SOIL ECOLOGY LETTERS

SEL | RESEARCH ARTICLE
Volume 6 / Issue 4 / 240242 / 2024
https://doi.org/10.1007/s42832-024-0242-6

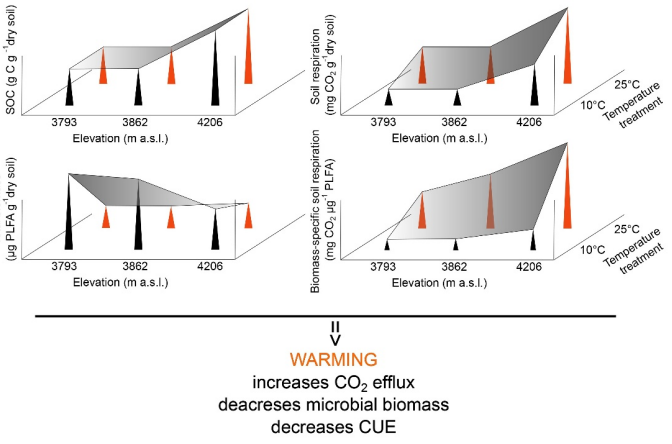
Experimental warming increases respiration and affects microbial communities of soil wetlands at different elevations of the Argentinean Puna

M. Fernanda Chiappero[1], María V. Vaieretti[1,2,*], Norma Gallardo[1], Andrea E. Izquierdo[1,3]

1 Multidisciplinary Institute of Plant Biology (IMBIV), National University of Córdoba -CONICET, Vélez Sársfield Avenue 1611, 5016 Córdoba, Argentina
2 Faculty of Exact, Physical and Natural Sciences, National University of Córdoba, Vélez Sarsfield Avenue 299, 5000 Córdoba, Argentina
3 Faculty of Natural Sciences and Miguel Lillo Institute, National University of Tucumán, Miguel Lillo 205, 4000 San Miguel de Tucumán, Tucumán, Argentina
* Corresponding author. E-mail: vvaieretti@imbiv.unc.edu.ar (M.V. Vaieretti)
Received January 4, 2024; Revised February 18, 2024; Accepted February 21, 2024

ABSTRACT

- Under warming soil respiration was higher, but soil microbial biomass was lower.
- Warming effect on soil respiration was higher in soil from the highest elevation.
- Soil respiration was higher in soil with higher soil carbon content.
- Warming increased biomass-specific respiration and enzyme activity.
- The Q_{10} did not differ among soils from different elevations.



Global warming is expected to increase the rate of soil carbon (C) efflux through enhanced soil microbial processes, mainly in systems, such as high elevation wetlands, storing large quantities of soil organic C. Here, we assessed the impact of experimental warming on respiration and microbial communities of high Andean wetland soils of the Puna region located at three different elevations (3793, 3862, 4206 m a.s.l.). We incubated soils at 10°C and 25°C for 68 days and measured the soil respiration rate and its temperature sensitivity (Q_{10}). Furthermore, we measured biomass and composition and enzymatic activity of soil microbial communities, and initial and final soil C content. Although warming increased soil respiration rates, with more pronounced effect in soils sampled from 4206 m a.s.l., Q_{10} did not differ between elevations. Soil C content was higher at the highest elevation. Soil microbial biomass, but not enzymatic activity, was lower for warmed soil samples. However, the biomass-specific respiration and biomass-specific enzymatic activity were higher under warming, and in soil from the highest elevation wetland. These results suggest that, in the short-term, warming could stimulate resource allocation to respiration rather than microbial growth, probably related to a reduction in the microbial carbon use efficiency. Simultaneously, soils with higher soil C concentrations could release more CO_2, despite the similar Q_{10} in the different wetlands. Overall, the soil of these high Andean wetlands could become C sources instead of C sinks, in view of forecasted increasing temperatures, with C-losses at regional scale.

Keywords high-altitude ecosystems, peatlands, temperature, microorganisms, soil CO_2 flux, *vegas*

1 Introduction

Andean wetlands located at high elevations (i.e., over 3000 m a.s.l.) are recognised for their capacity to store large quantities of soil organic carbon (SOC) (Hribljan et al., 2015; Benavides et al., 2023; Chimner et al., 2023). The accumulation of organic matter in these wetland soils results from high primary productivity and low decomposition rates due to waterlogging conditions and low temperatures (Maldonado-Fonkén, 2014; Chiappero et al., 2021). The increased temperatures driven by climate change might alter biochemical cycles and the C balance in these mountain wetlands (IPCC, 2022). At present, our understanding of soil processes in the Andean region in response to climate change scenarios is limited, making it crucial to fill this gap to accurately predict the consequences of warmer temperatures in the SOC dynamics of these wetlands.

Most climate scenarios for these high-elevation ecosystems

predict a temperature increase by the end of the 21st century (Urrutia and Vuille, 2009; IPCC, 2022). In this environmental context, soil respiration rate could increase and amplify the effect of climate change through SOC losses mediated by microbial decomposition (García-Palacios et al., 2021). In mountains, the response of soil respiration to warming is influenced by the strong variations in temperature and C content at different elevations (Hagedorn et al., 2019). For example, soil respiration rates under warming have been shown to increase along the elevation gradient as a result of larger SOC reservoirs at higher elevations (Wang et al., 2013; Li et al., 2018). However, the sensitivity of soil respiration to temperature (Q_{10}), which represents the range of increase in respiration rate for every 10°C increase in temperature (Davidson and Janssens, 2006), is not mainly associated with the amount of C itself, but rather with SOC quality. In this sense, recalcitrant SOC fractions show higher Q_{10} values as compared to labile SOC fractions (Nottingham et al., 2015). It has also been shown that the increase in the sensitivity of soil respiration to warming at lower elevations compared to at higher elevations could be a consequence of changes in the microbial community composition (Li et al., 2020). These changes in C availability and microbial communities could eventually affect, and interact with, warming effects on C cycling (Bardgett and Caruso, 2020).

In the short term, warmer temperatures usually stimulate the enzyme activity of microorganisms (Meng et al., 2020), promoting the consumption of C resources and their assignment to microbial growth (Walker et al., 2018; Wang et al., 2021). However, the stimulation of microbial activity due to an increase in temperature can promote the allocation of C to respiration rather than investing in growth biomass, with the reduction in the carbon use efficiency affecting microbial growth (Tian et al., 2023). It has also been shown that Q_{10} is a good indicator of the responses of microbial communities to changes in environmental factors, such as incubation temperature, substrate availability and microbial community composition (Li et al., 2020). Some authors have suggested that Q_{10} decreases at higher elevations (i.e., colder temperatures) because microorganisms are adapted to a greater daily thermal amplitude compared to lower elevations (Blagodatskaya et al., 2016). For soils belonging to cold environments, like those from higher elevations, constant warming, however, could also generate thermal damage to microorganisms and cause a reduction in their biomass (Li et al., 2020). Consequently, these changes could affect microbial community composition (Orwin et al., 2018). Sensitivity to thermal damage depends furthermore on the type of microorganisms involved. According to a global analysis carried out by Salazar et al. (2020), fungi are less sensitive than bacteria to increasing temperature. Among bacterial groups, Gram-positive (GP) bacteria are also more resistant than Gram-negative (GN) bacteria to warming when water is not a limiting factor (Yu et al., 2018). These changes in microbial communities caused by variations in temperature also determine the magnitude and direction of C fluxes, altering the dynamics of C cycling (de Vries and Shade, 2013).

