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Soil C:N:P stoichiometric signatures of grasslands differ between tropical and warm temperate climatic zones

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Abstract Climate and land management affect nutrient cycling in grassland ecosystems. We aimed to understand whether temperate and tropical grasslands differ in terms of soil organic carbon (SOC), nitrogen (N), and phosphorus (P) concentrations, and their C:N:P stoichiometric ratios in grazed and ungrazed natural grasslands and pastures. For this, we used a meta-analysis approach (1296 records, 241 papers), and regression models to explain the observed patterns in terms of mean annual precipitation (MAP), mean annual temperature (MAT), altitude, and latitude. SOC, N, and P concentrations were higher in temperate regions than in tropical ones, and they negatively correlated with MAT and MAP. The grassland type effect was more significant for tropical regions. In tropical regions, soil C:N ratios were higher in ungrazed than in grazed pastures, and soil N:P ratios in ungrazed sites were higher in pastures than in natural grasslands. Grazing increases soil N and SOC for natural grasslands in temperate regions. Our findings suggest that soil stoichiometric C:N:P stoichiometric signatures in grasslands differed between tropical and temperate regions on a global scale. P is a key element in regulation and restriction on soil C and N cycling in tropical regions but less in the temperate ones. Our findings suggest the direction of effects of grazing or grassland type on C:N:P stoichiometric signature. Since imbalances in soil stoichiometric ratios may have implications for ecosystem functioning, the assessment of these patterns could serve as a valuable tool for management and conservation of grasslands and pastures in both tropical and temperate regions.

Keywords Grazing lands · Pastures · Soil nutrients · Soil organic carbon · Stoichiometric patterns · Tropical grasslands

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Introduction

Carbon (C), nitrogen (N), and phosphorus (P) have complex global biogeochemical cycles that are strongly coupled (Ågren 2008). N and P synergistically affect many ecosystem processes as growth-limiting factors for organisms (Sterner and Elser 2002; Elser et al. 2007). The relationship between plant-available N and P varies widely among soils depending on the mineralogy, organic matter forms, climate, weathering, and other factors (Amundson 2021). Ratios between elements may provide additional information to ecosystem functioning related to that obtained with the individual concentrations of each element (Binkley and Fisher 2020). These elemental ratios (stoichiometric ratios) and their quantification in the environment reflect the impact of living organisms and can be considered a stoichiometric signature (Redfield 1958; Reiners 1986; Sterner and Elser 2002; Butler et al. 2021; Chang et al. 2021; Kempes et al. 2021). A chemical signature is defined as a pattern of elemental or molecular composition that has been employed for characterizing or tracking living organisms or tissues based on their composition or biochemical processes (Sterner and Elser 2002), or as evidence of life forms in astrobiology (Chan et al. 2019). For the purposes of this study, we designate the stoichiometric signature as a pattern in the ratios of chemical elements within the soil, with the intention of tracking the effects of environmental and management factors on grasslands soil. The importance of using this approach in living organisms is that despite the variability between the element concentrations, the ratios maintain a lower variation interval (e.g., Reiners 1986; Sterner and Elser 2008; Arhonditsis et al. 2019). This lower variability has also been reported for C:N:P ratios in grasslands soil on a global scale (Cleveland and Liptzin 2007). Stoichiometric signature is based on elemental mass ratios and depends on cycling elements and ecosystem processes (Reiners 1986; Sterner and Elser 2002; Butler et al. 2021). Quantifying the C:N:P ratios in soil can be a powerful tool to understand the influence of environmental variables and management on soil nutrients concentration.

Over the last two decades, there have been global and regional syntheses on the status of C and nutrient concentrations in grassland soils. Some studies have explored the effect of management, including grazing, mainly in soil C in grasslands at global scale (Conant et al. 2001, 2017; Pineiro et al. 2009; McSherry and Ritchie 2013), and some include effects in other nutrients (Abdalla et al. 2018; Rumpel et al. 2015; Byrnes et al. 2018; He et al. 2020). Other reviews have examined the concentrations and ratios of C and N in grassland soils comparing temperate and tropical zones (Pärtel et al. 2008), encompassing both natural grasslands and pastures (Xu et al. 2013), or only tropical ecosystems (Joergensen 2010). Consequently, it is well-established that soil nutrient transformation and cycling in grasslands are contingent upon climate and other factors, such as grazing (Pärtel et al. 2008). However, most of these studies predominantly explore the influence of individual factors (grassland type, grazing, or climate individually) on the concentrations of C and nutrients, such as N and P, as well as their respective ratios. Until now, only a limited number of studies have comprehensively investigated the simultaneous impact of multiple factors on C, N, and P concentrations and ratios, concurrently considering climatic effects (Pärtel et al. 2008; Abdalla et al. 2018). One key objective of this study is to elucidate comprehensive global stoichiometric patterns of C-N-P in soil, encompassing the contrast between temperate and tropical climate zones, in addition to the influences of temperature, precipitation, geographic location, and the altitude of grassland-associated ecosystems.

Grasslands are distributed in different climatic zones of the world (Blair et al. 2014; ILRI et al. 2021). For this study, we classified sites as natural grasslands (native grasslands, prairies, savannas) and pastures (cultivated and induced grasslands). Our analyses distinguished between temperate and tropical zones for all these classifications. Most pastures have been established in the equatorial and warm temperate zones, in regions corresponding to zone A (i.e., humid tropical) and C (i.e., temperate) in the Köppen-Geiger classification (Humphreys 1981; Suttie et al. 2005; Ramankutty et al. 2008; Reinermann et al. 2020). Several distinctions between grasslands in these two climatic zones can be highlighted. Temperate grasslands are predominantly characterized by C_3 plants, while tropical grasslands are dominated by C_4 grasses (Partel et al. 2008; Lehmann and Parr 2016). Soil organic matter (SOM) transformation processes occur more rapidly in tropical regions (van Keulen 2001; Nortcliff 2010), primarily driven by temperature and precipitation (Voroney and Heck 2015; Mitchell et al. 2021). The accelerated SOM transformation results in higher productivity (Chapin et al. 2012; Paul 2016), faster recycling rates (Zech et al. 1997; Saggar et al. 2011), and a greater turnover rate of soil carbon (C) in tropical grasslands compared to temperate grasslands (Horwath 2015; Paul 2016; Six and Jastrow 2017). Phosphorus (P) limitation is a constant factor in tropical biomes due to climate conditions, as well as historical soil development and geological factors (Vitousek et al. 2010; Sanchez 2019). In tropical regions, pastures are typically established in areas that were originally covered by natural forests, leading to the conversion of a significant portion of forested and wooded areas (Dias et al. 2016; Lerner et al. 2017; Aryal et al. 2018; Ávila-Bello et al. 2018). All these distinctions between temperate and tropical zones have implications for soil biogeochemical processes and may derive in a stoichiometric signature of grassland-associated ecosystems.

