

Linking historical vegetation to bacterial succession under the contrasting climates of the Tibetan Plateau

Haijun Yuan^{a,b,c}, Fanfan Meng^{c,d}, Masanobu Yamamoto^e, Xingqi Liu^f, Hailiang Dong^{g,h},
Ji Shenⁱ, Huaqun Yin^{a,b,*}, Jianjun Wang^{c,d,*}

^a School of Minerals Processing and Bioengineering, Central South University, Changsha 410083, China

^b Key Laboratory of Biometallurgy of Ministry of Education, Central South University, Changsha 410083, China

^c State Key Laboratory of Lake Science and Environment, Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences, Nanjing 210008, China

^d University of Chinese Academy of Sciences, Beijing 100049, China

^e Faculty of Environmental Earth Science, Hokkaido University, Kita-10, Nishi-5, Kita-ku, Sapporo 060-0810, Japan

^f College of Environmental Resources & Tourism, Capital Normal University, Beijing 100048, China

^g State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences, Beijing 100083, China

^h Department of Geology and Environmental Earth Science, Miami University, Oxford, OH 45056, United States

ⁱ School of Geography and Ocean Science, Nanjing University, Nanjing 210023, China

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ABSTRACT

Understanding the relationship between historical vegetation and bacteria is critical for disentangling spatio-temporal variations in microbial communities. However, the utility of historical vegetation as indicated by the reconstruction proxies like n-alkanes to explain microbial succession has been understudied, especially regarding aquatic microbes living under contrasting climates. Here, we studied bacterial and n-alkane succession in sediment cores from Kusai Lake and Lugu Lake under contrasting climates, that is, the drier and colder climates and the warmer and wetter conditions, respectively, and further explored how bacterial communities are affected by historical vegetation. In both lakes, the Shannon diversity of bacteria and n-alkanes consistently and significantly ($P < 0.05$) decreased towards deep-depth sediments, and their compositional dissimilarity Bray-Curtis increased with depth changes, with slopes of 0.00048 and 0.00027 in Kusai and Lugu lakes, respectively. Furthermore, there was strong synchrony between bacteria and historical vegetation, which was underpinned by similar ecological processes such as environmental selection (e.g., climatic perturbations). Compared to Lugu Lake, however, both the Shannon diversity and compositions of bacteria or n-alkanes changed faster in Kusai Lake, which was influenced by abiotic factors such as the sediment Na and loss-on-ignition. Except for abiotic variables, we found that bacterial diversity and composition were also affected by n-alkane attributes such as the C_{27}/C_{31} , carbon preference index, Shannon diversity and composition in both lakes. In particular, n-alkane attributes generally exerted stronger effects on bacterial characteristics than abiotic variables. For example, n-alkane attributes showed strong direct effects on bacterial community composition, with path coefficients of 0.485 and 0.976 ($P < 0.001$) in Kusai and Lugu lakes, respectively, while abiotic variables had no direct effect. Thus, our findings provide new evidence that historical vegetation could substantially explain variations in bacterial communities across temporal scales.

1. Introduction

Microbial communities play pivotal roles in driving aquatic (Treva-
than-Tackett et al., 2019; Wang et al., 2016) and terrestrial (Delgado-
Baquerizo et al., 2016) ecosystem functions and services. Understanding

and characterizing the complex patterns of microbial diversity and
community composition and identifying the relative importance of
abiotic and biotic factors that affect them are essential to better under-
stand microbial ecology (de Vries et al., 2012). It has long been recog-
nized that microbial communities can be regulated by abiotic properties,

* Corresponding authors at: State Key Laboratory of Lake Science and Environment, Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences, Nanjing 210008, China (J. Wang). School of Minerals Processing and Bioengineering, Central South University, Changsha 410083, China (H. Yin)

E-mail addresses: yinhuaqun_cs@sina.com (H. Yin), jjwang@niglas.ac.cn (J. Wang).

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such as the climate (Gaston, 2000), organic matter content (Hondt et al., 2009) and sediment salinity (Yang et al., 2016), pH (Xiong et al., 2012) and depth (Böer et al., 2009). Plant attributes can also explain variations in microbial communities (de Vries et al., 2012). For instance, plant richness (Lamb et al., 2011), evenness (Sun et al., 2019), cover (Delgado-Baquerizo et al., 2018) and biomass (Hiiesalu et al., 2014) have great effects on the microbial diversity and community composition in terrestrial ecosystems. More generally, soil multifunctionality can be affected by plant diversity and climate change (Valencia et al., 2018), microbial communities, including fungi, bacteria, and protists, are therefore well predicted by plant attributes (Leff et al., 2018).

While numerous studies support the above spatial relationships between plants and microbes, far less is known about the effects of plant attributes on the succession of sediment microbial communities at temporal scales. As an archive of lake ecosystem history, the sediment records the provenance, depositional processes and historical changes (Matys Grygar et al., 2016) and provides time-series information on the trajectories of n-alkane abundances (Zhang et al., 2020). For example, the vertical distribution of n-alkanes in lake sediments can effectively indicate distinct ages and origins (Bliedtner et al., 2020). As reported in numerous literatures regarding age-depth model in lake ecosystem, the relationships between sediment age and depth in Kusai (Liu et al., 2014; Wu et al., 2018) and Lugu lakes (Wang et al., 2014; Zhang et al., 2015) were well examined, which is widely based on ^{210}Pb and ^{137}Cs -based age or AMS- ^{14}C dating. Generally, the deeper the sediment, the older the sediment age. Accordingly, the historical vegetation in sediments can effectively reflect the temporal variation of vegetation, which provides a temporal scale for sediment depth (Blaauw et al., 2018). Currently, using n-alkane-based proxies has been found to be an effective approach to reconstructing historical vegetation or paleoclimates, including parameters such as the carbon preference index, P_{aq} and C_{27}/C_{31} ratio (Wang et al., 2019). Under the reconstruction of sediment and lake level, a broad synchrony is shown among the fluctuations in vegetation and climate change (Neumann et al., 2010). Notably, the legacy effects mediated by plants or soil are crucial for shaping community assembly and biodiversity, and they provide a source of variation that influences the microbes (Wurst and Ohgushi, 2015). For example, the community compositions of fungi and prokaryotes were previously reported to be greatly affected by the drought legacy effects in terrestrial ecosystems (Meisner et al., 2018). Based on the synchronous relationship above, and the influence of the vegetation types on microbial communities (Chu et al., 2011), the historical vegetation is expected to explain the succession of microbial communities at temporal and spatial scales.

Here, we collected sediment cores from two plateau lakes, Kusai Lake and Lugu Lake, which have contrasting climates, that is, the drier and colder climates and the warmer and wetter conditions, respectively. We examined the depth-related patterns in bacterial Shannon diversity and community dissimilarity in both lakes, and we further studied how bacterial succession was affected by historical vegetation as reconstructed using n-alkane-based proxies. Based on the relationships between historical vegetation and bacteria, we proposed the following hypotheses: (1) the succession of bacterial communities in drier and colder regions is faster than that in warmer and wetter regions, (2) the bacterial diversity and community composition are jointly affected by contemporary environments and historical vegetation, and (3) historical vegetation can explain the succession of bacterial communities even after accounting for abiotic variables.

