Journal of Soil Science and Plant Nutrition (2023) 23:2662–2672
https://doi.org/10.1007/s42729-023-01222-6

ORIGINAL PAPER

No Evidence of an Elevation Effect Caused by Temperature Differences on Soil Microbial Properties in a Walnut Fruit Forest in Kyrgyzstan

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Received: 7 November 2022 / Accepted: 20 March 2023 / Published online: 31 March 2023

Abstract
This study is to investigate the effect of differences in annual average temperature on soil microbial communities as caused by elevation in walnut-fruit forests in Kyrgyzstan with similar vegetation. Soil samples ($n = 10$ per site) were collected from top- and subsoil at three elevation levels (1000, 1300 and 1600 m above sea level) with an average temperature difference of 1.3 °C between sites and analysed for soil chemical and biological properties. All soil properties showed high variability within, but most revealed no differences between elevation levels. Microbial biomass, activity and community composition were largely similar at all sites with slightly higher fungal contribution based on internal transcribed spacer (ITS) sequence counts at high elevation, which, however was not reflected by ergosterol. Total soil organic carbon and nitrogen levels did not show elevation effects either. Mehlich-extractable elements revealed positive relationship with soil microbial properties, which was in particular pronounced for copper, manganese and zinc, highlighting the relevance of trace elements for soil microorganisms. The subsoil showed lower levels for all microbial properties even though they were on a comparably high level; it contained smaller sized bacteria and fungi, as revealed by MBC/dsDNA ratios, and fungal ITS counts/ergosterol ratios illustrating growth limitations for microorganisms in subsoils. Elevation with long-term average temperature differences did not yield pronounced differences in soil microbial properties, which were more potentially stronger affected by similar C input quantity and substrate quality from the similar vegetation. Consequently, climate change effects will more likely affect microbial properties indirectly via changes in vegetation.

Keywords Ergosterol · Fungi · Mehlich extractable · Microbial biomass · Microbial community · Ionome

1 Introduction

Climate change results in temperature increase, which is pronounced in Central Asia, where average temperature increased already with different estimates of 0.39 °C between 1979 and 2011 (Hu et al., 2014) or 0.28 °C between 1950 and 2016 (Haag et al., 2019). An increase of temperature by 1–2 °C until 2030–2050 is predicted for Central Asia (Lioubimtseva and Cole, 2006). According to climate modelling, it is expected that the average annual temperature in Kyrgyzstan will increase by 2.5 to 3.0 °C and the annual precipitation by 10–15% until 2100 (UNFCCC, 2003). Enhanced temperatures are expected to influence vegetation and directly as well as indirectly via vegetation changes shape soil microbial properties (Hatfield and Prueger, 2015). Especially the size, community composition and activity of soil microorganisms are affected by altered plant input quantities and qualities but also respond to changing temperature.

Microbial soil respiration rate is directly affected by global warming, because soil microorganisms and the processes they mediate are temperature sensitive (Bradford, 2013; Moinet et al., 2021). Further, it has been observed that bacterial abundance changed and that the bacteria to fungi ratio increased as a result of warming by 5 °C in a temperate forest soil (KM et al., 2015). Also, nitrogen (N) mineralization, especially nitrification, is affected by temperature

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(De Neve et al., 2003). This temperature sensitivity of soil organic matter (SOM) is critical, as SOM fulfils many functions in an ecosystems, such as water and nutrient storage, nutrient release, provision of habitat for soil organisms and better soil structure allowing faster water infiltration (Franzluebbers, 2002). Consequently, understanding the impact of temperature increase on soil microbial processes, nutrient dynamics and SOM is important to predict climate change effects.

As a proxy of future temperature increase elevation gradients within the same ecosystem and with comparable site properties, may act as living lab for investigating temperature effects on soil microbial processes, like C and N mineralization. However, in a recent study by Chen et al. (2022), it was shown, that slope aspect (south-facing and north-facing slopes) has a larger effect on bacterial community composition as compared to elevation level, likely reflecting the direct effect of radiation driven temperature and vegetation changes. Nonetheless, soil microbial responses likely are also influenced by the temperature extremes they are prone to. In the investigation area of the present study in the continental climate of Central Asia, temperature amplitudes from − 20 to + 30 °C throughout the year are common in the mountains (Mannig et al., 2013). Therefore, soil microbial communities under these conditions may be adapted to strong temperature changes and may not strongly respond to climate change induced temperature increase of 1 or 2 °C. A temperature decrease was observed along the elevational gradient in the middle Tian Shan Mountain area in Central Asia with temperature decline from high to low elevation by 0.71 ± 0.20 °C 100 m^{-1} and 0.59 ± 0.05 °C 100 m^{-1} on the northern and southern slopes respectively (Gheyret et al., 2020). A 500-m height difference therefore reflects the expected temperature difference caused by climate change that is likely to occur within the next 20 years in Central Asia. Thus, a current low elevation temperature regime likely reflects that present at higher elevation in the future. Consequently, low elevation sites with similar parent material, soil texture, ground water level, vegetation cover and human influence can therefore be used to predict soil microbial responses at high elevation sites.