Grazing also affects soil nutrient concentration and ratios by affecting the physical properties of the plant-soil system (Ash et al. 2011; Teague et al. 2013; Pulido et al. 2016). Vegetation consumption, plant trampling and soil compaction caused by livestock can affect nutrient storage and transformation in grasslands (Greenwood and McKenzie 2001; Taboada et al. 2011). A reduction in soil porosity, for example, affects the soil water retention capacity (Cerda et al. 1998; Bartley et al. 2010; Pulido et al. 2016) and microbial diversity (Northup et al. 1999; Pan et al. 2018), and these factors together affect the soil nutrients concentration and cycling (Semmartin et al. 2008; Schnyder et al. 2010; Wang et al. 2016). Grazing can alter coupling of C, N, and inorganic P cycles because it can modify soil organic matter storage and stimulate belowground biological activity (Rumpel et al. 2015). Studies on this topic are inconclusive on whether there is a positive or negative effect of grazing on soil element concentration (Conant et al. 2001, 2017; Pineiro et al. 2010; McSherry and Ritchie 2013; Zhou et al. 2017; Abdalla et al. 2018). However, adverse effects of grazing, particularly those related to grazing intensities, have been reported in temperate (Piñeiro et al. 2009; Pineiro et al. 2010; McSherry and Ritchie 2013; Abdalla et al. 2018; He et al. 2019) and in tropical regions (Ritchie 2014; Abdalla et al. 2018; Pasricha and Ghosh 2019; Pringle et al. 2014). The impact of grazing on total P in tropical soils has yet to be studied despite the limitation of total P occurring in many tropical soils (Joergensen 2010). Little is known about how grazing influences all soil C, N and P concentrations and their ratios in both natural grasslands and pastures and in tropical vs. temperate climates with different environmental and geographic conditions.

This study aimed to compare concentrations and stoichiometric ratios of soil organic C (SOC) and nutrients (N and P) of natural grasslands and pastures, grazed and ungrazed, in two different climatic zones (i.e., tropical vs. warm temperate). We also explored the relationship between environmental (mean annual temperature, MAT, and precipitation, MAP) and geographical (latitude, altitude) variables in soil elemental concentrations and ratios. The incorporation of environmental and geographical factors in the analysis could aid in elucidating stoichiometric patterns in temperate and tropical grasslands. Furthermore, we aim to ascertain whether these patterns persist when incorporating variables such as grassland type and grazing. We expect to observe differences in grassland soils between temperate and tropical zones, where the stoichiometric signatures will reflect a higher nutrient concentration in temperate zones (low C:N and C:P ratios) and a greater P limitation in tropical zones (high C:P and N:P ratios). In this regard, we expect to gain a deeper understanding of the relationship between soil nutrient concentrations and C:N:P stoichiometric signatures with environmental variables, such as MAT and MAP, and geographical coordinates, such as latitude and altitude. A higher C concentration in pasture soils is also expected, regardless of the climatic zone, due to accelerated nutrient (N and P) use in plant growth associated with grazing by livestock. On this point, we predict that grazing would lead to decreasing soil P more rapidly in tropical grasslands compared to soils from ungrazed sites. The effect of grazing on C:nutrients stoichiometry can be reflected in a stoichiometric signature of high soil C:P and N:P ratios.

Methods

Data sources and search terms

Using peer-reviewed papers published before April 2023 and with data available online, a database of

SOC, total N, and total P in grasslands was compiled, for two Köppen-Geiger climate zones: equatorial or humid tropical (zone A) and warm temperate or mesothermic (zone C). We compiled the papers using Scopus, with the following search terms: (soil carbon / soil organic carbon / nitrogen / phosphorus / nutrients) and (grasslands / rangelands / savanna / grazing lands / pastures / cultivated grasslands / tropical grasslands) and (grazing). We limited the search terms to title, keywords, and abstract. Given the limited coverage of studies in tropical regions and the southern hemisphere, mainly in Latin America and Africa, a second, broader search of other databases (Google Scholar, Scielo, and Redalyc) was made, including papers in English, Spanish, and Portuguese.

For a more thorough review, we examined the reference lists of collected papers on the comprehensive analysis of C and nutrient concentrations in grassland soils, focusing on previous reviews and meta-analyses that include effects of grazing (Conant et al. 2001, 2017; Pineiro et al. 2009; McSherry and Ritchie 2013; Rumpel et al. 2015; Abdalla et al. 2018; Byrnes et al. 2018; He et al. 2020), climate zones (Pärtel et al. 2008; Joergensen 2010) and grassland types (Xu et al. 2013). Our compilation has been enriched notably by a contribution from Xu et al. (2014). This database compile data about SOC, N, and P, and their ratios at biome and global scales (Xu et al. 2013). We extracted information for natural grasslands and pastures soils.

Criteria for selection of published studies

Each site reported in the source papers was considered an independent sample. When a site was reported in two different papers with complementary information, it was considered a single sample (e.g., Damian et al. 2020, 2021; Franzluebbers and Stuedemann 2005, 2009, references in supplementary information). Given that the present study did not aim to evaluate seasonal variation, and that total soil concentrations typically vary relatively little, we obtained a mean value when papers reported results at different times of the year for a given site. The following information was also obtained for each site: coordinates, MAT, MAP, soil type according to WRB (2015), sampling date and depth, grazing condition, grazer species, and stocking rate, when available. When geographical coordinates were unavailable in the source papers, data were estimated via Google Earth.

Since the relationships between elements in reactions occur on a molar basis (Sterner and Elser 2002), all data reported in different units were converted into molar units (mmol kg^{-1}). We omitted sites where data were presented as mass $area^{-1}$, unless bulk density and depth data were included, which allowed a conversion to mmol kg^{-1}. Only soil surface data (< 30 cm) were obtained. Since we have data at different depths, we do not distinguish between shallow depths less than 30 cm. We assume that the average values obtained may have a variation associated with confounded factors in the depth interval from 0 to 30 cm. Most of the data presented (~90%) corresponds to depths from 0 to 20 cm. Given that not all papers have information on all three elements (SOC, N, and P), the number of data points for stoichiometric ratios (C:N = SOC:nitrogen, C:P = SOC:phosphorus, and N:P = nitrogen:phosphorus) were different for each site.

Data classification

The collected information was classified into two climatic zones according to Köppen-Geiger: equatorial or humid tropical (Köppen-Geiger zone A) and warm temperate or mesothermic (Köppen-Geiger zone C). The climatic zone was determined following Kottek et al. (2006) based on the coordinates and site name if no data were provided by the respective reference. We only included grasslands in the A and C climatic zones since pastures have been established mainly in these regions (Humphreys 1981; Suttie et al. 2005; Ramankutty et al. 2008; Reinermann et al. 2020). Pastures have also been cultivated in hot semi-arid climate (Bsh) regions, but we did not consider these sites because they accounted for less than 2.0% of the retrieved data. Sites were classified as natural grasslands or pastures (cultivated or induced grasslands) and as grazed or ungrazed sites, as reported in the source papers. Grasslands include savannas, which are natural grasslands in tropical areas, which represent 4.1% of data. Induced grasslands (3.5% of the total data) were included in the pastures group (cultivated grasslands), as they were established in sites where original vegetation was replaced with grasses (Suttie et al. 2005; Sanchez 2019; Teutscherová et al. 2021). When the grazing condition was not specified in the original papers, we classified the sites as ungrazed.