2. Materials and methods

2.1. Sediment sampling and site characteristics

We studied the two plateau lakes Kusai Lake (35°30'–35°50'N, 92°30'–93°15'E) and Lugu Lake (27°41'–27°45'N, 100°45'–100°50'E), which are located in the northern (Hoh Xil region) and the southeastern (Yunnan Province) regions of the Qinghai-Tibetan Plateau, respectively.

These two lakes have either drier and colder, or warmer and wetter climates, respectively. In Kusai Lake region, dust storms is the most severe natural disaster interfering with agriculture and stock grazing in dust source regions (Fang et al., 1997), and affected by the temperature changes in the northern Qinghai-Tibetan Plateau (Liu et al., 2014). Although the coverage of natural grasslands shows a profound impact on dust outbreaks, with high frequency of dust storms, there are scattered vegetation and low abundance in the Hoh Xil region (Fang et al., 1997). Conversely, under the influence of the southwest monsoon, Lugu Lake region is one of the lakes least affected by human disturbance in China, with abundant rainfall, high plant diversity and vegetation cover of about 45% (Lee and Zhao, 2008). Based on the contrasting climates, the vegetation in Kusai Lake region is dominated by *Chenopodiaceae* and *Artemisia* (Liu et al., 2009), while Lugu Lake region is primarily the conifers *Pinus yunnanensis* var. *faranch* and *Pinus tabuliformis* (Wang et al., 2012). In Lugu Lake region, there are also other abundant terrestrial vegetation such as *abies*, *larix*, *quercus* and *picea* (Zhang et al., 2015) and aquatic vegetation like *Ottelia acuminata* var. *crispa*, *Myriophyllum spicatum*, *Ceratophyllum demersum*, *Najas major* and *Potamogeton pectinatus* (Guo et al., 2013). Kusai Lake is a saline lake with surface and catchment areas of 254.4 and 3,700 km², respectively, and its maximum water depth is approximately 50 m (Wu et al., 2018). The mean annual evaporation capacity of this lake is much greater than the mean annual precipitation of the Hoh Xil region, resulting in a salinity of 28.5 g/L for Kusai Lake (Liu et al., 2009). Additionally, the melting snow and ice from the Mt. Daxuefeng flows into Kusai Lake via Kusai River, which can greatly influence the daily temperatures of the lake water. Collectively, the Kusai Lake region shows a strong continental climate, with a large annual temperature difference and extremely low precipitation (Wu et al., 2018). Conversely, as a plateau freshwater lake, Lugu Lake has a surface area of ~50.5 km², an elevation of 2,685 m and a maximum water depth of 93.5 m (Wang et al., 2012). Lugu Lake is a semiclosed deep-water lake with a horseshoe shape that is primarily fed from ephemeral streams and precipitation. The climate of Lugu Lake is moderate, with distinct dry and wet seasons, with a mean annual precipitation of 1,000 mm and a mean air temperature of 12.8 °C (Wang et al., 2012). The pH value of water is 7.7 ~ 8.6 in Lugu Lake, while approximately 8.3 in Kusai Lake, which shows a small difference between the two lakes.

Using UWITEC coring equipment and gravity corers, we obtained two long cores of 750 and 1,180 cm in length from water depths of 22 m and 69.3 m in Kusai Lake and Lugu Lake, respectively. The sampling dates for the two cores were in September of 2010 and 2008, respectively. The detailed procedures are described in previous studies (Wu et al., 2018; Wang et al., 2012). The two cores were transferred to laboratory at -18 °C and then dissected into 1-cm-long sediment samples, which were stored at -20 °C. We then selected 29 and 20 samples from Kusai and Lugu Lakes, respectively, from approximately equal depth intervals. These samples were dried using a vacuum freeze dryer and stored in a -20 °C refrigerator for the following biotic and abiotic analyses.

2.2. Measuring the sediment properties

To measure the sediment properties, we obtained the water content, porosity, loss-on-ignition (LOI) and the contents of 20 elements (that is, P, Al, Ba, Be, Ca, Co, Cr, Cu, Fe, Li, K, Mg, Mn, Na, Ni, Pb, Sr, Ti, V, and Zn). The water content was measured by oven drying and pycnometer methods (Wang et al., 2007). The porosity, which describes the void or empty spaces in the sediment samples, was determined by referring to previous literature (Zhao et al., 2019). The LOI was measured to estimate the sediment organic matter by following the method described in Heiri et al. (Heiri et al., 2001). After 1.0 g of frozen-dried sediments were digested using the aqua regia digestion (USEPA 3050) (USEPA, 1996), the contents of the 20 elements were determined by inductively coupled plasma mass spectrometer (ICP-MS). We selected 18 element contents,

except for Na and Mg, to perform a principal component analysis (PCA), and we then used the first two components of the PCA (i.e., PC1.Ele and PC2.Ele) as additional abiotic variables (Wang et al., 2012).

2.3. n-Alkane attributes and historical vegetation reconstruction

For the extraction and fractionation of n-alkanes, we followed the method described in previous literature (Yamamoto et al., 2008; Yamamoto and Polyak, 2009), and then determined the contents of n-alkanes. In brief, after the freeze-dried samples were ground, the n-alkane contents were determined using a Hewlett Packard 5973 GC-mass selective detector (Waldbronn, Germany), and the authentic n-alkane standards (C₁₀₋₄₀) were measured. Based on the mass spectra of the target compounds, the individual n-alkanes were identified by their retention times in comparison with the authentic standards. According to the internal standards, the contents of individual n-alkanes were quantified.

The historical vegetation was reconstructed using n-alkane attributes because different types of plants contain leaf wax n-alkanes with differing carbon chain lengths (Nichols et al., 2006). Specifically, the n-alkanes differ compositionally according to their various sources (Meyers, 2003). Generally, short-chain n-alkanes (C_{14-C20}) primarily come from bacteria and algae (Han and Calvin, 1969), mid-chain n-alkanes (C_{21-C25}) are the dominant component of submerged and floating plants (Ficken et al., 2000), and long-chain n-alkanes (C_{26-C35}) are primarily derived from the leaf epicuticular waxes of higher plants (Eglinton and Hamilton, 1967).

Similar to the above 18 elements, the n-alkanes were also ordinated by PCA, and then the first two components of the PCA (i.e., PC1.Alk and PC2.Alk) were used as additional n-alkane parameters. We further obtained other n-alkane-based proxies, such as the total normal alkanes (TNA), C₂₇/C₃₁, carbon preference index (CPI) and the “P-aqueous” ratio (P_{aq}), which are usually applied to reconstruct the paleovegetation and paleoclimate (Wang et al., 2019). For example, the TNA was used to estimate or predict the variations in historical vegetation (He et al., 2020) and other organisms in sediments. The C₂₇/C₃₁ was applied to infer the vegetation (tree/grass) changes (Ling et al., 2017), because n-alkanes from grasses and woods are preferentially dominated by C₃₁ and C₂₇ (Cranwell, 1973; Cranwell et al., 1987), respectively. The CPI index can effectively reflect paleoclimate changes, and it usually increases in colder climates and declines in warmer ones (Cranwell et al., 1987; Xie et al., 2004). Given the degree of odd-over-even predominance (Naafs et al., 2019) and a large amount of C₂₇, C₂₉ and C₃₁ (Cranwell et al., 1987), the CPI value of terrestrial higher plants

is usually > 5. Importantly, the CPI index and the C₂₇/C₃₁ ratio can also be calculated to explore the vegetative evolution (Brincat et al., 2000). Based on the calculated formula of Cranwell (Cranwell et al., 1987), the CPI values were calculated using modified equation (Naafs et al., 2019) as follows:

$$\text{CPI} = \frac{1}{2} \left(\frac{\text{C}_{25} + \text{C}_{27} + \text{C}_{29} + \text{C}_{31} + \text{C}_{33}}{\text{C}_{24} + \text{C}_{26} + \text{C}_{28} + \text{C}_{30} + \text{C}_{32}} + \frac{\text{C}_{25} + \text{C}_{27} + \text{C}_{29} + \text{C}_{31} + \text{C}_{33}}{\text{C}_{26} + \text{C}_{28} + \text{C}_{30} + \text{C}_{32} + \text{C}_{34}} \right) \quad (1)$$

