



# Effects of temperature on the composition and diversity of bacterial communities in bamboo soils at different elevations

Yu-Te Lin<sup>1</sup>, Zhongjun Jia<sup>2</sup>, Dongmei Wang<sup>2</sup>, and Chih-Yu Chiu<sup>1</sup>

<sup>1</sup>Biodiversity Research Center, Academia Sinica, Taipei 11529, Taiwan

<sup>2</sup>State Key Laboratory of Soil and Sustainable Agriculture, Institute of Soil Science, Chinese Academy of Sciences, Nanjing 210008, People's Republic of China

Correspondence to: Zhongjun Jia (jia@issas.ac.cn) and Chih-Yu Chiu (bochiu@sinica.edu.tw)

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**Abstract.** Bamboo is an important resource distributed in mountain areas in Asia. Little is known about the impact of temperature changes on bamboo soil bacterial communities. In this study, responses of bacterial communities collected at 600, 1200, and 1800 m to different incubation temperatures (15, 20, and 35 °C) were examined using barcoded pyrosequencing and soil analyses. Soil respiration was greater at higher elevation and incubation temperature. The bacterial diversity decreased after 112 days of incubation at 35 °C. Before incubation, *Acidobacteria* and *Proteobacteria* were the most abundant phyla in all communities. The relative abundance of *Acidobacteria* generally decreased after 112 days of incubation at the three temperatures.  $\alpha$ -*Proteobacteria* showed a similar trend, while  $\gamma$ -*Proteobacteria* increased after incubation, except in samples from 1800 m incubated at 35 °C. Non-metric multi-dimensional scaling analysis revealed structural variability under different incubation times and temperatures. Principal component analysis indicated that the bacterial structure in samples incubated at 35 °C correlated with temperature and soil respiration, while structures in samples incubated at 15 and 20 °C correlated with time. These results suggest that a temperature rise could result in increasing soil respiration and soluble carbon and nitrogen consumption as well as differentially influence bacterial diversity and structure at different elevations.

## 1 Introduction

Temperature is one of the most important factors influencing soil organic matter decomposition and microbial communities. For example, temperature significantly affects the soil microbial phospholipid fatty acid composition associated with straw decomposition at the early stage (Zhou et al., 2016). Bacterial abundance increases in conditions of elevated temperature and CO<sub>2</sub> concentration (Castro et al., 2010). The complex responses of bacterial composition and diversity of bamboo soils across altitudinal gradients have been suggested to result from interactions with multiple factors, including temperature (Lin et al., 2015).

In Taiwan, moso bamboo (*Phyllostachys pubescens*) is an important versatile forest resource that is widely used for food, construction, and as a furniture material. It is distributed from low- to high-mountain regions at approximately 1800 m above sea level (a.s.l.). Management practices for increasing bamboo production, including regular removal of understory vegetation, tillage, and fertilizer application, can increase the soil CO<sub>2</sub> efflux (Liu et al., 2011) and water-soluble organic N concentration (Wu et al., 2010). However, these management practices can lower the microbial functional diversity (Xu et al., 2008). Considering the effects of bamboo plantations on soil properties and microbial communities, it is worth elucidating the changes in bamboo soil bacterial communities under environmental changes.

Our previous study revealed that bamboo invasion could increase bacterial diversity and alter the bacterial structure of adjacent cedar forest soils (Lin et al., 2014). Soil bacterial diversity in bamboo plantations showed a hump-backed trend, with less diversity at low and high elevations, and max-

imum diversity at middle elevations, and community structure formed different clusters at different elevations (Lin et al., 2015). Our parallel study showed that invasion of bamboo into adjacent forest soils increased humification of soil organic matter (SOM) (Wang et al., 2016b). In addition, changes in the SOM pool and the rate of humification with elevation were primarily affected by changes in climatic conditions along the elevation gradient in the bamboo plantations (Wang et al., 2016a). However, it is not known whether bamboo soil bacterial groups respond to temperature changes.

Soil bacterial communities include different phylotypes that likely represent different functional groups, and their relative abundances are affected by carbon (C) availability. For example, some members of *Proteobacteria* are considered copiotrophs, and their relative abundances appear to be higher in C-rich environments. In contrast, oligotrophs (e.g., *Acidobacteria*) can live in stressful environmental conditions (Fierer et al., 2007). However, little is known about how these two groups respond to the environmental temperature changes. Here, we hypothesized that the temperature changes would alter the structure and diversity of soil bacterial communities at different elevations, and that bacterial taxa, including copiotrophic and oligotrophic groups, would have distinct responses to altered nutrient availability caused by temperature changes. To test these hypotheses, soil communities sampled at bamboo plantations at three elevations were incubated at different temperatures and investigated by using the barcoded pyrosequencing technique. The objectives of this study were to elucidate (1) changes in soil organic carbon, nitrogen, and respiration at elevation gradients and at different incubation temperatures, (2) differences in bacterial structure and diversity under different incubation temperatures and periods, and (3) changes in the abundances of different phylogenetic groups at different incubation temperatures.

## 2 Methods

### 2.1 Site description and soil sampling

This study was conducted in Mt. Da'an, a subtropical mountain area in Nantou County, central Taiwan (23°42' N, 120°41' E). The soil samples were collected from moso bamboo plantations at 600, 1200, and 1800 m a.s.l. along a county road. The three sampling sites were all dominated by moso bamboo with few understory plants. Based on weather station records and the temperature–elevation correlation, the annual mean air temperature was estimated as 20.3 °C at 600 m, 17.2 °C at 1200 m, and 14.1 °C at 1800 m with a decrease of 0.52 °C per 100 m elevation gain (Wang et al., 2016a). At each elevation, three 25 m × 25 m plots were established along transect lines in March 2015. Within each plot, three subsamples were collected with a soil auger 8 cm in diameter and 10 cm deep and pooled. Visible detritus, such as

roots and litter, was manually removed prior to passing the soil through a 2 mm sieve. Soil samples collected at each elevation were combined and homogenized for further incubation and analysis. The sieved soils were stored at 4 °C before incubation experiments.