Database summary

We compiled a dataset of 1296 records from 241 papers (Online Resource 1, a list of data sources), which included samples from 40 countries, mainly Brazil (n = 31, 13.7% of total papers), New Zealand (n = 29 papers, 12.8%), the United States of America (n = 21, 9.3%), Mexico (n = 18, 8%), and the United Kingdom (n = 17, 7.5%). Most sites (70.0%) were located at latitudes outside the tropics, with extreme latitudes of 57º06’ N and 46º24’ S. One-third of the data (35.8%) were North of the Tropic of Cancer and 23.3% South of the Tropic of Capricorn (Fig. 1). Sites in equatorial or humid tropical regions (zone A) represent 36.2% of the total data. Pastures account for 59.3% of the entries, and 57.8% of sites were subject to grazing (Supplementary Appendix 1). Most of the data (90%) were collected as samples at 0–20 cm depth. The main soil types for tropical climate regions were Ferralsols, with 32.3% of data (according to the World Reference Base, WRB 2015; Oxisols according to US Soil Taxonomy classification), 26.5% of data were Acrisols and 19.8% Vertisols. 37.7% of data were Cambisols, 11.0% Acrisols and 8.6% Luvisols for sites in warm temperate regions (Supplementary Appendix 2). The mean clay content in soils for the climatic zones was 29.2% for the tropical zone (37.0% in Ferralsols, 21.0% in Acrisols, and 34.0% in Vertisols) and 22.5% for the temperate zone (27.5% in Cambisols, 20.1% in Acrisols, and 23.4% in Luvisols).

Data analyses

A three-way ANOVA with a Tukey’s post-hoc test ($p < 0.05$ level) was performed to examine the effect of the climatic zone (Köppen-Geiger zone A and zone C), grassland type (natural grassland and pasture), grazing regime (grazed and ungrazed), and the interactions between these three factors on soil elemental concentrations (SOC, N, and P) and their stoichiometric ratios (C:N, C:P, and N:P). We conducted exploratory analyses to test the assumptions of normal distribution of residuals (Shapiro-Wilks’s test) and homoscedasticity (Fligner-Killen’s test) (Jones et al. 2022). Since data were not normally distributed, log transformation was used for ANOVA models to reduce the effect of outliers and increase the power of the statistical tests employed.

We also explored the relationships between elemental concentrations and ratios with environmental factors (MAP, MAT, altitude, and latitude) using linear regression models (Lepš and Šmilauer 2020). A log-linear transformation was used to ensure data normality. For correlations between element concentrations and their ratios we used a Pearson linear correlation, and the slope value was tested with one-sided tests (Zar 2014). All statistical analyses were performed using the packages `agricolae´ 1.3–5 (Mendiburu and Yaseen 2020) and `ggplot2´ 3.3.6 (Wickham 2022) in R (R Core Team 2020). The significance level was set as $\alpha = 0.05$.

Results

Soil element concentrations and ratios according to climate, grassland type, and grazing

The SOC, N, and P concentrations were higher in warm temperate than tropical sites, whether in natural grasslands or pastures. The SOC and N concentrations were higher in pastures than in natural grasslands at the global level (Table 1). The C:N ratios were higher in pastures than in natural grasslands for ungrazed sites in both climate zones (Table 2). In the tropical zone, N:P ratios were higher in ungrazed pastures than in grazed or ungrazed natural grasslands sites (Table 1). Tropical pastures showed higher C:N ratio for ungrazed than for grazed sites (Table 1).

Concentrations of SOC, N, and C:P ratio differed when comparing climatic zones and grassland types ($p < 0.001$; Table 2). Total P differed when comparing climatic zones and C:N and N:P ratios differed among grassland types. However, these factors explain less than 10% of the variance in SOC and N concentrations but more than 25% in P concentration and C:P and N:P ratios (Table 2). Soil P concentration and C:P and N:P ratios did not show significant differences when we compared grazed and ungrazed sites, but the impact of grazing was significant for soil N concentration. The factors (climate, grassland type, and grazing) had an interactive effect on soil N concentration ($p = 0.02$) and N:P ($p = 0.03$) when considering climate and grassland

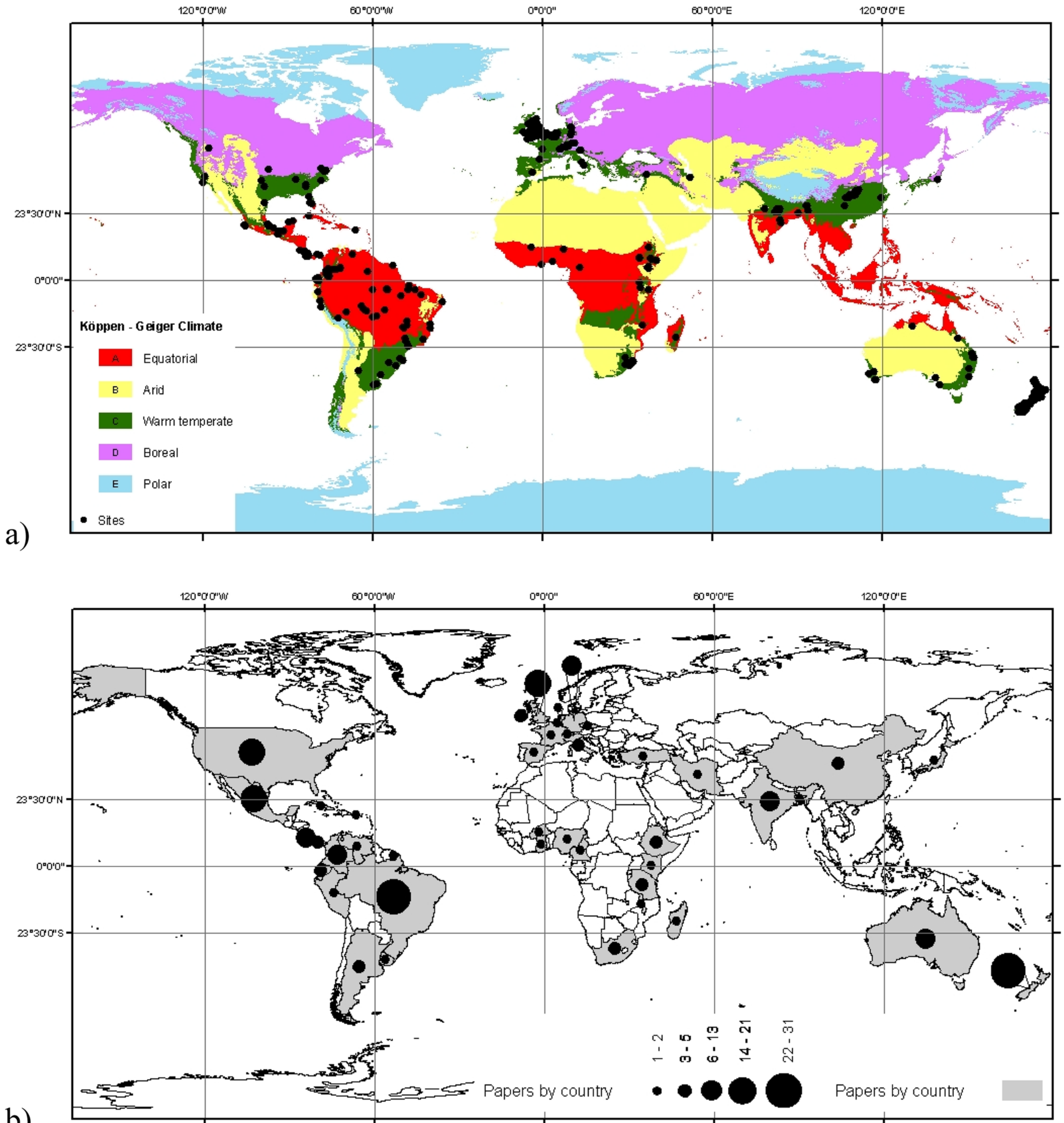

Fig. 1 Global distribution of the compiled information. **a** Site distribution in the climatic zones, **b** papers by country