The P_{aq} was calculated using formula (Ficken et al., 2000)

$$P_{\text{aq}} = \frac{\text{C}_{23} + \text{C}_{25}}{\text{C}_{23} + \text{C}_{25} + \text{C}_{29} + \text{C}_{31}} \quad (2)$$

The P_{aq} can quantify the abundance of aquatic macrophytes when compared to terrestrial plants (Ficken et al., 2000). The P_{aq} can also determine the source of organic matter: when P_{aq} < 0.1, the sources are mostly from terrestrial higher plants; when 0.1 < P_{aq} < 0.4, primarily from emergent aquatic plants; and when 0.4 < P_{aq} < 1, predominately from submerged plants and floating plants (Ficken et al., 2000). In addition, the higher P_{aq} values can indicate lake expansion and higher moisture levels (Ficken et al., 2000; Sun et al., 2013).

2.4. Microbial communities

The details from the DNA sequencing and analyses are described in previous studies (Wang et al., 2013). In brief, we extracted genomic DNA from 0.45 g of frozen sediments using the phenol chloroform method. The DNA quality was assessed by using a NanoDrop One/OneC UV-Vis spectrophotometer (Thermo Fisher Scientific, USA). We amplified the bacterial 16S rRNA genes using a 27F primer with the 454 Life Sciences ‘A’ sequencing adapter, and a 519R primer with an 8-bp barcode sequence and the 454 Life Sciences ‘B’ sequencing adapter (Hamady et al., 2008; Wang et al., 2012). The barcoded amplicons were sequenced using a FLX 454 pyrosequencer (Roche, Branford, CT, USA). The sequencing data were analyzed using QIIME pipeline (v1.9.0) (Caporaso et al., 2010). The bacterial communities were rarefied at 1,300 sequences for the following analyses.

2.5. Statistical analyses

The datasets from Kusai and Lugu lakes were independently analyzed for n-alkanes or bacteria. First, we performed PCA to explore the environmental differences between the two lakes. Ellipses were added at a confidence interval of 68% for the two lakes to show how their environmental conditions were separated. In addition, we applied nonmetric multidimensional scale analysis (NMDS) to depict the community compositions of n-alkanes and bacteria in both lakes, and we tested their significances between the two lakes using a permutational multivariate analysis of variance (Anderson, 2001).

Second, we used the Shannon diversity to estimate the alpha diversity (Reese and Dunn, 2018) for the bacteria and n-alkanes, and we explored the relationships between the sediment depth and bacterial or n-alkane Shannon diversity using linear and quadratic models. The better model was selected according to the lower value of Akaike’s information criterion (AIC) (Yamaoka et al., 1978).

Third, we applied the Bray-Curtis dissimilarity to examine the beta diversity (Tuomisto and Ruokolainen, 2006) of the bacteria and n-alkanes, and then we studied the sediment-depth patterns in the beta diversity for the two taxonomic groups within the distance-decay framework (Wang et al., 2013). The significance of the relationships was explored by Mantel test (9,999 permutations) (Mantel, 1969), and the trend was visualized with a linear regression.

Fourth, the associations between the bacteria and n-alkanes were explored regarding the alpha or beta diversity for each lake. For the alpha diversity, the relationships were modeled with linear and quadratic models, and the better model was selected according to the lower value of AIC value. For the beta diversity, we performed a Mantel test (9,999 permutations) (Mantel, 1969) to examine their correlations and used linear regressions to visualize the trends.

Fifth, we examined the explanatory variables on the bacterial Shannon diversity and community composition using a Pearson correlation and Mantel test (Mantel, 1969), respectively. Furthermore, we applied the random forest model (Feld et al., 2016) to determine the most important predictors of bacterial Shannon diversity. The explanatory variables included the abiotic variables and n-alkane attributes. We used Pearson’s rank correlation coefficients to evaluate the statistical dependence among these explanatory variables, and excluded the variables with high correlation coefficients (Pearson $r > 0.7$). Cross-validation was then used to obtain an optimal number of 2,000 trees (Elith et al., 2008). The importance of a predictor factor was determined by its frequency of selection (for splitting), weighted by a measure of improvement in the model given each split and averaged across all the trees (the contributions were scaled to sum to 100) (Wu et al., 2020). A canonical correspondence analysis (CCA) (Økland and Eilertsen, 1994) was performed to infer the underlying relationships between the bacterial community composition and the important explanatory factors, such as the n-alkane attributes and abiotic variables. All the explanatory variables were transformed by Z-score for better use of the analysis with

linear methods before CCA analysis.

We further partitioned the variations in the bacterial Shannon diversity into the three explanatory matrices, namely, the n-alkane attributes, abiotic variables and sediment depth, using a linear model (Anderson and Cribble, 1998; Borcard et al., 1992). We then performed a distance-based redundancy analysis to test the potential explanatory variables for the community composition with a Hellinger-transformation (Legendre and Gallagher, 2001). All the significant abiotic factors and n-alkane attributes were selected by forward selection against the bacterial biological characteristics data, with 9,999 permutations.

Finally, structural equation modeling (SEM) (Grace et al., 2012) was performed to estimate the direct and indirect effects of historical vegetation and abiotic variables on the bacterial Shannon diversity and community composition. The first axis of the NMDS was used to indicate the bacterial community composition. We first constructed a priori structural equation model as shown in Fig. S6 to hypothesize the underlying structure of causal pathways. To support the hypothesized paths or not, the bivariate relationships between all the variables transformed by Z-score were evaluated with regression equations before SEM analysis (Li et al., 2018). The significance of these models was tested using ANOVA. The best predictors are shown in Table S2. Similar to previous studies (Hu et al., 2020), the composite variables were used to explain the collective effects of the historical vegetation, abiotic variables and depth. Based on the full model of composite variables, AIC_c and overall model fit statistics were used to examine all the alternative models (Grace et al., 2010). The detailed information on all the alternative models is described in Table S3. The best model was selected based on the lowest value of AIC_c, a nonsignificant χ^2 test ($P > 0.05$) and low standardized root mean squared residual (SRMR < 0.05). Our SEMs were performed using the R package lavaan V.0.5.23 (Rosseel and lavaan, 2012), and the other statistical analyses were implemented with the packages vegan V2.5–5 (Oksanen et al., 2013) and randomForestSRC V2.9.0 (Ishwaran and Kogalur, 2017).