### 2.2 Incubation experiment and soil analysis

Three replicates (25 g each) from each elevation were incubated at 15, 20, or 35 °C for 112 days. The temperatures of 15 and 20 °C were selected based on the mean annual temperature, while 35 °C was selected to simulate the summer condition. During the entire incubation period, the soil moisture was maintained at 60 % of the water-holding capacity. At various incubation times, soil samples were taken from the same container. Soil respiration (CO<sub>2</sub>-C) was measured as described (Huang et al., 2014). Soluble organic carbon (SOC) and nitrogen (SON) were extracted from the soil samples after different incubation periods with 2 M KCl and measured with the Fisons NA1500 elemental analyzer (Thermo-Quest Italia, Milan, Italy) as described (Huang et al., 2014).

### 2.3 Barcoded pyrosequencing of the 16S rRNA genes

Soil community DNA was extracted using the PowerSoil® soil DNA isolation kit (MoBio Industries, Carlsbad, CA, USA) in accordance with the manufacturer's instructions. The V1 to V2 regions of the bacterial 16S rRNA gene were amplified using 27F and 338R primers (Lane, 1991). Polymerase chain reactions (PCR) were performed as described previously (Lin et al., 2015). Secondary PCR (using 3 cycles instead of 20) was carried out to barcode the DNA in each sample. The unique and error-correcting barcodes facilitated sorting of sequences from a single pyrosequencing run (Hamady et al., 2008). The barcoded PCR products were purified on a column filter using a PCR clean-up system (Vio-gene Biotek Corp., New Taipei City, Taiwan). The qualities and concentrations of the purified barcoded PCR products were determined using a NanoDrop spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA). Amplicon pyrosequencing was performed by Mission Biotech (Taipei, Taiwan) using the 454/Roche GS-FLX Titanium instrument (Roche, Branchburg, NJ, USA). All sequences have been submitted to the Short Read Archives under accession number SRS1923345.

### 2.4 Sequence analyses

The pyrosequences were processed through the RDP pyrosequencing pipeline (<http://pyro.cme.msu.edu>; RDP Release 11.5; release date: 30 September 2016). The sequences were assigned to the samples by recognition of the barcode from a tag file, followed by trimming of barcodes, primers, and linkers. The pyrosequences were filtered, and sequences that did not contain Ns, were more than 200 bp in length, and possessed quality scores > 25 were selected for further

analyses. Taxonomic information was analyzed using the naïve Bayesian rRNA classifier in RDP (Wang et al., 2007). The Shannon diversity index was calculated based on complete linkage clustering data for operational taxonomic units (OTUs), with an evolutionary distance of 0.03. The distribution of shared OTUs among the communities was obtained using the Mothur program (Schloss et al., 2009). Non-metric multi-dimensional scaling (NMDS) based on the distribution of shared OTUs was plotted by using the PRIMER V6 software (Clarke and Gorley, 2006). The Mantel tests as implemented in PRIMER V6 software was used to analyze the relationships between bacterial communities, phylogenetic groups and soil properties. Principal component analysis (PCA) to determine the relationship between bacterial community and soil properties was carried out using R v.3.2.1.

### 3 Results

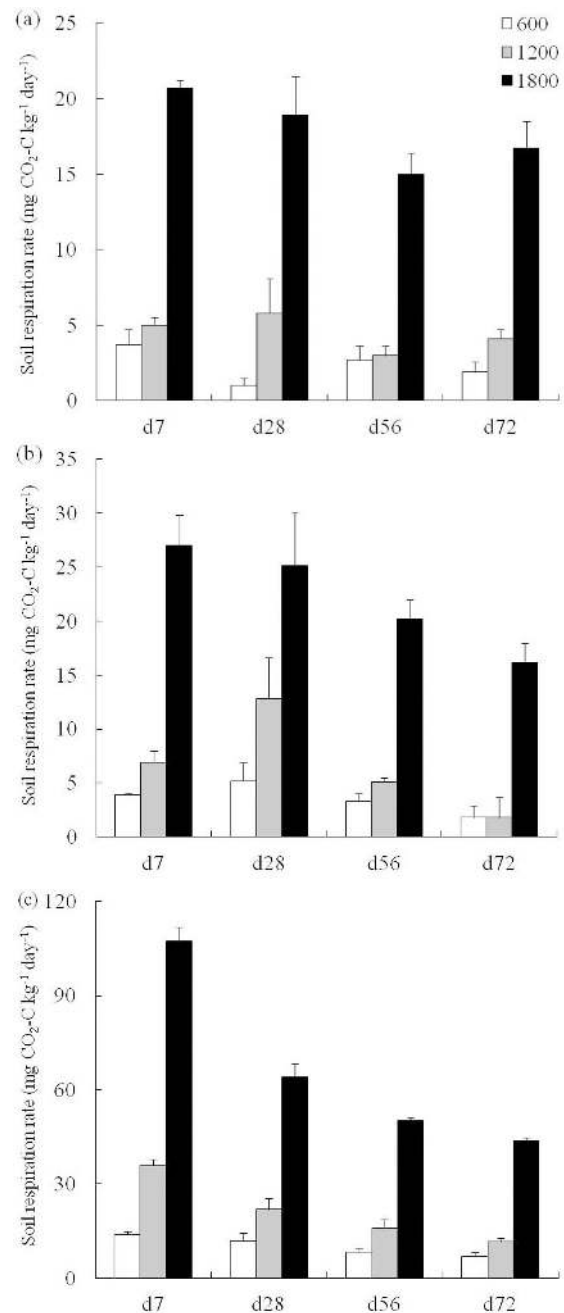
#### 3.1 Soil respiration, SOC, and SON

Data on soil respiration  $\text{CO}_2\text{-C}$  in samples taken from three elevations and incubated at different temperatures are shown in Fig. 1. Under the same temperature, the soil samples collected at higher elevation, especially those from 1800 m, had a significantly higher soil respiration rate than those obtained at lower elevation. The soil respiration rate increased with temperature within each elevation. At  $35^\circ\text{C}$ , the soil respiration rate decreased significantly with incubation time. At 15 and  $20^\circ\text{C}$ , the respiration rates of some soil samples slightly increased in the early incubation period (until day 28, d28) (Fig. 1). Because the respiration rate was stabilized after d72, respiration rate analyses were conducted only up to this time point.