For the Puna ecoregion in the Andean mountains, an increment in the monthly mean temperature of 0.01−0.04°C per decade, since the beginning of the 20th century, has been measured (Pabón-Caicedo et al., 2020), along with a decrease in precipitations with longer dry seasons (Morales et al., 2023). In the dry Argentinean Puna ecoregion, wetlands – locally called *vegas* – represent the primary source of fresh water and food for the fauna and human populations (Izquierdo et al., 2018a, 2018b), but also represent the main sink of C at a regional scale (Chiappero et al., 2021). Despite the relevance of these wetlands at local and regional scales, little is known about how soil processes could be affected by increasing temperature and the possible consequences for the accumulated C in their soils. Therefore, in this study we carried out a short-term experiment to assess the response of soil respiration to warming of three *vegas* located at different elevations (3793, 3862, 4206 m a.s.l.) in the Argentinean Puna. We carried out a soil laboratory incubation experiment at two temperatures, control (10°C) and warming (25°C), and evaluated differences in the soil respiration, measured as the CO_2 released and its temperature sensitivity (Q_{10}). To analyse the effects of the potential changes on soil respiration rates, we analysed: 1) differences in the biomass, composition and enzymatic activity of the microbial community after the exposure to temperature treatments, and initial and final soil C content, and 2) the relationship between microbial biomass and initial soil C content as a proxy to analyze the potential microbial C assimilation.

2 Materials and methods

2.1 Study area

The study area is located in the Puna ecoregion of the Catamarca province, Argentina (26.06° S, 67.39° W, Fig. S1). The region has an arid climate, with a strong seasonality. Precipitation is concentrated during the austral summer (from December to March), and the mean annual precipitation decreases from 400 to 100 mm along a northeast to southwest gradient. Thermal amplitude in the Puna region is high, reaching 15°C of difference between day and night (Navarro, 2020). The average annual temperature is around 10°C (Cabrera, 1971). Along the Puna region soils are classified mostly as Aridisols or Entisols (Soil Survey Staff, 2010). Within this arid landscape, wetlands develop in places that receive permanent inflows of groundwater and superficial

water, which are recharged from seasonal rainfall and snowmelt. The soils in these places are classified as Histosols due to the accumulation of SOC (Vargas Gil, 1990; Fig. S1). The limited water supply makes wetlands vulnerable to small changes in climate (Cooper et al., 2019).

We selected three representative *vegas* of high Andean wetlands in a similar region with similar floristic composition and eco-geographic characteristics according to Izquierdo et al. (2022), but located at different elevations: 3793, 3862, and 4206 m a.s.l. (Table 1, Fig. S1). Plant communities are characterised by the dominance of *Zameioscirpus atacamensis*, with the presence of *Eleocharis pseudoalbibracteata*, *Lobelia oligophylla* and *Phylloscirpus acaulis*, among others (Izquierdo et al., 2022). *Distichia muscoides* and *Oxichloe andina* are also abundant species which form a typical cushion and can be associated with grasses, like *Festuca nardifolia* and *Deyeuxia hackelii* (Izquierdo et al., 2022).

2.2 Soil sampling

In May 2021, within each selected *vega*, we collected four composite soil samples within the top 10 cm separated by at least 30 m from each other. We chose sampling points with similar plant species composition and with no superficial water courses. After collection, we transported the soil samples to the laboratory and stored them in sealed plastic bags in a fridge at 4°C until processing. Then, we carefully sieved the soil samples (2 mm mesh) and removed roots and stones. We separated 30 g of soil from each composite sample and placed these sub-samples into 100 mL vials and stored them in a fridge for 48 h at 10°C until the beginning of incubations, allowing microbial communities to stabilise after disturbance. We measured soil C concentration (%) in the soil samples prior to incubations (initial C content) and at the end of the experiment (i.e., final C content), using the Walkley and Black method (Nelson and Sommers, 1996). We also separated another sub-sample of 1 g, of each composite soil sample, to determine water soil humidity using the gravimetric method (i.e., oven-dry at 105°C for at least 24 h, Jarrell et al., 1999).

To characterise each sampled point in the field campaign, we measured the water table in dipwells installed near the sampling point at least 24 hours before the measurements (Navarro, 2020). We also collected soil composite samples up to 15 cm depth to determine in the laboratory soil pH (Thomas, 1996) and electrical conductivity (Rhoades, 1996) using a Hanna DIST 4 conductivity meter.

2.3 Soil incubation experiment

We set up a laboratory incubation experiment to test the responses of soil respiration to changes in temperature. We selected the CO_2 alkali trap method, which is a widely used and simple process for measuring soil respiration (Haney et al., 2008). Using a sealed plastic jar (1000 mL of volume) to create a closed system, we incubated the 30 g soil sub-samples in dark conditions at two temperatures: control (10°C) and warmed (25°C). We prepared a total of 24 sealed jars: four samples × three elevations × two temperature treatments. Each sealed plastic jar contained three vials inside: one vial of 100 mL size containing 30 g of wet soil sample (pre-incubated at 10°C, see above) and two smaller vials, one with 10 mL water (to maintain moisture level) and the other with 10 mL of NaOH 1 M (i.e., CO_2 alkali trap). We also prepared three additional sealed plastic jars used as blanks (without soil sample) for control and warming treatment, respectively. We measured the CO_2 released from soil samples at 9, 16, 28, 40, 54, and 68 days of incubations. Before titration, we added $BaCl_2$ (0.75 M) to precipitate the CO_3^- and the excess NaOH was back titrated with HCl (0.5 M) (Rice et al., 1996). We kept soil humidity constant

Table 1 Characterization of the three studied wetlands located at different elevations in the Argentinean Puna.

Characteristics	Studied wetlands		
Elevation (m a.s.l.)	3793	3862	4206
Latitude (S)	26.6913068°	26.0165419°	25.9894793°
Longitude (W)	67.1802228°	67.6942650°	67.2307396°
Soil			
pH†	8.64 (0.04) A	6.94 (0.17) B	6.84 (0.18) B
EC (μS cm^{-1}) †	846.0 (150.60) A	2517.50 (590.11) A	1524.25 (420.87) A
Organic carbon (%)‡	7.77 (0.85) A	7.75 (1.83) A	17.57 (0.87) B
Water content (%)‡	53.76 (1.62) A	52.73 (6.46) A	61.11 (1.59) A
Water table depth (cm)	7.63 (3.46) A	17.93 (4.76) A	16.38 (4.62) A

Data regarding elevation, geographic coordinates, and the averages (± SE) of soil characteristics (prior to incubations) and water table depth are given. Different letters, A and B, indicate significant differences between wetlands at $P < 0.05$, $n = 4$. EC: electrical conductivity.
†Measured at 15 cm depth. ‡ Measured at 10 cm depth.

during all the experiment; hence we added water to the soil after each measurement when necessary. We expressed soil respiration as $mgCO_2$ g^{-1} dry soil and $mgCO_2$ g^{-1} initial C dry soil.

We also calculated the temperature sensitivity (Q_{10}) of cumulative soil respiration (i.e., at the end of the experiment) using the following equation:

$$Q_{10} = (R_W/R_C)^{[10/(T_W - T_C)]}$$

where R is the accumulative soil respiration after 68 days of incubation, T is temperature (°C) and the subscripts W and C indicate the different temperatures of incubation at warming (25°C) and control (10°C), respectively.