3. Results

Generally, there were clear differences between Kusai and Lugu Lakes regarding the abiotic variables, n-alkane attributes and bacterial communities (Table 1; Figs. S2, S3). For the abiotic variables, the average of sediment Na was 16.44%, ranging from 8.75 to 34.37% in Kusai Lake, while it was 5.51%, ranging from 2.70% to 7.56%, in Lugu lake (Table 1). The average of LOI was 6.13%, ranging from 3.17 to 9.48%, in Kusai Lake, whereas it was 12.40%, ranging from 6.29 to 21.66%, in Lugu Lake (Table 1), showing that the organic matter content

was significantly ($P < 0.05$) higher in the freshwater sediments of Lugu Lake than in the saline sediments of Kusai Lake. The saline sediments were dominated by the sediment Na and Mg, while the freshwater sediments were largely related to the LOI and the first component of the PCA for the 18 elements (Fig. S2a).

For the bacterial communities, there was higher Shannon diversity in Lugu Lake than in Kusai Lake, with the mean values of 6.60 and 5.93, respectively. The sediment-depth patterns of the bacterial Shannon diversity decreased faster in Kusai Lake than in Lugu Lake, with the slopes of -0.0032 and -0.0013 , respectively (Fig. 1a). The Bray-Curtis dissimilarity of bacterial community increased with the sediment depth changes, with slopes of 0.00048 and 0.00027 in Kusai and Lugu Lakes, respectively (Fig. 1b). In addition, at the phylum level, the relative abundance of *Firmicutes*, *OP8* and *OP9* increased towards deep sediments in Kusai Lake while *Proteobacteria*, *Chloroflexi* and *Cyanobacteria* declined (Fig. S3a). In Lugu Lake, *Chloroflexi* was the most dominant bacterial phylum, whereas the relative abundance of *Elusimicrobia* increased and that of *Proteobacteria* declined towards the deep sediments (Fig. S3b).

For the n-alkane attributes, the average of P_{aq} was 0.11, ranging from 0.03 to 0.34, in Kusai Lake, while it was 0.54, ranging from 0.35 to 0.76 (Table 1). These results suggested that the historical vegetations in Kusai Lake primarily came from emergent aquatic plants, while Lugu Lake was dominated by submerged plants and floating plants. Moreover, the average of C_{27}/C_{31} was 0.32, ranging from 0.23 to 0.52, in Kusai Lake, but it was 1.49, ranging from 0.89 to 2.23 in Lugu Lake (Table 1), indicating that herbaceous plants historically predominated in the former, and woody plants were clearly dominant in the latter. Interestingly, n-alkanes had similar trends to bacteria regarding depth-related patterns in alpha and beta diversity (Fig. 1). In Kusai and Lugu lakes, for n-alkanes, Shannon diversity decreased along the depths, with slopes of -0.0066 and -0.0015 , respectively (Fig. 1c), their compositional dissimilarity increased with the depth changes, with slopes of 0.00038 and 0.00023, respectively (Fig. 1d).

In both lakes, bacteria showed high correlation with n-alkanes regarding diversity and composition (Figs. 2 and S4). For the Shannon diversity, bacteria were significantly positively correlated with n-alkanes (Kusai: $r = 0.79$, $P < 0.001$; Lugu: $r = 0.69$, $P < 0.001$) (Fig. 2a; Fig. S4a, S4b) and negatively correlated with the second component of PCA of n-alkanes (Kusai: $r = -0.78$, $P < 0.001$; Lugu: $r = -0.72$, $P < 0.001$) (Fig. S4a, S4b). For the community composition, bacteria had significant positive correlations with n-alkanes regarding community dissimilarity (Kusai: Mantel $r = 0.55$, $P < 0.001$; Lugu: Mantel $r = 0.26$, $P < 0.05$) (Fig. 2b). Additionally, the bacterial community dissimilarity was significantly positively correlated with the second component of

Table 1
The list of predictors used in this study.

Predictors	Variables	Acronym	Value range				Units
			Kusai Lake		Lugu Lake		
			Range	Mean	Range	Mean	
Abiotic variables	Depth	Depth	1–748	–	1–1171	–	cm
	Water content	WC	35–93	52	54–89	68.7	%
	Porosity	Por	54.98–91.71	69.45	65.49–83.26	73.40	%
	Sediment Mg	Mg	11.88–56.72	30.25	6.92–16.20	12.47	mg/g
	Sediment Na	Na	8.75–34.37	16.44	2.70–7.56	5.41	mg/g
	The first component of PCA* of other 18 elements	PC1.Ele	–0.97 to –0.47	–0.61	0.18–1.71	0.88	
	The second component of PCA of other 18 elements	PC2.Ele	–0.87 to +1.51	–0.17	–1.30 to +2.14	+0.24	
n-Alkane attributes	Loss-On-Ignition	LOI	3.17–9.48	6.13	6.29–21.66	12.40	%
	Total normal alkane	TNA	3.77–12.77	7.81	3.87–34.25	16.05	μg/g
	nC_{27}/nC_{31}	C27.C31	0.23–0.52	0.32	0.89–2.23	1.49	
	Carbon preference index	CPI	3.85–10.98	7.49	4.98–7.32	5.90	
	P_{aq}	Paq	0.03–0.34	0.11	0.35–0.76	0.54	
	The first component of PCA of n-alkanes	PC1.Alk	–0.03 to +0.71	0.42	–2.87 to +0.61	–0.60	
	The second component of PCA of n-alkanes	PC2.Alk	–1.68 to +1.08	0.08	–3.84 to +0.93	–0.12	
	Shannon diversity of n-alkanes	Shannon.Alk	4.64–11.85	7.11	9.04–15.95	11.42	

* PCA: principal component analysis.