At d0, the SOC and SON contents of the soils increased significantly with elevation (Fig. 2). Compared to d0, the concentration of SOC in the high-elevation soils (1800 m) decreased, while those at 600 and 1200 m increased after 112 days (d112) of incubation at three temperatures. Incubation at higher temperature ( $35^\circ\text{C}$ ) resulted in higher SOC content than that at lower temperatures (15 and  $20^\circ\text{C}$ ). In most samples, SON content increased until d28 of incubation, but was decreased at d112.

#### 3.2 Community diversity at different temperatures

The soil bacterial diversity at three elevations at different incubation temperatures was determined based on an OTU cutoff of  $\leq 0.03$ . Based on the Shannon diversity index, the bacterial diversity of soils incubated at  $35^\circ\text{C}$  decreased after long incubation (d112). Under incubation at 15 or  $20^\circ\text{C}$ , the bacterial diversity slightly increased at d7 and d28, and decreased at d112 (Fig. 3). Analysis of the  $\beta$ -diversity revealed that though incubated with different temperature, the

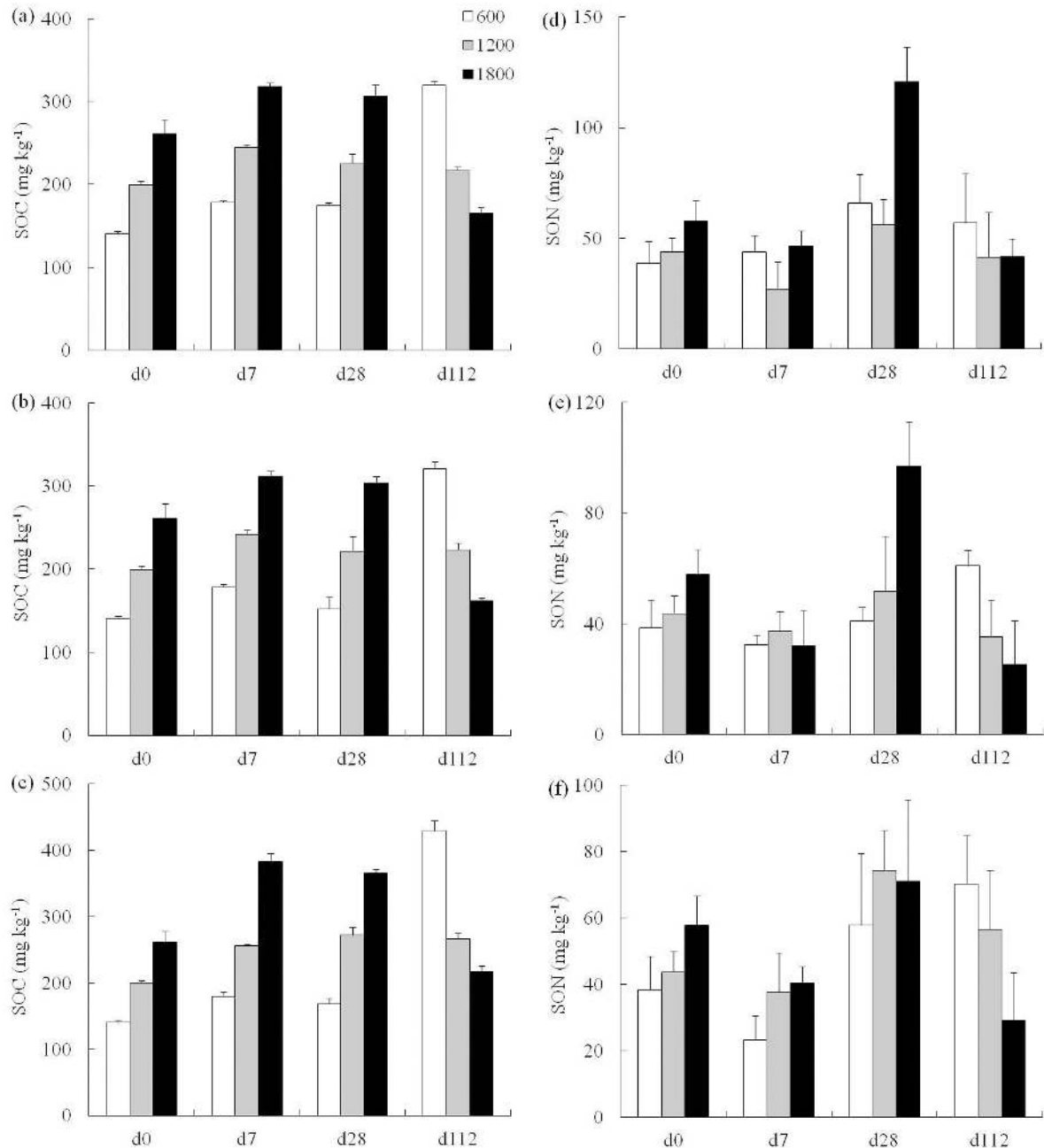


**Figure 1.** Respiration  $\text{CO}_2\text{-C}$  rate in soils sampled at three elevations under incubation at (a)  $15^\circ\text{C}$ , (b)  $20^\circ\text{C}$ , and (c)  $35^\circ\text{C}$ . Error bars represent SD.

communities at the same elevation formed a cluster different from those at other elevations (Supplement Fig. S1).