Based on this, the objective of our study was to evaluate elevation effects as a proxy of differences in temperature on the soil microbial community and their functions in a walnut-fruit forest in Kyrgyzstan, Central Asia. These unique walnut-fruit forests are ancient walnut forests present at different elevations, dating back at least 2000 years (Beer et al., 2008), and are home to a huge diversity of trees and shrubs (Hemery and Popov, 1998). Even though state owned, they harbour very important natural resources for the local communities (Beer et al., 2008). The following hypotheses were investigated using an elevation gradient between 1000 and 1600 m above sea level: (i) Increasing elevation and thus differences in temperature do not have pronounced short-term effects on soil microorganisms. (ii) Microbial biomass and abundances of microbial domains do not vary at the different elevation sites with different temperatures, as the vegetation is similar.

2 Materials and Method

2.1 Study Area

The investigation area is situated in the Jalal-Abad region on the slopes of the Fergana and Chatkal mountain ridges in southern Kyrgyzstan (Fig. 1). The investigated walnut-fruit forest is located on the south western Tian Shan between 41°25′ to 41°39′N and 72°88′ to 73°06′E. The study area is located in the major forestry districts (village name) Achi (Charbak), Kyzyl-Unkur (Kyzyl-Unkur) and Arslanbap (Jay-Terek), with sampling sites on south–east slopes, where a continental subtropical climate prevails. In the region, the long-term average minimum temperature is − 18 °C in winter and the average maximum is 26 °C in summer. The long-term average temperature (1983–2004) was 9.2 °C (Winter et al., 2009). The average daily temperatures of the study sites at 1000, 1300 and 1600 m above sea level (asl) are 23.5 °C, 22 °C and 20 °C in July as well as − 1.2, − 2.1 and − 3.2 °C in January, respectively. The majority of the annual precipitation, which ranges from 700 to 1000 mm at an elevation of 1000 to 2000 m asl, occurs during spring and winter (Table S3) (Sakbaeva et al., 2013).

The vegetation of the walnut forests is dominated by walnut (*Juglans regia* L.) associated with hawthorn (*Crataegus turkestanica* Pojark.) and wild apple (*Malus sieversii var. Kirgizorum*). According to Sakbaeva et al. (2013) who used the IFAS 2003 data, gray, gray brown, gray dark brown, chestnut-hued and brown soils are common on the mountain slopes between 1000 and 2500 m asl in the region.

2.2 Sampling and Storage

Soil samples were collected in October 2019 at three different elevations, which ranged from 1000 to 1600 m asl (Charbak at 1000 m asl, Kyzyl-Unkur at 1300 m asl and Jay-Terek at 1600 m asl). At every elevation in an area of 500 m^2, 10 trees per sampling site on the south-east slopes were randomly chosen with a mature walnut tree as central point. Soil samples were taken from the mineral topsoil at 0–30 cm and the subsoil at 30–60-cm depth with a soil corer during moist soil conditions. At every tree, ten sub-samples were taken in a star-shaped circle around the tree. Sub-samples were mixed forming one replicate soil sample per tree and were placed in plastic bags and stored at 4 °C. A sub-sample of each sample was stored frozen at −18 °C and transferred