type interaction. Also, an effect was observed for SOC ($p=0.004$, Table 2) and C:N ($p<0.001$, Table 2) for grassland type and grazing interaction, and interactive effect of climate zone and grazing was observed for C:N ratio ($p<0.001$, Table 2).

Relationships among soil elemental concentrations, and environmental and geographical variables

We found that SOC and N concentrations in grassland soils increased with altitude, latitude, and MAP but

Table 1 Concentrations (mmol kg soil^{-1}) of SOC, N, and P and their ratios in natural grasslands and pastures soils from equatorial or humid tropical (A) and warm temperate (C) Köppen-Geiger climatic zones

			Grazed		Ungrazed	
			Natural grassland	Pasture	Natural grassland	Pasture
SOC	A	*mean*	1344.9 d	1850.3 c	1424.8 cd	2214.6 bc
		se	121.1	71.3	173.9	188.3
		(n)	*(71)*	*(260)*	*(38)*	*(80)*
	C	*mean*	4060.9 a	3511.2 a	3112.0 b	3926.2 a
		se	311.7	160.6	199.9	219.2
		(n)	*(151)*	*(240)*	*(263)*	*(164)*
N	A	*mean*	87.7 e	134.9 cd	87.6 e	147.8 de
		se	6.1	5.1	7.7	16.5
		(n)	*(70)*	*(245)*	*(37)*	*(76)*
	C	*mean*	222.3 ab	247.0 a	189.6 bc	233.1 ab
		se	13.0	10.9	7.6	15.1
		(n)	*(111)*	*(223)*	*(236)*	*(122)*
P	A	*mean*	12.3 bc	11.6 c	17.6 c	17.2 c
		se	1.0	0.6	3.2	1.9
		(n)	*(16)*	*(57)*	*(10)*	*(19)*
	C	*mean*	21.1 ab	28.7 b	22.8 ab	26.1 ab
		se	1.0	1.0	0.7	1.5
		(n)	*(31)*	*(111)*	*(91)*	*(19)*
C:N	A	*mean*	13.7 c	14.8 bc	15.4 abc	16.6 a
		se	0.6	0.3	1.0	0.4
		(n)	*(67)*	*(228)*	*(37)*	*(72)*
	C	*mean*	15.0 ab	14.6 ab	13.5 c	15.9 ab
		se	0.4	0.2	0.3	0.4
		(n)	*(111)*	*(213)*	*(236)*	*(118)*
C:P	A	*mean*	185.4 ab	237.1 ab	167.9 ab	237.2 a
		se	11.7	9.2	16.9	20.3
		(n)	*(16)*	*(48)*	*(10)*	*(15)*
	C	*mean*	153.9 ab	170.2 ab	138.6 b	227.6 ab
		se	6.1	5.8	4.1	12.4
		(n)	*(31)*	*(107)*	*(91)*	*(19)*
N:P	A	*mean*	10.2 b	15.4 ab	8.9 b	17.3 a
		se	0.7	0.6	1.0	1.1
		(n)	*(16)*	*(57)*	*(10)*	*(15)*
	C	*mean*	10.1 b	12.2 ab	10.7 ab	14.1 ab
		se	0.4	0.4	0.2	0.4
		(n)	*(31)*	*(106)*	*(91)*	*(13)*

Soil elements: SOC = soil organic carbon; N = total nitrogen; P = total phosphorus. Ratios: C:N = SOC:nitrogen; C:P = SOC:phosphorus; N:P = nitrogen:phosphorus. Means, standard errors (*se*), and available data are shown for each variable (*n*). Different letters in a data block (data within lines [mean, *se*, *n*] for each element or ratio in both climate zones, A and C) for a parameter show significant differences ($p < 0.05$). Letter 'a' was associated to higher values

decreased with MAT (Fig. 2, Supplementary Appendix 3 and 4). Soil P concentration was negatively related to MAT but increased with latitude. Soil P increased for MAP and altitude in tropical grasslands (Fig. 2). The C:P and N:P ratios increased with MAT and MAP but decreased with latitude; C:P and C:N ratios increased with altitude in warm temperate but decreased with this variable in tropical grasslands. The C:N decreased with MAT and increased with latitude only for tropical natural grasslands (Fig. 2, Supplementary Appendix 3 and 4). The SOC and N concentrations had similar trends in grasslands of tropical and temperate regions. The highest values for SOC (> 10,000 mmol kg^{-1}) corresponded to montane

Table 2 Three-way ANOVA of soil element concentrations (mmol kg soil^{-1}) and ratios in natural grasslands and pastures from equatorial or humid tropical (A) and warm temperate (C) Köppen-Geiger climatic zones

Source of variation	SOC			N			P		
	% Var	*F*		% Var	*F*		% Var	*F*	
Climatic zone	8.5%	120.9	***	8.1%	100.6	***	23.5%	109.2	***
Grassland type	1.7%	24.6	***	1.7%	21.3	***	0.6%	2.7	
Grazing condition	0.0%	0.3		0.5%	6.4	*	0.6%	2.6	
ClimZ × GrTyp	0.2%	3.1		0.5%	5.7	*	0.4%	1.8	
ClimZ × GrzC	0.1%	1.7		0.0%	0.1		0.2%	1.0	
GrTyp × GrzC	0.6%	8.3	**	0.0%	0.0		0.4%	1.8	
ClimZ × GrTyp × GrzC	0.2%	2.2		0.2%	1.8		0.0%	0.0	
Error	88.7%	0.0		89.1%	0.0		74.4%	0.0	
Source of variation	C:N			C:P			N:P		
	% Var	*F*		% Var	*F*		% Var	*F*	
Climatic zone	0.1%	0.9		3.6%	12.7	***	0.4%	1.3	
Grassland type	2.2%	25.3	***	3.6%	12.8	***	4.8%	17.4	***
Grazing condition	0.2%	2.5		0.0%	0.0		1.0%	3.5	
ClimZ × GrTyp	0.0%	0.0		0.0%	0.1		1.4%	4.9	*
ClimZ × GrzC	1.1%	12.9	***	0.0%	0.2		0.0%	0.1	
GrTyp × GrzC	0.9%	10.3	**	0.9%	3.2		0.4%	1.5	
ClimZ × GrTyp × GrzC	0.3%	3.3		0.1%	0.4		0.3%	1.2	
Error	95.1%			91.8%			91.7%		

Soil elements: SOC = soil organic carbon; N = total nitrogen; P = total phosphorus. Ratios: C:N = SOC:nitrogen; C:P = SOC:phosphorus; N:P = nitrogen:phosphorus. % Var = % of explained variance for every variation source in the model. ClimZ = Climatic zone, GrTyp = Grassland type, GrzC = Grazing condition. Statistical significance: *** < 0.001; ** < 0.01; * < 0.05;. < 0.1

grasslands in the Andean region (see, Oliver et al. 2017; Oliveras et al. 2014), and led to some differences between SOC and N trends with latitude and altitude (Fig. 2). Soil total P concentration and related ratios (C:P, N:P) had different trends related to altitude and MAP when comparing tropical and warm temperate grasslands (Fig. 2, Supplementary Appendix 4).