2.4 Biomass, composition and enzymatic activity of soil microbial communities

We quantified the biomass and characterised the composition of active soil microbial communities after the short term exposure to different temperatures (i.e., at the end of the incubation experiment), using phospholipid fatty acid (PLFA) profiles (Bossio and Scow, 1998; Zelles, 1999). We separated 8 g from each of the 30 g of incubated soils and extracted PLFA using a mixture of chloroform, methanol, and phosphate buffer (1:2:0.8 by volume) and with extraction columns in solid phase (Silicic acid Sil350-Sigma). We used a gas chromatograph (Perkin-Elmer Clarus 500) equipped with an Elite-5 Crossbond 5 % diphenyl - 95 % dimethyl-polysiloxane column. An external standard (BAME mix, SUPELCO, St. Louis, USA) was used to identify fatty acids. For the quantification of peaks, methyl-nonadecanoate (*19:0*) provided an internal standard. We used the sum of *14:0*, *15:0*, *16:0*, *17:0*, *18:0* and *20:0* fatty acids as indicators of non-specific bacteria; the sum of *a-15:0*, *i-15:0*, *i-16:0* and *i-17:0* as indicators of Gram-positive (GP) bacteria; *cy17:0*, *cy19:0*, *16:1ω9c* for Gram-negative (GN) bacteria. All the aforementioned fatty acids were summed as total bacteria (B). As fungal (F) indicators, we used the sum of *18:2ω9c,12c* and *18:1ω9c* fatty acids (Willers et al., 2015; Orwin et al., 2018; Joergensen, 2022). We also calculated the F:B and GP:GN ratios. For each soil sample, total microbial biomass was calculated as the sum of the abundance of the different PLFA markers based on dry soil weight (µg PLFA g^{-1} dry soil).

Additionally, we separated 1 g of each incubated soil sample to quantify the microbial enzymatic activity using fluorescein di-acetate (FDA) hydrolysis (Adam and Duncan, 2001). We incubated 1 g of air-dry soil with phosphate buffer (60 mM, pH=7.6) and 100 µL FDA (2 mg mL^{-1}) for 2 h at 25°C. After the incubation, we quantified the concentration of fluorescein, which is a coloured end-product released by the action of microbial enzymes, with a spectrophotometer at a wavelength of 490 nm. Microbial enzymatic activity was expressed as the mass of fluorescein released per hour by microbes present in the 1 g of dry soil (µg g^{-1} dry soil h^{-1}).

2.5 Statistical analysis

Before running models, we tested for normality of the data but most of the variables, except Q_{10} values and water table depth, were log-transformed. Soil elevation provenance (hereafter, elevation) and temperature treatment were considered as categorical factors, whereas soil properties (pH, electrical conductivity, initial OC and water content), water table depth, soil respiration, final OC concentration, temperature sensitivity, quantity of PLFA and enzyme activity were the considered quantitative variables. We considered soil humidity as a covariable due to initial differences in water content in the soil samples.

We fitted linear models (LM) to analyse differences between the three elevations, and between the temperature treatments and also the interaction between these main factors (elevation x temperature treatment), in means of the cumulative soil respiration rate, soil C content, temperature sensitivity, biomass and activity of microorganisms at the end of the experiment. For that, we used the package *lme4* in R. To determine differences in means between elevations we used post-hoc comparisons with Tukey's test (α=0.05), whereas we applied Student's *t*-test (α=0.05) for pairwise comparison between temperature treatments.

We analysed the variations in microbial community composition at the end of the incubation experiment of soil samples exposure to different temperatures, from different elevations, with a principal component analysis (PCA) using the *factoextra* package in R. We considered the abundance of the different PLFA markers measured (*14:0*; *15:0*; *16:0*; *17:0*; *18:0*; *20:0*; *a-15:0*; *i-15:0*; *i-16:0*; *i-17:0*; *cy17:0*; *cy19:0*; *16:1ω9c*; *18:2ω9c,12c* and *18:1ω9c*).

As a proxy of microbial C assimilation, we estimated the relationship between microbial biomass (total PLFAs) and initial soil C content. In addition, we calculated the biomass-specific soil respiration and biomass-specific enzymatic activity rates (i.e., respiration rate and enzymatic activity per unit of microbial biomass). We analysed these variables using LM as described above. All analyses were done with R v.4.1.1 (R Core Team, 2019).

3 Results

3.1 Initial soil characteristics

Soil pH ranged between 6.3−8.7 and it was higher at 3793 m a.s.l. than at 3862 m a.s.l. (t value = 7.18, $P < 0.001$) and at 4206 m a.s.l. (t value = −7.69, $P < 0.001$). The values of electrical conductivity were highly variable within each

wetland. For all points sampled the electrical conductivity ranged from 541 to 3531 μS cm^{-1} and we did not find differences among elevations (P > 0.05, Table 1). Initial soil OC concentration ranged between 2.9% and 19.2%, and it was higher at 4206 m a.s.l. than at 3793 m a.s.l. (t value = 3.13, P < 0.05) and at 3862 m a.s.l. (t value = 3.13, P < 0.05). The values found for water table depth ranged from 0 to 30 cm and did not differ between elevations (P > 0.05, Table 1).

3.2 Cumulative respiration rate and temperature sensitivity

After 68 days of incubation, the cumulative respiration rate was significantly higher (by a factor of two) in soil from 4206 m a.s.l. compared to soils from 3793 m a.s.l. (t value = 2.82, P < 0.05) and 3862 m a.s.l. of elevation (t value = 2.51, P < 0.05) (Fig. 1a). Additionally, the soil subjected to warming treatment had a threefold larger respiration rate than that of the control (t value = −5.68, P < 0.001), and we found a positive association with initial soil water content. When we compared the association of release of CO_2 and the initial soil OC content, we found no significant differences between *vegas* soils from different elevations (P > 0.05). But we found that samples subjected to warming treatment released fourfold more CO_2 per soil OC gram than the control treatment (t value = −10.62, P < 0.0001) (Fig. 1b). Soil respiration rate relative to C content was negatively correlated to soil water content.

At the end of the incubations, values of soil C concentration ranged between 2.7 and 19.1%, being these values similar to the C content before the incubations. Soil from 4206 m a.s.l. had twofold more C concentration than soil from 3793 m a.s.l. (t value = 4.68, P < 0.001) and 3862 m a.s.l. (t value = 4.82, P < 0.0001) (Fig. 2). We did not find differences in the soil C concentration between the control and warming treatments (P > 0.05). Final soil C content was positively correlated with soil water content.

The Q_{10} values range between 1.68 and 2.83. The variation range of the Q_{10} at 3793 m a.s.l. was 1.75−2.83, and 1.68−2.35 at 3862 m a.s.l., while at the highest elevation it was 2.06−2.36. We did not find significant differences in the Q_{10} between elevations (Fig. 3).

3.3 Biomass, composition and enzymatic activity of soil microbial communities after exposure to temperature treatments

Axis 1 and 2 of the PCA analysis explained 62.5% of the total variance in the composition of PLFA markers of the soil samples from *vegas* located at different elevations and subjected to different temperatures (Fig. 4). We found that soil samples with higher relative abundance of the unspecific bacteria markers *18:0*, were grouped to the negative extreme of axis 1, and they corresponded to soil samples from 3793 and 3862 m a.s.l. exposed to control treatment. Axis 2 separated soil samples with higher relative abundance of fungal markers (*18:2ω9c,12c* and *18:1ω9c* markers) towards the negative extreme, which correspond mainly to soil samples from all elevations and subjected to warming treatment; except for two samples from the lower elevation that were grouped with soil samples from 4206 m a.s.l. subjected to control treatment at the positive extreme of axis 2, which presented higher relative abundance mainly of GN bacteria (*cy17:0*, *16:1ω9c* markers) (Fig. 4; Table S1).