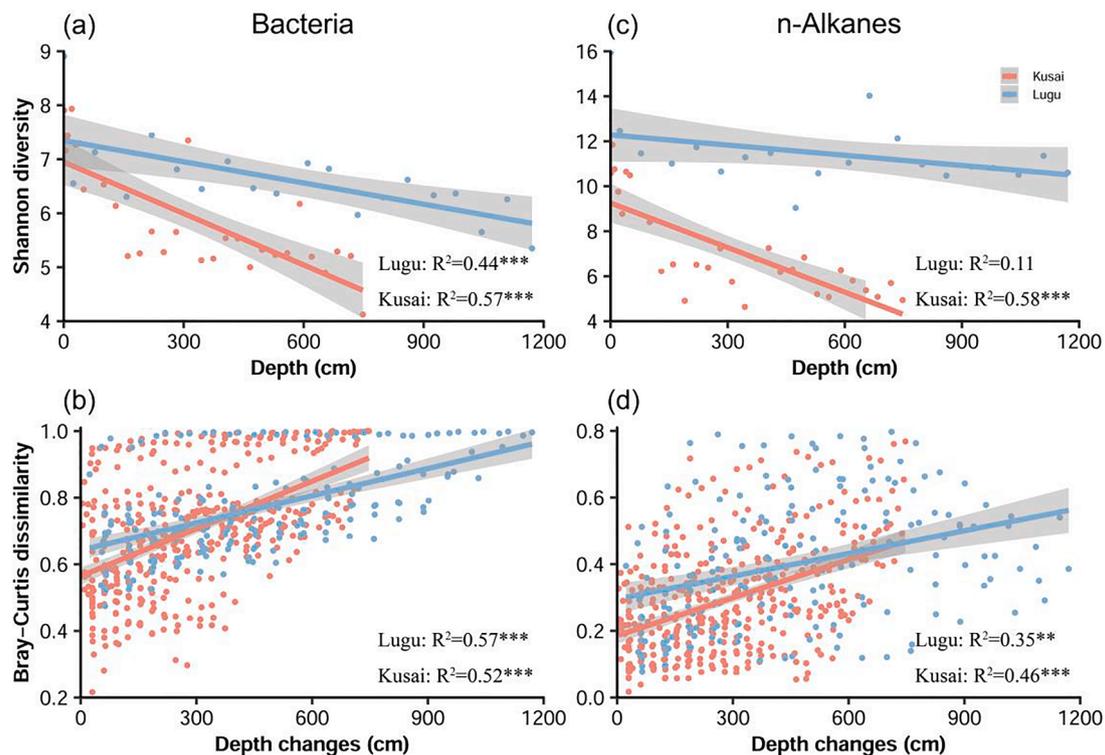


Fig. 1. Sediment-depth biodiversity patterns for bacteria and n-alkanes. We considered the two facets of composition characteristics of bacteria (a, b) and n-alkanes (c, d), that is Shannon diversity (a, c) and Bray-Curtis dissimilarity (b, d). The relationships between depth and Shannon diversity were modeled with linear and quadratic models, and the best model was selected according to the lowest value of Akaike's information criterion. The correlations between community dissimilarities and the changes in sediment depth were explored by Mantel test (9,999 permutations) and their relationships were visualized by a linear model. * $P \leq 0.05$; ** $P < 0.01$; *** $P < 0.001$.

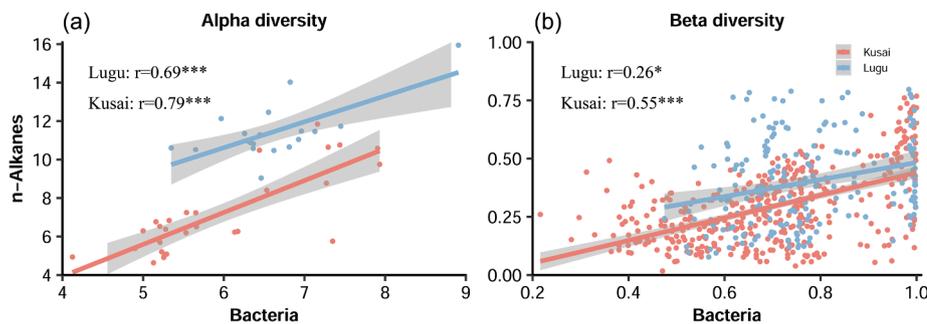


Fig. 2. Relationship between bacteria and n-alkanes regarding their alpha (a) and beta diversity (b). The relationships for Shannon diversity (a) between bacteria and n-alkanes were modeled with linear and quadratic models, and the best model was selected according to the lowest value of Akaike's information criterion. The correlations for Bray-Curtis dissimilarity (b) between bacteria and n-alkanes were explored by Mantel test (9,999 permutations) and their relationships were visualized by a linear model. * $P \leq 0.05$; ** $P < 0.01$; *** $P < 0.001$.

PCA (Kusai: Mantel $r = 0.55$, $P = 0.001$; Lugu: Mantel $r = 0.56$, $P = 0.017$) and the Shannon diversity (Kusai: Mantel $r = 0.48$, $P = 0.001$; Lugu: Mantel $r = 0.41$, $P = 0.028$) of n-alkanes, and the sediment Na (Kusai: Mantel $r = 0.62$, $P = 0.001$; Lugu: Mantel $r = 0.46$, $P = 0.001$) (Fig. S4c, S4d).

For the bacterial Shannon diversity, random forest analysis showed that the relative contributions of the second component of PCA and the Shannon diversity of n-alkanes and CPI in Kusai Lake were 15.09%, 12.96% and 7.98%, respectively (Fig. 3a). Similarly, in Lugu Lake, the relative contributions of the C_{27}/C_{31} , Shannon diversity and the second PCA component of n-alkanes were 12.93%, 11.23% and 9.62%, respectively (Fig. 3b). In addition, the CCA showed that the n-alkane attributes had important effects on the bacterial communities (Fig. 3c, 3d), such as the second PCA component and the Shannon diversity of n-alkanes, C_{27}/C_{31} and TNA, although the abiotic variables such as porosity and water content were also pivotal.

In the variation partitioning analyses, abiotic variables only explained 3.0% and 2.0% of the total variation in the Shannon diversity

in Kusai and Lugu lakes, respectively, while the pure effects of the n-alkane attributes unexpectedly accounted for 8.0% and 11.0% (Fig. S5a, S5b). For the bacterial community composition, the n-alkane attributes accounted for 3.0% and 2.0% of the total variations in Kusai and Lugu Lakes, respectively, while the pure effects of the abiotic variables explained 10.0% and 11.0% (Fig. S5c, S5d). Additionally, the joint effects of the abiotic variables, depth and n-alkane attributes explained 53.0% and 25.0% of the total variation in the bacterial Shannon diversity in Kusai and Lugu Lakes, respectively (Fig. S5a, S5b). For the community composition, the joint effects accounted for 8.0% and 6.0% of the total variations for the two lakes, respectively (Fig. S5c, S5d).

Finally, the SEM indicated that 83.5% and 82.5% of variations in the bacterial Shannon diversity were jointly explained by the depth, n-alkane attributes and abiotic variables for the Kusai and Lugu lakes, respectively (Fig. 4a, 4b). The path coefficients for the direct effects of n-alkane attributes and abiotic variables were 0.497 ($P < 0.001$) and 0.471 ($P < 0.001$) in Kusai Lake (Fig. 4a). In Lugu Lake, the path coefficient of n-alkane attributes was 0.742 ($P < 0.001$), and there was no direct effect