Correlations between SOC, N, and P and their ratios

At a global level, a strong positive correlation was found between SOC and N (r = 0.9) and between C:P and N:P (r = 0.89) (Figs. 3a and 3f, Table 3). Correlations between SOC and P (r = 0.49), N and P (r = 0.58), and C:N and C:P (r = 0.36) were significant ($p < 0.0001$) (Fig. 3b to 3d, Table 3). When comparing both warm temperate and tropical climate zones, the pattern observed for SOC and N was the same as the one observed at a global level (see Table 3). The same thing occurs for correlations between SOC and P, and N and P (Figs. 3b and 3c). The correlation between C:P and N:P was weaker for warm temperate grasslands (r = 0.80) than for tropical sites (r = 0.91) (Fig. 3f). The correlations observed between C:N and C:P at a global level (r = 0.36, $p < 0.001$) were different when comparing both climate zones: significant for warm temperate regions (r = 0.66, $p < 0.0001$) but non-significant for tropical grasslands (r = 0.19, p = 0.09) (Fig. 3d, Table 3).

Discussion

Grasslands are ecosystems distributed worldwide and subject to conditions related to climate and management that determine the availability of soil C and nutrients (Westoby et al. 1989; Jouany et al. 2011; Vendramini et al. 2014). According to our results, soils of natural grasslands and pastures in the humid

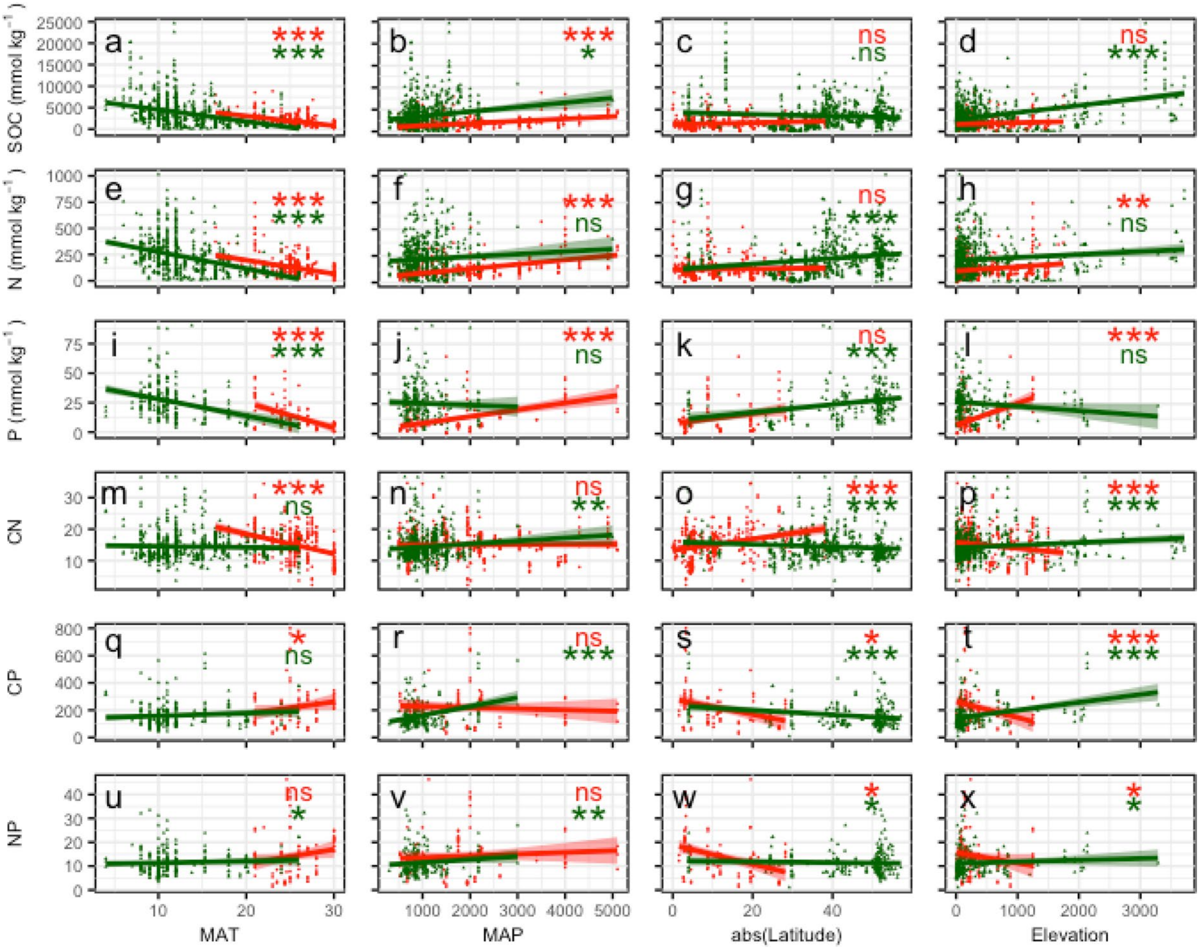

Fig. 2 Regression plots of elemental concentrations and ratios with environmental and geographical factors. Soil elements: SOC = soil organic carbon (panels "a" to "d"); N = total nitrogen ("e" to "h"); P = total phosphorus ("i" to "l"). Ratios: C:N = SOC:nitrogen ("m" to "p"); C:P = SOC:phosphorus ("q" to "t"); N:P = nitrogen:phosphorus ("u" to "x". MAT, mean annual temperature; MAP, mean annual precipitation. Red points, sites in the equatorial or humid tropical climatic zone (A); green points, sites in the warm temperate climatic zone (C). Statistical significance: *** < 0.001; ** < 0.01; * < 0.05; ns = non-significant. Complementary information in Supplementary Appendix 3 and 4

tropics have lower SOC concentration and higher C:P and N:P ratios than those from warm temperate regions on a global scale. However, other factors lead to different patterns at regional scales. For example, grazing has a significant effect in increasing soil N concentration and SOC, especially in temperate climates. For C:P and N:P ratios, the direction of the effect depends on grassland type and climatic zone. Soil stoichiometric signatures of grasslands differ between temperate and tropical climatic zones at global scales, although patterns at regional scales change when factors such as grassland type, grazing, temperature, precipitation, latitude, and altitude are included in the analysis.