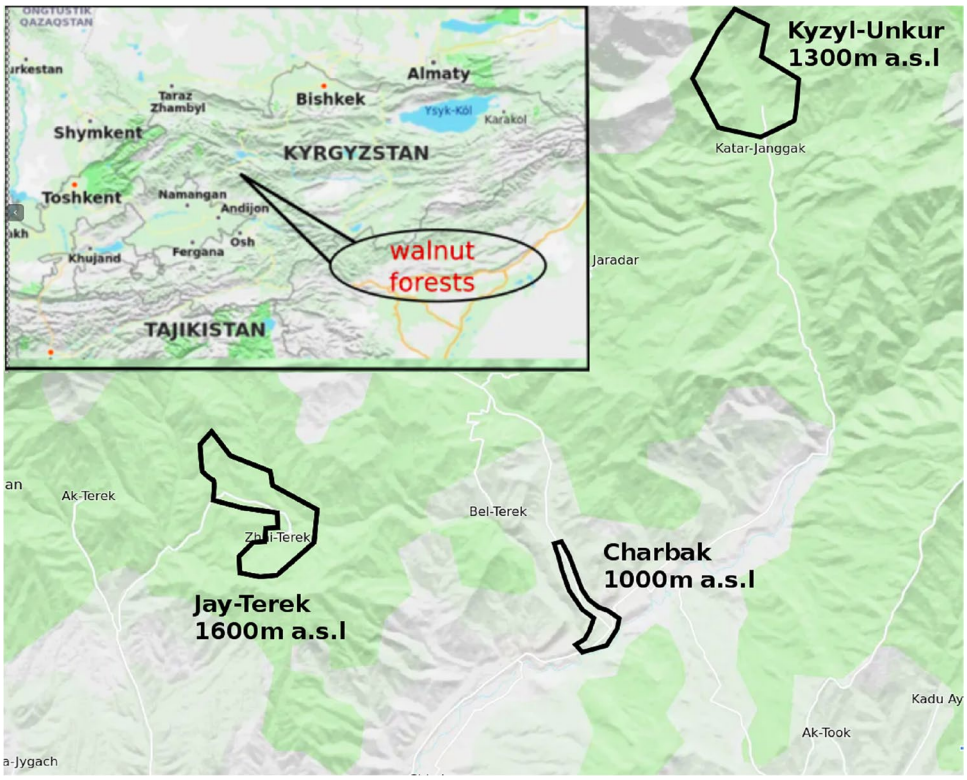

Fig. 1 Map of the walnut-fruit forest of Southern Kyrgyzstan showing sampling sites at different elevation (source: http://www.bing.com/maps)

to the laboratory in Germany for microbial analyses. All soil samples were sieved (< 2 mm) prior to analyses and air-dried prior to analysis if necessary.

2.3 Soil Physical and Chemical Properties

Soil texture was analysed according to Gee and Or (2018). The soils contained 39–40% clay, 51–57% silt and 1.3–7.7% sand at the three sites. Soil colour varied from dark brown (10YR4/3) to very dark brown (10YR2/2) according to the Munsell Soil Color Charts.

Soil pH was assessed using air-dried sieved soil and water (1:5 w/w). Extractable elements Ca, K, Mg, Na, P, Cu, Fe, Mn and Zn were extracted in Mehlich-3 solution and analysed by ICP-OES (Optima 8000, Perkin Elmer, Waltham, USA). Extractable carbon was determined in the 0.5 M K_2SO_4 non-fumigated extracts. Total soil C, N and S were determined using gas chromatography after combustion (Watson et al., 2021).

2.4 Soil Microbial Properties

To measure microbial basal respiration, moist soils were incubated for 28 days at 22 °C and 50% water holding capacity in the dark after pre-incubation for 7 days. Soil basal respiration and microbial N mineralization were assessed as described by Watson et al. (2021). Microbial biomass carbon (MBC) and nitrogen (MBN) were determined in moist sub-samples at the end of the incubation experiment using the chloroform fumigation extraction method (Brookes et al., 1982; Vance et al., 1987) as described by Wichern et al. (2020). $CHCl_3$-labile microbial derived secondary and trace elements (MB_{STE}) magnesium (Mg), potassium (K), sodium (Na), copper (Cu), manganese (Mn) and Zn (zinc) were determined using fumigation extraction using 0.01 M $CaCl_2$ instead of 0.5 M K_2SO_4. The extracts were filtered and analysed by ICP-OES (Optima 8000, PerkinElmer, Waltham, USA). MB_{STE} were calculated as the difference of fumigated and non-fumigated soils. As an index for fungal biomass, ergosterol was measured in soil samples after incubation according to Djajakirana et al. (1996) and as described by Watson et al. (2021).

As microbial biomass index (Bardelli et al., 2017), dsDNA was extracted from frozen soil samples using the FastDNA® Spin Kit for Soil (MP Biomedicals, Santa Ana, USA) following the manufacturer's protocol, modified by Hemkemeyer et al. (2014). Using this extracted dsDNA, microbial domains were determined using quantitative real-time *q*PCR in a LightCycler® 480 II (Roche, Penzberg, Germany) as described by Watson et al. (2021). Primers, probes and *q*PCR reaction conditions are documented in Table S1.

The specific *CO_2 evolution* of the microbial biomass, the metabolic quotient (qCO_2), is calculated from the basal respiration as follows: (µg CO_2–C d^{-1} g^{-1} soil evolved during the last 7 days of incubation)/(µg microbial biomass C g^{-1}

soil at the end of the incubation experiment) × 1000 = mg CO_2–C g^{-1} microbial biomass C d^{-1} (Wichern et al., 2006).

2.5 Statistics

The open-source programming language R 3.6.3 with the R-Studio version 1.3.1073 was used for statistical analysis and graphical visualization. Normal distribution and variance homogeneity of the data were checked using the normal Q-Q plot and residuals vs. fitted values plot, respectively. One-way ANOVA was used for evaluation of site and soil depth differences followed by Tukey HSD when data was parametric. Kruskal-Wallis test was used for non-parametric data to test for significant differences between soil sites and soil depths followed by Dunn's post hoc test. Significant differences were detected at $p < 0.05$. Results are arithmetic means of ten replicates and based on dry soil weight. Pearson correlation coefficient was used for correlation test with a $p < 0.05$ significance threshold using Corrplot. Correlation coefficient interpretation is as described by Rumsey (2016). Results for simple linear and multiple linear regression were transformed to the natural log.

