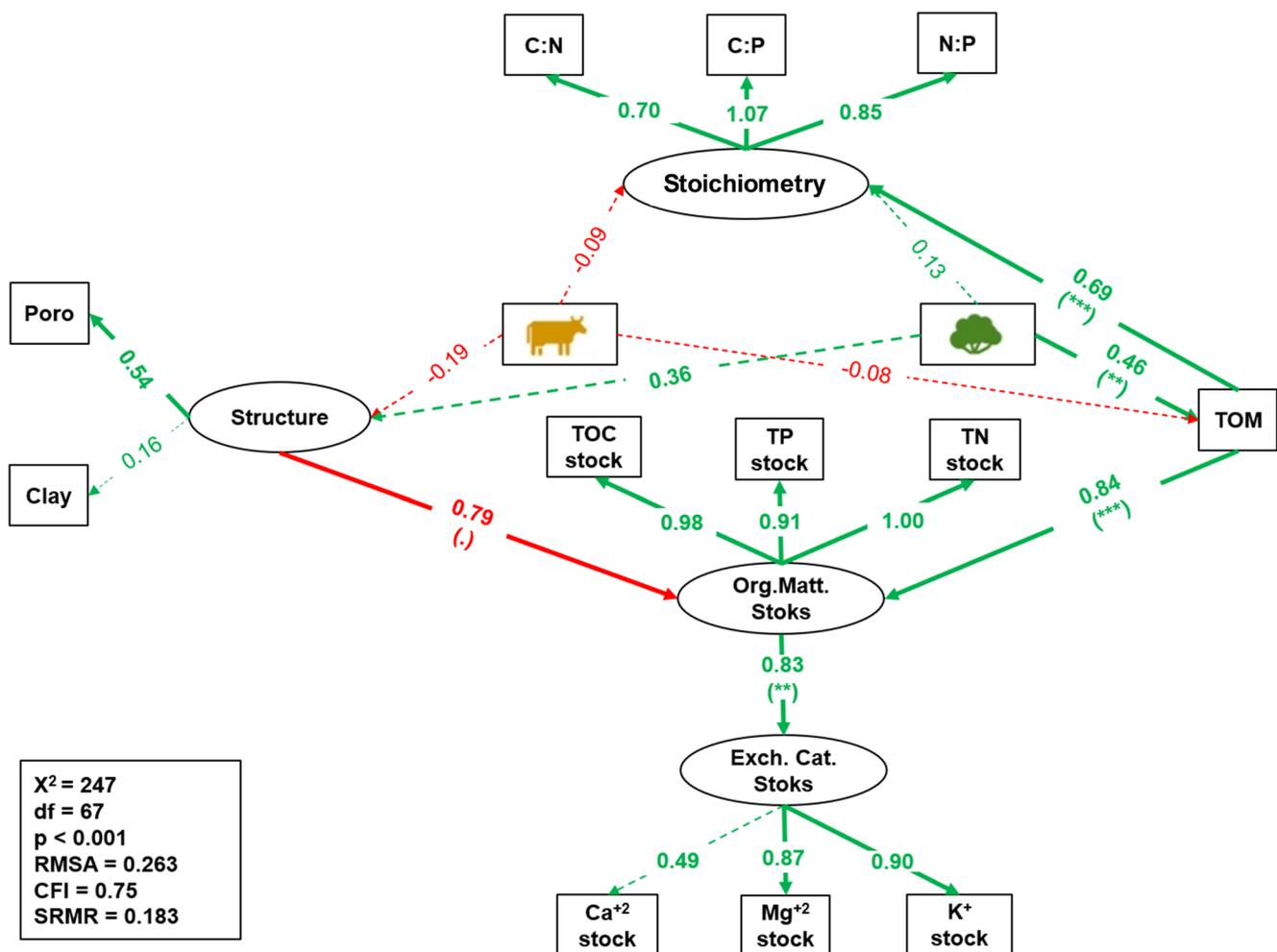

Fig. 3 Conceptual model depicting paths among the main and secondary factors to explain the cascade effect of Shrubs and Grazing (main factors) on C: N:P stoichiometry (C: N, N: P, and C: P), C-N-P stocks (TOCstock, TNstock and TPstock), and exchangeable cations' stocks (Ca^{+2}stock, Mg^{+2}stock, K^+stock) through secondary factors; i.e., Total organic matter (TOM) and the Structure latent variable, constructed by Clay and Porosity (Poro) data. Links significance (***$p < 0.001$; **$p < 0.01$; *$p < 0.05$). Arrow width is proportional to standardized path coefficients (shown beside arrows) and the colour represents the sign of the association (Red: negative associations between variables; green: positive associations between variables). Model fit measures: χ^2: chi-square test statistic; df: degrees of freedom; p-value of chi-square test; RMSEA: Root Mean Square Error of Approximation; SRMR: Standardized Root Mean Square Residual; CFI: Comparative Fit Index. Abbreviations as in Table 1

and C-N-P stocks. Structure has a negative near-significant direct effect on C-N-P stocks. C-N-P stocks have a significant direct effect on exchangeable cations' stocks.