We found that soils from 3793 and 3862 m a.s.l. had higher total microbial biomass after being subjected to 10°C (control treatment) compared to soils from the same two elevations and subjected to 25°C (warming treatment). However, we did not find differences between temperature treatments in soil of the *vega* from 4206 m a.s.l. (Fig. 5a). The same pattern was found for total bacteria biomass (i.e., the sum of unspecific bacteria, GP and GN bacteria PLFA

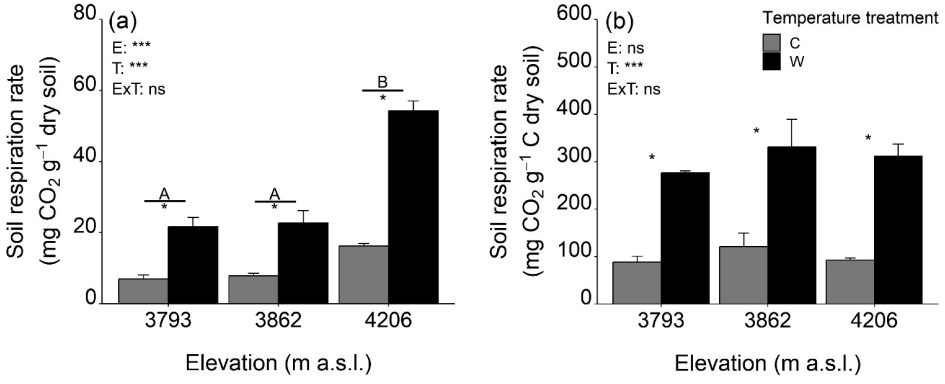


Fig. 1 Cumulative soil respiration rate after 68 days of incubation of soils from different elevations of the Argentinean Puna incubated at two temperatures: C=Control (10°C), W=warmed (25°C). (a) CO_2 released per g of dry soil and (b) CO_2 released per g of initial soil C content. The error bars represent ±1 standard error. Different capital letters denote significant differences between elevations (P < 0.05), and asterisks indicate significant differences between temperature treatments at the same elevation (P < 0.05). E=elevation; T=temperature treatments; E×T=interaction of elevation and temperature treatment. ns=not significant.

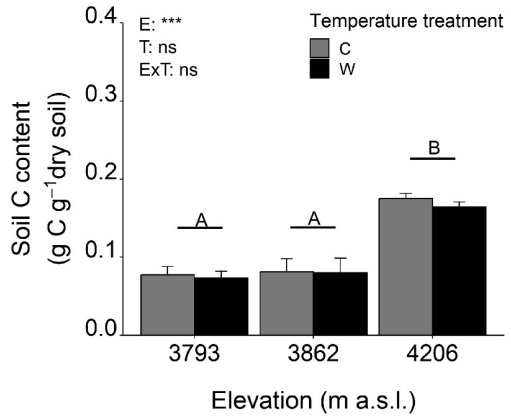


Fig. 2 Soil organic carbon (C) content, of wetland soils from different elevations of the Argentinean Puna, at the end of incubation at two different temperatures. C=Control (10°C), W=warmed (25 °C). The error bars represent ± 1 standard error. Different capital letters denote significant differences between elevations ($P < 0.05$) and asterisks indicate significant differences between temperature treatments at the same elevation ($P < 0.05$). E=elevation; T=temperature treatments; E×T= interaction of elevation and temperature treatment. ns=not significant.

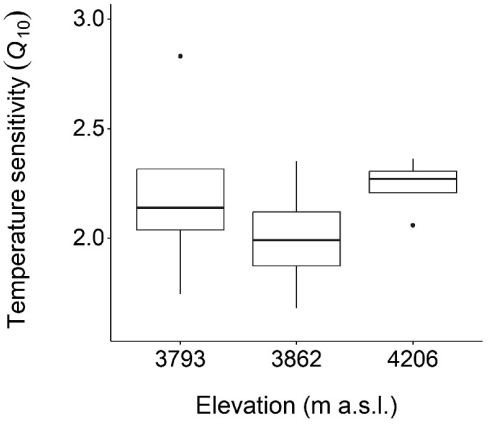


Fig. 3 Boxplot of temperature sensitivity of soil respiration (Q_{10}) to warming in wetland soils of the Argentinean Puna located at different elevations.

markers) (Fig. 5b). Nevertheless, we found different patterns for the different bacterial groups. Independently of temperature treatment, GP bacteria biomass was higher in soil from the low elevation (3793 m a.s.l.) and lower in soil from intermediate elevation (3862 m a.s.l.), with intermediate biomass in soil from higher elevation (4206 m a.s.l.). Furthermore, we found higher GP bacteria biomass in soil samples incubated under control treatment than soil samples incubated under warming treatment (Fig. 5c). In soil from 4206 m a.s.l, the GN bacteria biomass was higher when incubated at 10° C than when incubated at 25°C, but we did not find similar differences between temperature treatments in soils from the other two elevations (Fig. 5d). In the case of fungal biomass, we found higher values in soil samples incubated at 10°C than in soil samples incubated at 25°C, for the three

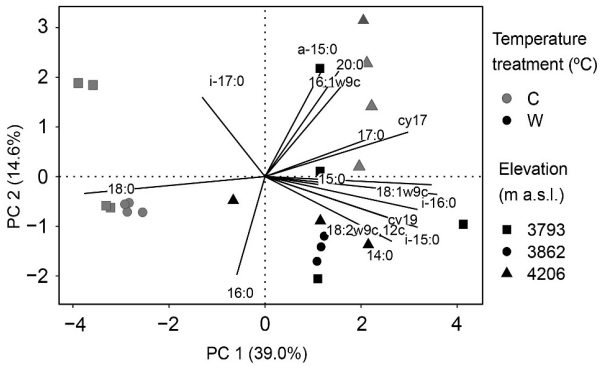


Fig. 4 Diagram of principal component analysis (PCA) showing the ordination of soil samples from wetlands located at different elevations, based on their soil microbial composition after the laboratory incubation under different temperature treatments. C=Control (10°C), W=warmed (25°C). The contribution of different PLFA markers to the ordination is shown. The percentage of variability explained by each axis is shown in parentheses.

elevations (Fig. 5e). We found significant interaction effects of elevation and temperature treatment on F:B and GP:GN ratios. F:B ratio was lower in soils from 3793 and 3862 m a.s.l. incubated at 10°C than in those incubated at 25°C or in soil from 4206 m a.s.l. (Fig. 5f). GP:GN ratio was higher in soil from 3793 m a.s.l. incubated at 10ºC than in soils from the other two elevations incubated at both temperatures (Fig. 5g). Finally, microbial enzymatic activity (FDA) showed higher values in soil from the highest elevation than in soils from the other two elevations, but we did not find significant differences between temperature treatments (Fig. 5h). None of the microbial parameters measured were related to water content.

3.4 Metabolic responses of soil microbial communities to warming

We found that microbial biomass per unit of initial soil C content was lower in warmed than control sample soils from 3793 and 3862 m a.s.l. However, we did not find differences between temperature treatments in soil from 4206 m a.s.l. (Fig. 6a). Biomass-specific soil respiration was tenfold higher in soil samples subjected to warming than in control samples, and was significantly higher in soil from 4206 m a.s.l. than in soils from 3793 and 3862 m a.s.l (Fig. 6b). We also found that biomass-specific enzymatic microbial activity was higher (fourfold) under warming than control treatment, and higher in soil from the highest elevation compared to soils from the other elevations (Fig. 6c).