#### 3.3 Community composition at different incubation temperatures

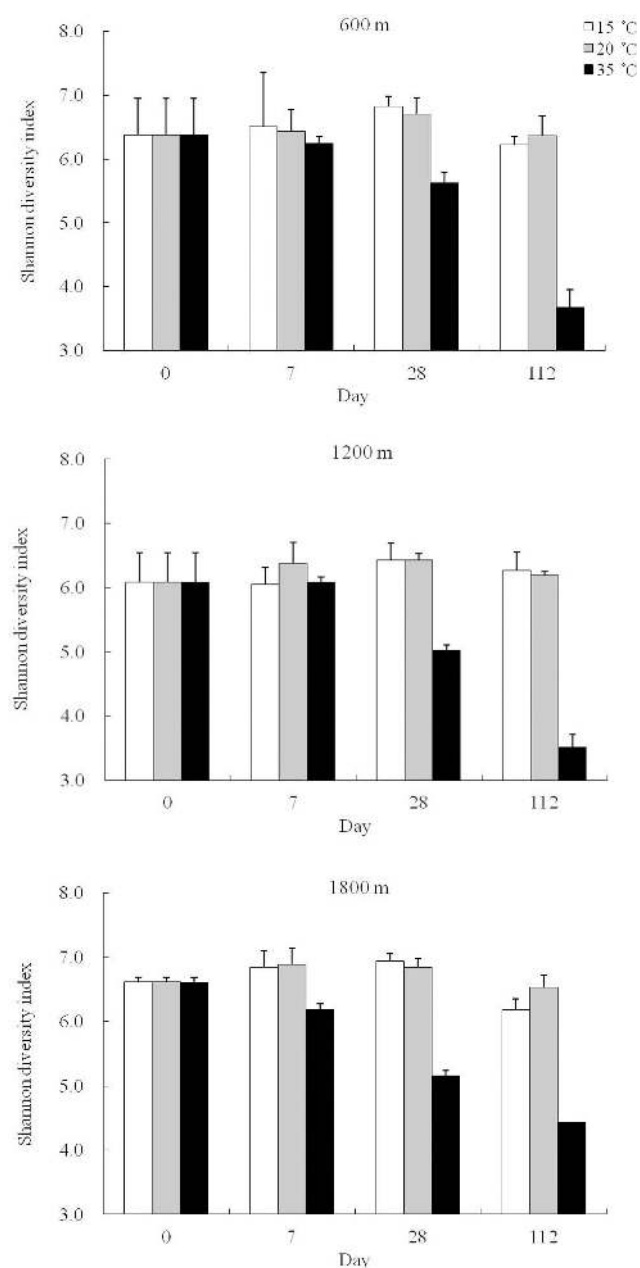
Before incubation, *Acidobacteria* and *Proteobacteria* were the two most abundant phyla in soils from all three eleva-



**Figure 2.** Concentration of (a–c) soluble organic carbon (SOC) and (d–f) nitrogen (SON) in bamboo soils sampled at three elevations and incubated at (a, d) 15 °C, (b, e) 20 °C, and (c, f) 35 °C. Error bars represent standard deviation.

tions, together representing more than 60 % of the soil bacterial communities (Table 1). Within the *Proteobacteria*,  $\alpha$ -*Proteobacteria* were predominant (Table 1). At 1800 m, *Bacteroidetes* accounted for 8 % of the community, while they comprised only 2–4 % of the communities at the two other elevations. The relative abundance of *Actinobacteria* was 4–6 %, and the other phylogenetic groups represented less than 3 % of the communities.

Bacterial groups of the soil communities showed different responses to the incubation temperature. The relative abundance of *Acidobacteria* at 600 and 1200 m gradually decreased over the entire incubation period at all temperatures (Fig. 4a–f). At 1800 m, it increased during the first 7 days of incubation at 35 °C, and decreased thereafter at all temperatures (Fig. 4i). The relative abundance of  $\alpha$ -*Proteobacteria* showed similar trends; it gradually decreased at 600 and 1200 m over the entire incubation period at different tempera-



**Figure 3.** Changes in bacterial diversity of soil community at 600, 1200, and 1800 m incubated at different temperatures.

tures, except at d7 at 600 m, 20 °C, and at d7 at 1200 m, 35 °C (Fig. 4a–f). At 1800 m, the changes in abundance were different. *α-Proteobacteria* were elevated at d7 and d112, but were lower at d28 of incubation at 15 and 20 °C. Their abundance decreased over time under incubation at 35 °C (Fig. 4g–i). With regard to *γ-Proteobacteria*, their relative abundance mostly increased over incubation, except in soils sampled at 1800 m under incubation at 35 °C, in which it was increased at d7 but decreased at d28 and d112 (Fig. 4i). The relative abundance of *Chloroflexi* also increased over incubation, ex-

**Table 1.** Relative abundances (%) of different phylogenetic groups in the bamboo soil bacterial communities at different elevations.