The effect of shrubs and grazing on C: N:P stoichiometry and C-N-P stocks may be exerted through the secondary variables, TOM and Structure. The effect of shrubs and grazing on exchangeable cations' stocks may be exerted through the TOM, structure, C:N: P stoichiometry, and C-N-P stocks, describing a cascade effect.

4 Discussion

Shrub presence and grazing jointly structured soil C: N:P stoichiometry and nutrient stocks in rehabilitated mine soils, highlighting the role of vegetation–herbivory interactions in early ecosystem recovery.

Shrub presence increased the C: N ratio, indicating a lower proportion of labile carbon and slower organic matter decomposition (López-Marcos et al. 2020; Muñoz-Cerro et al. 2023), consistent with the accumulation of coarse, lignin-rich litter typically found beneath leguminous shrubs (Condron and Newman 1998). In contrast, grazing reduced the C: N ratio, likely due to decreased carbon inputs from herbaceous vegetation by browsing (Piñeiro et al. 2010) and accelerated decomposition caused by trampling, which disrupts soil aggregates and enhances microbial activity (Liu et al. 2022). However, grazing exerted little influence on soil nitrogen content, aligning with studies reporting weaker trampling effects on nitrogen storage (He et al. 2019). The lack of nitrogen enrichment suggests low stocking rates, as nitrogen inputs from livestock excreta or root turnover appear minimal in the absence of shrub cover (Wan et al. 2021; Muñoz-Cerro et al. 2023). Overall, under low to moderate grazing, shrubs primarily promote carbon accumulation and C: N shifts, whereas grazing mainly modulates carbon inputs and decomposition, markedly increasing nitrogen pools.

Shrubs-grazing interactions were most evident in C: P and N: P ratios, reflecting how microsite conditions and management shape elemental balance. The highest ratios occurred beneath shrubs in grazed areas, indicating a synergistic effect of shrub and grazing on nutrient enrichment and stoichiometric patterns. Similarly, C-N-P stocks were greater beneath shrubs in grazed areas, in line with findings in arid systems (Allington and Valone 2014; Muñoz-Cerro et al. 2023). Although N-fixing species often increase C: P and N: P ratios by elevating nitrogen demand and phosphorus uptake (Woś et al. 2022; Mitran et al. 2018; Ardanuy et al. 2021), such effects were not dominant here. Instead, the positive relationship between TOC and TP suggests the stabilization through shared soil processes (Doetterl et al.

2015; He et al. 2021; Sato et al. 2019), even though phosphorus content is largely governed by pedogenesis and substrate characteristics (Cao et al. 2015). Taken together, these patterns indicate that shrub–grazing interactions enhance C: P and N: P ratios and nutrient stocks mainly through physical and biogeochemical stabilization of organic matter and phosphorus, rather than by strong N-fixation effects.

Patterns of phosphorus availability and N: P ratios across microsites further illustrate how shrub–grazing interactions reorganize nutrient cycling in this post-mining ecosystem. While low C: P ratios typically promote microbial mineralization and phosphorus availability (Tian et al. 2010), we found higher available phosphorus beneath shrubs in grazed areas. This likely reflects the combined influence of dung inputs, litter accumulation, and surface nutrient redistribution through trampling (Zarekia et al. 2012; Muñoz-Cerro et al. 2023), which concentrates phosphorus beneath shrub canopies when grazing occurs. Conversely, the decline in soil N: P ratios in grazed open areas may result from selective herbivory on nitrogen-fixing herbs (Sigcha et al. 2018), soil compaction limiting organic matter accumulation (Šantrůčková et al. 1993), and increased nitrogen losses under grazing (Li et al. 2025). Microbial phosphorus translocation from phosphorus-rich coal substrates may also contribute to these trends (López-Marcos et al. 2020), and grazing exclusion has similarly been linked to reduced phosphorus stocks in other systems (Li et al. 2022).

Despite high C: P and N: P ratios often signaling nutrient immobilization, the relatively low C: N values observed (<15) suggest sufficient nitrogen availability for microbial activity (Brust 2019). The increase in C: P and N: P ratios under shrub-grazing interaction suggests advancing ecological succession and greater stoichiometric complexity over time (Ma et al. 2020). Thus, shrub–grazing microsites emerge as localized hotspots where phosphorus inputs, microbial activity, and stoichiometry dynamics together promote nutrient availability and successional progression.

These stoichiometric effects were mirrored at the level of total C-N-P stocks, underscoring the central role of shrub–grazing interactions in nutrient build-up in rehabilitated mine soils. Stocks were significantly higher beneath shrubs in grazed areas, indicating a synergistic interaction between vegetation and herbivory. Leguminous shrubs enhance nutrient inputs through nitrogen fixation and litterfall, while moderate grazing redistributes nutrients via trampling and organic returns (Tessema et al. 2011; Muñoz-Cerro et al. 2023). In ungrazed areas, no significant differences in TOC, TN, or TP stocks were detected between shrub-covered and open microsites, suggesting that shrubs alone may be insufficient to substantially alter nutrient pools and that grazing amplifies their influence, possibly by stimulating grass productivity and organic matter turnover. Similar dynamics

have been reported in arid ecosystems, where grazing under shrub canopies supports nutrient accumulation (Allington and Valone 2010).