3 Results

3.1 Soil Chemical Properties

Soil chemical properties did not show elevation gradients in the topsoil or subsoil (Table 1), except soil pH significantly decreasing with increasing elevation. Soil pH was the only property, which increased with depth, whereas the contents of soil organic carbon (SOC), K_2SO_4 extractable C and total N declined with depth.

The contents of Mehlich-3 extractable metals declined in the order Mg > K > Fe > Mn > Na > P > Zn. These metal fractions also did not exhibit any consistent elevation gradients in the topsoil and in the subsoil (Table 2). The contents of Mehlich-3 extractable K, P, Mn and Zn at 0–30-cm depth significantly exceeded respective contents at 30–60-cm depth, whereas those of Mg, Na, Cu and Fe did not show a depth gradient. Mehlich-3 extractable K, P, Mn and Zn were positively correlated with SOM related properties, i.e. SOC, K_2SO_4 extractable C and total N (Fig. 2).

3.2 Microbial Biomass and Activity Indices

MBC varied around 650 µg g^{-1} soil at 0–30-cm depth and around 180 µg g^{-1} soil at 30–60 cm without any elevation gradient (Fig. 3a). MBN values at 0–30 cm and 30–60 cm did not show elevation effect either (Fig. 3b). MBN followed MBC with an average MB-C/N ratio of 5.4 (Table 3), and they were both positively related to Mehlich-3 extractable Zn (Table 4). The contributions of MBC to SOC ratio and that of MBN to total N were 1.30% and 3.6%, respectively, in the topsoil and only 0.70% and 2.6% in the subsoil (Table 3). The dsDNA contents followed MBC with a mean ratio of 67 in the topsoil and 39 in the subsoil. Both biomass indices were significantly correlated with $r = 0.85$ (Fig. S1a). In contrast to MBC, dsDNA was not affected by Mehlich-3 extractable Zn but by total N (Table 4). At 1000-m elevation, the dsDNA content was significantly lower in comparison with the higher sites, leading to a significant higher dsDNA/MBC ratio (Table 3).

The content of $CHCl_3$-labile Mn in the topsoil at 1300 and 1600 m was roughly 10 times higher than the mean content of 40 µg g^{-1} soil measured at 1000 m in the topsoil and at all sites in the subsoil. $CHCl_3$-labile Mn was solely related to Mehlich-3 extractable P (Table 4), but on markedly lower level than the other microbial properties.

Table 1 Soil chemical properties along an elevation gradient at two soil depths

Elevation (m asl)	pH (H_2O)	SOC	Total N	SOC/total N	K_2SO_4-Extractable C	
		(mg g^{-1} soil)			(µg g^{-1} soil)	(% SOC)
0–30-cm soil depth						
1000	7.9 a	56 a	3.7 b	15.2 a	206 a	0.37 a
1300	7.2 b	66 a	4.7 a	13.7 ab	121 b	0.19 b
1600	6.9 c	58 a	4.6 a	12.6 a	151 b	0.26 ab
CV (± %)	5.5	18	16	8.0	28	36
P value	< 0.01	NS	0.01	< 0.01	< 0.01	< 0.01
30–60 cm soil depth						
1000	8.5 a	35 a	1.4 b	25.8 a	64 b	0.18 b
1300	7.4 b	27 b	2.1 a	12.8 b	44 b	0.18 b
1600	7.4 b	29 b	2.2 a	13.7 b	101 a	0.34 a
CV (± %)	9.2	18	21	20	54	39
P value	0.01	0.02	0.01	< 0.01	0.01	0.02

CV, mean coefficient of variation between replicate samples ($n = 10$); NS, not significant; asl, above sea level; SOC, soil organic carbon

Table 2 Mehlich-3 extractable elements in soils along an elevation gradient at two soil depths

Elevation	K	Mg	Na	P	Cu	Fe	Mn	Zn
(m asl)				(μg g^{-1} soil)				
0–30-cm soil depth								
1000	485 a	421 b	12 b	11 b	6.4 a	146 b	217 a	5.4 a
1300	318 b	506 a	52 a	27 a	7.8 a	250 a	159 b	6.1 a
1600	433 a	484 a	17 b	21 ab	6.5 a	238 a	190 ab	5.7 a
CV (± %)	11	10	42	32	31	13	14	23
P value	< 0.01	0.01	< 0.01	< 0.01	NS	< 0.01	< 0.01	NS
30–60-cm soil depth								
1000	348 a	402 a	16 b	1.2 b	5.0 a	85 b	108 ab	1.6 a
1300	228 b	446 a	43 a	8.9 a	5.6 a	194 a	90 b	1.9 a
1600	304 a	439 a	18 b	5.1 ab	6.7 a	175 a	130 ab	2.1 a
CV (± %)	19	15	47	48	32	22	27	34
P value	< 0.01	NS	0.02	0.01	NS	< 0.01	0.03	NS