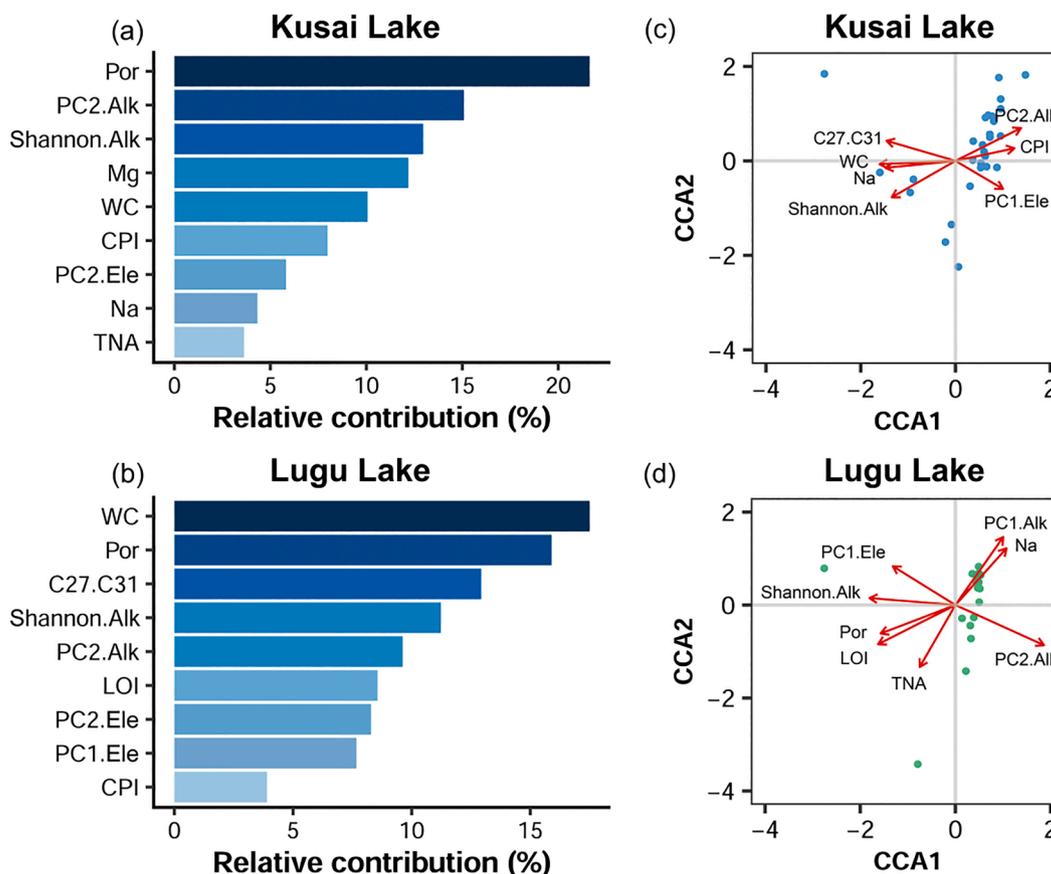


Fig. 3. The abiotic and biotic factors explaining bacterial diversity and community composition. Random forest analysis was performed to show the relative contributions of important predictors in explaining bacterial Shannon diversity for Kusai (a) and Lugu (b) lakes. Ordination plots of canonical correspondence analysis showed the relationships between bacterial communities and the explanatory factors of n-alkane attributes and abiotic variables for Kusai (c) and Lugu (d) lakes. n-Alkane attributes: Paq, C27.C31, Shannon.Alk, PC1.Alk, PC2.Alk, TNA and CPI; Abiotic variables: WC, Por, PC1.Ele, PC2.Ele, LOI, Mg and Na. More details of explanatory factors are described in Table S4. * $P \leq 0.05$; ** $P < 0.01$; *** $P < 0.001$.

for the abiotic

variables (Fig. 4b). For the bacterial community composition, 81.7% and 95.3% of the total variations were explained for the Kusai and Lugu Lakes, respectively (Fig. 4c, 4d), and the path coefficients of n-alkane attributes were 0.485 ($P < 0.001$) and 0.976 ($P < 0.001$), respectively. There was no direct effect between the abiotic variables and bacterial community composition in both lakes (Fig. 4c, 4d).

4. Discussion

Determining the temporal succession patterns and underlying drivers of community composition is a major aim of microbial ecology (Thompson et al., 2017). In addition to the environmental variables, plants are reported to play a crucial role in explaining the spatial variations in microbial diversity and community composition. To the best of our knowledge, this is the first study to link historical vegetation to the succession patterns of bacterial communities. We studied the sediment depth patterns of bacteria and n-alkanes in Kusai and Lugu Lakes under contrasting climates, and we further explored the relative importance of n-alkane attributes and abiotic variables. We found that (1) there were predictable sediment-depth patterns for the Shannon diversity or beta diversity of bacteria and n-alkanes in both lakes, whereas these patterns changed faster in Kusai Lake. (2) There was significant congruence between bacteria and n-alkanes regarding Shannon diversity or beta diversity. (3) n-Alkane attributes had greater effects on the bacterial diversity and community composition in comparison to contemporary environments.

4.1. Vertical trends in bacterial and n-alkane diversity and community composition

For the alpha diversity, our findings revealed the decreasing patterns along sediment depth for bacteria (Fig. 1a) and n-alkanes (Fig. 1c) in the two lakes, the former of which was concordant with previous studies on lakes (Koizumi et al., 2003) and seas (Walsh et al., 2016a, 2016b). For example, the monotonously decreasing pattern in the bacterial Shannon diversity in sediments was observed in the northern Lake Biwa based on the fingerprinting analysis of reversely-transcribed 16S rRNA (Koizumi et al., 2003). Similarly, there were strong vertical gradients in the bacterial Shannon diversity, Chao1, and Simpson indices, which gradually decreased along the depth in the abyssal sediments of the northwest Pacific Ocean (Hiraoka et al., 2020). In our two lakes, the depth-related patterns in Shannon diversity were similar between bacteria and n-alkanes, which reflects the consequence of sediment characteristic changes or paleoclimatic variations along depth gradients. Compared to the bacteria, the Shannon diversity of n-alkanes is less studied along sediment depths, and their decreasing pattern towards deep sediments probably results from biodegradation (Ye et al., 2017) or mineralization (del Giorgio and Duarte, 2002).

Similar to the alpha diversity, we found that the community dissimilarity of bacteria (Fig. 1b) and n-alkanes (Fig. 1d) increased with the sediment depth changes in both lakes. This congruence indicated a parallel pattern between the bacteria and historical vegetation, which could be underpinned by similar ecological processes such as environmental selection (e.g., climatic perturbations) (Shade et al., 2018). In general, the distribution of vegetation around the world is primarily