The highest TP stocks under shrubs in grazed areas align with the known co-stabilization of phosphorus and organic carbon through aggregate formation and mineral association (Doetterl et al. 2015; He et al. 2021; Sato et al. 2019). Conversely, soil compaction in grazed open areas may reduce phosphorus uptake by plants, lowering available phosphorus (Barzegar et al. 2006). While total phosphorus availability is also shaped by weathering, parent material, and climate (Cao et al. 2015), our findings indicate that biotic factors such as shrub cover and grazing significantly modulate its spatial distribution.

Moreover, grazing exclusion has been associated with reduced phosphorus stocks (Li et al. 2022), reinforcing the role of controlled herbivory in maintaining nutrient levels. In addition, microbial biomass beneath shrubs may act as a nitrogen reservoir, particularly where faecal nitrogen inputs from livestock are captured and retained within organic matter pools (van der Wal et al. 2004; Barthelemy et al. 2015; Li et al. 2021).

Taken together, these results indicate that shrub presence combined with grazing enhances C-N-P stocks through increased organic matter inputs and nutrient retention mechanisms, creating localized hotspots of soil fertility that support early ecosystem recovery during initial soil development in post-mining landscapes.

Although N-fixing shrubs can improve soil fertility and nutrient cycling, their effects depend strongly on species identity and environmental context. Increased nitrogen availability mediated by N_2-fixing species may also entail ecological risks, even when these species are natives. For instance, in post-mining forests, native N_2-fixing trees characteristic of later successional stages have been shown to promote soil development in ways that favour strong competitors and ultimately reduce understory plant diversity (Mudrák et al. 2010). This highlights that the effects of N_2-fixing species depend on successional stage and dominant growth form, and thus may differ between forest-dominated systems and early, nutrient-poor post-mining grasslands colonized by shrubs, such as in the system examined here. Moreover, in some post-mining areas, non-native N-fixing shrubs (i.e., *Eleagnus umbellata*) have hindered ecosystem development and altered successional trajectories (Franke et al. 2018). This contrasts with our study system, where *Cytisus scoparius* and *Genista florida* are native, spontaneously colonizing shrubs that represent a natural successional stage in Mediterranean post-mining pastures (Milder et al. 2013; Alday et al. 2016). Previous research in this mine and similar ecosystems has shown that native shrubs enhance nutrient accumulation, improve soil structure, and promote

the establishment of late-successional species (Alday et al. 2014; Costa et al. 2017; Muñoz-Cerro et al. 2023). Therefore, while non-native shrubs may generate adverse effects, our findings apply to naturally occurring native shrubs within low-intensity grazing systems, where they act as effective microsite facilitators, enhancing soil restoration.

Exchangeable cations exhibited spatial patterns consistent with these nutrient hotspots. Shrubs' presence combined with grazing increased the stocks of exchangeable macronutrients such as potassium (K^+) and magnesium (Mg^{2+}). This likely reflects greater litter deposition, enhanced microbial activity, and organic matter accumulation in these microsites (Gómez-Aparicio et al. 2005; Celestina et al. 2019), as well as reduced soil compaction, which otherwise limits nutrient uptake by roots (Barzegar et al. 2006).

The structural equation model (SEM) confirmed a strong positive relationship between C-N-P stocks and exchangeable cations, reinforcing the idea that nutrient-rich organic matter supports cation storage. Soil organic matter, rich in carbon and nitrogen, drives cation exchange capacity and sorption processes, particularly in disturbed or nutrient-poor substrates such as mine soils (Tipping et al. 2016).

Interestingly, while K^+ and Mg^{2+} followed organic matter trends, Ca^{2+} showed higher stocks in ungrazed areas outside shrub canopies. This may reflect reduced soil degradation under livestock exclusion, as trampling destabilises soil aggregates and reduces Ca^{2+} retention (Yao et al. 2022). Previous findings in the study area also indicate improved porosity and lower bulk density in ungrazed soils, which may facilitate Ca^{2+} accumulation (Muñoz-Cerro et al. 2023). Additionally, browsing can limit litterfall and reduce calcium inputs from plant material (García-Palacios et al. 2016; Hu et al. 2022).

In contrast, sodium (Na^+) showed higher stocks in grazed areas outside shrub canopies, likely due to concentrated livestock excreta deposition in open spaces (Zarekia et al. 2012) and exclusion of Na^+ by shrub root systems, which often results in Na^+ enrichment in inter-shrub areas (Jobbágy and Jackson 2001). Although Na^+ can negatively affect soil structure by impairing aggregation (Feng et al. 2021), concentrations observed in this study are likely below thresholds for structural degradation (Garrido-Valero 1993). Nonetheless, its highest levels occurred in compacted, low-porosity soils, suggesting potential localized effects on soil quality.

