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

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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, 1,200, and 1,800 m to different incubation temperatures (15°C, 20°C, and 35°C) were examined using barcoded pyrosequencing and soil analyses. Soil respiration was greater at higher elevation and incubation temperature. The bacterial diversity in samples incubated at 35°C decreased after 112 days of incubation. 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. α-*Proteobacteria* showed a similar trend, while the abundance of γ-*Proteobacteria* increased after incubation, except those from 1,800 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 bacterial structure incubated at 35°C correlated with temperature and soil respiration, while structures in samples incubated at 15°C and 20°C correlated with time. These results suggest that a temperature rise could result in increasing soil respiration and soil soluble carbon and nitrogen consumption, influencing the bacterial diversity and structure at different elevations.

Keywords: temperature, bamboo, soil

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1. Introduction

Temperature is known as 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_2 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 and construction and as a furniture material. It distribute from low mountain region to high mountain at about 1,800 m a.s.l. Management practices for increasing bamboo production, including regular removal of understory vegetation, tillage, and fertilizer application, could increase the soil CO_2 efflux (Liu et al., 2011) and water-soluble organic N concentration (Wu et al., 2010). Because of the decrease in bamboo prices, many bamboo plantations are in an unmanaged condition. Under the unmanaged conditions, the aboveground biomass of old bamboo has been sharply increasing (Chen et al., 2016). Considering the effects of environmental factors, it is worth elucidating the changes in bamboo soil bacterial communities, under managed and unmanaged conditions.

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, and community structure formed different clusters along with elevations (Lin et al., 2015). Our parallel study showed that bamboo increased humification of soil organic

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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 the temperature changes.

Bacteria could have distinct ecological classification that different phylogenetic groups could represent different functional groups, and their relative abundance affected by C availability. For example, as copiotroph, the relative abundance of *Proteobacteria* is more abundant under C rich environment. In contrast, oilgotrophic groups (e.g., *Acidobactreria*) could maintain viability under stressful environmental conditions (Fierer et al., 2007). However, little is known about how these two distinct groups respond to the environment changes caused by temperature. 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 reveal distinct responses to different nutrient availability cause 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) responses of different phylogenetic groups to the temperature changes.

2. Methods

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2.1. Site description and soil sampling

This study was conducted in Mt. Da-an, a subtropical montane area in Nantou County, central Taiwan (23°42' N, 120°41' E). The soil samples were collected from moso bamboo plantations at 600, 1,200, and 1,800 m a.s.l. along a county road. The three sampling sites were all dominated by moso bamboo with few understory plants. Based on the record from weather stations and temperature-elevation correlation, the annual mean air temperature was estimated as 20.3°C at 600 m, 17.2°C at 1,200 m, and 14.1°C at 1,800 m with a decrease of 0.52°C per 100 m elevation gain (Wang et al., 2016a). At each elevation, three 25 × 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, were 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

The three replicates (25 g for each replicate) from each elevation were incubated at 15°C, 20°C, and 35°C for 112 days. Temperature 15°C, 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. Soil samples of different incubation times were taken from the same container. Soil respiration (CO_2-C) was measured as described (Huang et al., 2014). Soluble organic carbon (SOC) and

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nitrogen (SON) were extracted from the soil samples at different incubation times with 2 M KCl, and measured with the Fisons NA1500 elemental analyser (ThermoQuest 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 bar codes 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 cleanup system (Viogene 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: 2016.09.30). The

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sequences were assigned to the samples by recognition of the bar code from a tag file, followed by trimming of bar codes, 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 analysed 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). The abundance-based Jaccard similarities among communities (β-diversity) at an evolutionary distance of 0.03 was computed with Mothur program. Pairwise similarity values were converted to distances and used to construct dendrogram. Non-metric multi-dimensional scaling (NMDS) based on the distribution of shared OTUs was plotted by using the PRIMER V6 software (Clarke & Gorley, 2006). The Mantel tests as implemented in PRIMER V6 software was used to analyse 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

The results of soil respiration CO_2-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 1,800 m, had a significantly higher soil respiration rate than those obtained at lower elevation. The

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soil respiration rate was also increased with temperature within each elevation. At 35°C, the soil respiration rate decreased significantly with incubation time. At 15°C and 20°C, the respiration rates of some soil samples slightly increased in the early incubation period (d28) (Fig. 1). Because the respiration rate after d72 was similar, we only applied the rate up to d72 for further analysis.

