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Article *in* Journal of Soil Science and Plant Nutrition · September 2022

DOI: 10.1007/s42729-022-01002-8

Journal of Soil Science and Plant Nutrition
https://doi.org/10.1007/s42729-022-01002-8

ORIGINAL PAPER

A Fundamental Role of Slope Aspect and Elevation in Controlling Diversity Patterns of Soil Bacterial Communities: Insights from an Arid-Montane Ecosystem in China

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Received: 5 April 2022 / Accepted: 12 September 2022

Abstract

In montane ecosystems, slope aspect and elevation are the main topographic parameters that produce environmental heterogeneity related to microclimate, pedogenic processes, and vegetation patterns. However, their effects on belowground microbes are not well understood. In particular, there are few studies on how bacteria community responds to slope aspect. Here, we selected a shaded north-facing slope and a sunny south-facing slope, and investigated the influences of slope aspect and elevation on bacterial communities along transects at 2400 to 3800 m in the Qilian Mountains, a typical arid-montane ecosystem of northwestern China. The results showed that bacterial alpha and beta diversity differed significantly with slope aspect and elevation. North-facing slope had higher bacterial richness and abundance than south-facing slope, and the bacterial community composition differed significantly between slope aspects (stress = 0.062, $R^2 = 0.849$, $p < 0.001$) as revealed by non-metric multidimensional scaling analysis. Bacterial richness and diversity increased significantly with elevation and then decreased on both north-facing and south-facing slopes, with the highest values at 3500 m, and the community composition differed dramatically along elevation, as shown with quadratic relationships ($R^2_{\text{south-facing}} = 0.78$; $R^2_{\text{north-facing}} = 0.66$) between beta diversity indices and elevation. Redundancy analysis further revealed that the variations in soil pH, soil organic carbon, and soil carbon/nitrogen ratios induced by slope aspect and elevation contributed significantly to the diversity patterns of soil bacterial communities. These findings indicated a fundamental role of slope aspect and elevation in controlling diversity patterns of bacterial communities in arid-montane ecosystems, providing new insights into microbial relationships with topography.

Keywords Bacteria · Community diversity and composition · Biogeographic patterns · Topography · Slope aspect · Arid-montane ecosystems

1 Introduction

Despite accounting for only 12% of the terrestrial surface, mountain ecosystems provide a major habitat and refuge for biodiversity (Körner 2007; Moret et al. 2019; Hagedorn et al. 2019), and biogeographic patterns of plants, animal, and macrofauna and their interactions with environmental factors have been widely studied (Coblentz and Riitters 2010; Moret et al. 2019; Tan et al. 2021). By comparison, the diversity patterns of belowground microbes, in terms of their complex diversities and compositions, are not well understood (Delgado-Baquerizo et al. 2018; Tajik et al. 2020; Ivashchenko et al. 2021).

Growing evidence demonstrates that soil, plant, and climatic characteristics are often among the most important environmental predictors of microbial diversity and composition in soils (Nielsen et al. 2010; Siles and Margesin 2016; Nottingham et al. 2018; Shen et al. 2019). In montane ecosystems, slope aspect and elevation are the main topographic parameters that produce environmental heterogeneity related to microclimate, pedogenic processes, and plant traits; thus,

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they are likely to contribute to soil microbial variability (Coblentz and Riitters 2010; Seibert et al. 2007; Stage and Salas 2007; Mendez-Toribio et al. 2016; Zeng et al. 2019; Ivashchenko et al. 2021). For example, slope aspect alters net solar radiation received, and creates different microenvironment and opportunities for soil formation and development, and vegetation establishment (Sidari et al. 2008; Bennie et al. 2008; Liu et al. 2013). Climatic gradients along elevation can modify hydrothermal processes, further affecting plant traits and soil-forming processes (Wang et al. 2003; Deng et al. 2019; Chen et al. 2022). Accordingly, a greater understanding is needed of topographic controls on soil microbial communities, especially in montane ecosystems.

Soil bacteria, ranking among the most abundant and diverse group of soil microorganisms, play an important role in maintaining multiple functions of terrestrial ecosystems, including nutrient and carbon cycling, plant production, and greenhouse gas emissions (Tiedje et al. 1999; Bardgett and van der Putten 2014; Delgado-Baquerizo et al. 2018). The immense diversity of soil bacterial communities has stymied efforts to characterize their biogeographic patterns (Delgado-Baquerizo et al. 2018). Recently, an increasing number of researchers began to explore the role of topographic factors in controlling bacterial diversity patterns. However, different and sometimes contradictory results have been produced. For example, bacterial community diversity along increasing elevations include decreasing (Li et al. 2016), increasing (Margesin et al. 2009), unimodal (Praeg et al. 2020), and hollow (a dip in diversity at mid-altitude) patterns (Singh et al. 2014; Liu et al. 2016). Fewer work focused on the influence of slope aspect on bacterial communities compared with elevation, and the limited results were inconclusive. For example, some studies reported greater richness of arbuscular mycorrhizal fungi (AMF) and bacteria on sunny south-facing slope than on shaded north-facing slope (Chu et al. 2016; Liu et al. 2017; Wei et al. 2021). However, Ai et al. (2018) and Xue et al. (2018) reported that fungi and bacteria were more abundant on north-facing slope, while Schlatter et al. (2018) and Tajik et al. (2020) reported relatively minor differences in bacterial communities over varied slope aspects. Those inconclusive results indicated that the biogeographic patterns of bacterial communities were more complex than expected; thus, new work on bacterial communities facilitates a better understanding of the microbial relationships with topography.

The Qilian Mountains, constituting a major biodiversity hotspot in the arid northwestern China, are marked by complicated topography with abrupt elevations, creating high heterogeneity in climate, soil, and vegetation. Moreover, the mountains have been identified as a National Nature Reserve since 1988, greatly limiting human interference and enhancing the capacity for investigating the effects of topography on microbial communities. Thus, we selected a shaded north-facing slope and a sunny south-facing slope, and investigated the influence of slope aspect and elevation on bacterial communities along transects at 2400 to 3800 m in the Qilian Mountains. In particular, we addressed two main questions: (1) whether slope aspect and elevation had significant effects on bacterial communities and (2) which environmental variables associated with slope aspect and elevation contributed to the biogeographic patterns of bacterial communities.