CV, mean coefficient of variation between replicate samples (n = 10); NS, not significant; asl, above sea level

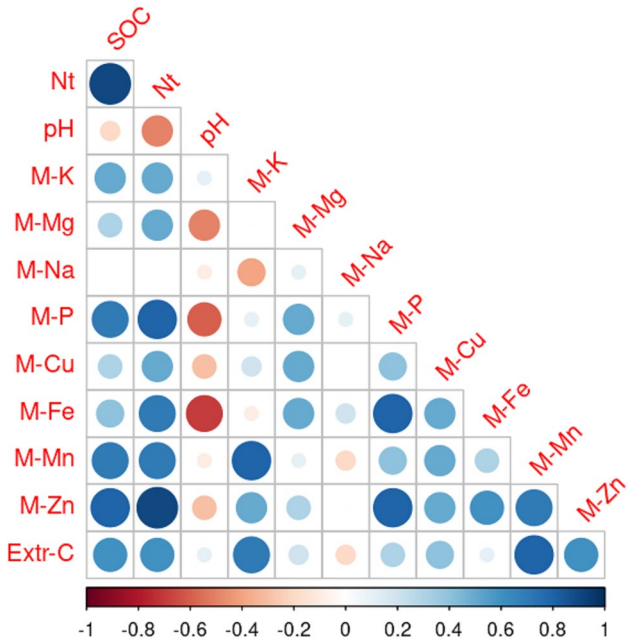

Fig. 2 Correlation matrix between soil chemical properties in soils along an elevation gradient at two soil depths. M-element refers to Mehlich-3 extractable elements (M-element), soil organic carbon (SOC), total nitrogen (N_t) and extractable carbon (Extr-C). Colour intensity in circle size show the strength of correlation with red negative and with blue positive

Basal respiration and net N mineralization rate did not show elevation gradients. Basal respiration was positively related to K_2SO_4 extractable C, Mehlich-3 extractable K and Fe (Table 4). The metabolic quotient qCO_2 varied around 20 μg CO_2-C mg^{-1} MBC d^{-1} throughout the profile. In the topsoil, the qCO_2 was significantly lowest at 1300 m (Table 4).

3.3 Microbial Domains

The gene copy numbers for the main microbial domains were higher in the topsoil compared with the subsoil (Table 5).

This difference in fungal abundance was not reflected by ergosterol, although both fungal indices showed a significant relationship with $r = 0.75$ (Fig. S1b). The ergosterol/MBC ratio constantly varied around 0.23% throughout the whole soil profile at the three different elevation levels. In contrast, the average fungal counts/ergosterol ratios varied around 1.3 in the topsoil and around 1.9 in the subsoil. The ratios of bacteria/fungi and bacteria/archaea varied around rather stable means of 145 and 21 throughout the soil profiles, despite some site-specific significant variation.

The gene copy numbers of bacteria, archaea and fungi were all positively related to Mehlich-3 extractable Mn (Table 4). Bacterial and fungal counts were additionally affected by total N, whereas archaeal counts by SOC.

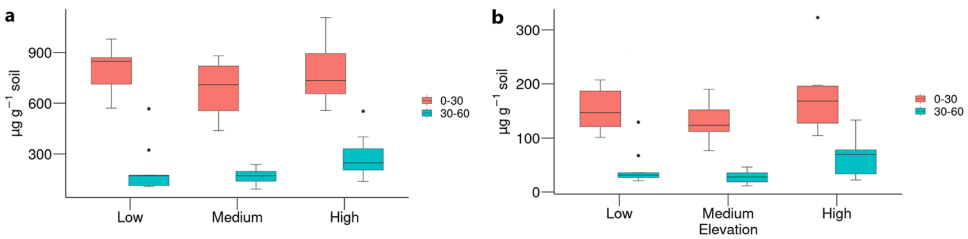

Fig. 3 Soil microbial biomass carbon (MBC) (**a**) and nitrogen (MBN) (**b**) along an elevation gradient (low = 1000 m asl; medium = 1300; high 1600; asl = above sea level) at 0–30 cm and 30–60-cm soil depths

Table 3 Contents of dsDNA and $CHCl_3$-labile Mn, basal respiration and net-N mineralization rates as well as the ratios MB-C/N, MBC/SOC, MBN/total N and metabolic quotient qCO_2 in soils along an elevation gradient at two soil depths