At the beginning of incubation at day 0 (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 (1,800 m) decreased, while those at 600 and 1,200 m increased after 112 days (d112) of incubation at three temperatures. Incubation at higher temperature (35°C) resulted higher SOC content than that at lower temperature (15°C and 20°C). In most samples, SON content increased over the first 28 days (d28) of incubation, but 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 the OTUs formed at an evolutionary distance ≤ 0.03. Based on the Shannon diversity index, the bacterial diversity of soils incubated at 35°C decreased after long incubation (d112). Under incubation at 15°C or 20°C, the bacterial diversity slightly increased at d7 and d28, and decreased at d112 (Fig. 3). Analysis of the β-diversity revealed that though incubated with different temperature, the communities at the same elevation formed a cluster different from those at other elevation (Supplementary Fig. 1).

3.3. Community composition at different incubation temperatures

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Before incubation, *Acidobacteria* and *Proteobacteria* were the two most abundant phyla in soils from all three elevations, together representing more than 60% of the soil bacterial communities (Fig. 4a). Within the *Proteobacteria*, α-*Proteobacteria* were predominant (Fig. 4b). At 1,800 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 1,200 m gradually decreased over the entire incubation period at all temperatures (Fig. 5a-5f). At 1,800 m, it increased during the first seven days of incubation at 35°C, and decreased thereafter at all temperatures (Fig. 5i). The relative abundance of α-*Proteobacteria* showed similar trends; it gradually decreased at 600 and 1,200 m over the entire incubation period at different temperatures, except at d7 at 600 m, 20°C, and at d7 at 1,200 m, 35°C (Fig. 5a-5f). At 1,800 m, the changes in abundance were different. α-*Proteobacteria* were elevated at d7 and d112, but were lower at d28 of incubation at 15°C and 20°C. Their abundance decreased over time under incubation at 35°C (Fig. 5g-5i). With regard to γ-*Proteobacteria*, their relative abundance mostly increased over incubation, except in soils sampled at 1,800 m under incubation at 35°C, in which it was increased at d7, but decreased at d28 and d112 (Fig. 3c). The relative abundance of *Chloroflexi* also increased over incubation, except that at 600m incubated at 15 °C, d112. Some other phyla demonstrated inconsistent changes under increased temperature. The abundances of *Actinobacteria* at 1,200 m and 1,800 m increased at higher temperature (Fig. 5d-5i), while it decreased in samples taken at 600 m (Fig. 5a-5c). Likewise, *Bacteroidetes*

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showed inconsistent changes after different incubation times and temperatures (Fig. 5a-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 1,800 m formed a different cluster from those at 600 and 1,200 m. Incubation at higher temperature (35°C) led to a bacterial structure different from those at 15°C and 20°C. Incubation time also changed the bacterial structure. The bacterial structure at long incubation time (d112) was different from those at d7 and d28.

PCA analysis revealed the correlation between bacterial structure and environmental factors. When incubated at 35°C, bacterial structure correlated with temperature and soil respiration CO_2-C, while at 15°C 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 at higher elevation after long incubation. The soil respiration CO_2-C rate was greater at higher elevation. Similarly, a previous study in tundra soils using different incubation temperatures 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 could also be the result of nutrient

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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.

The bacterial community structure varied over different incubation periods and temperatures. The communities at the three elevations formed different clusters as compared to the results of our previous study (Lin et al., 2015). Soils at different elevation have distinct soil SOC and SON contents, which could result in different forces to alter bacterial communities. Incubation temperature 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_2 flux has been shown to increase under warming condition (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 labile carbon degradation in a tall-grass prairie ecosystem in Central Oklahoma, USA, 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°C and 20°C, it correlated with incubation time (Fig. 5). Warming has been shown to change the bacterial structure of alpine meadow soils (Xiong et al., 2014) and to cause thermal adaption in 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

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(Yergeau et al., 2012) or even only a few months (Xiong et al., 2014). However, some studies revealed no significant community changes due to warming across time (Allison et al., 2010; Zhou et al., 2011). The present work revealed community structure differences after incubation for only about four months, suggesting that the bacterial communities in bamboo soils at elevation are highly sensitive to temperature changes, even though they faced a relative 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). Warming conditions in the soil could increase substrate availability and might favour fast-growing (copiotrophic) microorganisms. Thus, the decreases in the abundance of *Acidobacteria* could reflect their interactions with copiotrophic species. This phylum may be an indicator of climate warming in soil ecosystems (Xiong et al., 2014).