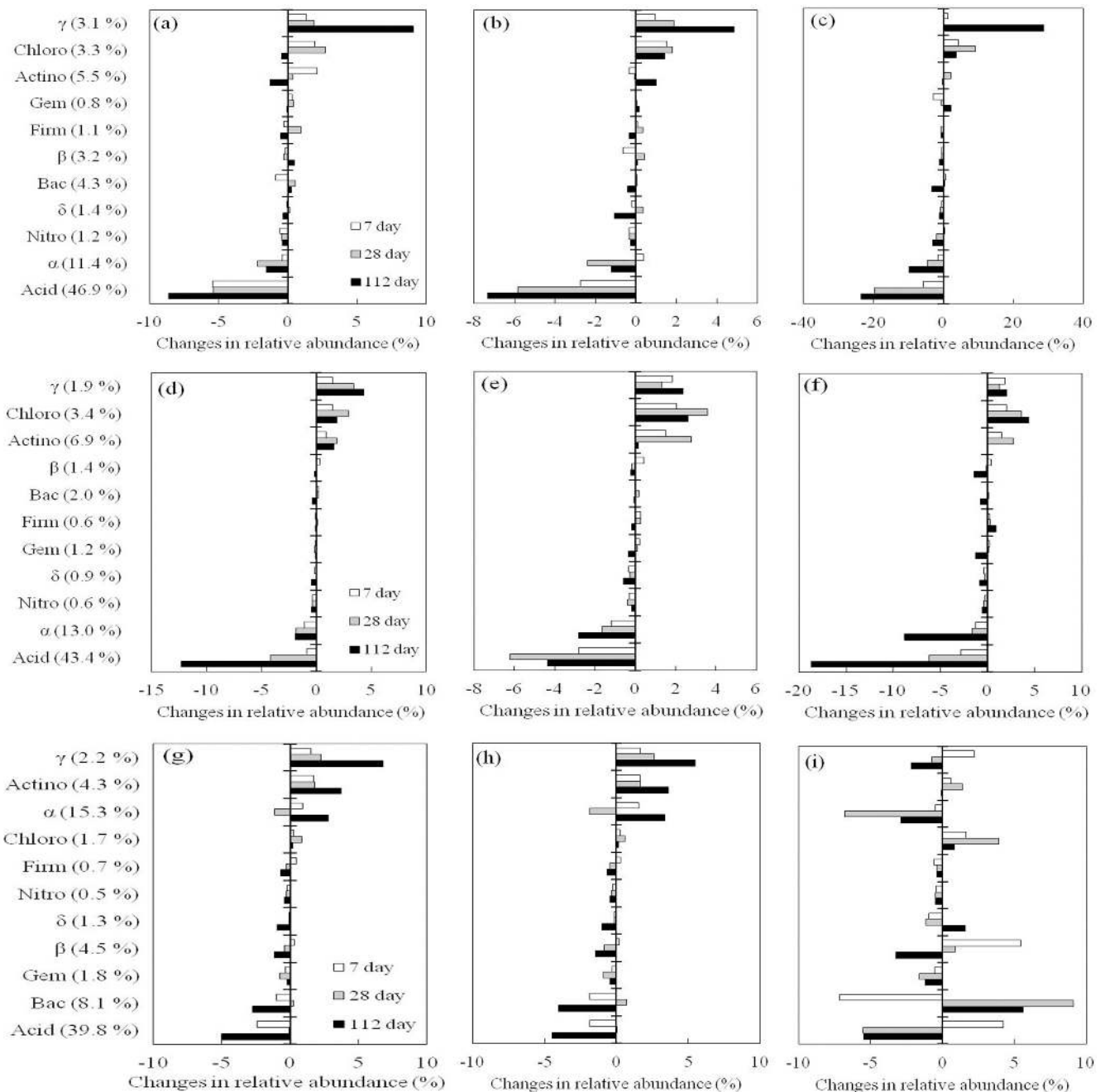
Phylogenetic groups	600 m	1200 m	1800 m
<i>Acidobacteria</i>	46.9	43.6	39.8
<i>Actinobacteria</i>	5.5	6.9	4.3
<i>Bacteroidetes</i>	4.3	2.0	8.1
<i>Chloroflexi</i>	3.3	3.4	1.7
<i>Firmicutes</i>	1.1	0.6	0.7
<i>Gemmatimonadetes</i>	0.8	1.2	1.8
<i>Nitrospirae</i>	1.2	0.6	0.5
<i>Alphaproteobacteria</i>	11.4	13.0	15.3
<i>Betaproteobacteria</i>	3.2	1.4	4.4
<i>Gamma</i> proteobacteria	3.1	1.9	2.2
<i>Deltaproteobacteria</i>	1.4	0.9	1.3
<i>Proteobacteria, others</i>	6.2	6.3	7.1
Others	11.6	18.2	12.8

cept in samples taken at 600 m, incubated at 15 °C, on d112. Some other phyla demonstrated inconsistent changes under increased temperature. The abundances of *Actinobacteria* at 1200 and 1800 m increased at higher temperature (Fig. 4d–i), while it decreased in samples taken at 600 m (Fig. 4a–c). Likewise, *Bacteroidetes* showed inconsistent changes after different incubation times and temperatures (Fig. 4a–i).

The changes in relative abundance of some abundant genera are shown in Fig. 5. The relative abundance of acidobacterial-GP1 generally decreased over the entire incubation period at all temperatures, except at 35 °C (Fig. 5i). The *α*-proteobacterial *Bradyrhizobium* showed similar trends, while its relative abundance at 1800 m increased at all three incubation temperatures (Fig. 5g–i). Within *β-Proteobacteria*, the relative abundance of *Burkholderia* at 1200 m decreased over incubation, except in samples incubated at 15 °C in the first 7 days (Fig. 5d). With regard to *γ-Proteobacteria*, *Dyella* in samples from 1200 m decreased under all three incubation temperatures (Fig. 5d–f), and its abundance increased mostly in communities at 600 m and 1800 m (Fig. 5a–c and g–i). The relative abundance of *Mucilaginibacter* of *Bacteroidetes* at 1800 m increased greatly in samples incubated at 35 °C on d28 and d112 (Fig. 5i).

NMDS analysis based on the distribution of shared OTUs also revealed the variability in bacterial structure under different incubation times and temperatures (Fig. 6). The bacterial community at 1800 m formed a different cluster from those at 600 and 1200 m. Incubation at higher temperature (35 °C) led to a bacterial structure different from those at 15 and 20 °C. Incubation time also changed the bacterial structure. The bacterial structure under long incubation (at d112) was different from those at d7 and d28.