2 Methods

2.1 Study Area

The study sites were situated in the Dayekou watershed (100°03′E–100°23′E, 38°23′–38°48′N, 2250–3980 m above sea level) in central Qilian Mountains, northwestern China. Native vegetation in the catchment was shaped by slope aspect and elevation, and forms two distinctly vegetation zones (Chen et al. 2016): grasslands on south-facing slopes and grassland-forest-shrubland on north-facing slopes (*Picea crassifolia* forests are distributed at elevations between 2500 and 3300 m, and shrublands are found at elevations from 3250 to 3650 m). Soil type is dominated by Haplic podsol according to the FAO classification system.

2.2 Experimental Design and Sampling

In August 2013, five sample sites were set up at about 2400, 2800, 3200, 3500, and 3800 m on selected north-facing and south-facing slopes. Site characteristics were given in Table S1. Three replicate sampling plots (30 m × 30 m) were randomly established in each site, and the distance between each plot was at least 50 m. Mean annual precipitation (MAP) and mean annual temperature (MAT) for each plot were monitored by standing tipping-bucket pluviographs and thermo-hygrometers, respectively.

In early August 2018, one composite sample comprising twelve soil cores at depths of 0–20 cm was collected for each plot, giving a total of 30 soil samples. Subsequently, visible roots and litter debris were removed from each soil sample, which was then sieved through a 2-mm soil sieve. Then, samples were divided into two portions: one portion for physicochemical analysis was air-dried and the other portion for molecular analysis was immediately stored at − 80 °C. At the same time, five undisturbed soil cores were obtained from each plot for determining soil bulk density (BD). The details for vegetation survey were present in Chen et al. (2016).

For each plot, twelve litter nets (1.0 × 1.0 m^2) were randomly installed 50 cm above the ground to collect the aboveground litter of trees and shrubs, ten quadrats (1.0 × 1.0 m^2)

were randomly selected to collect the aboveground litter of herbs and understory vegetation, and twelve soil cores (9 cm in diameter and 20 cm in depth) were collected, and fine roots (< 2 mm in diameter) were gently separated from the soil manually. Collected litter and fine roots were ground finely to determine carbon and nitrogen.

2.3 Analysis of Soil Physicochemical Properties and Plant Characteristics

Carbon (C) and nitrogen (N) concentrations in collected litter and fine roots were detected using a CHNS/O Elemental Analyzer (PerkinElmer, USA). Detailed analysis methods and procedures of soil pH, soil organic carbon (SOC), total nitrogen (TN), ammonium nitrogen (NH_4^+-N), nitrate nitrogen (NO_3^--N), total phosphorus (TP), and available phosphorus (AP) were present in He et al. (2018).

2.4 DNA Extraction and Sequence Analysis

Soil total DNA was isolated with the MoBio Power Soil DNA Isolation kit. The primer set 338F/806R was adopted to quantify the V3–V4 region of the 16S Rrna (Zhu et al. 2018). PCR reactions were conducted for amplification, and the amplification conditions and programs were present in Zhao et al. (2019). The PCR amplicons were purified using a gel extraction kit, quantified using Qubit fluorometer, and then paired-end sequenced using an Illumina Miseq PE 250 platform (San Diego, CA, USA).

The raw reads were clustered into the same OTUs (operational taxonomic units) at 97% nucleotide similarity with the UPARSE software (http://drive5.com/usearch/). 16S rRNA sequences were assigned to a taxonomic unit based on the bacterial SILVA reference database (Release138 http://www.arb-silva.de) using the RDP classifier v.11.5 (http://rdp.cme.msu.edu/). We identified a total of 13,682,118 high-quality 16S sequences, ranging from 30,012 to 74,319 sequences per sample, and these sequences were classified into 8313 OTUs at 97% similarity level.

2.5 Statistical Analysis

Taxonomic diversity indices were estimated with MOTHUR v.1.34.4 (http://www.mothur.org/). Two-way analysis of variance (ANOVA) was used to detect the differences in soil physicochemical properties, plant characteristics, and bacterial alpha diversity between slope aspect and elevation, and multiple comparisons were performed by the Duncan's new multiple range tests. The differences in bacterial beta diversity at OTU level were explored by non-metric multidimensional scaling (NMDS) analysis based on Bray–Curtis distances, and the significance of the observed differences was estimated by Adonis using 999 permutations. The compositional variance within groups, measured as distances to centroids, was evaluated using the betadisper function. The relationships between distances to centroids and elevation were evaluated by ordinary least squares (OLS) regression. Redundancy analysis (RDA) was performed to estimate the correlations among environmental variables and bacterial community. The environmental variables with variance inflation factor (VIF) > 10 were considered to have strong collinearity with other environmental variables, and removed from the RDA analysis. The VIF values of MAT, MAP, BD, TN, NO_3^--N, and AP > 10 were removed. In addition, Pearson correlation (PC) analysis was adopted to estimate the relationships between distances to centroids and environmental variables, and between bacteria abundance and environmental variables. The ANOVA, NMDS, Adonis test, OLS, RDA, and PC analyses were performed using "multcomp," "vegan," "vegan," "basicTrendline," "vegan," and "psych" packages in R v.3.2.3, respectively (Boix-Amorós et al. 2016; Ziegler et al. 2017; Zhao et al. 2019).

3 Results

3.1 Soil Physicochemical Properties and Plant Characteristics

Generally, soil pH, BD, SOC, soil C/N ratios, NO_3^--N, and AP varied significantly with slope aspect and elevation, TN and NH_4^+-N varied significantly with elevation, while TP showed no significant difference with slope aspect or elevation (Table 1). Notably, SOC, soil C/N ratios, NO_3^--N, and AP on north-facing slope were significantly higher than those on south-facing slope, while soil pH on north-facing slope was significantly lower than that on south-facing slope (Table 1). Furthermore, SOC, soil C/N ratios, NO_3^--N, and AP on both south-facing and north-facing slopes increased initially and then decreased with elevation, while soil pH and BD on both south-facing and north-facing slopes decreased initially and then increased with elevation (Table 1).

Nutrient levels of aboveground litter and fine roots also changed with slope aspect and elevation. Specifically, the N concentrations and C/N ratios of aboveground litter and the C concentrations of fine roots varied significantly with slope aspect and elevation; the C concentrations of aboveground litter varied significantly with slope aspect; the C/N ratios of fine roots varied significantly with elevation (Table 2). Notably, the C concentrations and C/N ratios of aboveground litter and the C concentrations of fine roots on north-facing slope were higher than those on south-facing slope, and the C/N ratios of aboveground litter on both south-facing and north-facing slopes increased initially and then decreased with elevation (Table 2).