SOC, N, and P concentrations were higher in sites in warm temperate than in tropical zones

Natural grasslands and pastures soils in humid tropical zones (Köppen-Geiger zone A) tend to have lower SOC, N, and P concentrations than soils in warm temperate zones (Köppen-Geiger zone C). These results can be explained by the fact that organic matter transformation processes are faster in the tropics (van Keulen 2001; Nortcliff 2010). Soil net primary production

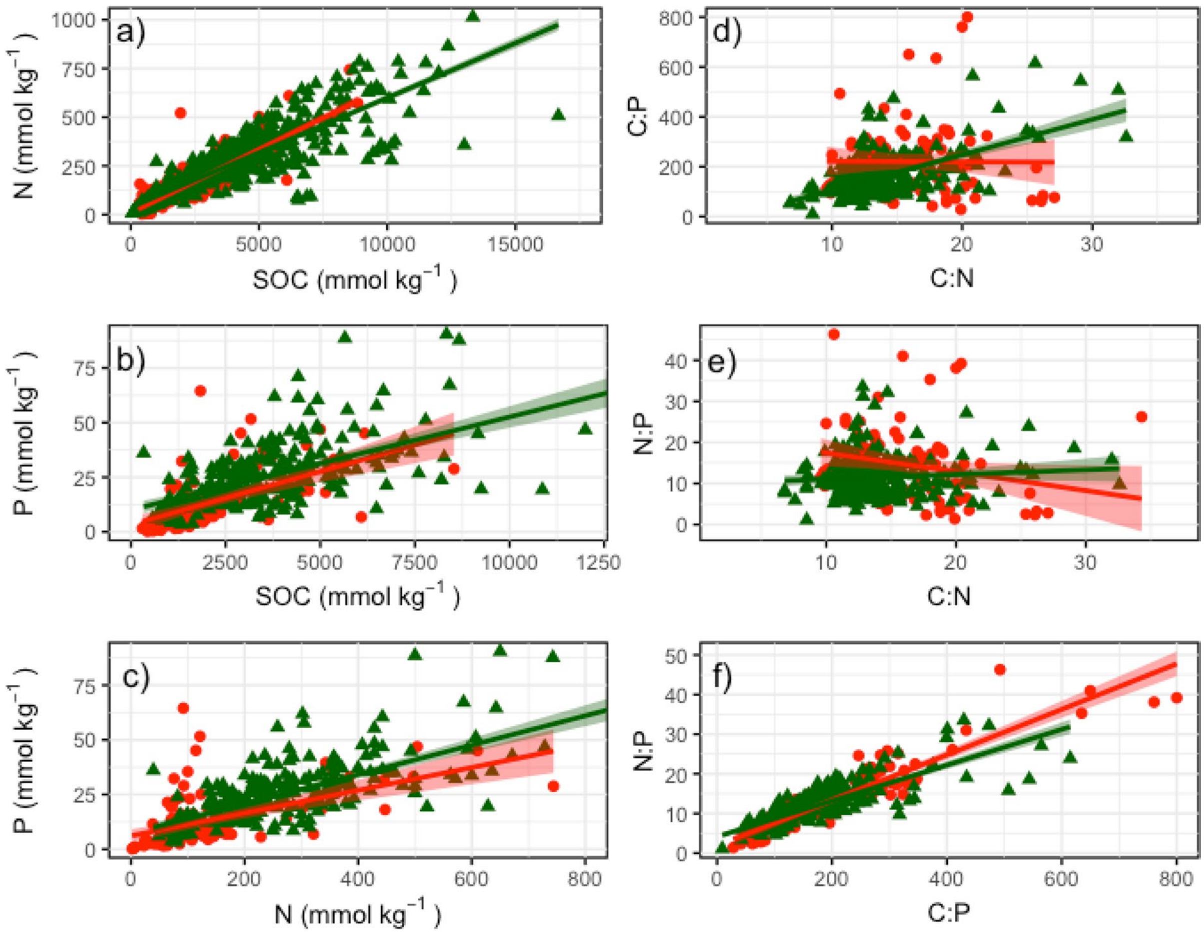

Fig. 3 Correlations between element concentrations and their ratios. Red points represent the sites in the equatorial or humid tropical climatic zone (A) and green triangles correspond to sites in the warm temperate climatic zone (C) (models and correlation parameters in Table 3)

(Chapin et al. 2012; Paul 2016) and C turnover rate (Trumbore 1993; Feller and Beare 1997; Šantrůčková et al. 2000; Six et al. 2002; Horwath 2015; Paul 2016; Six and Jastrow 2017) are higher in tropical than in temperate grasslands. High temperatures promote faster litter decomposition, nutrient transformation, recycling rates (Haynes and Williams 1993; Zech et al. 1997; Saggar et al. 2011), and microbial biomass production (Joergensen 2010). Changes in SOC are likely to affect soil total N due to a close association between SOC and total N in soil organic matter (Pineiro et al. 2010; Pringle et al. 2014). It has been reported that a higher microbial decomposition of SOC is related to increases in MAT and consequently lower concentrations of SOC and soil total N can be seen (Amundson 2021). This can be observed in our results, since SOC and N concentrations were negatively related to MAT and positively related to MAP (Fig. 2, Supplementary Appendix 3 and 4).

The lower total soil P concentrations in tropical compared to temperate regions (Fig. 2) could be explained by factors such as temperature, precipitation, and soil types. Soil total P concentration and C:P ratio decreased with MAT and MAP (Figs. 2, Supplementary Appendix 3 and 4), but it increased with SOC and N (Fig. 3). Sites with high total P concentrations are mainly located in temperate zones (Hou et al. 2018), with some exceptions for P-rich soils (Andosols, Mollisols) in volcanic and fertile tropical rainy regions (Cleveland et al. 2003; Huth et al. 2012). In temperate regions, high temperatures can promote soil P transformation from extractable to

Table 3 Models for correlation between elements and their stoichiometric ratios for both climate zones: equatorial or humid tropical (A) and warm temperate (C)