4 Discussion

Our results showed that experimental short-term warming increased respiration rate in soils from *vegas* located at

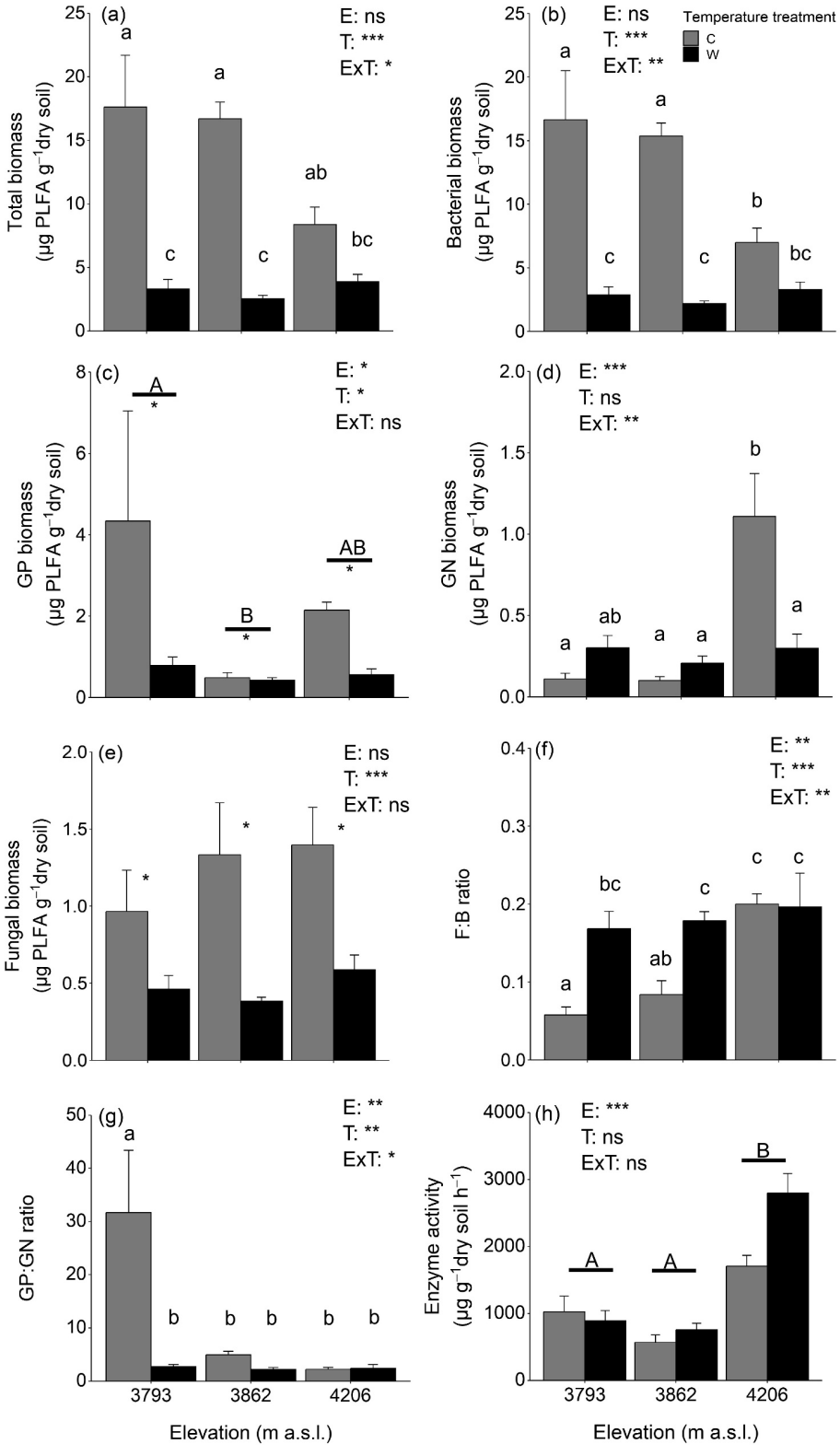


Fig. 5 Soil microbial biomass and enzymatic activity at the end of incubation. (a) Total microbial biomass (total PLFA), (b) biomarkers PLFA for total bacteria, (c) Gram-positive (GP) bacteria, (d) Gram-negative (GN) bacteria, (e) fungi, (f) fungi: bacteria (F:B) ratio, (g) GP:GN ratio and (h) microbial enzymatic activity (FDA). C=Control (10°C), W=warmed (25°C). The error bars represent ±1 standard error. Different capital letters denote significant differences between elevations ($P < 0.05$), and asterisks indicate significant differences between temperature treatments of soil from the same elevation ($P < 0.05$). When the interaction of elevation and temperature treatment was significant ($P < 0.05$), the differences between treatments are indicated with lowercase letters. E=elevation; T=temperature treatments; E×T= interaction of elevation and temperature treatment. ns =not significant.

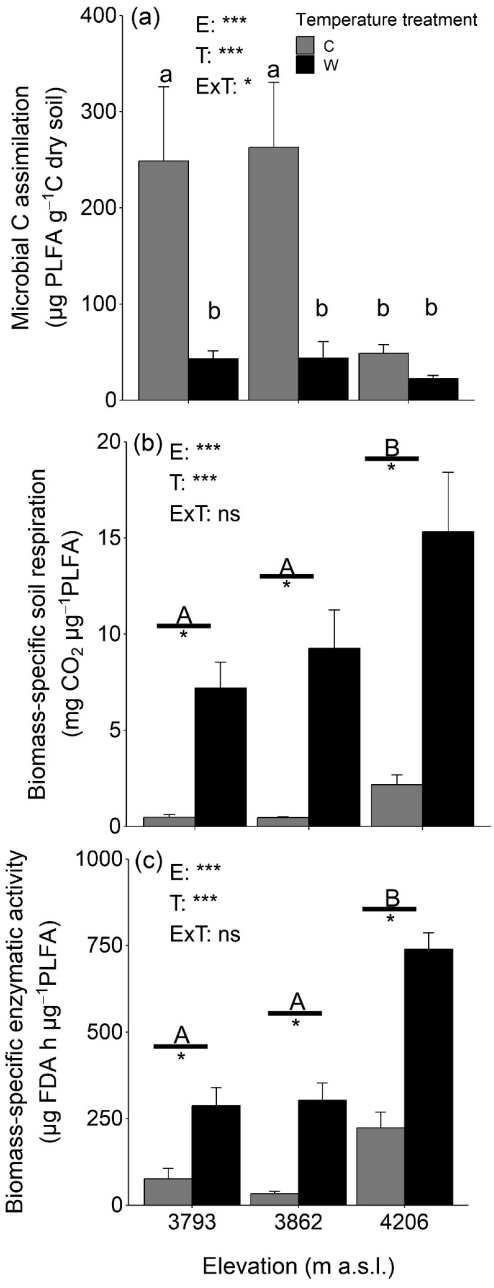


Fig. 6 Changes in soil microbial communities at the end of incubation. (a) microbial biomass per unit soil carbon; (b) biomass-specific respiration and (c) biomass-specific enzymatic activity. C=Control (10°C), W=warmed (25°C). The error bars represent ±1 standard error. Different capital letters denote significant differences between elevations ($P < 0.05$), and asterisks indicate significant differences between temperature treatments for samples from the same elevation ($P < 0.05$). When the interaction of elevation and temperature treatment was significant ($P < 0.05$), the differences between treatments are indicated with lowercase letters. E=elevation; T=temperature treatments; E×T= interaction of elevation and temperature treatment. ns =not significant.

different elevations in the Argentinean Puna. In addition, warming decreased total soil microbial biomass, relative to control treatment, but biomass-specific respiration and biomass-enzyme activity were increased. Finally, our findings showed that the soil of *vegas* at different elevations had similar temperature sensitivity of SOC mineralization. These results suggest that in the short-term, the soil of *vegas* could become C sources instead of C sinks in view of the forecast increasing temperatures, with the consequence of C-losses at regional scale.