Overall, these findings indicate that the spatial distribution of exchangeable cations in rehabilitated mine soils is closely linked to shrub presence and grazing activity, with organic matter and nutrient interactions playing a central role in their accumulation and stabilization.

The mechanistic basis for these patterns is captured by the cascade-like interaction revealed by variance

partitioning and SEM analyses: shrubs and grazing first influence soil total organic matter (TOM) and structure, which in turn affect C-N-P stocks and exchangeable cations. Shrubs exert a strong positive effect on TOM through persistent litter inputs and slow decomposition rates associated with high lignin content (Condron and Newman 1998), whereas grazing negatively affects soil structure via trampling, reducing porosity, and increasing compaction (Muñoz-Cerro et al. 2023).

TOM emerged as the main mediator in this system, showing significant positive effects on both C: N:P stoichiometry and nutrient stocks. This aligns with its role as a reservoir of organic nutrients and a key component in nutrient retention and sorption (Tipping et al. 2016). Meanwhile, soil structure —represented by a latent variable combining clay content and porosity (Poro)— showed a near-significant negative effect on C-N-P stocks. Compaction-related reduction in pore space may limit nutrient mobility and root access (Johannes et al. 2019; Obour et al. 2019).

Interestingly, the SEM did not reveal a significant direct link between C: N:P stoichiometry and nutrient or cation stocks, suggesting that stoichiometric ratios reflect the outcome of underlying biophysical processes rather than actively driving nutrient dynamics. In other words, stoichiometry appears as a response variable within the cascade, not a controlling factor.

These findings underline the central role of TOM in modulating nutrient availability and cation retention and highlight how its accumulation is strongly promoted by shrub presence. Although grazing can degrade soil structure, under low stocking rates —as observed in the study area— its negative impacts remain limited (Teague et al. 2011). Overall, the cascade model demonstrates that the indirect effects of shrubs and grazing, mediated through TOM and structure, are more influential than their direct impacts on nutrient dynamics. This emphasizes the importance of managing both biotic and abiotic components when aiming to restore soil function in post-mining ecosystems.

5 Conclusions

Our results demonstrated that the native leguminous shrubs, *Genista florida* and *Cytisus scoparius*, active colonizers of opencast coal mines rehabilitated to pastures in northern Spain, promote mine-soil nutrient storage and have positive synergistic effects with grazing. The presence of shrubs in grazing post-mining pastures with low stocking rates maintained the levels of C: N:P stoichiometry and nutrient stocks similar to those found in the absence of grazing. Furthermore, the effect of shrubs and grazing on soil C: N:P stoichiometry and nutrient stocks is mediated by secondary factors

such as soil organic matter and structure (a latent variable constructed by clay and porosity). These findings highlight the role of N-fixing legume shrubs as a Nature-based Solution in grazed post-mining pastures to increase soil nutrient storage, reducing the adverse effects of grazing on soil degradation.

Author Contribution Elena Muñoz-Cerro: Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft. Juan García-Duro: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Writing – review & editing. Carolina Martínez-Ruiz: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing. Daphne López-Marcos: Formal analysis, Investigation, Methodology, Resources, Supervision, Visualization, Writing –review & editing.

Data Availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

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

References

Alday JG, Marrs RH, Martínez Ruiz C (2011) Vegetation succession on reclaimed coal wastes in Spain: The influence of soil and environmental factors. Appl Veg Sci 14:84–94. https://doi.org/10.1111/j.1654-109X.2010.01104.x

Alday JG, Santana VM, Marrs RH, Martínez-Ruiz C (2014) Shrub-induced understory vegetation changes in reclaimed mine sites. Ecol Eng 73:691–698. https://doi.org/10.1016/j.ecoleng.2014.09.079

Alday JG, Zaldívar P, Torroba-Balmori P, Fernández-Santos B, Martínez-Ruiz C (2016) Natural forest expansion on reclaimed coal mines in Northern Spain: the role of native shrubs as suitable microsites. Environ Sci Pollut Res 23:13606–13616. https://doi.org/10.1007/s11356-015-5681-2

Allen SE (1989) Chemical analysis of ecological materials. Blackwell scientific publications.

Allington GRH, Valone TJ (2014) Islands of fertility: A byproduct of grazing? Ecosystems 17:127–141. https://doi.org/10.1007/S10021-013-9711-Y

Aramrak S, Chittamart N, Wisawapipat W, Rattanapichai W, Phun-Iam M, Aramrak A (2021) Dynamics of soil aggregate stability as induced by potassium in a soil-plant system. Soil Sci Plant Nutr 67:371–379. https://doi.org/10.1080/00380768.2021.1939151

Ardanuy A, Walker JKM, Kritzler U, Taylor AFS, Johnson D (2021) Tripartite symbioses regulate plant–soil feedback in alder. Funct Ecol 35:1353–1365. https://doi.org/10.1111/1365-2435.13799

Barthelemy H, Stark S, Olofsson J (2015) Strong Responses of Subarctic Plant Communities to Long-Term Reindeer Feces Manipulation. Ecosystems 18:740–751. https://doi.org/10.1007/s10021-015-9856-y