	Global data			Equatorial or humid tropical climate (zone A)			Warm temperate climate (zone C)		
	Model	p	r	Model	*p*	r	Model	*p*	r
SOC *vs.* N	N = 7.95 + 0.065 • SOC	< 0.001	0.92	N = 7.95 + 0.065 • SOC	< 0.001	0.87	N = 37.1 + 0.056 • SOC	< 0.001	0.88
SOC *vs.* P	P = 7.00 + 0.005 • SOC	< 0.001	0.72	P = 3.26 + 0.0049 • SOC	< 0.001	0.56	P = 10.1 + 0.0042 • SOC	< 0.001	0.59
N *vs.* P	P = 6.21 + 0.068 • N	< 0.001	0.81	P = 6.07 + 0.052 • N	< 0.001	0.54	P = 7.24 + 0.07 • N	< 0.001	0.71
C:N *vs.* C:P	C:P = 18.83 – 10.96 • C:N	< 0.001	0.36	**C:P = 223.89—0.25 • C:N**	**0.95**	**– 0.01**	C:P = -35.8 + 14.2 • C:N	< 0.001	0.59
C:N *vs.* N:P	**N:P = 12.24 – 0.007 • C:N**	**0.20**	**– 0.07**	N:P = 22.02 – 0.46 • C:N	0.04	– 0.22	**N:P = 9.90 + 0.12 • C:N**	**0.18**	**0.09**
C:P *vs.* N:P	N:P = 3.17 + 0.051 • C:P	< 0.001	0.89	N:P = 1.82 + 0.057 • C:P	< 0.001	0.92	N:P = 4.14 + 0.05 • C:P	< 0.001	0.83
SOC *vs.* C:N	C:N = 13.37 + 0.0005 • SOC	< 0.001	0.31	C:N = 13.42 + 0.0009 • SOC	< 0.001	0.37	C:N = 12.80 + 0.0005 • SOC	< 0.001	0.33
SOC *vs.* C:P	C:P = 148.2 + 0.009 • SOC	< 0.001	0.21	C:P = 217.8 + 0.001 • SOC	0.52	0.07	C:P = 100.5 + 0.017 • SOC	< 0.001	0.42
SOC *vs.* N:P	N:P = 10.39 + 0.0006 • SOC	< 0.001	0.24	N:P = 11.73 + 0.0013 • SOC	0.04	0.22	N:P = 8.52 + 0.0008 • SOC	< 0.001	0.35
N *vs.* C:N	**C:N = 15.1 – 0.002 • N**	**0.47**	**– 0.02**	C:N = 16.12 – 0.009 • N	< 0.001	– 0.18	**C:N = 14.60 – 0.0005 • N**	**0.62**	**– 0.02**
N *vs.* C:P	**C:P = 176.2 + 0.01 • N**	**0.11**	**0.09**	**C:P = 221.2 – 0.008 • N**	**0.94**	**– 0.01**	C:P = 138.9 + 0.092 • N	0.02	0.15
N *vs.* N:P	N:P = 10.44 + 0.008 • N	< 0.001	0.25	N:P = 11.87 + 0.016 • N	0.02	0.23	N:P = 8.61 + 0.011 • N	< 0.001	0.33
P *vs.* C:N	C:N = 15.75—0.051 • P	< 0.001	– 0.26	**C:N = 16.24 – 0.0019 • P**	**0.96**	**– 0.005**	C:N = 15.10 – 0.043 • P	0.012	– 0.16
P *vs.* C:P	C:P = 249.1 – 3.24 • P	< 0.001	– 0.53	C:P = 302.81 – 5.85 • P	< 0.001	– 0.52	C:P = 216.9 – 2.21 • P	< 0.001	– 0.35
P *vs.* N:P	N:P = 15.90 – 0.17 • P	< 0.001	– 0.42	N:P = 18.61 – 0.32 • P	< 0.001	– 0.45	N:P = 14.12 – 0.11 • P	< 0.001	– 0.31

Soil elements: SOC = soil organic carbon; N = total nitrogen; P = total phosphorus. Ratios: C:N = SOC:nitrogen; C:P = SOC:phosphorus; N:P = nitrogen:phosphorus. Relationships are considered significant when $p < 0.05$. The models highlighted in bold were not significant more stable forms (Siebers et al. 2017). Temperature and soil moisture enhance P-mineralization. Rainfall can increase inorganic P-fraction leaching (Arenberg and Arai 2019), but P organic fraction may be sequestered geochemically. In highly weathered tropical soils (Oxisols, Ultisols), these processes lead to a lower concentration of soil nutrients (Lopes et al. 2004; Peña-Peña and Irmler 2018; Vitousek and Sanford 1986; Vitousek et al. 2010) and high C:P ratios (Tipping et al. 2016), as we observed in our study. Low relative P-availability in tropical regions is also associated to sorption by allophanes in young volcanic soils (e.g. Andosols) and sesquioxide clays (e.g., Oxisols) (Vitousek and Sanford 1986; Gijsman et al. 1997; Hou et al. 2018). In this context, P could be a key element of regulation and restriction on soil C and N cycling in tropical regions more than in temperate zones.

Stoichiometric signatures differ according to climatic zones and environmental variables

Although SOC and N showed lower concentrations in tropical than in temperate grasslands, there were no significant differences in the C:N ratio for both climatic zones (Table 2). C:N values do not show differences between climatic zones (Table 1). Ratios of 14:1 have been previously reported for C:N, based on total C (Cleveland and Liptzin 2007) and of 13:1 for SOC:N (Xu et al. 2013). The C:N ratio is a litter decomposition driver and therefore promotes organic matter formation (Horwath 2015; Amundson 2021). This stoichiometric signature indicates an increase in SOC recalcitrance (for natural grasslands or pastures) or lower total N, leading to higher C:N ratios. Therefore, it stimulates N-immobilization, reducing its availability to plants (Robertson and Groffman 2015) and limiting soil organic matter, SOC formation and storage (Pineiro et al. 2010). The C:N ratios remained within intervals of 2 to 36 (> 90% of data are between 8 and 22), with higher variation in N:P ratios, which ranged from 1 to 46 (5 to 22 for 90% of data). Similar intervals have been reported on a global scale for the C:N ratio (2 to 30) but wider range for N:P (1 to 77), reflecting a strong coupling between the C and N cycles, but a decoupling of the total P from C and N concentration (Cleveland and Liptzin 2007). This association between SOC and total N has also been observed at regional or local scales (Pineiro et al. 2010; Tian et al. 2010; Pringle et al. 2014). A C:P ratio of 230:1 was found for tropical soils and of 158:1 for temperate sites, regardless of whether they were pastures or natural grasslands. A C:P ratio of 166:1 has been previously reported for grasslands globally (Cleveland and Liptzin 2007). This pattern has also been reported in forests (McGroddy et al. 2004) and other ecosystems (Yan et al. 2016), where the N:P ratio increases towards equatorial regions, following an increase in MAT. In our study, N:P ratios were 15:1 for grasslands in equatorial zones and 11:1 for sites in warm temperate regions.

Soil C:N:P stoichiometry among grassland types

Grassland-type (natural grassland or pasture) had a significant effect on SOC and nutrient concentrations in both climatic regions. We can explain this partially, due to characteristics of plant communities established in these ecosystems. Temperate grasslands are dominated by C_3 grasses, while C_4 grasses occur predominantly in tropical regions (Woodward et al. 2004; Lehmann and Parr 2016). As mentioned before, pastures in tropical regions are generally cultivated in sites whose original vegetation was forest (predominantly C_3 plants), and it is replaced mainly with exotic C_4 grasses (Oliveras and Malhi 2016). Grasslands dominated by C_4 grasses store more SOC and N than those dominated by C_3 plants, as has been reported for both temperate (Tilman and Wedin 1991; Yang et al. 2019) and tropical regions (Nyameasem et al. 2020). Tropical C_4 grasses (e. g. *Panicum*, *Pennisetum*) metabolism is more efficient in terms of photosynthetic activity indicators (e. g. use efficiency of resources such as light, water, or nutrients) compared to C_3 grasses from temperate climates (da Silva et al. 2015; Volenec and Nelson 2020). Given their higher photosynthetic efficiency, C_4 grasses use less water, but also have higher lignin content (Volenec and Nelson 2020) and produce lower quality litter, which is more slowly incorporated into soil (Thomas and Asakawa 1993). The introduction of African deep-rooted C_4 grasses into native savannas could increase soil C storage (Fisher et al. 1994; Fujisaki et al. 2015) but also higher C:N ratios (Williams and Baruch 2000), so the combination with N-fixing legumes could increase soil N content. This functional type of grasses also increases the P stock in their tissues and makes efficient use of this element, but further research is required. This C_3/C_4 grass communities composition contributes to explain SOC higher concentrations and nutrients in tropical pastures than in natural grasslands.