Several studies have demonstrated an increasing rate of soil respiration with increasing temperature (Eliasson et al., 2005; Allison et al., 2010; Li et al., 2020), related to the physical and chemical principles of enzyme kinetics (Davidson and Janssens, 2006). Our results are consistent with this, since rate of soil CO_2 release was increased threefold for warmed soils from all elevations. In addition, we showed that soil from 4 206 m a.s.l had respiration rates twice as high as those of soils from the other two elevations. Both quantity and quality of organic matter are drivers of soil microbial activities (Allison et al., 2010). Hence, a higher soil respiration in soil from the *vega* at 4 206 m a.s.l. could be related to a larger SOC content at this elevation, as we observed this effect for control and for warming treatments. These findings also agree with the expectation that soils with larger standing C-stocks could release more CO_2 under warmer conditions (Crowther et al., 2016).

Despite having differences in the initial amount of soil C, all soils from different elevations had similar C mineralization rates, for both temperature treatments, when we analysed the respiration rates as a function of the SOC content. These results could indicate that the activity of microorganisms in these soils would not be limited by resource availability, which is consistent with the similarity of Q_{10} values among elevations (Min et al., 2019). Contrary to our results, Blagodatskaya et al. (2016) and Li et al. (2020) observed that temperature sensitivity was higher for soils at higher than lower elevations, probably due to the larger soil temperature variation associated with a greater altitudinal difference between sites that they selected and/or the difference between the altitude of the selected sites; our studied sites were located above 3 000 m a.s.l.. Conversely, in our studied *vegas*, with lower altitudinal difference between them, preliminary soil temperature measurements in the field showed that they had similar mean annual temperature (~10°C), as well as daily and seasonal temperature variation (data not shown). Therefore, despite differences in the C content between the three studied elevations, the similarity of soil temperature parameters between *vegas* suggest that raising temperatures over the Puna region, in the short-term, could increase CO_2 emissions from wetlands located at similar elevations to those studied here.

The increase of soil respiration subjected to warming could be associated with changes in microbial community composition in the short term, as well as their activity. In this sense, we found that, mainly in soils from the two lower

elevations, warming caused differences in the soil microbial communities' composition and significantly decreased the total biomass compared to findings for control samples. Although we did not determine the composition of microbial communities prior to the incubations, it is probable that the temperature of control treatment did not affect microorganisms' communities due to the similar temperatures of field conditions. Therefore, we could hypothesize that temperature treatments caused a reduction in the biomass of microorganisms, which could be associated with thermal stress in communities adapted to cold environments (Li et al., 2020; Song et al., 2021). The reduction of microbial biomass and the simultaneous increase in rate of microbial respiration could also be related to a reduction in the carbon use efficiency, which would mean that increasing temperature enhances resource allocation to respiration rather than microbial growth (Allison et al., 2010; Lehmeier et al., 2013). We provided two results that are in line with this expectation. Firstly, we found that microbial biomass per unit soil C was lower in warmed than in control treatment in soils from the lower and intermediate elevations. Secondly, we observed an increased biomass-specific respiration and biomass-enzymatic activity in warmed samples as compared to those in control samples. Total microbial activity, measured as FDA production, did not differ between temperature treatments, and this lack of difference suggests the important role of substrate availability in determining the response of soil enzyme activity in these wetlands (Hartley et al., 2008). Hence, the higher enzyme activity in soil from 4 206 m a.s.l. could be related to a larger amount of initial soil C at this elevation. These initial differences in the soil C among elevations could also explain higher biomass-specific respiration and enzyme activity at 4 206 m a.s.l. than at the other two elevations in warming treatment and also in control temperature treatment.

Laboratory incubation experiments are useful for disentangling the effects of raising temperature on soil processes, avoiding confounding factors. Here, we set up a short-term experiment in which we observed a fast and positive soil respiration response to warming consistent with literature. However, it is possible that under field conditions higher temperatures interact with other environmental factors (for example soil moisture, nutrient availability and substrate concentration) driving neutral or negative responses of soil respiration to warming (Carey et al., 2016). In the high Andean Plateau climate change is thought to increase aridity conditions over the region (Carilla et al., 2013), which could reduce the water supply to wetlands and reduce soil humidity, hence exerting a limiting factor on the rate of soil processes (Jing et al., 2014). In addition, in the long term different mechanisms, such as changes in microbial communities, thermal adaptation or changes in microorganisms' use of C could reduce the effects of sustained warming on soils (Romero-Olivares et al., 2017). Therefore, for a more comprehensive understanding on how changes in temperature will impact the soil functioning and the net balance of C between soils and the atmosphere in these wetlands, it would be highly valuable to set up long-term warming studies combining field and laboratory experimental approaches.

5 Conclusions

In the soils of the Argentinean Puna´s *vegas*, experimental short-term warming stimulated the efflux of CO_2 through increased soil microbial respiration and this effect was more pronounced for the highest elevation *vega* studied (i.e., 4 206 m a.s.l.), which also contained more SOC than the other two elevations. However, the SOC mineralization in all studied *vegas*' soils had similar temperature sensitivity (Q_{10}). This suggests that, within the range of elevation considered here, soils with higher SOC could release more CO_2, although all soils showed similar temperature sensitivity of soil respiration. Warming also affected soil microbial communities, leading to a lower biomass, different composition, and higher activity per unit microbial biomass than in the control treatment. These results suggest that, in the short-term, warming stimulates resource allocation to respiration rather than to microbial growth, which could be related to a reduction in carbon use efficiency by microorganisms. Overall, these results indicate that, in the short-term, edaphic processes in these high elevation wetlands could be affected by rising temperature over the Puna region with the consequence of C-losses at regional scale.

Acknowledgements

We are grateful to Dr. Kowaljow for his assistance with laboratory work and Dr. Ignacio Gasparri for his valuable comments to initial results. This work was supported by FONCYT (Grant Nos. PICT 2016-2173, PICT 2018-04228). The authors are researchers and fellows from CONICET.

Author contributions

M. Fernanda Chiappero, M.V. Vaieretti and Andrea E. Izquierdo contributed to the study conception and design. Material preparation, data collection and analysis were performed by M. Fernanda Chiappero, M.V. Vaieretti, Norma Gallardo and Andrea E. Izquierdo. The first draft of the manuscript was written by M. Fernanda Chiappero, M.V. Vaieretti and Andrea E. Izquierdo and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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.

Electronic supplementary material

Supplementary material is available in the online version of this article at https://doi.org/10.1007/s42832-024-0242-6 and is accessible for authorized users.

References

Adam, G., Duncan, H., 2001. Development of a sensitive and rapid method for the measurement of total microbial activity using fluorescein diacetate (FDA) in a range of soils. Soil Biology and Biochemistry 33, 943–951.

Allison, S.D., Wallenstein, M.D., Bradford, M.A., 2010. Soil-carbon response to warming dependent on microbial physiology. Nature Geoscience 3, 336–340.

Bardgett, R.D., Caruso, T., 2020. Soil microbial community responses to climate extremes: resistance, resilience and transitions to alternative states. Philosophical Transactions of the Royal Society B: Biological Sciences 375, 20190112.

Benavides, J.C., Vitt, D.H., Cooper, D.J., 2023. The high-elevation peatlands of the northern Andes, Colombia. Plants 12, 955.

Blagodatskaya, E., Blagodatsky, S., Khomyakov, N., Myachina, O., Kuzyakov, Y., 2016. Temperature sensitivity and enzymatic mechanisms of soil organic matter decomposition along an altitudinal gradient on Mount Kilimanjaro. Scientific Reports 6, 22240.

Bossio, D.A., Scow, K.M., 1998. Impacts of carbon and flooding on soil microbial communities: phospholipid fatty acid profiles and substrate utilization patterns. Microbial Ecology 35, 265–278.

Cabrera, A.L., 1971. Fitogeografía de la república argentina. Boletín de la Sociedad Argentina de Botánica 14, 1–42.