Table 1 Soil physicochemical properties along an altitudinal gradient on south-facing and north-facing slopes

		Soil pH	BD (g cm^{-3})	SOC (g kg^{-1})	TN (g kg^{-1})	C/N	TP (g kg^{-1})	NH_4^+-N (mg kg^{-1})	NO_3^--N (mg kg^{-1})	AP (mg kg^{-1})
South-facing slope	S38	7.76 (0.11) dA	0.84 (0.03) cA	80.30 (3.24) bB	7.82 (0.29) bB	10.27 (0.39) bB	1.51 (0.26) bA	3.54 (0.68) aA	95.99 (3.80) bB	13.68 (0.56) bB
	S35	7.63 (0.10) dA	0.76 (0.03) cA	92.56 (2.77) aB	8.04 (0.14) bB	11.51 (0.15) aB	1.33 (0.06) bB	4.18 (0.77) aA	113.88 (8.14) aB	15.77 (0.47) aB
	S32	8.03 (0.03) cA	0.75 (0.07) cA	90.19 (3.23) aB	9.11 (0.25) aA	9.90 (0.15) bcB	2.90 (0.75) aA	2.40 (0.67) aA	115.10 (5.94) aB	15.65 (0.55) aB
	S28	8.57 (0.09) bA	0.95 (0.06) bA	41.63 (1.79) cB	4.27 (0.13) cB	9.75 (0.14) cB	1.75 (0.30) bA	3.91 (1.26) aA	52.55 (7.27) cB	8.43 (1.25) cB
	S24	8.99 (0.11) aA	1.08 (0.05) aA	21.98 (1.70) dB	2.28 (0.20) dB	9.63 (0.09) cB	1.83 (0.45) bA	4.32 (0.55) aA	26.27 (5.46) dB	6.11 (0.54) dB
North-facing slope	N38	7.46 (0.07) cB	0.76 (0.03) bcB	91.22 (0.46) cA	7.96 (0.01) bB	11.46 (0.07) cA	1.98 (0.46) aA	4.32 (1.02) abA	106.31 (5.13) bcA	15.21 (0.62) bcA
	N35	7.19 (0.16) cB	0.71 (0.03) cA	123.36 (9.55) aA	10.20 (0.20) aA	12.09 (0.43) cA	2.10 (0.14) aA	3.02 (1.64) abA	161.71 (7.31) aA	23.64 (1.24) aA
	N32	7.75 (0.04) bB	0.73 (0.02) bcA	102.49 (6.89) bA	5.02 (0.85) cB	20.45 (2.25) aA	1.37 (0.09) aB	2.29 (0.13) bA	125.21 (0.91) bA	17.40 (1.04) bA
	N28	7.97 (0.07) bB	0.81 (0.02) bcB	84.28 (1.61) cA	5.26 (0.16) cA	16.22(0.62) bA	1.84 (0.48) aA	5.09 (1.10) aA	96.11 (6.39) cA	14.02 (0.68) cA
	N24	8.64 (0.14) aB	1.01 (0.07) aA	34.31 (1.97) dA	2.97 (0.08) dA	11.57(0.95) cA	1.59 (0.17) aA	3.26 (0.27) abB	47.16 (10.43) dA	7.51 (0.81) dA
Slope aspect		***	***	***	0.28	***	0.53	0.82	***	***
Altitude		***	***	***	***	***	0.28	**	***	***
Slope aspect × altitude		0.08	0.24	***	***	***	***	0.13	***	***

Values of p are the significance by the two-way ANOVA. S38, S35, S32, S28, and S24 represent sites at 3800, 3500, 3200, 2800, and 2400 m on south-facing slope; N38, N35, N32, N28, and N24 represent sites at 3800, 3500, 3200, 2800, and 2400 m on north-facing slope. BD, SOC, TN, C/N, TP, NH_4^+-N, NO_3^--N, and AP indicate soil bulk density, soil organic carbon, total nitrogen, soil carbon/nitrogen ratios, total phosphorus, ammonia nitrogen, nitrate nitrogen, and available phosphorus. The data were expressed as mean (SE). Lowercase letters following the mean values indicated significantly different between elevations within slope aspect, and uppercase letters following the mean values indicated significantly different between aspects at the same elevation

***$p < 0.001$; **$p < 0.01$

Table 2 Carbon and nitrogen concentrations and their ratios for aboveground litter and fine roots along an altitudinal gradient on south-facing and north-facing slopes

		Aboveground litter			Fine roots		
		C_{litter} (mg g^{-1})	N_{litter} (mg g^{-1})	C/N_{litter} (mg g^{-1})	C_{roots} (mg g^{-1})	N_{roots} (mg g^{-1})	C/N_{roots} (mg g^{-1})
South-facing	S38	365.08 (55.77) aA	14.28 (2.71) aA	26.58 (0.98) bB	387.20 (67.19) aA	7.69 (0.90) aA	50.11 (3.02) aA
slope	S35	376.88 (20.58) aB	13.12 (2.94) aA	28.78 (0.37) aA	490.38 (29.40) aB	8.75 (0.80) aA	56.41 (7.03) aA
	S32	369.10 (45.52) aB	14.91 (1.68) aA	24.73 (0.36) bcB	407.21 (67.23) aA	8.67 (0.86) aA	45.59 (7.91) aA
	S28	359.19 (24.66) aB	14.75 (1.22) aA	24.37 (0.35) bcB	460.35 (57.55) aA	9.91 (1.21) aA	46.76 (7.14) aA
	S24	363.78 (24.55) aA	15.11 (0.96) aA	24.08 (0.21) cB	473.47 (51.18) aB	8.97 (0.77) aA	53.02 (7.09) aA
North-facing	N38	426.03 (32.44) aA	14.79 (1.45) aA	28.66 (0.17) cA	478.41 (44.69) abA	8.91 (0.70) aA	53.83 (5.09) bcA
slope	N35	424.45 (39.92) aA	14.09 (0.36) aA	32.03 (2.07) cA	582.69 (34.23) aA	9.31 (0.32) aA	62.71 (5.71) aA
	N32	502.64 (93.06) aA	9.77 (0.76) cB	51.13 (5.63) aA	457.89 (54.88) bA	8.81 (1.06) aA	51.97 (1.19) bcA
	N28	413.28 (14.25) aA	10.17 (0.94) bcB	40.54 (1.55) bA	480.03 (38.40) abA	9.61 (0.27) aA	49.93 (2.83) cA
	N24	383.18 (38.82) aA	13.32 (1.94) bA	29.83 (2.37) cA	584.09 (37.21) aA	9.40 (0.40) aA	62.15 (3.56) aA
Slope aspect		**	**	***	***	0.24	0.08
Altitude		0.374	*	***	**	0.06	*
Slope aspect × altitude		0.476	*	***	0.53	0.48	0.89