Elevation	MB-C/N	MBC	MBN	dsDNA	MBC/	CO_2C	net-Nmin	qCO_2 (mg CO_2C	$CHCl_3$-labile Mn
(m asl)		(% SOC)	(% total N)	(μg g^{-1} soil)	dsDNA	(μg g^{-1} soil d^{-1})		g^{-1} MBC d^{-1})	(ng g^{-1} soil)
0–30-cm soil depth									
1000	5.4 a	1.42 a	4.1 a	8.4 b	94 a	15.3 a	0.20 a	22 a	40 b
1300	5.4 a	1.10 a	2.9 b	14.7 a	48 b	8.2 b	0.10 b	12 b	395 a
1600	5.0 a	1.36 a	4.0 a	13.9 a	60 b	16.8 a	0.33 a	22 a	493 a
CV (± %)	24	24	35	26	30	36	47	36	90
P value	NS	NS	0.05	< 0.01	< 0.01	0.01	0.01	0.01	0.01
30–60-cm soil depth									
1000	4.8 b	0.59 b	3.2 a	5.6 a	44 a	4.7 a	0.06 b	27 a	23 a
1300	6.8 a	0.63 b	1.4 b	6.1 a	28 a	2.2 b	0.04 b	15 a	76 a
1600	4.9 b	0.97 a	2.8 a	6.1 a	45 a	5.9 a	0.14 a	23 a	42 a
CV (± %)	24	49	63	24	49	46	64	50	103
P value	0.02	0.05	0.02	NS	NS	< 0.01	0.01	NS	NS

CV, mean coefficient of variation between replicate samples ($n = 10$); NS, not significant; asl, above sea level; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; SOC, soil organic C; dsDNA, double stranded deoxyribonucleic acid; qCO_2, microbial metabolic quotient; net-Nmin, net nitrogen mineralization

Table 4 Simple linear and multiple linear or non-linear regressions between soil microbial indices as the dependent variable and soil chemical properties as independent variables in soils along an elevation gradient at two soil depths

Dependent variable	Intercept	Independent variables	R^2 (%)
CO_2C (ln μg g^{-1} soil d^{-1})	− 0.586	0.006**** K_2SO_4-C (μg g^{-1} soil)	73.0
		0.004*** Mehlich-K (μg g^{-1} soil)	
		0.003** Mehlich-Fe (μg g^{-1} soil)	
MBC (ln μg g^{-1} soil)	4.455****	0.756**** Mehlich-Zn (ln μg g^{-1} soil)	74.3
		0.004** Mehlich-Mn (μg g^{-1} soil)	
MBN (ln μg g^{-1} soil)	3.026****	1.041**** Mehlich-Zn (ln μg g^{-1} soil)	70.3
		0.002* Mehlich-K (ln μg g^{-1} soil)	
$CHCl_3$-labile Mn (ln ng g^{-1} soil)	− 5.889****	1.340**** Mehlich-P (ln μg g^{-1} soil)	31.4
dsDNA (ln μg g^{-1} soil)	1.251****	0.272**** total N (mg g^{-1} soil)	69.1
Bacteria (ln n 10^{-8})	3.362****	0.311**** total N (mg g^{-1} soil)	74.0
		0.003** Mehlich-Mn (μg g^{-1} soil)	
Archaea (n 10^{-8})	− 14.428****	0.037**** Mehlich-Mn (μg g^{-1} soil)	68.4
		4.431*** SOC (ln mg g^{-1} soil)	
Fungi (ln n 10^{8})	− 1.982****	0.008*** Mehlich-Mn (μg g^{-1} soil)	56.7
		0.230** total N (mg g^{-1} soil)	
Ergosterol (ln μg g^{-1} soil)	− 6.091****	1.079**** SOC (ln mg g^{-1} soil)	75.3
		0.005**** K_2SO_4-C (μg g^{-1} soil)	
		0.003** Mehlich-Mg (μg g^{-1} soil)	

ln, transformed to the natural log rhythm; $^{**}P < 0.01$; $^{***}P < 0.001$; $^{****}P < 0.0001$; R^2, adjusted coefficient of determination; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; SOC, soil organic C; dsDNA, double stranded deoxyribonucleic acid

4 Discussion

The chosen elevation gradient represents a proxy of future temperature development, with the temperature at the lowest elevation representing the future temperature of the highest elevation. Our results, however, showed that microbial biomass, microbial stoichiometry, community composition and microbial activity were largely similar at the three study sites not showing any major effects of slightly higher temperature at the low elevation site as compared to higher elevation. This may be due to the fact that the soil microbial communities experience large temperature amplitudes on an annual basis with large differences between winter and summer and within seasons and

Table 5 Gene copies number of bacteria, archaea and fungi as well as the ratios fungi/ergosterol, bacteria/fungi and bacteria/archaea in soils along an elevation gradient at two soil depths