Carey, J.C., Tang, J.W., Templer, P.H., Kroeger, K.D., Crowther, T. W., Burton, A.J., Dukes, J.S., Emmett, B., Frey, S.D., Heskel, M. A., Jiang, L.F., Machmuller, M.B., Mohan, J., Panetta, A.M., Reich, P.B., Reinsch, S., Wang, X., Allison, S.D., Bamminger, C., Bridgham, S., Collins, S.L., de Dato, G., Eddy, W.C., Enquist, B. J., Estiarte, M., Harte, J., Henderson, A., Johnson, B.R., Larsen, K.S., Luo, Y.Q., Marhan, S., Melillo, J.M., Peñuelas, J., Pfeifer-Meister, L., Poll, C., Rastetter, E., Reinmann, A.B., Reynolds, L. L., Schmidt, I.K., Shaver, G.R., Strong, A.L., Suseela, V., Tietema, A., 2016. Temperature response of soil respiration largely unaltered with experimental warming. Proceedings of the National Academy of Sciences of the United States of America 113, 13797–13802.

Carilla, J., Grau, H.R., Paolini, L., Mariano, M., 2013. Lake fluctuations, plant productivity, and long-term variability in high-elevation tropical Andean ecosystems. Arctic, Antarctic, and Alpine Research 45, 179–189.

Chiappero, M.F., Vaieretti, M.V., Izquierdo, A.E., 2021. A baseline soil survey of two peatlands associated with a lithium-rich salt flat in the Argentine Puna: physico-chemical characteristics, carbon storage and biota. Mires and Peat 27, 16.

Chimner, R.A., Resh, S.C., Hribljan, J.A., Battaglia, M., Bourgeau-Chavez, L., Bowser, G., Lilleskov, E.A., 2023. Mountain wetland soil carbon stocks of Huascarán National Park, Peru. Frontiers in Plant Science 14, 1048609.

Cooper, D.J., Sueltenfuss, J., Oyague, E., Yager, K., Slayback, D., Caballero, E.M.C., Argollo, J., Mark, B.G., 2019. Drivers of peatland water table dynamics in the central Andes, Bolivia and Peru. Hydrological Processes 33, 1913–1925.

Crowther, T.W., Todd-Brown, K.E.O., Rowe, C.W., Wieder, W.R., Carey, J.C., Machmuller, M.B., Snoek, B.L., Fang, S., Zhou, G., Allison, S.D., Blair, J.M., Bridgham, S.D., Burton, A.J., Carrillo, Y., Reich, P.B., Clark, J.S., Classen, A.T., Dijkstra, F.A., Elberling, B., Emmett, B.A., Estiarte, M., Frey, S.D., Guo, J., Harte, J., Jiang, L., Johnson, B.R., Kröel-Dulay, G., Larsen, K.S., Laudon, H., Lavallee, J.M., Luo, Y., Lupascu, M., Ma, L.N., Marhan, S., Michelsen, A., Mohan, J., Niu, S., Pendall, E., Peñuelas, J., Pfeifer-Meister, L., Poll, C., Reinsch, S., Reynolds, L.L., Schmidt, I.K., Sistla, S., Sokol, N.W., Templer, P.H., Treseder, K.K., Welker, J.M., Bradford, M.A., 2016. Quantifying global soil carbon losses in response to warming. Nature 540, 104–108.

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173.

de Vries, F.T., Shade, A., 2013. Controls on soil microbial community stability under climate change. Frontiers in Microbiology 4, 265.

Eliasson, P.E., McMurtrie, R.E., Pepper, D.A., Strömgren, M., Linder, S., Ågren, G.I., 2005. The response of heterotrophic CO_2 flux to soil warming. Global Change Biology 11, 167–181.

García-Palacios, P., Crowther, T.W., Dacal, M., Hartley, I.P., Reinsch, S., Rinnan, R., Rousk, J., van den Hoogen, J., Ye, J.S., Bradford, M.A., 2021. Evidence for large microbial-mediated losses of soil carbon under anthropogenic warming. Nature Reviews Earth & Environment 2, 507–517.

Hagedorn, F., Gavazov, K., Alexander, J.M., 2019. Above- and below-ground linkages shape responses of mountain vegetation to climate change. Science 365, 1119–1123.

Haney, R.L., Brinton, W.F., Evans, E., 2008. Soil CO_2 respiration: comparison of chemical titration, CO_2 IRGA analysis and the Solvita gel system. Renewable Agriculture and Food Systems 23, 171–176.

Hartley, I.P., Hopkins, D.W., Garnett, M.H., Sommerkorn, M., Wookey, P.A., 2008. Soil microbial respiration in arctic soil does not acclimate to temperature. Ecology Letters 11, 1092–1100.

Hribljan, J.A., Cooper, D.J., Sueltenfuss, J., Wolf, E.C., Heckman, K. A., Lilleskov, E.A., Chimner, R.A., 2015. Carbon storage and long-term rate of accumulation in high-altitude Andean peatlands of Bolivia. Mires and Peat 15, 12.

IPCC, 2022. Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge University Press.

Izquierdo, A.E., Blundo, C., Carilla, J., Foguet, J., Navarro, C.J., Casagranda, E., Chiappero, M.F., Vaieretti, M.V., 2022. Floristic types of high-Andean wetlands from northwest Argentina and their remote-sensed characterization at a regional scale. Applied Vegetation Science 25, e12658.

Izquierdo, A.E., Carilla, J., Nieto, C., Osinaga Acosta, O., Martin, E., Grau, H.R., Reynaga, M.C., 2020. Multi-taxon patterns from high

Andean peatlands: assessing climatic and landscape variables. Community Ecology 21, 317–332.

Izquierdo, A.E., Grau, H.R., Navarro, C.J., Casagranda, E., Castilla, M.C., Grau, A., 2018a. Highlands in transition: urbanization, pastoralism, mining, tourism, and wildlife in the Argentinian Puna. Mountain Research and Development 38, 390–400.

Izquierdo, A.E., Navarro, C.J., Aragón, R., Casagranda, E., 2018b. Humedales de la Puna: principales proveedores de servicios ecosistémicos de la región. In: Grau, R., Babot, J., Izquierdo, A. E., Grau, A., eds. La Puna Argentina: Naturaleza y Cultura. San Miguel de Tucumán, Argentina: Fundación Miguel Lillo, 96–111.

Jarrell, W.M., Armstrong, D.E., Grigal, D.F., Kelly, D.F., Monger, H. C., Wedin, D.A., 1999. Soil water and temperature status. In: Robertson, G.P., Coleman, D.C., Bledsoe, C.S., Sollins, P., eds. Standard Soil Methods for Long-Term Ecological Research. Oxford, UK: Oxford University Press, 55–73.

Jing, X., Wang, Y.H., Chung, H., Mi, Z.R., Wang, S.P., Zeng, H., He, J.S., 2014. No temperature acclimation of soil extracellular enzymes to experimental warming in an alpine grassland ecosystem on the Tibetan Plateau. Biogeochemistry 117, 39–54.

Joergensen, R.G., 2022. Phospholipid fatty acids in soil—drawbacks and future prospects. Biology and Fertility of Soils 58, 1–6.

Lehmeier, C.A., Min, K., Niehues, N.D., Ballantyne, F., Billings, S.A., 2013. Temperature-mediated changes of exoenzyme-substrate reaction rates and their consequences for the carbon to nitrogen flow ratio of liberated resources. Soil Biology and Biochemistry 57, 374–382.

Li, J.Q., Yan, D., Pendall, E., Pei, J.M., Noh, N.J., He, J.S., Li, B., Nie, M., Fang, C.M., 2018. Depth dependence of soil carbon temperature sensitivity across Tibetan permafrost regions. Soil Biology and Biochemistry 126, 82–90.