Values of p are the significance by the two-way ANOVA. S38, S35, S32, S28, and S24 represent sites at 3800, 3500, 3200, 2800, and 2400 m on south-facing slope; N38, N35, N32, N28, and N24 represent sites at 3800, 3500, 3200, 2800, and 2400 m on north-facing slope. C_{litter}, N_{litter}, and C/N_{litter} indicate the carbon and nitrogen concentrations and their ratios for aboveground litter; C_{roots}, N_{roots}, and C/N_{roots} indicate the carbon and nitrogen and their ratios for fine roots. The data were expressed as mean (SE). Lowercase letters following the mean values indicated significantly different between elevations within slope aspect, and uppercase letters following the mean values indicated significantly different between aspects at the same elevation

$^{***}p<0.001$; $^{**}p<0.01$; $^{*}p<0.05$

3.2 Patterns of Soil Bacterial α-Diversity

Generally, the number of OTUs and Chao index varied significantly with slope aspect and elevation, and the Shannon index varied significantly with elevation (Table 3). Specifically, the number of OTUs at 2400, 2800, and 3200 m on north-facing slope was significantly higher than that on south-facing slope, and the Chao index on north-facing

Table 3 Bacterial richness and diversity estimators along an altitudinal gradient on south-facing and north-facing slopes

		Observed OTUs	Chao1 estimator	Shannon index
South-facing	S38	2701 (167.29) abA	3344.73 (73.37) aB	6.70 (0.03) aA
slope	S35	2834 (184.86) aA	3727.99 (296.68) aA	6.71 (0.02) aA
	S32	2410 (94.62) bB	3292.71 (88.17) aB	6.56 (0.03) bA
	S28	2049 (105.67) cB	2770.79 (219.97) bB	6.38 (0.05) cA
	S24	2038 (133.97) cB	2525.04 (86.17) bB	6.27 (0.08) cA
North-facing	N38	2769 (201.58) abA	3695.73 (193.64) abA	6.65 (0.04) aA
slope	N35	2980 (98.09) aA	4060.01 (140.37) aA	6.68 (0.04) aA
	N32	2755 (121.97) abA	3839.04 (110.79) abA	6.51 (0.08) abA
	N28	2715 (74.36) abA	3798.12 (133.88) abA	6.43 (0.05) abA
	N24	2471 (101.71) bA	3597.15 (104.72) bA	6.37 (0.09) bA
Slope aspect		***	***	0.91
Altitude		***	***	***
Slope aspect × altitude		*	*	0.34

Values of p are the significance by the two-way ANOVA. S38, S35, S32, S28, and S24 represent sites at 3800, 3500, 3200, 2800, and 2400 m on south-facing slope; N38, N35, N32, N28, and N24 represent sites at 3800, 3500, 3200, 2800, and 2400 m on north-facing slope. The data were expressed as mean (SE). Lowercase letters following the mean values indicated significantly different between elevations within slope aspect, and uppercase letters following the mean values indicated significantly different between aspects at the same elevation

$^{***}p<0.001$; $^{*}p<0.05$

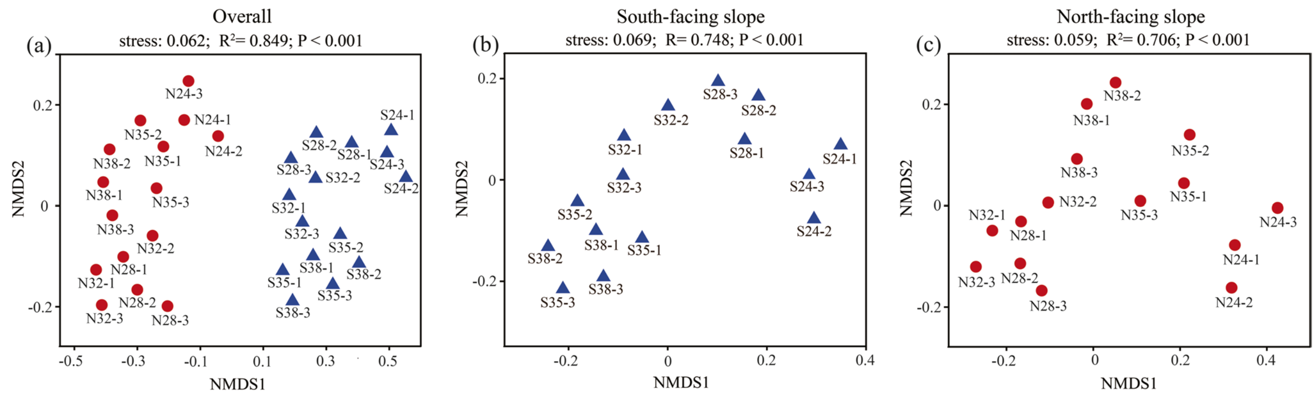


Fig. 1 Non-metric multidimensional scaling (NMDS) ordination of bacterial communities based on Bray–Curtis similarities for the overall (**a**), south-facing slope (**b**), and north-facing slope (**c**) and the significance of the observed differences was estimated by Adonis using 999 permutations. S38, S35, S32, S28, and S24 represent sites at 3800, 3500, 3200, 2800, and 2400 m on south-facing slope; N38, N35, N32, N28, and N24 represent sites at 3800, 3500, 3200, 2800, and 2400 m on north-facing slope

slope was significantly higher than that on south-facing slope, except at elevation of 3500 m. However, no significant differences were detected in Shannon index between north-facing and south-facing slopes (Table 3). The number of OTUs, Chao index, and Shannon index on both south-facing and north-facing slopes increased significantly with elevation up till 3500 m and then decreased, exhibiting a unimodal pattern (Table 3).