Elevation (m asl)	Bacteria	Archaea	Fungi	Ergosterol		Fungi/ergosterol (n μg^{-1} 10^8)	Bacteria/fungi	Bacteria/archaea
	(n gene copies 10^8 g^{-1} soil)			(μg g^{-1} soil)	(%MBC)			
0–30-cm soil depth								
1000	209 a	11.2 a	2.0 b	1.84 a	0.24 a	1.1 b	116 b	19 b
1300	231 a	10.3 a	1.3 b	1.52 a	0.24 a	1.0 b	174 a	23 ab
1600	256 a	10.4 a	3.5 a	1.84 a	0.25 a	1.9 a	92 b	26 a
CV (± %)	32	28	62	34	40	42	31	23
P value	NS	NS	< 0.01	NS	NS	0.01	< 0.01	0.05
30–60-cm soil depth								
1000	86 a	6.6 a	0.6 b	0.57 a	0.34 a	1.3 a	170 a	15 b
1300	68 a	3.9 b	0.5 b	0.29 a	0.18 a	2.0 a	216 a	19 b
1600	83 a	3.6 b	1.1 a	0.50 a	0.18 a	2.4 a	96 b	25 a
CV (± %)	46	44	90	57	51	112	36	37
P value	NS	0.04	0.01	NS	NS	NS	< 0.01	0.02

CV, mean coefficient of variation between replicate samples (n = 10); NS, not significant; asl, above sea level; dsDNA, double stranded deoxyribonucleic acid; MBC, microbial biomass carbon

are likely adapted to large temperature amplitudes, as soil microorganisms possess the capability to regulate their homeostasis and to adapt to warming (Li et al., 2022).

It has been shown that microbial community structure in Alpine forest soils was not significantly affected by elevation (Merino-Martín et al., 2022; Siles et al., 2016), supporting our first hypothesis. In contrast, other studies that investigated elevation effects on microbial communities in forests showed contrasting results, with for example an increase (Chen et al., 2022; Xiong et al., 2022; Zhao et al., 2022) or a decrease (Hu et al., 2016; Nottingham et al., 2018; Yang et al., 2017) in bacterial and fungal richness. The composition of microbial communities influences microbial N mineralization and nitrification. Earlier studies found that N mineralization decreased with increasing elevation in forest soils, highlighting temperature as a controlling parameter (Durán et al., 2016; Hart and Perry, 1999). Our results, however, showed an opposite trend. Likely, elevation and associated average temperature differences do not directly affect N mineralization (Smith et al., 2002). In our investigation, N mineralization was higher at the highest elevation with lower average temperature.

Next to temperature differences, water availability plays an important role in soil microbial functioning and is reflected by changes in microbial biomass and activity (Rangel-Vasconcelos et al., 2015). Our investigation sites did not differ in average annual precipitation and water availability. Thus, water effects on soil microbial communities can be excluded. Often differences in mineralization rate can be explained by differences in organic matter availability as affected by vegetation type (Knoepp and Swank, 1998). This is because microorganisms rely on C input from vegetation for maintenance and growth (Schimel and Schaeffer, 2012).

Differences in vegetation result in differences in C input quantity (Cotrufo et al., 2013; Kuzyakov and Domanski, 2000) and quality (Guo et al., 2016) and are thus often a major driver for differences in microbial biomass (Ravindran and Yang, 2015; Wu et al., 2018), microbial community composition (Chen et al., 2004; Wang et al., 2022) and microbial activity (Bauhus and Pare, 1998; Pang et al., 2019). It has been shown that for SOM content, the impact of vegetation differences is larger than temperature differences caused by elevation level (Massaccesi et al., 2020). The investigated forests at different elevations in terms of species composition and especially in terms of productivity did not show any differences between sites (Mujawamariya et al., 2018). The shift in plant species with elevation had a higher impact on SOC contribution throughout the soil profile than temperature (Chang et al., 2015). The temperature sensitivity of productivity in temperate forests is influenced by forest structure and species diversity (Bohn et al., 2018). The species distribution index and forest height seem to be the most important forest properties influencing temperature sensitivity (Bohn et al., 2018). Xiong et al. (2022) quantified C input in tropical montane wet forest and concluded that changes in water, light and nutrient availability strongly influence C fluxes to increasing temperature.

At our investigation sites, vegetation of the walnut-fruit forest was similar as shown by Toktoraliev et al. (2018) and Ionov and Lebedeva (2002). This suggests that the same vegetation at different elevation levels does not differ in biomass and carbon quality and quantity (Mujawamariya et al., 2018) and most likely contributed strongly to the similar SOC

content, microbial properties and C and N dynamics at the three sites. However, large variability within sites may have masked differences between sites related to elevation and thus temperature. The heterogeneity of sites as it has been described for soil chemical properties and for walnut fruit properties in the same ecosystem (Meisen et al., 2021) may override elevation effects. Dassen et al. (2017) showed that plant functional identity had a strong effect on soil microbial community composition, which supports our second hypothesis that with similar vegetation and comparable soil properties, no differences in microbial properties occur at the different elevation sites, irrespective of the difference in average temperature. Thus, we conclude that vegetation is the main driver and factor influencing the microbiological properties of soil (Massaccesi et al., 2015; Merino-Martín et al., 2022; Pang et al., 2019) and not elevation and temperature differences at the studied sites.