Under increased temperature, some phyla in our study responded differently from previous studies. Increasing α-*Proteobacteria* abundance has been observed in short warming conditions (Xiong et al., 2014) and in a range of Antarctic environments (Yergeau et al., 2012). α-*Proteobacteria* are mostly fast-growing (copiotrophic) bacteria, and known to be positively correlated with soil available C pools (Nemergut et al., 2010). The decreases in the abundance of α-*Proteobacteria* in the present study could reflect the decrease in SOC content, which was exhausted by soil respiration CO_2-C after incubation. Increased in the abundance of γ-*Proteobacteria* after incubation in our study also differed from that in the soil

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community subjected elevated soil temperature. The γ-*Proteobacteria* showed a lower relative abundance under elevated temperature treatment compared to ambient control (Ren et al., 2015). 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. The results of previous study suggest the relationship of elevation and temperature to the decomposition of recalcitrant C (Wang et al., 2016a). After decomposition of labile C, the availability of recalcitrant C could also serve an important factor to affect the community. Moreover, based on the literature survey by Ho et al. (2017), the consistency in the oligotrophic and copiotrophic phyla of bacterial communities is little. The microorganisms could process a variety of metabolic characteristics; adjust between high and low substrate use efficiency, to adapt environmental changes. Therefore, shifts in the relative abundances of bacterial taxa may not necessarily indicate their life strategies in oilgotroph or copiotroph. It would just reveal the response of community to the local factors (Ho et al., 2017). Further study, including more comprehensive temperature gradients and more detailed time course analysis, will be necessary to elucidate the exact influences of temperature to soil communities. In addition, an interesting pattern was shown at some bacterial groups. The *Acidobacteria* and α-*Proteobacteria*, comprised more than 10% of the communities before incubation, revealed decreasing response in relative abundance after incubation. The groups with lower abundance of communities before incubation, especially γ-*Proteobacteria*, responded in increasing trend after incubation. This patter was similar to that shown in communities of a rice paddy and desert soils (Wang et al., 2012; Ren et al., 2015). The numerically dominant bacterial phyla/classes were reduced, while original rare groups increased in relative

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abundance after exposed to environmental changes. These results suggest the shifts of the bacterial populations faced to the environmental changes may follow a predictable pattern. The dominant bacterial groups will become less abundant or even rare taxa, while initial less/rare abundant groups will become dominant after a period of incubation time (Ren et al., 2015).

In conclusion, our results revealed that an increase in temperature could result in increased soil respiration CO_2-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 physiologic and ecologic roles of soil bacterial members, such as *Acidobacteria*, α- and γ-*Proteobacteria*, in climatic change in forest ecosystems.

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Author Contributions

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

Competing financial interests

The authors declare that they have no competing interests.

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Figure legends

Fig. 1. Respiration CO_2-C rate in soils sampled at three elevations and incubated at (a) 15 °C, (b) 20 °C and (c) 35 °C. Error bars represent standard deviation.

Fig. 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 15 °C, (b, e) 20 °C and (c, f) 35 °C. Error bars represent standard deviation.

Fig. 3. Changes in bacterial diversity of soil community at 600 m, 1,200 m, and 1,800 m incubated at different temperatures.

Fig. 4. Relative abundances of (a) all phylogenetic groups and (b) all phylogenetic groups except *Acidobacteria* in the bamboo soil bacterial communities at different elevations.

Fig. 5. 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) 1,200 m, 15 °C, (e) 1,200 m, 20 °C, (f) 1,200 m, 35 °C, (g) 1,800 m, 15 °C, (h) 1,800 m, 20 °C and (i) 1,800 m, 35 °C. Abbreviation: Acid: *Acidobacteria*; Actino: *Actinobacteria*; Bac: *Bacteroidetes*; Chloro: *Chloroflexi*; Firm: *Firmicutes*; Gem: *Gemmatimonadetes*; Nitro: *Nitrospirae*; α, β, γ, δ: α-, β-, γ- and δ-*Proteobacteria*.

Fig. 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 m, 1,200 m and 1,800 m elevation, respectively. The

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analysis was based on the distribution of OTUs formed at an evolutionary distance of 0.03.

Fig. 7. PCA analysis of bamboo soil bacterial communities and environmental properties. Symbols are the same as in Fig. 4.