Barzegar AR, Nadian H, Heidari F, Herbert SJ, Hashemi AM (2006) Interaction of soil compaction, phosphorus and zinc on clover growth and accumulation of phosphorus. Soil Tillage Res 87:155–162. https://doi.org/10.1016/j.still.2005.03.004

Bell FG, Donnelly LJ (2006) Mining and its Impact on the Environment. Taylor & Francis, London and New York

Bremner J, Mulvaney CS (1982) Nitrogen-total. In: Black CA (ed) Methods of Soil Analysis. American Society of Agronomy Inc., Madison, pp 595–624

Brust GE (2019) Management strategies for organic vegetable fertility, safety and practice for Organic Food. Elsevier Inc. https://doi.org/10.1016/B978-0-12-812060-6.00009-X

Cao J, Yan W, Xiang W, Chen X, Lei P (2015) Stoichiometry characterization of soil C, N, and P of Chinese fir plantations at three different ages in Huitong, Hunan province. Sci Silvae Sin 51:1–8. https://doi.org/10.11707/j.1001-7488.20150701

Celestina C, Hunt JR, Sale PWG, Franks AE (2019) Attribution of crop yield responses to application of organic amendments: A critical review. Soil Tillage Res 186:135–145. https://doi.org/10.1016/j.still.2018.10.002

Condron LM, Newman RH (1998) Chemical nature of soil organic matter under grassland and recently established forest. Eur J Soil Sci 49:597–603. https://doi.org/10.1046/j.1365-2389.1998.4940597.x

Costa A, Villa S, Alonso P, García-Rodríguez JA, Martín FJ, Martínez-Ruiz C, Fernández-Santos B (2017) Can native shrubs facilitate the early establishment of contrasted co-occurring oaks in Mediterranean grazed areas? J Veg Sci 28:1047–1056. https://doi.org/10.1111/jvs.12550

Day PR (1965) Particle fractionation and particle-size analysis. In: Black CA (ed) Methods of Soil Analysis. American Society of Agronomy Inc., Madison, pp 545–567. https://doi.org/10.2134/agronmonogr9.1.c43

Doetterl S, Stevens A, Six J, Merckx R, Van Oost K, Casanova Pinto M, Boeckx P (2015) Soil carbon storage controlled by interactions between geochemistry and climate. Nat Geosci 8:780–783. https://doi.org/10.1038/ngeo2516

Eldridge DJ, Beecham G, Grace JB (2015) Do shrubs reduce the adverse effects of grazing on soil properties? Ecohydrology 8:1503–1513. https://doi.org/10.1002/eco.1600

Feng H, Wang S, Gao Z, Pan H, Zhuge Y, Ren X, Li C (2021) Aggregate stability and organic carbon stock under different land uses integrally regulated by binding agents and chemical properties in saline-sodic soils. Land Degrad Dev 32:4151–4161. https://doi.org/10.1002/ldr.4019

Franke ME, Zipper C, Barney JN (2018) Native Hardwood Tree Seedling Establishment Following Invasive Autumn-Olive (*Elaeagnus umbellata*) Removal on a Reclaimed Coal Mine. INVAS PLANT SCI MANA 11(3):155–161. https://doi.org/10.1017/inp.2018.19

García-Palacios P, McKie BG, Handa IT, Frainer AHáttenschwiler S (2016) The importance of litter traits and decomposers for litter decomposition: a comparison of aquatic and terrestrial ecosystems within and across biomes. Funct Ecol 30:819–829. https://doi.org/10.1111/1365-2435.12589

Garrido-Valero MS (1993) Interpretación de análisis de suelos. Guía práctica para muestrear los suelos e interpretar sus análisis. Instituto Nacional de Reforma y Desarrollo Agrario, Madrid. [in Spanish]

Gómez-Aparicio L, Gómez JM, Zamora R, Boettinger JL (2005) Canopy vs. Soil effects of shrubs facilitating tree seedlings in Mediterranean montane ecosystems. J Veg Sci 16:191–198. https://doi.org/10.1111/j.1654-1103.2005.tb02355.x

González-Alday J, Marrs RH, Martínez-Ruiz C (2009) Soil seed bank formation during early revegetation after hydroseeding in reclaimed coal wastes. Ecol Eng 35:1062–1069. https://doi.org/10.1016/j.ecoleng.2009.03.007

Grace JB (2006) Structural equation modeling and natural systems. Cambridge University Press, Cambridge

Hassan N, Li X, Wang J, Zhu H, Nummi P, Wang D, Finke D, Zhong Z (2021) Effects of grazing on C:N:P stoichiometry attenuate from soils to plants and insect herbivores in a semi-arid grassland. Oecologia 195:785–795. https://doi.org/10.1007/s00442-021-04873-3

He M, Zhou G, Yuan T, Groenigen KJV, Shao J, Zho X (2019) Grazing intensity significantly changes the C:N:P stoichiometry in grassland ecosystems. Glob Ecol Biogeogr 29:355–369. https://doi.org/10.1111/geb.13028

