Postprint: Altitudinal and Seasonal Variations in Soil Carbon Sequestration Microbial Community Characteristics in Meadows of the Northern Tibetan Plateau

Authors: Gao Jing, MUHANMMAD, In recent years, deep learning has achieved breakthrough advances in areas such as image classification and natural language processing. However, deep neural networks typically require large amounts of annotated data for training, which is difficult to satisfy in many practical applications. To address this issue, researchers have proposed transfer learning methods, which pre-train models on the source domain and then transfer them to the target domain for fine-tuning, thereby significantly reducing the demand for annotated data in the target domain. Although transfer learning has achieved success in many tasks, its performance is still limited by the distribution discrepancy between the source and target domains. When the distribution discrepancy between the source and target domains is large, the performance of transfer learning degrades significantly. Therefore, how to reduce the inter-domain distribution discrepancy and achieve more effective knowledge transfer has become a core problem in the field of transfer learning.

Domain Adaptation (DA), as an important branch of transfer learning, aims to improve the generalization performance of models on the target domain by reducing the distribution discrepancy between the source and target domains. According to whether target domain data is available, domain adaptation methods can be divided into Unsupervised Domain Adaptation (UDA) and Semi-supervised Domain Adaptation (SDA). Among them, UDA assumes that the target domain has no annotated data, while SDA allows the use of a small amount of annotated target domain data. Although UDA is theoretically more challenging, it has received increasing attention in recent years due to its wide applicability in practical scenarios.

Existing UDA methods can be mainly divided into two categories: methods based on statistical distances and methods based on adversarial learning. Methods based on statistical distances achieve domain alignment by minimizing the statistical distance between the feature distributions of the source and target domains (such as Maximum Mean Discrepancy (MMD) [**?**], Wasserstein distance [**?**], etc.). Such methods typically require carefully designed feature extractors to

ensure that the reduction of statistical distance can truly improve domain adaptation performance. However, since statistical distances are usually computed at the global level, such methods often struggle to capture the local structural information of data, leading to suboptimal adaptation effects in certain complex scenarios.

Methods based on adversarial learning draw inspiration from Generative Adversarial Networks (GANs) [**?**], introducing a domain discriminator to distinguish features from the source and target domains, while simultaneously training the feature extractor to 'fool' the domain discriminator, thereby achieving the extraction of domain-invariant features. Such methods have achieved remarkable success in tasks such as image classification [**?**, **?**]. However, methods based on adversarial learning also suffer from several issues. First, the adversarial training process is often unstable, prone to problems such as mode collapse and gradient vanishing. Second, the domain discriminator can only provide binary feedback (source or target domain), unable to provide fine-grained domain discrepancy information, which limits its application in complex domain adaptation scenarios.

To overcome the limitations of the aforementioned methods, this paper proposes a novel unsupervised domain adaptation framework, termed Structure-Preserving Domain Adaptation (SPDA). The core idea of this framework is to preserve the intrinsic structural information of data while performing domain alignment. Specifically, we design a structure-preserving loss function that constrains the feature extractor through Graph Laplacian Regularization, ensuring that similar data points remain close to each other in the feature space. Furthermore, we introduce an attention mechanism-based feature alignment module that can adaptively focus on feature regions more important for domain adaptation, thereby achieving finer-grained domain alignment. Experimental results demonstrate that the proposed SPDA method achieves superior performance compared to existing methods on multiple standard domain adaptation datasets.

The main contributions of this paper can be summarized as follows:

- We propose a novel unsupervised domain adaptation framework SPDA, which preserves the intrinsic structural information of data through Graph Laplacian Regularization, thereby enhancing domain adaptation performance.
- We design an attention mechanism-based feature alignment module that can adaptively focus on important feature regions, achieving finer-grained domain alignment.
- We conduct extensive experiments on multiple standard domain adaptation datasets, validating the effectiveness of the proposed method and achieving state-of-the-art performance levels.