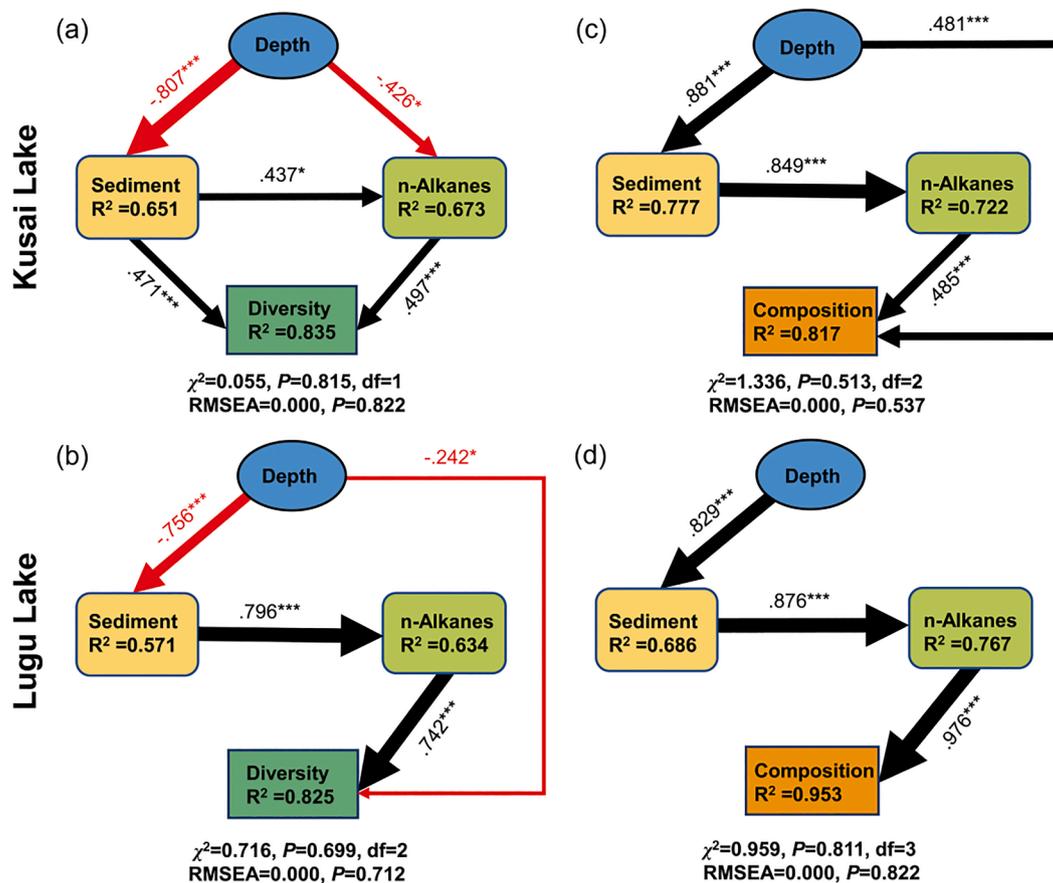


Fig. 4. The effects of depth, abiotic variables, and n-alkane attributes on bacterial diversity (a, b) and community composition (c, d). Diversity and community composition were quantified with Shannon diversity and the first axis of the nonmetric multidimensional scaling, respectively. In each structural equation models, we considered the composite variables of sediment abiotic variables (that is, Sediment) and n-alkane attributes (that is, n-Alkanes), and the observable variable of sediment depth (that is, Depth). Black and red arrows denote positive and negative effects, respectively. The width of the lines and numbers adjacent to arrows represent the standardized path coefficients. R^2 indicates the proportion of explained variance. RMSEA: root-mean-square error of approximation. Significance levels of each predictor: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. More details of the model fit are described in Tables S2 and S3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

determined by climatic conditions, such as frost and drought (Tinner and Lotter, 2001). Given that monsoon areas with warmer and wetter climates can facilitate the expansion of vegetation, and the eastern Tibetan Plateau is strongly affected by the Asian summer monsoon (Zhao et al., 2020), the Lugu Lake region shows higher plant species richness, while the Kusai Lake region has less vegetation. In addition, based on the age-depth models of Kusai (Wu et al., 2018) and Lugu lakes (Wang et al., 2014), there were temporal variations in the bacterial communities in the sediments of the two lakes, which might be related to the terrestrial inputs of historical vegetation. Based on the environmental selection, there were unique bacterial phyla in the sediments between both lakes. For example, *Chloroflexi* was the most abundant in Lugu Lake (Fig. S3), which might partly result from the high concentration of sediment organic matters. *Bacteroidetes* and *Firmicutes* were the unique or primary saprophytic microbes in Kusai Lake but were minor or absent from Lugu Lake (Fig. S3), which might cause the organic matter degradation of historical vegetation in Kusai Lake. It should be noted that organic matter is among the most important factors driving sediment microbial diversity and composition, such as in mangroves (Chen et al., 2016).

As expected, there was a significant positive correlation between bacteria and n-alkanes regarding the alpha (Fig. 2a) and beta diversity (Fig. 2b), which further consolidated the synchrony between historical vegetation and bacteria at temporal and spatial scales. The depth-related patterns of historical vegetation substantially reveal a temporal variation and provide a temporal scale along the sediment depth.

Additionally, there are age-depth models reflecting such relations between sediment age and depth in Kusai (Wu et al., 2018) and Lugu lakes (Wang et al., 2014), which is largely underpinned by previous literatures regarding ^{210}Pb and ^{137}Cs -based age or AMS- ^{14}C dating. Accordingly, the succession patterns of bacterial communities are disentangled in temporal scale. Generally, cross-taxon congruence can happen once when different organisms spatially covary spatially regarding either diversity or community composition (Rooney and Azeria, 2015). For bacterial alpha diversity, this type of congruent relationship is also observed among macro- and microorganisms. For example, seagrass vegetation shows a positive correlation with bacterial abundance in the meadow sediments of the Baltic Sea, and it provides organic matter and habitat to facilitate the growth of microbes (Jankowska et al., 2015). For the bacterial beta diversity, there is a similar correlation between plant and soil microbes (i.e., bacteria, archaea and fungi) across temperate grasslands globally, suggesting that the patterns in the microbial community composition can be predicted by plant diversity (Prober et al., 2015). Intriguingly, there is a significant parallel pattern between microbial and macroinvertebrate communities regarding beta diversity, but a contrasting pattern in the alpha diversity of the marine lakes of Palau (Rapacciuolo et al., 2019), presumably due to a shared spatial-temporal and environmental context.

Notably, the depth-related patterns in Shannon diversity or community compositions of bacteria and n-alkanes changed faster in Kusai Lake than in Lugu Lake (Fig. 1), which might be due to the overall contrasting climates and the local environmental drivers. For the

bacterial Shannon diversity, climate is a major factor driving biogeographic patterns (Gaston, 2000). For example, temperature and precipitation can effectively drive the elevational patterns of stream microbes including bacteria, archaea and fungi at continental scales (Picazo et al., 2020). Especially in the Kusai Lake region, the temperature variations in the northern Qinghai-Tibetan Plateau can directly affect their less or more dusty future, and dust can largely drive the climate changes via altering atmospheric circulation, global biogeochemical and hydrologic cycling (Liu et al., 2014). Under the strong influence of climate fluctuations (Zhao et al., 2020), there is historically low diversity in vegetation in Kusai Lake, whereby their terrestrial inputs only provide less organic matter as a nutrient for the growth of microbes. Furthermore, salinity also responds sensitively to climate change (Perri et al., 2020), and it rapidly drives global patterns of bacterial diversity, which has frequently been reported in previous studies (Lozupone and Knight, 2007). For bacterial community composition, the variations should be caused by the environmental differences between the two lakes, such as organic matter content (Hondt et al., 2009), salinity (Yang et al., 2016) and climate (Gaston, 2000). For example, there was a significant positive correlation between salinity and microbial community composition in surface sediments of the Tibetan lakes (Yang et al., 2016), namely, the sediments with similar salinity have parallel patterns of total microbial beta diversity. Furthermore, compared to Lugu Lake, Kusai Lake shows stronger climatic variations at a higher elevation and a harsh environment such as lower nutrients, higher salinity, and dryer and colder conditions, which results in the rapid succession of bacteria towards deep-depth sediments.

4.2. Abiotic and biotic variables in explaining sediment-depth patterns

We found that the abiotic variables showed significant correlations (Fig. S4) and strong relative contributions (Fig. 3) to the bacterial diversity and community composition in both lakes. For the bacterial Shannon diversity, our SEMs indicated that abiotic variables such as porosity and sediment Mg had a high direct effect in Kusai Lake, but a strong indirect effect in Lugu Lake (Fig. 4a, b). This indirect effect indicates that abiotic factors could govern the pattern of bacterial diversity by directly influencing the n-alkanes. Similarly, given the significant correlations between the salinity and the n-alkane-based proxies such as the CPI, the distribution of n-alkanes is strongly constrained by salinity, presumably in relation to microbial degradation (Wang et al., 2019). For the bacterial community composition, our findings revealed that the abiotic variables, such as porosity, sediment Na and the composition of the 18 elements, substantially showed the pure effects by accounting for 10.0% and 11.0% of total variations in the Kusai and Lugu Lakes, respectively (Fig. S5c, 5d; Table S1). Consistent with this trend, increasing salinity can improve the salt tolerance of bacteria, and further facilitates the shifts in the bacterial community composition, such as in Lake O'Connor of western Australia (Rath et al., 2019). Additionally, our results also showed that abiotic factors could explain a greater proportion of the microbial succession than the sediment depth, which is in line with Wang et al (Wang et al., 2008).