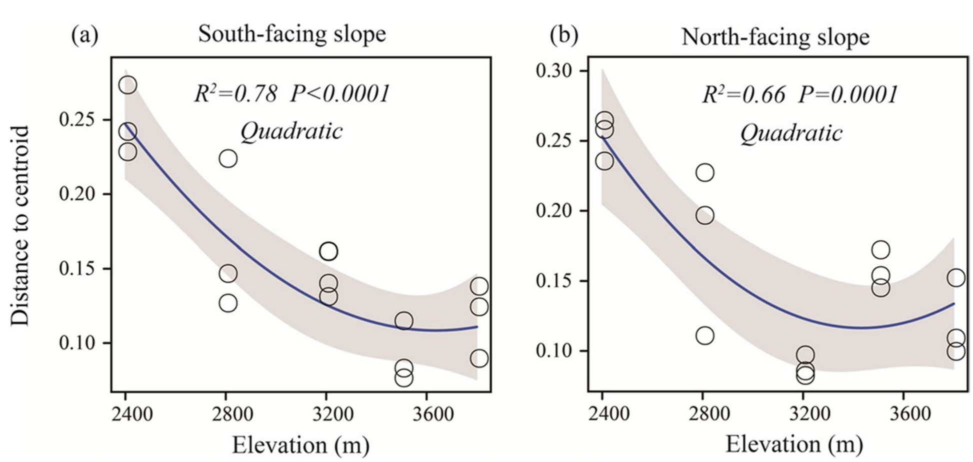
3.3 Patterns of Soil Bacterial β-Diversity

NMDS analysis revealed significant differences in bacterial beta diversity with slope aspect (stress = 0.062, $R^2 = 0.849$, $p < 0.001$) (Fig. 1a). Furthermore, NMDS analysis also revealed significant differences in bacterial beta diversity with elevation on both south-facing slope (stress = 0.069, $R^2 = 0.748$, $p < 0.001$) and north-facing slope (stress = 0.059, $R^2 = 0.706$, $p < 0.001$) (Fig. 1b, c). On south-facing slope, bacterial communities at elevations of 3800 and 3500 m grouped together, and were obviously separated from those at 3200, 2800, and 2400 m, which were also separated from each other (Fig. 1b). On north-facing slope, bacterial communities at elevation of 3200 and 2800 m grouped together, and were obviously separated from those at elevations of 3800, 3500, and 2400 m, which were also separated from each other (Fig. 1c). A regression analysis showed that distances to centroids were significantly correlated with elevation on both south-facing and north-facing slopes, and the relationships were described by quadratic models (Fig. 2a, b; Table S2).

3.4 Patterns of Soil Bacterial Community Compositions

The top 10 dominant phyla were *Actinobacteria* (17.58–32.63%), *Proteobacteria* (15.35–36.56%), *Acidobacteria* (8.99–23.09%), *Chloroflexi* (8.07–16.47%), *Bacteroidetes* (2.76–4.42%), *Gemmatimonadetes* (1.96–5.62%),

Fig. 2 Relationships of elevation with distances to centroids on south-facing slope (**a**) and north-facing slope (**b**). The quadratic models were selected by comparing adjusted R^2 and AIC



Firmicutes (0.18–7.84%), *Nitrospirae* (0.39–4.25%), *Verrucomicrobia* (0.59–2.35%), and *Cyanobacteria* (0.04–7.31%) (Fig. 3a). Notably, *Actinobacteria*, *Chloroflexi*, *Gemmatimonadetes*, and *Cyanobacteria* were more abundant on south-facing slope than those on north-facing slope; while *Proteobacteria* and *Nitrospirae* were less abundant on south-facing slope than those on north-facing slope (Fig. 3b).

The top 10 dominant classes were *Actinobacteria* (17.58–36.16%), *Acidobacteria* (8.99–23.09%), *Alphaproteobacteria* (11.54–18.39%), *Betaproteobacteria* (1.27–11.36%), *Gemmatimonadetes* (1.98–5.62%), *Thermomicrobia* (0.25–8.69%), *Deltaproteobacteria* (1.80–3.93%), *Nitrospirae* (0.39–4.25%), *Bacilli* (0.07–7.54%), and *Cyanobacteria* (0.04–7.31%) (Fig. 4a). Notably, *Actinobacteria*, *Thermomicrobia*, *Gemmatimonadetes*, and *Cyanobacteria* were more abundant on south-facing slope than those on north-facing slope, while *Alphaproteobacteria*, *Betaproteobacteria*, and *Nitrospirae* were less abundant on south-facing slope than those on north-facing slope (Fig. 4b).

3.5 Relationships of Soil Bacterial Community with Environmental Variables

RDA indicated that slope aspect ($r^2 = 0.929$, $p < 0.001$), soil C/N ratios ($r^2 = 0.805$, $p < 0.001$), SOC ($r^2 = 0.270$, $p < 0.05$), and soil pH ($r^2 = 0.234$, $p < 0.05$) were the major environmental variables significantly affecting bacterial community composition (Fig. 5a; Table 4). For south-facing slope, elevation ($r^2 = 0.840$, $p < 0.001$), soil pH ($r^2 = 0.886$, $p < 0.001$), SOC ($r^2 = 0.772$, $p < 0.001$), and soil C/N ratios ($r^2 = 0.677$, $p < 0.01$) were the major environmental variables significantly affecting bacterial community composition (Fig. 5b; Table 4). For north-facing slope, elevation ($r^2 = 0.890$), soil C/N ratios ($r^2 = 0.779$), soil pH ($r^2 = 0.673$), and SOC ($r^2 = 0.549$) were the major environmental variables significantly affecting bacterial community composition (Fig. 5c; Table 4). This finding was confirmed with regression analyses, which demonstrated that aspect, soil C/N ratios, SOC, and soil pH were significantly correlated with distances to centroids. For both south-facing and north-facing slopes, elevation, soil pH, SOC, and soil C/N ratios were significantly correlated with distances to centroids (Table S3).