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Abstract

Investigating the abundance, community structure, diversity differences, and influencing factors of soil carbon sequestration microorganisms is of great significance for understanding soil carbon cycling and carbon sequestration potential on the Tibetan Plateau. Using quantitative PCR (qPCR), terminal restriction fragment length polymorphism (T-RFLP), clone library, and sequencing methods, this study examined the variations in abundance and community structure of carbon sequestration microorganisms in Tibetan Plateau meadow soils with altitude and season. The main results are as follows: 1) The abundance of carbon sequestration microorganisms in alpine meadow soils increased significantly with altitude, but showed no obvious seasonal variation. The abundance of microbial carbon sequestration gene cbbL across different categories was in the order: Form IC > Form IAB > Form ID, with Form IC carbon sequestration microorganisms reaching up to 10^8 copies/g soil. The abundance of the cbbL gene was positively correlated with altitude, soil water content, and ammonium nitrogen content (NH4+-N), and negatively correlated with soil temperature and pH; 2) The diversity and richness of carbon sequestration microorganisms increased with altitude, reaching a maximum at 4800 m, and both were less affected by season. The community structure gradually changed with altitude, being mainly influenced by soil pH, altitude, and soil moisture; 3) Form IC carbon sequestration microorganisms mainly included Actinobacteria and Proteobacteria, with Alphaproteobacteria being the dominant carbon sequestration microbial group in alpine meadow soils. This study contributes to understanding the functional roles of soil microbial communities and their involvement in soil carbon cycling processes, providing a scientific basis for more accurate assessment of carbon cycling processes in alpine meadow soils.

Full Text

Preamble

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Title: Changes in CO -fixing microbial community characteristics with elevation and season in alpine meadow soils on the northern Tibetan Plateau

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Abstract

Soil microbial autotrophs play an important role in CO fixation in terrestrial ecosystems, particularly in vegetation-constrained ecosystems with environmental stresses such as the Tibetan Plateau, which is characterized by low temperature, drought, and high UV radiation. However, soil microbial autotrophic communities and their driving factors remain less appreciated in these terrestrial ecosystems. To understand carbon sequestration by soil microbial autotrophs and the carbon cycle in alpine meadow soils on the Tibetan Plateau, we explored autotrophic microbial abundance, community structure, diversity, and their driving environmental factors along an elevation gradient from 4400 m to 5200 m. Additionally, the seasonal change in soil microbial autotrophs was explored at each elevation. The autotrophic microbial communities were characterized by quantitative PCR (qPCR), terminal restriction fragment length polymorphism (T-RFLP), and cloning/sequencing methods targeting four types of genes encoding the large subunit of the CO -fixing protein ribulose-1,5-bisphosphate carboxylase/oxygenase (RubisCO): Form IA/B, IC, and ID.

The main results were as follows: (1) The abundance of carbon-fixing microbes in alpine meadow soils significantly increased with elevation, but showed minimal seasonal change. Among the four types of microbial autotrophs, Form IC carbon-fixing gene *cbbL* abundance was highest (reaching 10 copies/g soil), followed by Form IA/B and Form ID. Form IC abundance was positively correlated with elevation, soil water content, and NH -N content, and negatively correlated with soil temperature and pH ($P < 0.01$). (2) Carbon-fixing microbial diversity and richness increased with elevation, peaking at 4800 m, and were less affected by season. Community structure gradually changed with elevation, mainly driven by soil water content, pH, and elevation. (3) Form IC carbon-fixing microbes were dominated by Actinobacteria and Proteobacteria, with Proteobacteria being the dominant phylum in alpine meadow soils, including typical rhizobia such as *Bradyrhizobium*, *Mesorhizobium*, and *Rhizobium*. This study helps understand soil microbial community function and its role in soil carbon cycling, providing a scientific basis for more accurately assessing carbon cycling processes in alpine meadow soils.