High lignin content in C_4 grasses may limit the incorporation of plant matter into soil, a condition that is also favored by P deficiency (Lopes et al. 2004; García-Oliva et al. 2006; Vendramini et al. 2014). This P deficiency is reflected in P lower concentration and high C:P and N:P ratios in pastures (C:P, 211:1, N:P, 14:1), usually higher than in natural grasslands (C:P, 152:1; N:P, 11:1). When considering the climatic zone, the average values for both ratios were higher in tropical regions than in temperate regions. On a global scale, higher C:P and N:P ratios have also been reported for pastures (169:1 and 12:1) compared to natural grasslands (143:1 and 11:1) (Xu et al. 2013). This trend of lower relative P concentration is also observed in C:P ratios in pastures and has also been reported in previous studies (Xu et al. 2013). The lower relative content of nutrients in pasture soils can limit the SOC use by organisms in the system (Abbas et al. 2013; Achat et al. 2016).

Grazing impacts on soil C:N:P stoichiometry

The grazing influence on SOC and soil nutrient concentrations depended on the type of grassland. In natural grasslands, the highest concentrations of SOC, N, and P were found in grazed sites, but higher C:P and N:P ratios were observed in ungrazed tropical pastures (Table 1). Grazing can inhibit the growth of tropical plants with high efficiency characteristics in the acquisition of soil nutrients, while without grazing, these plants can grow, uptake nutrients, and establish themselves. More research is needed on this topic. The most used livestock management method in tropical grasslands is extensive grazing (Dubeux et al. 2007; Teutscherová et al. 2021). This method promotes selective forage consumption leading to zonal degradation (Kothmann 2009), and urine and dung patches unevenly distributed. Two effects can be expected about this grazing management method: (1) an increase in N-recycling and availability when nutrients remain and storage on site, or (2) an increase in N-losses through volatilization and leaching (Dubeux et al. 2007; Pineiro et al. 2010). In the first case, the plant-soil system can store more N in part by biomass microbial immobilization. In the second case, if available N exceeds the short-term requirements of pastures around dung patches, losses will occur (Haynes and Williams 1993). Even when these patches can contribute to an increase in SOC and N, compaction and intense rainfall can promote nutrient losses by surface runoff and limit soil N inputs (Greenwood and McKenzie 2001; Taboada et al. 2011). Increased soil C stocks by improvements in grazing management (i.e., stocking density management, rotation grazing) have been reported (Conant et al. 2017). Grazing effects also can depend on grass composition (C_3 or C_4 grasses) and environmental conditions (McSherry and Ritchie 2013; Abdalla et al. 2018; He et al. 2020). The effect of grazing on SOC concentration also depends on other specific factors at more local scales, such as environmental conditions (precipitation, temperature), soil properties, land topography (Pineiro et al. 2009), and grazing improvements (Conant et al. 2017).

Effect of geographical variables on stoichiometric signature patterns

Geographical variables (i.e., altitude and latitude) have consistent effects on SOC and N concentrations, which both increase with altitude and latitude. The highest (Andean) montane grasslands soil, and the northernmost (England) and southernmost (New Zealand) regions are the richest. Decreases in annual mean temperature (5.5ºC) generally have been calculated for every increase of 1000 m in altitude above sea level, or for increases of 15º in latitude above 10º North or South (Humphreys 1981). Following this pattern, increases in SOC and N concentrations proportional to altitude and latitude would be expected in grasslands, which is supported by our results. Increasing SOC and total N concentrations with altitude have also been observed at a local level (Gerschlauer et al. 2016). The higher concentrations of SOC we found (up to 24,000 mmol kg^{-1}) have been reported in Andean montane grasslands, over 3000 m.a.s.l. (Oliver et al. 2017; Oliveras et al. 2014). It is important to note that N-mineralization increases with soil moisture (Singh et al. 1991) but also with elevation (Gerschlauer et al. 2016), and thus if N is not taken up or immobilized, then it could be lost by leaching or runoff. Furthermore, if increasing temperature and limited water availability lead to a decline in microbial growth, then there is also a decline in C-use efficiency (Manzoni et al. 2012). At low P concentrations N_2 fixation is limited and N availability for plants can be reduced (Sardans and Peñuelas 2012). These results are an invitation to study and compare patterns of nutrient concentration and transformation in altitudinal gradients in other mountain systems, such as other grassland areas in the Andes, Kilimanjaro, the Himalayas, and mountain regions in Mexico, Central America, and New Zealand, to name a few examples.

Limitations and future work

This study investigated soil organic C, N, and P among warm temperate and tropical grassland, and the underlying mechanisms. Although meta-analysis approach allows a synthesis to establish global and regional patterns that cannot be observed through individual studies, a few limitations have been identified and will be addressed in our future work. First, intrinsic diversity in grassland ecosystems leads to a high variability in C, N, and P concentrations. This variability has also been found in other reviews and is a source of uncertainty. Second, the relative lack of information about soil P has also been a frequent issue in previous reviews (Cleveland and Liptzin 2007; Tian et al. 2010). Third, there is a lack of standardized methodologies for determining elemental concentrations as a source of heterogeneity in datasets. Fourth, the conclusions related to effects of grazing on concentrations and ratios evaluated are limited by the necessary non-random sample of grazed vs. ungrazed sites. Despite all these methodological issues as a source of uncertainty, our findings can contribute to increase knowledge of factors affecting the status of elements in grazed and ungrazed grassland soils, particularly in pastures of tropical regions. There remains a clear gap of information in these tropical ecosystems, as can be seen from the collected data (Table 1, Supplementary Appendix 1) and from previous reviews.

Conclusions

Our findings suggest that soil stoichiometric C:N:P stoichiometric signatures in grasslands differed between tropical and temperate regions on a global scale. Our results can be partly attributed to the effect of mean annual temperature (MAT) and mean annual precipitation (MAP) on soil C and nutrient reduction, resulting in higher C:P and N:P ratios in tropical pastures. It could be hypothesized that in tropical regions, in contrast to temperate regions, P is a key element in regulating and limiting soil C and N cycling. Changes in soil P concentrations can have significant effects on soil C and N stoichiometric ratios, highlighting the importance of understanding the mechanisms behind soil P reduction in elucidating the functioning of tropical regions. Imbalances in soil C:N:P stoichiometric ratios could lead to cascading stoichiometric changes in N and P availability throughout the ecosystem. As nitrogen (N) and phosphorus (P) are elements that regulate the growth rate of organisms, these changes could affect both living organisms, such as plants, microorganisms and herbivores, and inorganic reservoirs of the ecosystem, including the atmosphere and water. Such imbalances can therefore affect ecosystem functioning and productivity, and taking these patterns into account can be a valuable tool for planning management and conservation of natural grasslands and pastures.

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Data availability Data will be made available on request.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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