He X, Augusto L, Goll DS, Ringeval B, Wang Y, Helfenstein J, Huang Y, Yu K, Wang Z, Yang Y, Hou E (2021) Global patterns and drivers of soil total phosphorus concentration. Earth Syst Sci Data 13:5831–5846. https://doi.org/10.5194/essd-13-5831-2021

Hudson G, Hart S, Verbeek A (2023) State-of-play and way forward for public and private financial measures in Europe. Investing in Nature-Based Solutions. European Investment Bank, Luxemburgo. https://doi.org/10.2867/031133

Hu J, Li Q, Huang Y, Zhang Q, Zhou D (2022) Distributions of medium mineral elements with long-term grazing exclusion in a semi-arid grassland of Inner Mongolia. Ecol Indic 143:109384. https://doi.org/10.1016/j.ecolind.2022.109384

IEA (2019) Energy Policy Review Spain 2021. Int. Energy Agency. https://iea.blob.core.windows.net/assets/2f405ae0-4617-4e16-884c-7956d1945f64/Spain2021.pdf

IUCN (2020) Nature Based Solutions Standard 1–22. https://doi.org/10.2305/IUCN.CH.2020.09.en

Jobbágy EG, Jackson RB (2001) The distribution of soil nutrients with depth: Global patterns and the imprint of plants. Biogeochemistry 53:51–77. https://doi.org/10.1023/A:1010760720215

Johannes A, Weisskopf P, Schulin R, Boivin P (2019) Soil structure quality indicators and their limit values. Ecol Indic 104:686–694. https://doi.org/10.1016/j.ecolind.2019.05.040

Lal R (2004) Soil carbon sequestration to mitigate climate change. Geoderma 123:1–22. https://doi.org/10.1016/j.geoderma.2004.01.032

Li J, Wang K, Shangguan Z, Deng L (2022) Coupling and decoupling of soil carbon, nitrogen and phosphorus stocks following grazing

exclusion in temperate grasslands. CATENA 211:106003. https://doi.org/10.1016/j.catena.2021.106003

Li L, Zhang J, He XZ, Hou F (2021) Different effects of sheep excrement type and supply level on plant and soil C: N: P stoichiometry in a typical steppe on the loess plateau. Plant Soil 462:45–58. https://doi.org/10.1007/s11104-021-04880-6

Li S, Li K, Zhang T, Tang S, Zhang Z, Chen H, Ke Jin K (2025) The global effects of grazing on grassland soil nitrogen retention. Agric Ecosyst Environ 383:109516. https://doi.org/10.1016/j.agee.2025.109516

Liu Y, Fu L, Lu X, Yan Y (2022) Characteristics of Soil Nutrients and Their Ecological Stoichiometry in Different Land Use Types in the Nianchu River Basin. Land 11:1001. https://doi.org/10.3390/land11071001

López-Marcos D, Martínez-Ruiz C, Turrión MB, Jonard M, Titeux H, Ponette Q, Bravo F (2018) Soil carbon stocks and exchangeable cations in monospecific and mixed pine forests. Eur J Res 137:831–847. https://doi.org/10.1007/s10342-018-1143-y

López-Marcos D, Turrión MB, Bravo F, Martínez-Ruiz C (2021) Overyielding in mixed pine forests with belowground complementarity: impacts on understory. Eur J Res 140:777–791. https://doi.org/10.1007/s10342-021-01365-0

López-Marcos D, Turrión MB, Martínez-Ruiz C (2020) Linking soil variability with plant community composition along a mine-slope topographic gradient: Implications for restoration. Ambio 49:337–349. https://doi.org/10.1007/s13280-019-01193-y

Manso Arribas M, Tesón-Yudego A, Martínez-Ruiz C, García-Duro J (2024) The role of nurse shrubs in the biodiversity conservation of post-coal-mining gradsslands in Palencia mountains. In: Abstract book of XVIII Young Foresters Researchers Meeting, Palencia, Spain, p. 27

MAPA (1994) Tomo III. In: Métodos oficiales de Análisis, Ministerio de Agricultura, Pesca y Alimentación, Madrid, Spain. [in Spanish]

Ma R, Hu F, Liu J, Wang C, Wang Z, Liu G, Zhao S (2020) Shifts in soil nutrient concentrations and C:N:P stoichiometry during long-term natural vegetation restoration. PeerJ 8:e8382. https://doi.org/10.7717/peerj.8382

Martínez-Ruiz C, Milder AI, López-Marcos D, Zaldívar P, Fernández-Santos B (2021) Effect of the forest-mine boundary form on woody colonization and forest expansion in degraded ecosystems. Forests 12:773. https://doi.org/10.3390/f12060773

Milder AI, Fernández-Santos B, Martínez-Ruiz C (2013) Colonization patterns of woody species on lands mined for coal in Spain: preliminary insights for forest expansion. Land Degrad Dev 24:39–46. https://doi.org/10.1002/ldr.1101