Keywords: alpine meadow; carbon-fixing microorganisms; RubisCO; elevation; Tibetan Plateau

1 Study Area Description

The study area is located in Dangxiong County, north of Lhasa City, approximately 170 km from Lhasa urban center (91°05 E, 30°51 N), with an average elevation of 4300–4700 m, backed by the Nyenchen Thanglha Mountains. The region has a plateau monsoon climate with brief, rainy summers and cold, dry winters, large diurnal temperature variations, and distinct seasonal precipitation patterns. The multi-year average temperature is 1.5°C (1960–2000), with annual precipitation of 476.8 mm concentrated in the growing season. The soil type is alpine meadow soil, and the ecosystem is typical alpine meadow. Vegetation mainly consists of dominant species such as dwarf sedge (*Kobresia pygmaea*), interspersed with *Potentilla* species and cushion plants like *Androsace tapete*. Vegetation type changes little with elevation, though aboveground biomass increases.

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2 Sample Collection and Processing

Sampling was conducted on the southern slope of Nyenchen Thanglha Mountain during three seasons: May (spring), July (summer), and September (autumn) in 2015. Sampling sites were distributed at elevations of 4400, 4650, 4800, and 5200 m, with three replicate plots at each elevation. Each replicate soil sample was a composite of five soil cores (2.5 cm diameter) collected at 0–10 cm depth. Soils were sieved through a 2.0 mm mesh. One portion was sealed in sterile bags, rapidly frozen in liquid nitrogen, and stored at -80°C for microbial community analysis. Another portion was air-dried for determination of soil physicochemical properties.

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3 Determination of Soil Physicochemical Factors

Soil carbon and nitrogen-related physicochemical factors were measured using standard methods. Total organic carbon (TOC) was determined using a TOC analyzer (TOC-L, SHIMADZU, Japan). Ammonium nitrogen (NH -N) and nitrate nitrogen (NO -N) were measured using a flow analyzer (AQ2, SEAL Analytical Inc., UK). Soil water content (SWC) was determined by the oven-drying method (105°C for 24 h). Soil temperature at each elevation was measured using automatic weather stations (Onset Inc., Bourne, MA, USA). Soil pH was measured using a pH meter (PB-10, Sartorius, Germany) at a soil:water ratio of 1:2.5.

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4 Soil DNA Extraction

Soil DNA was extracted from 0.25 g of frozen soil samples using the PowerSoil® DNA Isolation Kit (MOBIO, USA) following the manufacturer's protocol. After extraction, 2 L of DNA was used to assess concentration and purity using a NanoDrop® ND-1000 spectrophotometer (USA), and integrity was checked by agarose gel electrophoresis.

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5 Gene Abundance Determination

Quantitative PCR (qPCR) was used to determine the abundance of carbon-fixing microbial *cbbL* genes. Amplification primers were specific for each gene form (Table 1). qPCR was performed on a Roche LightCycler® 480 II (Roche, USA) using SYBR Green kits (TaKaRa, Japan). Reaction mixtures (10 L) contained 0.5 L of each primer, 1 L of DNA template, and SYBR Green master mix. Reaction conditions were: pre-denaturation at 95°C for 2 min, followed by 35 cycles of 94°C for 30 s, annealing at specific temperatures (Form IA/B: 61°C, Form IC: 63°C, Form ID: 53°C) for 30 s, and extension at 72°C for 30 s. Fluorescence signals were collected during each cycle. Standard curves were generated using 10-fold serial dilutions of plasmids containing target fragments.

Table 1 Primers used in this study

Primer	Sequence (5 -3)
Form IC-F	GAA CAT CAA YTC KCA GCC CTT TGG
Form IC-R	TGC ATC TGV CCG GCR TG
Form ID-F	GAT GAT GAR AAY ATT AAC TC
Form ID-R	ATT TGD CCA CAG TGD ATA CCA
Form IA/B-F	TCI GCI TGR AAC TAY GGT CG
Form IA/B-R	GGC ATR TGC CAI ACR TGR AT

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6 Carbon-Fixing Microbial Community Structure Analysis

Form IC carbon-fixing microbes showed the highest abundance in meadow soils, representing the dominant carbon-fixing microbial group. Terminal restriction fragment length polymorphism (T-RFLP) was used to analyze Form IC community structure and diversity. The functional gene was amplified using fluorescently labeled primers. PCR products were purified using an AxyPrep™ DNA Gel Extraction Kit (Axygen). Purified products were digested with the restriction enzyme *Msp*I. Terminal restriction fragments (T-RFs) were sized and quantified using an ABI 3730xl DNA Analyzer (Applied Biosystems, CA, USA). Relative abundances of different T-RFs were used to calculate community structure and diversity indices.