4 Discussion

To our knowledge, the present study is as one of the few studies in arid-montane ecosystems to investigate the influence of slope aspect on soil bacterial communities. Our findings revealed that bacterial communities differed significantly between north-facing and south-facing

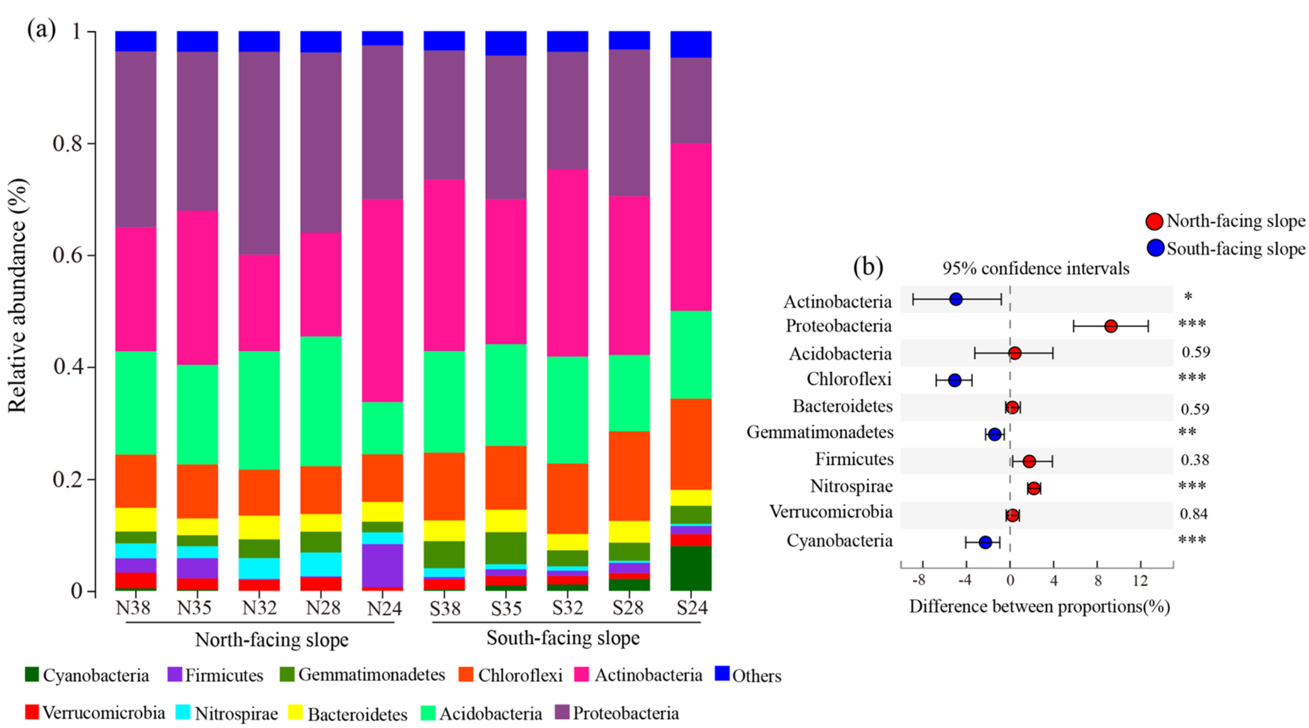


Fig. 3 Distributions of the top 10 dominant phyla at the different sampling sites (**a**) and the difference in the relative abundance of the dominant class between on south-facing and north-facing slopes (**b**). ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$. S38, S35, S32, S28, and S24 represent sites at 3800, 3500, 3200, 2800, and 2400 m on south-facing slope; N38, N35, N32, N28, and N24 represent sites at 3800, 3500, 3200, 2800, and 2400 m on north-facing slope

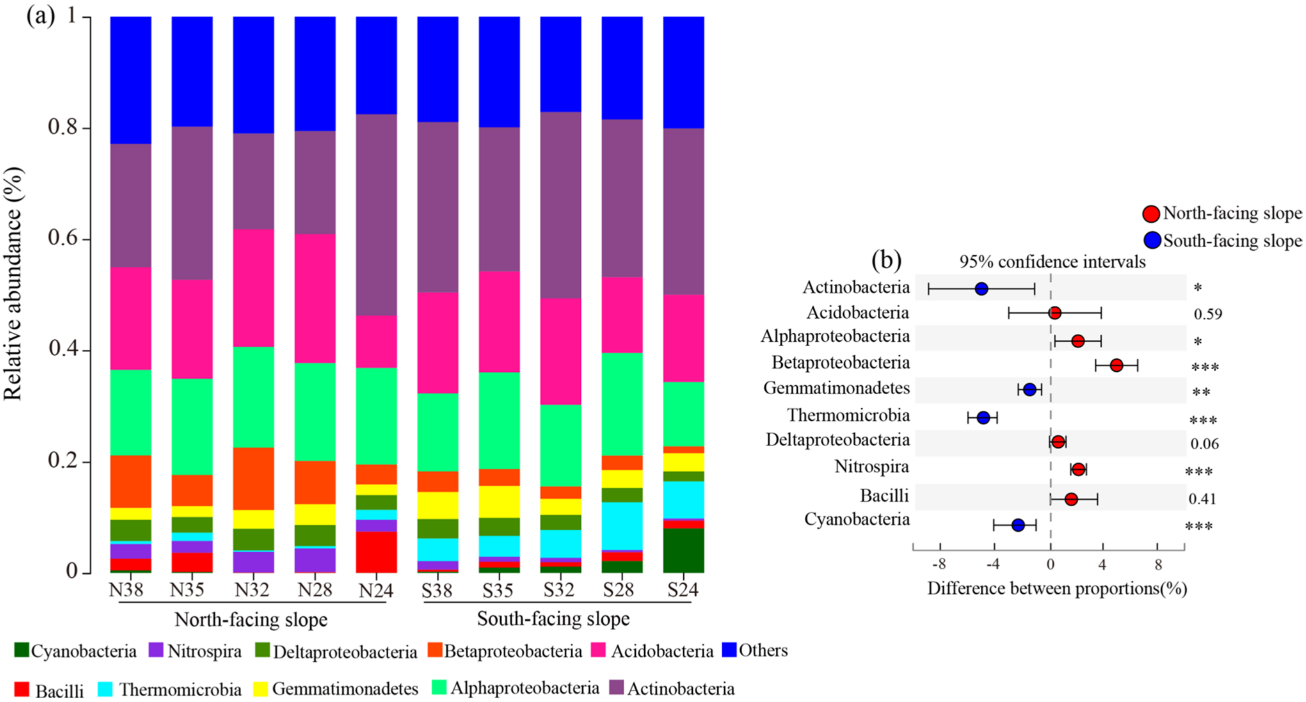


Fig. 4 Distributions of the top 10 dominant class at the different sampling sites (**a**) and the difference in the relative abundance of the dominant phyla between south-facing and north-facing slopes (**b**). $^{***}p<0.001$; $^{**}p<0.01$; $^{*}p<0.05$. S38, S35, S32, S28, and S24 represent sites at 3800, 3500, 3200, 2800, and 2400 m on south-facing slope; N38, N35, N32, N28, and N24 represent sites at 3800, 3500, 3200, 2800, and 2400 m on north-facing slope