Yet, some differences were observed for some sites. For example, soil samples from 1600-m elevation showed a higher fungal abundance, which was not reflected by the membrane component ergosterol, which is in agreement with previous studies (Ni et al., 2018) where higher fungal abundance at higher elevation sites was shown. An important reason could be differences in the fungal community composition at this site. A larger abundance of fungi such as *Mortierellaceae* or *Glomeromycota* (Olsson et al., 2003), which do not produce ergosterol, increase the ratio of fungal counts to ergosterol. *Entomophthorales* contain 24-methyl cholesterol (Weete and Gandhi, 1997) as a major sterol. According to Tedersoo et al. (2014), the studied area contains a high amount of *Mortierellomycotina* which can affect the total fungal biomass.

In our study, the topsoil showed higher microbial biomass and higher abundance of microbial abundances activity compared to subsoil. Overall, values were on a high level as compared to other studies in temperate forest ecosystems, especially in the subsoil (Frey et al., 2021). However, in line with earlier studies, contents of MBC (Lepcha and Devi, 2020), MBN (Chen et al., 2021) and ergosterol content (Guevara-Rozo et al., 2020) declined with depth in the current study.

The higher ratio of fungal counts to ergosterol in the topsoil in comparison with the subsoil indicates that fungal cells are larger at 0–30 cm than at 30–60-cm depth (Schroeder et al., 2020). This is in line with the higher MBS/dsDNA ratio in the topsoil in comparison with the subsoil, which indicates that microbial cells are generally larger in the topsoil than in the subsoil.

The MBC/SOC ratio is usually negatively correlated with the metabolic quotient qCO_2, i.e. the ratio of basal respiration and MBC (Anderson and Domsch, 2010). The qCO_2 is an important indicator for the demand of a starving and, thus, dormant soil microbial population for maintenance energy, provided by SOM decomposition (Joergensen and Wichern, 2018). However, in our current study, the qCO_2 values were similar at both soil depths, probably due to the relatively high SOM contents in the subsoil (Struecker and Joergensen, 2015).

Microbial C and nutrient use efficiency are proposed to be related to the stoichiometry of the organisms and of the available substrates assuming homeostasis of elements in soil microorganisms (Manzoni et al., 2012). In our investigation, the microbial biomass C/N was not different between sites and similar, thus indicating homeostasis for N. Until now, all studies on soil microbial stoichiometry focused mainly on MBC, MBN and MBP, with other elements essential for soil microbial processes (Hemkemeyer et al., 2021) usually ignored. In our study, $CHCl_3$-labile elements in particular Mn varied substantially without revealing any elevation or site effect on the soil microbial ionome. Thus, soil microorganisms may not be homeostatic for certain elements. This warrants further investigations to understand microbial functions in relation to their nutrient status.

Nutrient availability at the three sites was similar as revealed by Mehlich-3 extractable elements. Interestingly, Mehlich-3 extractable elements showed strong positive effects on soil microbial properties revealing that availability of nutrients is important for efficient microbial functioning in soil. Further research is needed to unravel the interaction between available (e.g. Mehlich-3 extractable) nutrients in soil microbial ionome (e.g. $CHCl_3$-labile elements) and microbial functions.

5 Conclusions

The current study sites provide the unique opportunity to compare different elevation levels and, thus, mean temperatures in ecosystems similar in soil properties, vegetation, and precipitation. Increasing elevation of the three sites reflecting a decrease in average temperature did not show an effect on soil microbial properties. Microbial biomass, domains and activity were largely similar at the three study sites, likely because vegetation at three studied sites are similar, thus providing similar carbon input quantity and substrate quality, which increases the ability of microbial communities to manage with temperature and being the main driver of microbial properties in line with our hypothesis. Consequently, climate change induced changes on vegetation, such as drought or heat waves that will more strongly affect soil microbial properties and functioning than direct temperature increase in the investigated walnut fruit forest system. Future studies should investigate potential changes in organic matter input quantity and quality along with temperature and moisture effects on soil microbial functioning.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s42729-023-01222-6.

Acknowledgements We would like to thank Dr. Lia Morena-Codinachs for the ICP measurements, Dr. Conor Watson for the soil chemistry advice, Sabrina-Alica Meisen for the ergosterol measurements, and Dr. Michael Hemkemeyer for the soil microbiology advice.

Funding Open Access funding enabled and organized by Projekt DEAL. This work was funded by German Academic Exchange Service (DAAD) Grant number: 57440921.

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