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2 **Fig. 1.**

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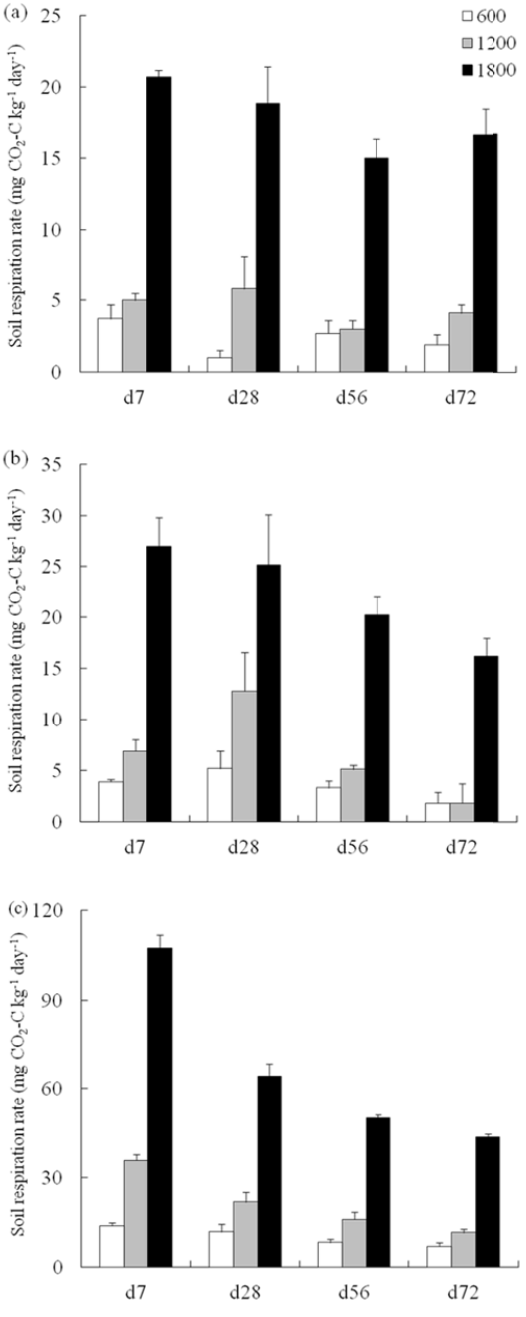

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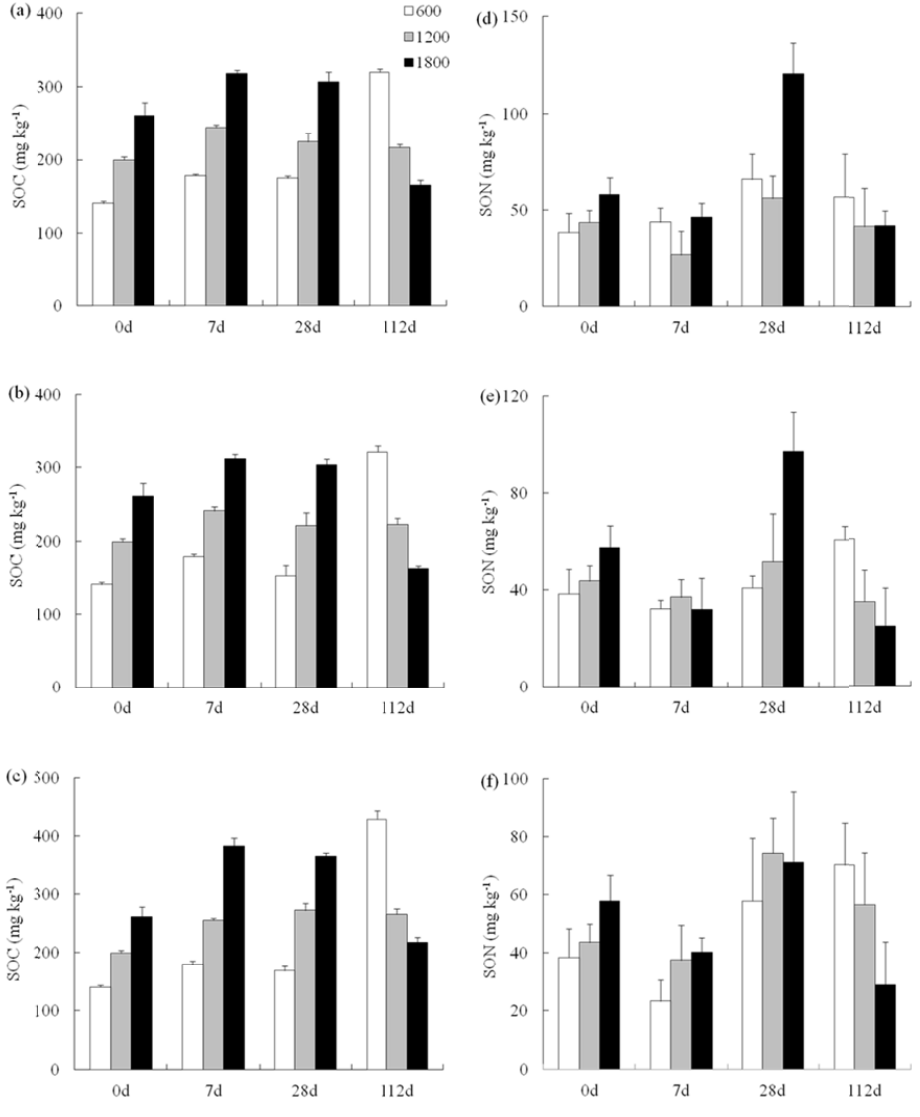
Fig. 2.