Li, X.J., Xie, J.S., Zhang, Q.F., Lyu, M., Xiong, X.L., Liu, X.F., Lin, T., Yang, Y.S., 2020. Substrate availability and soil microbes drive temperature sensitivity of soil organic carbon mineralization to warming along an elevation gradient in subtropical Asia. Geoderma 364, 114198.

Maldonado-Fonkén, M.S., 2014. An introduction to the bofedales of the Peruvian High Andes. Mires and Peat 15, 05.

Meng, C., Tian, D.S., Zeng, H., Li, Z.L., Chen, H.Y.H., Niu, S.L., 2020. Global meta-analysis on the responses of soil extracellular enzyme activities to warming. Science of the Total Environment 705, 135992.

Min, K., Buckeridge, K., Ziegler, S.E., Edwards, K.A., Bagchi, S., Billings, S.A., 2019. Temperature sensitivity of biomass-specific microbial exo-enzyme activities and CO_2 efflux is resistant to change across short- and long-term timescales. Global Change Biology 25, 1793–1807.

Morales, M.S., Crispín-DelaCruz, D.B., Álvarez, C., Christie, D.A., Ferrero, M.E., Andreu-Hayles, L., Villalba, R., Guerra, A., Ticse-Otarola, G., Rodríguez-Ramírez, E.C., LLoccla-Martínez, R., Sanchez-Ferrer, J., Requena-Rojas, E.J., 2023. Drought increase since the mid-20th century in the northern South American Altiplano revealed by a 389-year precipitation record. Climate of the Past 19, 457–476.

Navarro, C.J., 2020. Respuesta funcional de las vegas de la Puna argentina a la interacción entre cambios climáticos y cambios de uso del suelo. Ph.D. Dissertation. Universidad Nacional de Tucumán, San Miguel de Tucumán, Argentina.

Nelson, D.W., Sommers, L.E., 1996. Total carbon, organic carbon, and organic matter. In: Sparks, D.L., Page, A.L., Helmke, P.A., Loeppert, R.H., Soltanpour, P.N., Tabatabai, M.A., Johnston, C. T., Sumner, M.E., eds. Methods of Soil Analysis: Part 3 Chemical Methods. Madison: Soil Science Society of America, Inc., 961–1010.

Nottingham, A.T., Whitaker, J., Turner, B.L., Salinas, N., Zimmermann, M., Malhi, Y., Meir, P., 2015. Climate warming and soil carbon in tropical forests: insights from an elevation gradient in the Peruvian Andes. BioScience 65, 906–921.

Orwin, K.H., Dickie, I.A., Holdaway, R., Wood, J.R., 2018. A comparison of the ability of PLFA and 16S rRNA gene metabarcoding to resolve soil community change and predict ecosystem functions. Soil Biology and Biochemistry 117, 27–35.

Pabón-Caicedo, J.D., Arias, P.A., Carril, A.F., Espinoza, J.C., Borrel, L.F., Goubanova, K., Lavado-Casimiro, W., Masiokas, M., Solman, S., Villalba, R., 2020. Observed and projected hydroclimate changes in the Andes. Frontiers in Earth Science 8, 61.

R Core Team, 2019. The R Project for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rhoades, J.D., 1996. Salinity: electrical conductivity and total dissolved solids. In: Sparks, D.L., Page, A.L., Helmke, P.A., Loeppert, R.H., Soltanpour, P.N., Tabatabai, M.A., Johnston, C.T., Sumner, M.E., eds. Methods of Soil Analysis: Part 3 Chemical Methods. Madison, USA: Soil Science Society of America, 417–435.

Rice, C.W., Moorman, T.B., Beare, M., 1996. Role of microbial biomass carbon and nitrogen in soil quality. In: Doran, J.W., Jones, A.J., eds. Methods for Assessing Soil Quality. Madison, WI, USA: Soil Science Society of America, Inc., 203–215.

Romero-Olivares, A.L., Allison, S.D., Treseder, K.K., 2017. Soil microbes and their response to experimental warming over time: a meta-analysis of field studies. Soil Biology and Biochemistry 107, 32–40.

Salazar, A., Rousk, K., Jónsdóttir, I.S., Bellenger, J.P., Andrésson, Ó.S., 2020. Faster nitrogen cycling and more fungal and root biomass in cold ecosystems under experimental warming: a meta-analysis. Ecology 101, e02938.

Soil Survey Staff, 2010. Keys to Soil Taxonomy. 11th ed. Washington: USDA-Natural Resources Conservation Service.

Song, Y.Y., Liu, C., Song, C.C., Wang, X.W., Ma, X.Y., Gao, J.L., Gao, S.Q., Wang, L.L., 2021. Linking soil organic carbon mineralization with soil microbial and substrate properties under warming in permafrost peatlands of Northeastern China. CATENA 203, 105348.

Thomas, G.W., 1996. Soil pH and soil acidity. In: Sparks, D.L., Page, A.L., Helmke, P.A., Loeppert, R.H., Soltanpour, P.N., Tabatabai, M.A., Johnston, C.T., Sumner, M.E., eds. Methods of Soil Analysis: Part 3 Chemical Methods. Madison, WI, USA: Soil Science Society of America, Inc., 475–490.

Tian, Y., Schindlbacher, A., Malo, C.U., Shi, C.P., Heinzle, J., Kwatcho Kengdo, S., Inselsbacher, E., Borken, W., Wanek, W., 2023. Long-term warming of a forest soil reduces microbial biomass and its carbon and nitrogen use efficiencies. Soil Biology

and Biochemistry 184, 109109.

Urrutia, R., Vuille, M., 2009. Climate change projections for the tropical Andes using a regional climate model: temperature and precipitation simulations for the end of the 21st century. Journal of Geophysical Research: Atmospheres 114, D02108.

Vargas Gil, J., 1990. Provincia de Catamarca. In: Instituto Nacional de Tecnología Agropecuaria, ed. Atlas de Suelos de la República Argentina. Buenos Aires: Centro de Investigaciones de Recursos Naturales, 207–247.

Walker, T.W.N., Kaiser, C., Strasser, F., Herbold, C.W., Leblans, N.I. W., Woebken, D., Janssens, I.A., Sigurdsson, B.D., Richter, A., 2018. Microbial temperature sensitivity and biomass change explain soil carbon loss with warming. Nature Climate Change 8, 885–889.

Wang, C., Morrissey, E.M., Mau, R.L., Hayer, M., Piñeiro, J., Mack, M.C., Marks, J.C., Bell, S.L., Miller, S.N., Schwartz, E., Dijkstra, P., Koch, B.J., Stone, B.W., Purcell, A.M., Blazewicz, S.J., Hofmockel, K.S., Pett-Ridge, J., Hungate, B.A., 2021. The temperature sensitivity of soil: microbial biodiversity, growth, and carbon mineralization. The ISME Journal 15, 2738–2747.

Wang, G.B., Zhou, Y., Xu, X., Ruan, H.H., Wang, J.S., 2013. Temperature sensitivity of soil organic carbon mineralization along an elevation gradient in the Wuyi Mountains, China. PLoS One 8, e53914.

Willers, C., Jansen van Rensburg, P.J., Claassens, S., 2015. Phospholipid fatty acid profiling of microbial communities-a review of interpretations and recent applications. Journal of Applied Microbiology 119, 1207–1218.

Yu, H.Y., Ma, Q.H., Liu, X.D., Xu, Z.Z., Zhou, G.S., Shi, Y.H., 2018. Short- and long-term warming alters soil microbial community and relates to soil traits. Applied Soil Ecology 131, 22–28.

Zelles, L., 1999. Fatty acid patterns of phospholipids and lipopolysaccharides in the characterisation of microbial communities in soil: a review. Biology and Fertility of Soils 29, 111–129.