Consistent with our hypothesis, historical vegetation also had non-negligible effects on the biological characteristics of bacterial communities, showing that n-alkane attributes such as Shannon diversity and composition, C_{27}/C_{31} and CPI were relatively important for the bacterial diversity or community composition (Fig. 3). For example, our results revealed that the n-alkane attributes of TNA or Shannon diversity explained a large proportion of the bacterial Shannon diversity in both lakes (Fig. S5a, S5b; Table S1). Similarly, the abundance and composition of organic matters are reported to have critical roles in shaping the bacterial community structure in the sediments of the eastern China Marginal Seas (Qiao et al., 2018). Moreover, our SEMs showed that the bacterial diversity was strongly affected by the CPI index in both lakes (Fig. 4a, 4b; Table S2), which records the changes in colder or warmer climates of past and usually increases in colder climates and declines in

warmer ones (Cranwell et al., 1987; Xie et al., 2004).

For the bacterial community composition, our SEMs showed that n-alkane attributes such as the TNA, C_{27}/C_{31} and Shannon diversity had strong effects in both lakes, while the abiotic variables had no direct effect (Fig. 4 c, 4d; Table S2). The types of historical vegetation indicated by the C_{27}/C_{31} ratio thus presumably affected the bacterial community composition, and showed the contrasting differences between the Kusai and Lugu lakes, which were historically dominant by herbaceous and woody plants, respectively. The modern vegetation in Kusai Lake is dominated by *Chenopodiaceae* and *Artemisia* (Liu et al., 2009), while the vegetation around Lugu Lake is primarily the *conifers Pinus yunnanensis* var. *faranch* and *Pinus tabuliformis* (Wang et al., 2012). For modern vegetation, it has a substantial correlation with the microbial biogeography patterns across global (Opik et al., 2006), regional (Griffiths et al., 2011) and local (Mitchell et al., 2010) scales. For instance, plant phylogeny and plant species identities can strongly affect the succession of fungal communities in the natural mountains of eastern China (Yang et al., 2019). In particular, the patterns of bacterial and fungal community compositions can be well predicted by the plant diversity in temperate grasslands worldwide (Prober et al., 2015). Additionally, our SEMs also showed that the n-alkane index CPI and P_{aq} had strong effects on both the bacterial diversity and community composition in Lugu Lake (Fig. 4b, 4d; Table S2). Because these n-alkane indexes could effectively indicate the paleoclimate and the vegetation type of aquatic plants (Wang et al., 2019), it further indicates that the types of historical vegetation can predict the succession of bacterial communities.

Compared to abiotic factors, we found that the historical vegetation unexpectedly showed stronger effects on the bacterial diversity and community composition in both lakes. For the bacterial Shannon diversity, our results showed that n-alkane attributes explained 8.0% and 11.0% of the total variation in the Kusai and Lugu Lakes, respectively (Fig. S5a, S5b), which are much higher than those of the abiotic variables. These findings are inconsistent with the previous literature, in which abiotic variables such as pH, rather than biotic attributes, mostly affect the sediment bacterial alpha diversity of the Tibetan lakes (Xiong et al., 2012). For the bacterial community composition, the n-alkane attributes showed strong significant direct effects in both lakes (Fig. 4c, 4d), while the abiotic factors had no direct effect. These results, together with those reported in the previous literature (Walker et al., 2010), collectively indicate that bacterial succession was strongly constrained by historical vegetation across terrestrial to aquatic ecosystems, which is especially interesting because this finding is rarely reported regarding the effects of historical vegetation.

In summary, the importance of historical vegetation on bacterial succession could be understood from the following two perspectives. First, there is a synchrony between historical vegetation and bacteria regarding the Shannon diversity and composition in both lakes. This significant congruence was previously reported for terrestrial ecosystems, showing that the patterns of soil microbial diversity and community composition can be well predicted using the plant alpha (Lamb et al., 2011) and beta (Prober et al., 2015) diversity, respectively. Based on the influence of the monsoon climate (Zhao et al., 2020), there are contrasting vegetation types (Chu et al., 2011) and compositions (Mitchell et al., 2010) in historical vegetation between the two lakes, which are the major drivers underlying the biogeographic patterns in the bacterial communities. In brief, this synchronous relationship not only exhibited a far greater range of spatial-temporal variation, but it also provided insight into the similar processes (i.e., environmental selection by factors such as climatic perturbations (Ranta et al., 1995) that govern the parallel patterns in diversity and composition from microbes to macrobes (Shade et al., 2018).

Second, the historical vegetation can provide organic matter, including n-alkanes, as nutrients and energy for microbial communities. Most terrestrial organic inputs to the lakes primarily originate from plants (Sollins et al., 2007) and are composed of materials such as woody debris, grass residues, leaf litter and dead roots (Wardle et al., 2004).

Given that distinct organic matter is generated from different types of historical vegetation (Nichols et al., 2006), the abundance and composition of the organic matter may be the key drivers shaping the bacterial community structure (Qiao et al., 2018), and may also greatly influence to the succession of sediment bacterial communities.

5. Conclusion

Overall, our findings provide new perspectives for explaining the succession of bacteria in lacustrine environments by showing the strong effect of historical vegetation. We found that there were similar depth-related patterns between bacteria and n-alkanes regarding alpha or beta diversity in both lakes, which implied a long-term synchrony among bacteria and historical vegetation. Notably, this significant cross-taxonomic congruence might be primarily underpinned by similar processes such as environmental selection (e.g., climate perturbations). Compared to Lugu Lake, however, there were faster changes in the bacteria and n-alkanes in terms of the alpha and beta diversity in Kusai Lake, which might be driven by the high salinity and low nutrients in response to the extreme climate. Additionally, our findings also revealed that the bacterial communities were jointly affected by the historical vegetation, abiotic factors and depth. Although the historical vegetation and bacteria were constrained by the environments, the n-alkane attributes exerted greater effects on the bacterial diversity and community composition than the abiotic variables. Thus, our findings provide new evidence that historical vegetation could substantially explain the succession of bacterial communities in lake sediments under contrasting climates. Future studies are encouraged to confirm our findings by comparing the relationships between historical vegetation and other microbes in aquatic or terrestrial ecosystems under contrasting climatic conditions.

CRedit authorship contribution statement

Haijun Yuan: : Formal analysis, Visualization, Writing - original draft. **Fanfan Meng:** Software, Visualization. **Masanobu Yamamoto:** Validation, Methodology, Data curation. **Xingqi Liu:** Data curation, Investigation. **Hailiang Dong:** Writing - review & editing. **Ji Shen:** Funding acquisition, Supervision. **Huaqun Yin:** Project administration, Writing - review & editing, Resources. **Jianjun Wang:** Conceptualization, Writing - review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contributions

JW conceived the idea and designed the study. JW, XL, MW, HD conducted field sampling and provided physiochemical and biological data. FM performed bioinformatic analyses. HY analyzed the data and wrote the first version of the manuscript. JW and HY finalized the manuscript. All of the authors assisted in writing the manuscript, discussed the results, and commented on the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2021.107625>.

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