Misebo AM, Pietrzykowski M, Woś B (2022) Soil carbon sequestration in novel ecosystems at post-mine sites—a new insight into the determination of key factors in the restoration of terrestrial ecosystems. Forests 13:63. https://doi.org/10.3390/f13010063

Mitran T, Meena RS, Lal R, Layek J, Kumar S, Datta R (2018) Role of Soil Phosphorus on Legume Production. In: Meena R, Das A, Yadav G, Lal R (eds) Legumes for Soil Health and Sustainable Management. Springer, Singapore. https://doi.org/10.1007/978-981-13-0253-4_15

Mudrák O, Frouz J, Velichová V (2010) Understory vegetation in reclaimed and unreclaimed post-mining forest stands. Ecol Eng 36:783–790. https://doi.org/10.1016/j.ecoleng.2010.02.003

Muñoz-Cerro E, Armijos-Montaño AR, López-Marcos D, Martínez-Ruiz C, García-Duro J (2026) Twelve-year oak seedling survival and growth in post-coal mining pastures of northern Spain: Combined effects of nurse shrubs and grazing exclusion. Ecol Manage 600:123291. https://doi.org/10.1016/j.foreco.2025.123291

Muñoz-Cerro E, García-Duro J, Martínez-Ruiz C, López-Marcos D (2023) Soil amelioration induced by nurse shrubs in coal mines reclaimed to pastures and their synergistic effects with grazing.

Agric Ecosyst Enviro 350:108483. https://doi.org/10.1016/j.agee.2023.108483

Mushinski RM, Zhou Y, Hyodo A, Casola C, Boutton TW (2024) Interactions of long-term grazing and woody encroachment can shift soil biogeochemistry and microbiomes in savanna ecosystems. Geoderma 441: 116733 https://doi.org/10.1016/j.geoderma.2023.116733

Nafría-García DA, Garrido-del-Pozo N, Álvarez-Arias MV et al (2013) Atlas agroclimático de Castilla y León, 1st ed. Instituto Tecnológico Agrario, Junta de Castilla y León- Agencia Estatal de Meteorología. http://atlas.itacyl.es [in Spanish]

Obour PB, Keller T, Lamandé M, Munkholm LJ (2019) Pore structure characteristics and soil workability along a clay gradient. Geoderma 337:1186–1195. https://doi.org/10.1016/j.geoderma.2018.11.032

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2020) Vegan: Community Ecology Package. R package version 2.5-7. https://CRAN.R-project.org/packa ge=vegan

Olde Venterink H, Wassen MJ, Verkroost AWM, De Ruiter PC (2003) Species richness-productivity patterns differ between N-, P-, and K-limited wetlands. Ecology 84:2191–2199. https://doi.org/10.1890/01-0639

Piñeiro G, Paruelo JM, Oesterheld M, Jobbágy EG (2010) Pathways of Grazing Effects on Soil Organic Carbon and Nitrogen. Rangel Ecol Manage 63:109–119. https://doi.org/10.2111/08-255.1

Pinheiro JC, Bates DM (2000) Linear mixed-effects models: basic concepts and examples. Mix. Model. S S-Plus 3–56. https://www.R-project.org/

Pinheiro JC, Bates DM, R-Core Team (2023) Nlme: Linear and Nonlinear Mixed Effects Models. R package version 3 1-162. https://CRAN.R-project.org/package=nlme

Pugnaire FI, Armas C, Valladares F (2004) Soil as a mediator in plant-plant interactions in a semi-arid community. J Veg Sci 15:85–92. https://doi.org/10.1111/j.1654-1103.2004.tb02240.x

R-Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Rhoades JD (1982) Cation exchange capacity. In: Methods of soil analysis. Part 2. Chemical and Microbiological Properties. In: Page AL (ed) Methods of Soil Analysis, Agronomy Monographs. American Society of Agronomy, Inc. Soil Science Society of America, Madison, Wisconsin, pp. 149–157. https://doi.org/10.2134/agronmonogr9.2.2ed

Richards SA (2005) Testing ecological theory using the information-theoretic approach: examples and cautionary results. Ecology 86:2805–2814. https://doi.org/10.1890/05-0074

Rosseel Y (2012) lavaan: An R Package for Structural Equation Modeling. J Stat Softw 48:1–36. https://doi.org/10.18637/jss.v048.i02

Šantrůčková H, Heinemeyer O, Kaiser EA (1993) The influence of soil compaction on microbial biomass and organic carbon turnover in micro- and macroaggregates. Geoderma 56:587–598. https://doi.org/10.1016/B978-0-444-81490-6.50047-9

Sardans J, Peñuelas J (2021) Potassium control of plant functions: Ecological and agricultural implications. Plants 10:419. https://doi.org/10.3390/plants10020419

Sato CF, Strong CL, Holliday P, Florance D, Pierson J, Lindenmayer DB (2019) Environmental and grazing management drivers of soil condition. Agric Ecosyst Environ 276:1–7. https://doi.org/10.1016/j.agee.2019.02.003