7 Carbon-Fixing Microbial Clone Library and Phylogenetic Analysis

Clone libraries of Form IC carbon-fixing microbes were constructed from July soil samples at 4800 m. Amplification used the same primers as T-RFLP analysis. PCR products were purified and ligated into pGEM®-T vectors (Promega, USA) following the manufacturer' s instructions, then transformed into DH5 competent cells (ComWin Biotech, China). Positive clones were identified by blue-white screening, and clones with insert lengths matching the target fragment (40–45 bp) were selected for Sanger sequencing (ABI 3730xl DNA Analyzer). Phylogenetic analysis was performed on sequences with >97% similarity using MEGA 6.0 software (neighbor-joining method). Diversity indices were calculated using Mothur v.1.33.3. Community structure analysis was conducted using the "vegan" package in R v.3.1.3. Correlations and significance tests were performed using Canoco 5 and SPSS 23.

8 Data Analysis

Clone library sequences were analyzed using MEGA 6.0 (neighbor-joining phylogenetic tree). Diversity indices were calculated using Mothur v.1.33.3. Statistical analyses and visualizations were performed using SigmaPlot 10.0, Excel, and R 3.1.3.

2 Results and Analysis

2.1 Changes in *cbbL* Gene Abundance with Elevation and Season

The abundance of Form IA/B genes in soils increased gradually with elevation from 4400 m to 4800 m, then remained stable or decreased slightly above 4800 m. Form IA/B showed the greatest increase in abundance with elevation, while Form ID showed the smallest variation. Two-way ANOVA revealed that elevation significantly affected Form IA/B abundance ($P < 0.05$), while season and its interaction with elevation had no significant effect ($P > 0.631$).

Form IC gene abundance increased significantly with elevation, rising rapidly from 4400 m to 4800 m, then stabilizing or decreasing slightly above 4800 m. Compared with other months, July showed the highest Form IC abundance at each elevation. Two-way ANOVA indicated that both elevation and season significantly affected Form IC abundance ($P < 0.05$), and their interaction also had a significant effect ($P < 0.01$).

Form ID gene abundance showed minimal change with elevation, with no significant seasonal variation. Among the three carbon-fixing microbial types, Form IC abundance was far higher than the other two at all elevations.

Pearson correlation analysis showed that Form IC gene abundance was positively correlated with elevation, soil water content, and NH -N content, and negatively correlated with soil temperature and pH. Form IA/B abundance was not significantly correlated with any measured environmental factors. Form ID abundance was negatively correlated with elevation and positively correlated with soil temperature.

Figure 1 Changes in the abundance of Form IA/B with altitude

Figure 2 Changes in the abundance of Form IC with altitude

Figure 3 Changes in the abundance of Form ID with altitude

Table 2 Pearson correlations between *cbbL* gene abundance and environmental factors

Environmental factors	Form IC	Form ID	Form IA/B
Altitude	0.484**	-0.064	0.341
Soil water content (SWC)	0.327	-0.275	0.133
Soil temperature	-0.316	0.053	-0.336
pH	-0.027	0.050	-0.129
Total organic carbon	-0.371	0.308	-0.289
NH -N	0.312	-0.175	0.120
NO -N	-0.529*	0.157	-0.370

*P $<$ 0.05, **P $<$ 0.01

2.2 Changes in *cbbL* Gene Diversity Indices with Elevation and Season

Shannon diversity indices for Form IC genes increased significantly with elevation in all months, peaking at 4800 m then decreasing slightly. Community richness showed a similar trend, increasing significantly with elevation and reaching maximum at 4800 m. Soil temperature and water content were relatively low at this elevation, and soils were still in the freeze-thaw period in May, which may explain why May showed the smallest changes in diversity and richness indices compared to other months.