PCA revealed the correlation between bacterial structure and environmental factors. When incubated at 35 °C, bacterial structure correlated with temperature and soil respiration

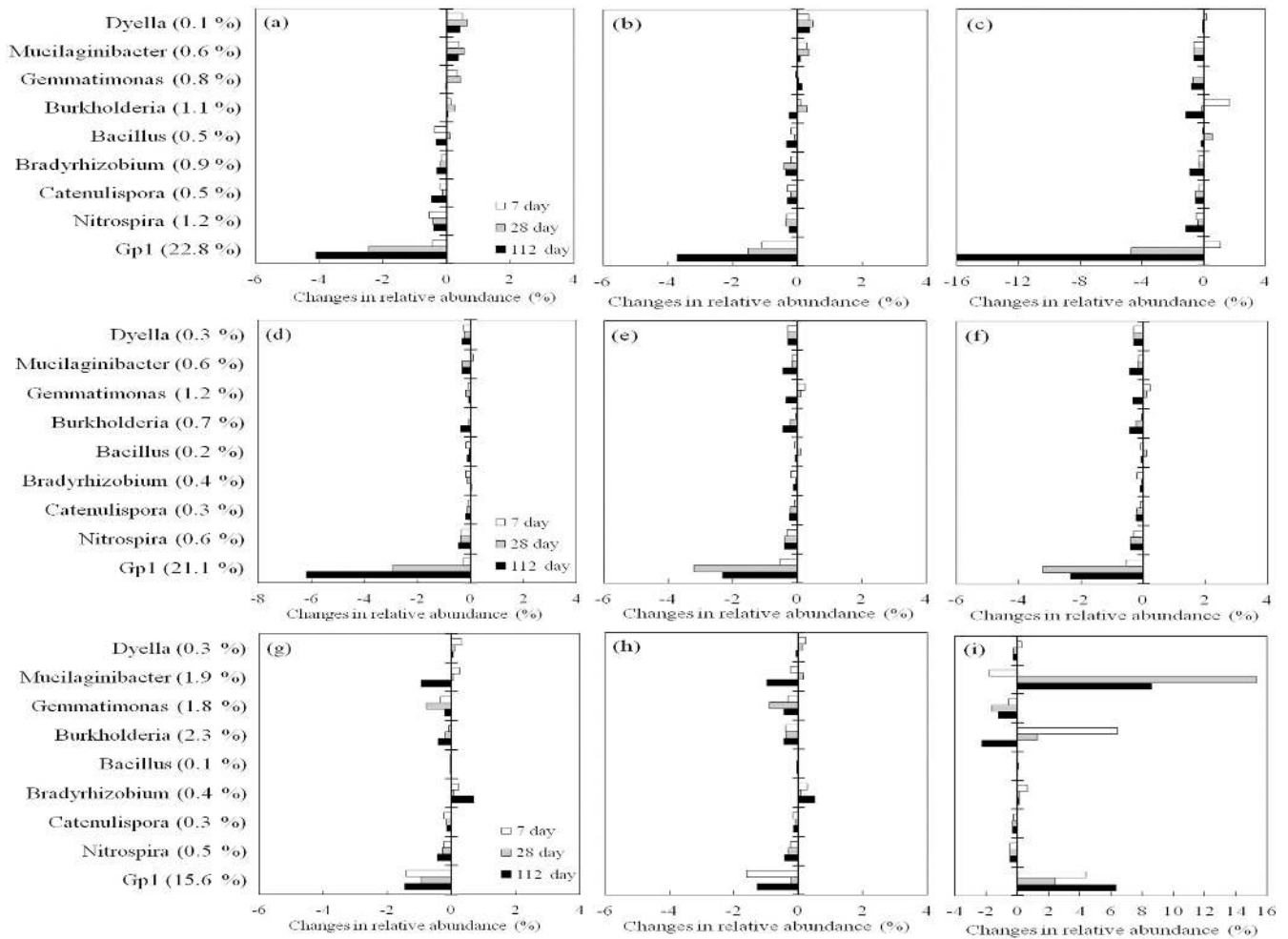


**Figure 4.** Changes in relative abundance of phylogenetic groups of bamboo soil bacterial communities at (a) 600 m, 15 °C; (b) 600 m, 20 °C; (c) 600 m, 35 °C; (d) 1200 m, 15 °C; (e) 1200 m, 20 °C; (f) 1200 m, 35 °C; (g) 1800 m, 15 °C; (h) 1800 m, 20 °C; and (i) 1800 m, 35 °C. Abbreviation: Acid: *Acidobacteria*; Actino: *Actinobacteria*; Bac: *Bacteroidetes*; Chloro: *Chloroflexi*; Firm: *Firmicutes*; Gem: *Gemmatimonadetes*; Nitro: *Nitrospirae*;  $\alpha$ ,  $\beta$ ,  $\gamma$ ,  $\delta$ :  $\alpha$ -,  $\beta$ -,  $\gamma$ -, and  $\delta$ -*Proteobacteria*.

CO<sub>2</sub>-C, while at 15 and 20 °C, bacterial structure correlated with incubation time (Fig. 7).

#### 4 Discussion

The present study revealed that the SOC content was higher at high incubation temperature and decreased with increasing elevation after long incubation. The soil respiration CO<sub>2</sub>-C rate was greater at higher elevation. Similarly, a previous study in tundra soils using different incubation temperatures



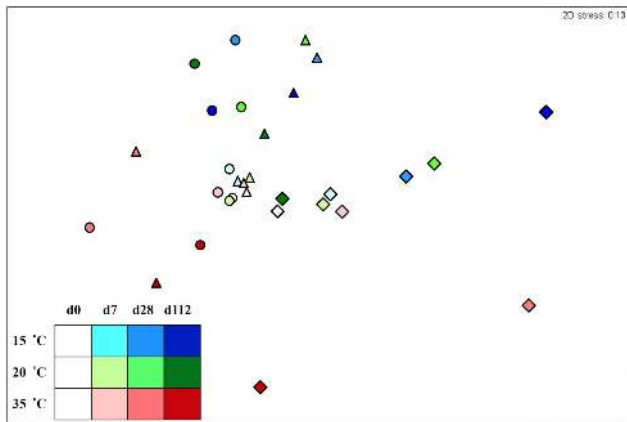
**Figure 5.** Changes in relative abundance of abundant genera of bamboo soil bacterial communities at (a) 600 m, 15 °C; (b) 600 m, 20 °C; (c) 600 m, 35 °C; (d) 1200 m, 15 °C; (e) 1200 m, 20 °C; (f) 1200 m, 35 °C; (g) 1800 m, 15 °C; (h) 1800 m, 20 °C; and (i) 1800 m, 35 °C.