Schollengberger CJ, Simon RH (1945) Determination of exchange capacity and exchangeable bases in soil—ammonium acetate method. Soil Sci 59:13–24. https://doi.org/10.1097/00010694-194501000-00004

Sigcha F, Pallavicini Y, Camino MJ, Martínez-Ruiz C (2018) Effects of short-term grazing exclusion on vegetation and soil in early

succession of a Subhumid Mediterranean reclaimed coal mine. Plant Soil 426:197–209. https://doi.org/10.1007/s11104-018-3629-2

Soil Survey Staff (2022) Keys to soil taxonomy, 13th edn. USDA-Natural Resources Conservation Service

Sokal RR, Rohlf FJ (1995) Biometry: The principles and practice of statistics in Biological research. W.H. Freeman and Company, New York

Talavera S, Castroviejo S (1999) Flora Iberica: plantas vasculares de la Península Ibérica e Islas Baleares: Vol. VII (I) Leguminosae (partim). CSIC-CSIC, Madrid. [in Spanish]

Teague WR, Dowhower SL, Baker SA, Haile N, DeLaune PB, Conover DM (2011) Grazing management impacts on vegetation, soil biota and soil chemical, physical and hydrological properties in tall grass prairie. Agric Ecosyst Environ 141:310–322. https://doi.org/10.1016/j.agee.2011.03.009

Tessema ZK, de Boer WF, Baars RMT, Prins HHT (2011) Changes in soil nutrients, vegetation structure and herbaceous biomass in response to grazing in a semi-arid savanna of Ethiopia. J Arid Environ 75:662–670. https://doi.org/10.1016/j.jaridenv.2011.02.004

Tian H, Chen G, Zhang C, Melillo JM, Hall CA (2010) Pattern and variation of C: N: P ratios in China's soils: a synthesis of observational data. Biogeochemistry 98:139–151. https://doi.org/10.1007/s10533-009-9382-0

Tipping E, Somerville CJ, Luster J (2016) The C:N:P:S stoichiometry of soil organic matter. Biogeochemistry 130:117–131. https://doi.org/10.1007/s10533-016-0247-z

Torroba-Balmori P, Zaldívar P, Alday JG, Fernández-Santos B, Martínez-Ruiz C (2015) Recovering Quercus species on reclaimed coal wastes using native shrubs as restoration nurse plants. Ecol Eng 77:146–153. https://doi.org/10.1016/j.ecoleng.2015.01.024

Tränkner M, Tavakol E, Jákli B (2018) Functioning of potassium and magnesium in photosynthesis, photosynthate translocation and photoprotection. Physiol Plant 163:414–431. https://doi.org/10.1111/ppl.12747

Van Bemmelen JM (1890) Über die Bestimmung des Wassers, des Humus, des Schwefels, der in den colloïdalen Silikaten gebundenen Kieselsäure, des Mangans usw im Ackerboden. Die Landwirthschaftlichen Versuchs-Stationen 37:e290. https://edepot.wur.nl/211282 [in German]

Van der Wal R, Brooker RW (2004) Mosses mediate grazer impacts on grass abundance in arctic ecosystems. Funct Ecol 18:77–86. https://doi.org/10.1111/j.1365-2435.2004.00820.x

Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Tilman DG (1997) Human alteration of the global nitrogen cycle: sources and consequences. Ecol Appl 7:737–750. https://doi.org/10.1890/1051-0761(1997)007[0737:HAOTGN]2.0.CO;2

Walkley A, Black IA (1934) An examination of the degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. Soil Sci 37:29–38. https://doi.org/10.1097/00010694-193401000-00003

Wan B, Mei X, Hu Z, Guo H, Chen X, Griffiths BS, Liu M (2021) Moderate grazing increases the structural complexity of soil micro-food webs by promoting root quantity and quality in a Tibetan alpine meadow. Appl Soil Ecol 168:104161. https://doi.org/10.1016/j.apsoil.2021.104161

Wang Y, Zheng Y, Liu Y, Huang J, Mamtimin A (2022) Spatial prediction models for soil stoichiometry in complex terrains: A case study of Schrenk's spruce forest in the Tianshan mountains. Forests 13:1407. https://doi.org/10.3390/f13091407

Woś B, Chodak M, Józefowska A, Pietrzykowski M (2022) Influence of tree species o Influence of tree species on carbon, nitrogen, and phosphorus stocks and stoichiometry under different soil regeneration scenarios on reclaimed and afforested mine and post-fire forest sites. Geoderma 415:115782. https://doi.org/10.1016/j.geoderma.2022.115782

Yao Y, Chen J, Li F, Sun M, Yang X, Wang G, Ma J, Sun W (2022) Exchangeable Ca^{2+} content and soil aggregate stability control the soil organic carbon content in degraded Horqin grassland. Ecol Indic 134:108507. https://doi.org/10.1016/j.ecolind.2021.108507

Zarekia S, Jafari M, Arzani H, Javadi SA, Jafari AA (2012) Grazing effects on some of the physical and chemical properties of soil. World Appl Sci J 20:205–212. https://doi.org/10.5829/idosi.wasj.2012.20.02.1624