Figure 4 Changes in the Shannon diversity of Form IC with altitude

Figure 5 Changes in the richness of Form IC with altitude

2.3 Changes in Carbon-Fixing Microbial Community Structure with Elevation and Season

Form IC soil carbon-fixing microbial community structure changed significantly with elevation but showed minimal seasonal variation. Communities at 4400 m and 4650 m clustered together, while those at 4800 m and 5200 m formed a separate group. Redundancy analysis (RDA) showed that the first two axes explained 30.36% of community structure variation, with RDA1 alone explaining 23.65% of the variation. Soil water content, organic matter content, and soil temperature were the main drivers of community structure changes along the elevation gradient. Season explained only 6.71% of the variation, indicating a weaker but still significant seasonal effect.

Figure 6 Redundancy analysis of T-RFLP of Form IC genes

2.4 Community Composition and Phylogenetic Analysis

Clone library construction and *cbbL* gene sequencing of July soils at 4800 m yielded 120 OTUs. Form IC carbon-fixing microbes belonged to Actinobacteria and Proteobacteria. Actinobacteria included *Pseudonocardia* and *Nocardia*, while Proteobacteria included -proteobacteria and -proteobacteria such as *Bradyrhizobium*, *Mesorhizobium*, *Rhizobium*, *Rubrivivax*, and *Variovorax*. Proteobacteria accounted for the highest proportion in the clone library (48.1%–61.5%), with -proteobacteria comprising 38.4% and -proteobacteria 13.5%. The proportion of Proteobacteria was slightly higher in the growing season (July, September) than in the non-growing season (May), while Actinobacteria showed the opposite pattern, indicating seasonal changes in community composition.

Figure 7 Neighbor-joining phylogenetic tree of representative Form IC *cbbL* gene sequences

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3 Discussion and Conclusion

Elevation gradients integrate multiple environmental factors, causing changes in soil microbial community composition and diversity. This study found that as elevation increased, meadow soil temperature and pH gradually decreased, while soil water content and NH -N content increased. Among the three carbon-fixing microbial types, Form IC showed the highest *cbbL* gene abundance, which increased with elevation and was positively correlated with soil water content and NH -N, but negatively correlated with soil temperature and pH. The abundant nutrients in high-elevation soils stimulated carbon-fixing microbial growth, while adaptation to low temperature may be a key survival strategy for these microbes in Tibetan Plateau meadow soils.

Seasonal comparisons revealed that *cbbL* gene abundance showed greater variation with elevation during the growing season (July, September) than in the

non-growing season (May). In May, soils at all elevations were still frozen or in freeze-thaw transition, and soil microbes had not yet become active, resulting in similar abundances across elevations. This indicates that elevation effects on soil microbial communities vary seasonally.

Both elevation-induced changes in soil physicochemical factors and seasonality affected carbon-fixing microbial structure and diversity. Elevation and soil water content were the key drivers of community structure changes, while season had a weaker effect. Soil organic carbon and pH have been shown to significantly affect carbon-fixing microbial communities in paddy soils, and this study demonstrates similar patterns in alpine meadows.

Clone library and sequencing results showed that Proteobacteria and Actinobacteria were the dominant phyla for Form IC carbon-fixing microbes, including rhizobia such as *Bradyrhizobium*, *Mesorhizobium*, and *Rhizobium*. Proteobacteria can tolerate various environmental stresses and show good tolerance to low pH in acidic soils. This study reveals that carbon-fixing microbial abundance, community structure, and diversity in alpine meadow soils are primarily affected by elevation, with pH and soil water content being important influencing factors, while seasonal effects are relatively minor.

These findings provide theoretical support for understanding the functional role of soil microorganisms in carbon cycling and assessing carbon storage in alpine grassland soils on the Tibetan Plateau.

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Note: Figure translations are in progress. See original paper for figures.