slopes, and that bacterial richness and abundance were higher on the north-facing slope than on the south-facing slope. Furthermore, we also detected remarkably elevational diversity patterns of soil bacterial communities on both north-facing and south-facing slopes. In that, bacterial richness and diversity increased significantly with elevation up to 3500 m, and then decreased, and community composition differed dramatically along elevation as shown with the significant quadratic relationships between beta diversity indices and elevation. These findings indicated a fundamental role of slope aspect and elevation in controlling diversity patterns of soil bacterial communities in arid-montane ecosystems. RDA further revealed that slope aspect has the greatest effect on

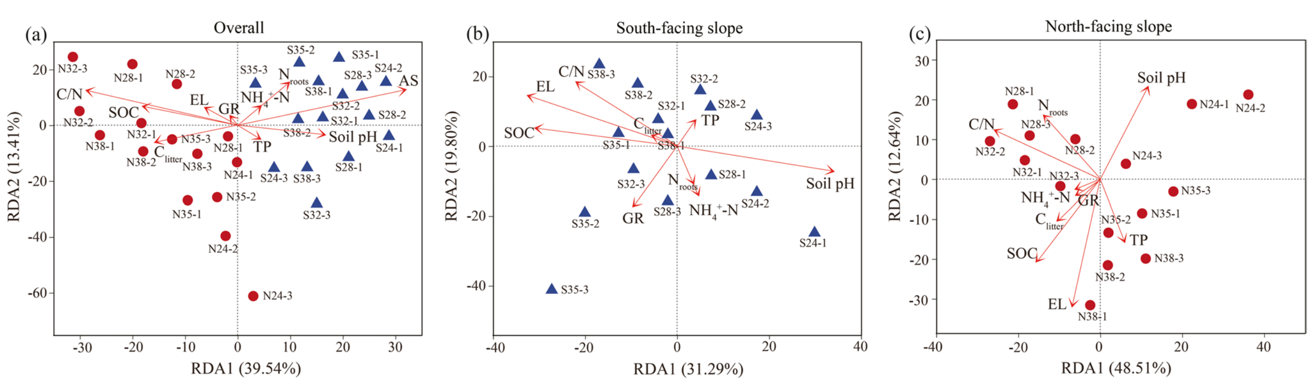


Fig. 5 Redundancy analysis identifying the relationships between bacterial community structures and environmental variables for the overall (**a**), south-facing slope (**b**), and north-facing slope (**c**). S38, S35, S32, S28, and S24 represent sites at 3800, 3500, 3200, 2800, and 2400 m on south-facing slope; N38, N35, N32, N28 and N24 represent sites at 3800, 3500, 3200, 2800, and 2400 m on north-facing slope. AS, EL, GR, SOC, C/N, TP, NH_4^+-N, C_{litter}, and N_{roots} indicate aspect, elevation, gradient, soil organic carbon, soil carbon/nitrogen ratios, total phosphorus, ammonia nitrogen, carbon concentrations for aboveground litter, and nitrogen concentrations for fine roots, respectively

Table 4 Correlation between soil properties and bacterial communities (OTU abundance) as evaluated by redundancy analysis

	VIF	Overall				South-facing slope				North-facing slope			
		Axis 1	Axis 2	r^2	p	Axis 1	Axis 2	r^2	p	Axis 1	Axis 2	r^2	p
Aspect	3.055	0.946	−0.325	0.929	***	/	/	/	/	/	/	/	/
Altitude	4.857	−0.686	−0.728	0.053	0.480	−0.898	0.439	0.840	***	−0.200	−0.980	0.890	***
Gradient	1.523	−0.299	−0.954	0.008	0.910	−0.587	−0.810	0.130	0.447	−0.953	−0.304	0.025	0.835
Soil pH	8.492	0.987	0.163	0.234	*	0.978	−0.210	0.886	***	0.335	0.942	0.673	**
SOC	5.509	−0.945	−0.327	0.270	*	−0.984	0.176	0.772	***	−0.547	−0.837	0.549	*
C/N	2.835	−0.934	−0.359	0.805	***	−0.601	0.799	0.677	**	−0.942	0.336	0.779	***
TP	1.639	0.637	0.771	0.028	0.691	0.852	0.523	0.037	0.768	0.321	−0.947	0.219	0.210
NH_4^+-N	1.253	0.333	−0.943	0.020	0.784	0.260	−0.966	0.204	0.249	−0.922	−0.388	0.028	0.857
C_{litter}	1.766	−0.998	0.062	0.174	0.121	−0.727	0.686	0.002	0.993	−0.737	−0.675	0.139	0.433
N_{roots}	1.961	0.335	−0.942	0.114	0.196	0.400	−0.917	0.068	0.667	−0.591	0.807	0.319	0.106

VIF, SOC, C/N, TP, NH_4^+-N, C_{litter}, and N_{roots} indicate variance inflation factor, soil organic carbon, soil carbon/nitrogen ratios, total phosphorus, ammonia nitrogen, carbon concentrations for aboveground litter, and nitrogen concentrations for fine roots, respectively

***$p < 0.001$, **$p < 0.01$, *$p < 0.05$

bacterial community composition for the whole catchment. At this spatial scale, elevation has no significant effect on bacterial community composition. However, within both south-facing and north-facing slopes, elevation was the most important environmental variable affecting bacterial community composition. These results indicated that the effect of slope aspect and elevation on bacterial community composition depends on spatial scale in arid-montane ecosystems.