reported higher respiration rate at high temperatures (Stark et al., 2015). Incubation at increasing temperatures enhanced the soil microbial activity and led to an increase in soil respiration in forest mesocosms (Lin et al., 2001). In our study, the respiration rate decreased after long incubation. This could be due to the exhaustion of labile compounds after microbial decomposition (Zhou et al., 2016). The decrease in bacterial diversity at high elevation and high incubation temperature, calculated from abundance data of the phylogenetic groups, could also be the result of nutrient exhaustion after long incubation. In addition, the correlation between soil respiration and bacterial structure in the soil samples under incubation at 35 °C suggests the adaption and high activity of bacterial communities at higher temperature.

In d0 samples, which represent the original composition of the bamboo soils, the bacterial diversity was higher in the 1800 m soils, followed by the 600 and 1200 m soils. Communities with higher diversity are reportedly more resistant to environmental changes (Loreau and de Mazancourt, 2013).

In a study by Ren et al. (2015) in rice paddies, the diverse soil communities were more resistant to elevated CO<sub>2</sub> and temperature than the less diverse foliar bacterial communities. The increasing concentration of recalcitrant C with increasing elevation (Wang et al., 2016a) could be helpful in providing more carbon resources to the community at high elevation. Together, these findings indicate that bamboo soil bacterial communities with higher diversity could be more capable of maintaining soil community and function when exposed to climatic changes and subjected to management at high elevation (1800 m).

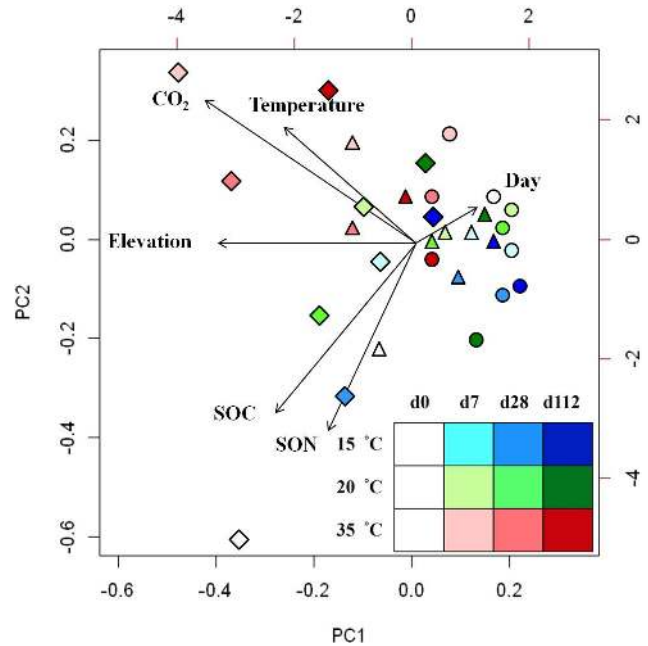
The bacterial community structure varied over different incubation periods and temperatures. Based on the abundance data of phylogenetic groups, the communities at the three elevations formed different clusters as compared to the results of our previous study (Lin et al., 2015). The different soil bacterial structures at different elevations can be explained by differences in soil management. The effects of management practices on soil microbial community can persist over



**Figure 6.** NMDS analysis of bamboo soil bacterial communities sampled at three elevations and incubated at different temperatures. Circles, triangles, and diamonds represent communities at 600, 1200, and 1800 m elevation, respectively. The analysis was based on the distribution of OTUs formed at an evolutionary distance of 0.03.

time (Keiser et al., 2011). Recently, bamboo shoot harvest and timber production has moved from about 600 to 1200 m in the study area. Soils at different elevation have distinct soil SOC and SON contents, which could result in different forces to alter bacterial communities. Incubation temperature also had an effect on community structure. Warming in the experimental field in a previous study in the Arctic environment caused a significant increase in the abundance of fungi and bacteria (Yergeau et al., 2012). The quantity of SOC and CO<sub>2</sub> flux has been shown to increase under warming conditions (Zhang et al., 2005; Zhou et al., 2011). Increasing temperature increased relative bacterial growth in arable soils from southern Sweden (Bárcenas-Moreno et al., 2009) and, particularly, the abundance of genes involved in labile carbon degradation in a tall-grass prairie ecosystem in central Oklahoma, USA (Zhou et al., 2011), and led to C loss. In the present study, the shifts in bacterial communities at three elevations could reflect differences in nutrient availability, including SOC and SON, and bacterial activity under different incubation temperatures and at distinct time points during incubation.

Bacterial community structure under incubation at 35 °C was affected by temperature, while under incubation at 15 and 20 °C it correlated with incubation time (Fig. 7). Warming has been shown to change the bacterial structure of alpine meadow soils (Xiong et al., 2014) and to cause thermal-adaptation functional shift of microbial communities (Rousk et al., 2012). Recent studies have observed changes in temperature sensitivity of microbial communities along incubation time. Shifts in microbial communities in response to warming occur after a few years (Yergeau et al., 2012) or even only a few months (Xiong et al., 2014). However, some studies revealed no significant community changes over time



**Figure 7.** PCA of bamboo soil bacterial communities and environmental properties. Symbols are the same as in Fig. 6.

owing to warming (Allison et al., 2010; Zhou et al., 2011). The present work revealed community structure differences after incubation for only about 4 months, suggesting that the bacterial communities in bamboo soils at elevation are highly sensitive to temperature changes, even though they faced a relatively short-time warming condition.