The importance of elevation in controlling soil microbial diversity and community composition has been shown in other montane ecosystems; nevertheless, different and even contradictory elevational distribution patterns have been documented (Liu et al. 2016; Shen et al. 2019). A recent synthesis of more than 20 studies revealed that elevational trends of microbial diversity were related to the tree line (Shen et al. 2019). Studies began above the tree line and extended upwards that tended to show declining diversity trends with elevation (Li et al. 2016); whereas others that extended across the tree line showed other diversity trends with elevation, including increasing (Margesin et al. 2009), unimodal (Peng et al. 2018; Praeg et al. 2020), and hollow patterns (Singh et al. 2014; Liu et al. 2016). A unimodal pattern was documented in this study for bacterial diversity from 2400 to 3800 m on both north-facing and south-facing slopes (tree line was at about 3300 m a.s.l). Our findings supported those of Peng et al. (2018) and Praeg et al. (2020) from Taibai Mountain in China and the Central European Alps, respectively.

Fewer studies focused on microbial relationships with slope aspect than with elevation. Slope aspect is the main topographic parameter generating environmental heterogeneity by altering the effects of solar radiation and hydrothermal processes (Sidari et al. 2008; Bennie et al. 2008; Liu et al. 2013; Chen et al. 2016). It has been well documented that slope aspects play a primary role in shaping soil biogeochemical processes and vegetation patterns (Coblentz and Riitters 2010; Xue et al. 2018). Recently, the influence of slope aspect on AMF communities also attracted attention because of the observed close association between plant diversity and AMF communities (Hiiesalu et al. 2014; Prober et al. 2015; Liu et al. 2017). Previous studies have revealed that aspect-induced changes in plant communities had strong direct effects on AMF community diversity (Chu et al. 2016; Ai et al. 2018; Wei et al. 2021). However, little is known about the response of bacterial communities to slope aspect. Interestingly, in this study, significant differences were observed in soil bacterial diversity and composition with slope aspect in the arid-montane ecosystem, supporting earlier evidence of the importance of slope aspect in regulating the diversity pattern of bacterial communities in arid-montane ecosystems.

The significant influence of slope aspect on bacterial community composition was demonstrated by the significant difference in dominant bacterial abundance between north-facing and south-facing slopes. Notably, *Actinobacteria*, *Gemmatimonadetes*, *Cyanobacteria*, and *Thermomicrobia* within *Chloroflexi* were more abundant on south-facing slope than those on north-facing slope, while *Alphaproteobacteria* and *Betaproteobacteria* within *Proteobacteria* and *Nitrospirae* were less abundant on south-facing slope than those on north-facing slope. *Actinobacteria* and *Thermomicrobia* are oligotrophic groups, and prefer nutrient deficient conditions (Eichorst et al. 2007; Sorokin et al. 2012; Lazcano et al. 2013; Song et al. 2018), while *Alphaproteobacteria*, *Betaproteobacteria*, and *Nitrospirae* have copiotrophic life history strategies, and are more abundant in nutrient-enriched environment (Fierer et al. 2007; Chu et al. 2010; Goldfarb et al. 2011;

Daims et al. 2015; Wang and Hua 2022). Thus, the higher abundance of *Alphaproteobacteria*, *Betaproteobacteria*, and *Nitrospirae* and lower abundance of *Actinobacteria* and *Thermomicrobia* on north-facing slope than on south-facing slope can be attributed to higher availability of substrate and nutrient supply on north-facing slope. Our interpretations were further confirmed with a Pearson correlation analysis, in which *Actinobacteria* and *Thermomicrobia* were significantly negatively correlated with SOC and available nutrient contents, while *Alphaproteobacteria*, *Betaproteobacteria*, and *Nitrospirae* were significantly positively correlated with SOC and available nutrients. In addition, *Cyanobacteria* are phototrophs and have been demonstrated be more abundant in south-facing slope (Kuritz 1998); *Gemmatimonadetes* prefer arid conditions (Chanal et al. 2006; DeBruyn et al. 2011), explaining their higher abundance on drier south-facing slope than on moister north-facing slope.

Furthermore, our results also revealed that the variations in soil pH, SOC, and soil C/N ratios caused by slope aspect and elevation contributed significantly to the diversity patterns of soil bacterial communities in this arid-montane ecosystem; this finding was confirmed with correlation analyses, which demonstrated that soil pH, SOC, and soil C/N ratios were significantly correlated with alpha and beta diversity indices of bacterial community. Soil pH-driven elevational patterns of microbial diversity and composition have been described across a variety of spatial scales (Fierer and Jackson 2006; Delgado-Baquerizo et al. 2018; Malard et al. 2019). Our observations were in line with studies mentioned above, and emphasized the importance of soil pH in mediating the influence of slope aspect on bacterial diversity and community composition in arid-montane ecosystem. SOC, as the fundamental substrate and energy source for soil microbes, and soil C/N ratios, indicating substrate quality (Nilsson et al. 2012; Deng et al. 2018; Zhao et al. 2021), are supposed to influence elevational diversity patterns of microbial communities by affecting their metabolism (Smith et al. 2002; Xiang et al. 2014; Peng et al. 2018). Our observations supported the role of slope aspect in controlling bacterial diversity and composition by altering SOC and soil C/N ratios.

5 Conclusions

Our work is as one of the few studies in arid-montane to explore the influence of slope aspect on bacterial communities in arid-montane ecosystems. The results revealed that bacterial alpha and beta diversity significantly differed with slope aspect and elevation, indicating a fundamental role of slope aspect and elevation in regulating diversity and composition of bacterial communities in the arid-montane ecosystems. The strong effect of slope aspect on bacterial communities was demonstrated by the shifts in dominant bacterial abundance between north-facing and south-facing slopes. Our results further emphasized the importance of soil pH, soil organic carbon, and soil carbon/nitrogen ratios in mediating the influence of slope aspect on bacterial diversity and community composition in arid-montane ecosystem. Overall, our findings provide new insights into microbial relationships with topography and have important implications for biodiversity conservation in arid-montane ecosystems in China.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s42729-022-01002-8.

Funding The study was funded by the Key Program of the Chinese Academy of Sciences (QYZDJ-SSW-DQC040), the Second Tibetan Plateau Scientific Expedition and Research (STEP) program (Grant No. 2019QZKK0303), and the Strategic Priority Research Program of the Chinese Academy of Sciences (CAS) (XDA23060301).

Declarations

Conflict of Interest The authors declare no competing interests.

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