The responses of phylogenetic abundances to temperature differed. As for *Acidobacteria*, the abundance generally decreased with increasing temperature. This is in accordance with previous studies showing decreases in the relative abundance of *Acidobacteria* in warming soils (Xiong et al., 2014; Yergeau et al., 2012). *Acidobacteria* are known as slow-growing (oligotrophic) bacteria that prefer low nutrient availability (Fierer et al., 2007) and possess high maximum growth efficiency (Roller and Schmidt, 2015). Warming conditions in the soil could increase substrate availability and might favor fast-growing (copiotrophic) microorganisms, which are more sensitive to nutrient availability (Männistö et al., 2016). Thus, the decreases in the abundance of *Acidobacteria* could reflect their interactions with copiotrophic species. The abundance of *Acidobacteria* could also be limited by high temperatures (Stark et al., 2015).

Under increased temperature, some phyla in our study responded differently from previous studies. Increasing  $\alpha$ -*Proteobacteria* abundance has been observed in short warming conditions (Xiong et al., 2014) and in a range of Antarctic environments (Yergeau et al., 2012).  $\alpha$ -*Proteobacteria* are mostly fast-growing (copiotrophic) bacteria and are known to be positively correlated with soil available C pools (Nemergut et al., 2010). The decreases in the abundance of



$\alpha$ -*Proteobacteria* in the present study could reflect the decrease in SOC content, which was exhausted by soil respiration CO<sub>2</sub>-C after incubation. *Bradyrhizobium* of  $\alpha$ -*Proteobacteria* at 1800 m increased at all three incubation temperatures. This genus includes species capable of nitrogen fixation and may significantly contribute to soil function (Yarwood et al., 2009). The increase in their abundance might explain the elevated SON. Moreover, these bacteria are plant-growth-promoting bacteria, stimulating plant growth by fixing N<sub>2</sub>, increasing the availability of nutrients in the rhizosphere, positively influencing root growth and morphology, and promoting other beneficial plant–microbe symbioses (Vessey, 2003). Their response to incubation temperatures indicates their potential roles in bamboo growth and responses to application of fertilizers under climatic change.

The increase in abundance of  $\gamma$ -*Proteobacteria* after incubation in our study differed from that in the soil community sampled at elevated soil temperature.  $\gamma$ -*Proteobacteria* showed a lower relative abundance under elevated temperature than in the ambient temperature control (Ren et al., 2015). Within  $\beta$ -*Proteobacteria*, the abundant genus *Burkholderia* is nutritionally versatile and is commonly found in rhizosphere soils. Their functional diversity, including nitrogen fixation and plant growth promotion (Coenye and Vandamme, 2003), could help maintain soil community stability. In addition, *Actinobacteria* and *Bacteroidetes* showed variable responses at different temperatures. These phyla also prefer nutrient-rich environments (Nemergut et al., 2010). Differences in vegetation and litter quality among the study sites might explain this variation. *Actinobacteria* are involved in the organic matter degradation. Under climatic changes, managements of bamboo forests need to consider the responses of *Actinobacteria* to temperature, especially that in N fertilizers, since the abundance of this phylum was positively affected by N fertilization treatments (Zhou et al., 2015). The *Mucilaginibacter* species of *Bacteroidetes* are capable of degrading polysaccharides (Pankratov et al., 2007); thus, the increase in their abundance can be explained by the increase in plant residues in the soil. A previous study suggested the relationship of elevation and temperature with the decomposition of recalcitrant C (Wang et al., 2016a). After decomposition of labile C, the availability of recalcitrant C can strongly affect the community. Moreover, based on a literature survey by Ho et al. (2017), there is little consistency in oligotrophic and copiotrophic phyla of bacterial communities. The microorganisms can display a variety of metabolic characteristics and adjust between high and low substrate use efficiency to adapt to environmental changes. Therefore, shifts in the relative abundances of bacterial taxa may not necessarily indicate their life strategies as an oligotroph or copiotroph but might just reveal the response of a community to such local factors (Ho et al., 2017). Further study, including more comprehensive temperature gradients and more detailed time-course analysis, will be neces-

sary to elucidate the exact influences of temperature on soil communities.

*Acidobacteria* and  $\alpha$ -*Proteobacteria*, which comprised more than 10% of the communities before incubation, tended to decrease after incubation. Groups with lower abundance before incubation, especially,  $\gamma$ -*Proteobacteria*, showed an increasing trend after incubation. These patterns were similar to those shown in communities of a rice paddy and desert soils (Wang et al., 2012; Ren et al., 2015), in which numerically dominant bacterial phyla/classes were reduced, while originally rare groups increased in relative abundance after exposure to environmental changes. These results suggest that shifts in bacterial populations facing environmental changes may follow predictable patterns.

## 5 Conclusions

Our results revealed that an increase in temperature could result in increased soil respiration CO<sub>2</sub>-C and consumption of SOC and SON contents, which directly or indirectly influence the bacterial diversity and structure of bamboo soils at different elevations. In addition, the different responses of bacterial groups to the temperature changes suggest the adaptation of soil communities to global-warming-related climatic changes. This study highlights the need for further research on the physiological and ecological roles of soil bacterial members, such as *Acidobacteria*,  $\alpha$ - and  $\gamma$ -*Proteobacteria*, in response to climatic change in forest ecosystems.

*Data availability.* All sequences have been submitted to the Short Read Archives under accession number SRS1923345.

**The Supplement related to this article is available online at <https://doi.org/10.5194/bg-14-4879-2017-supplement>.**

*Author contributions.* YTL performed statistical analyses; ZJ built statistical models; CYC interpreted ecological rationale; CYC and ZJ formulated the study hypothesis and developed the methodology; and YTL wrote and ZJ and CYC edited the manuscript. All authors read and approved the final manuscript.

*Competing interests.* The authors declare that they have no competing interests.

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