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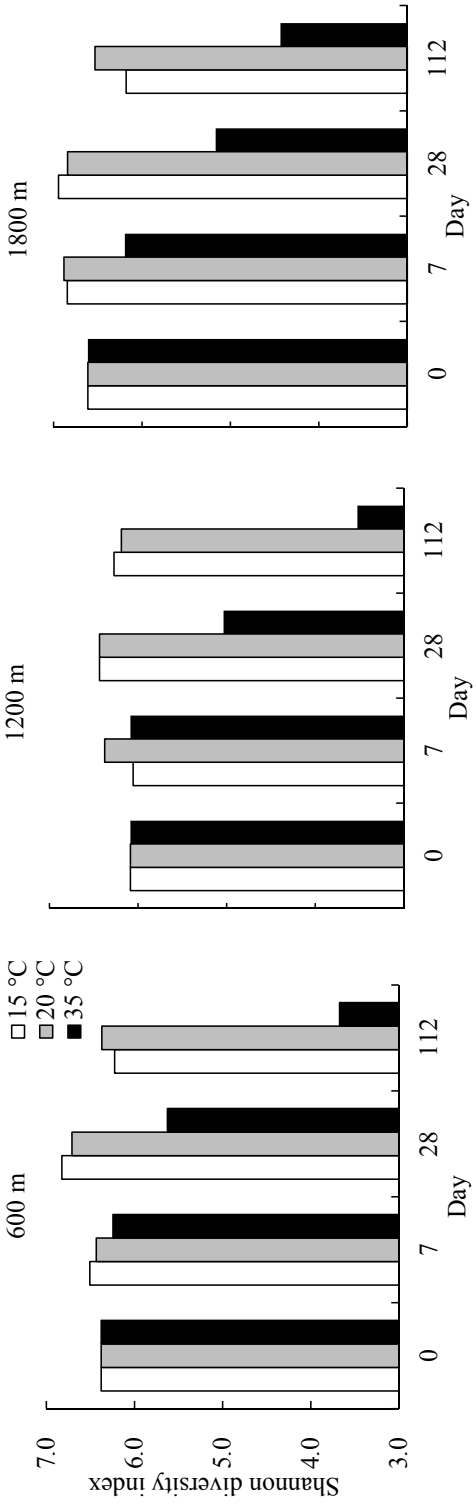

Fig. 3.

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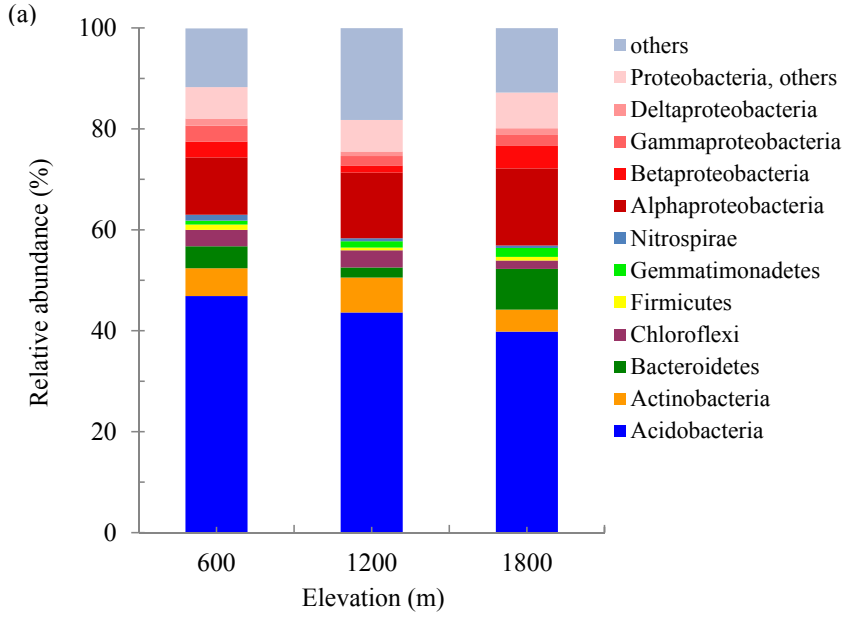
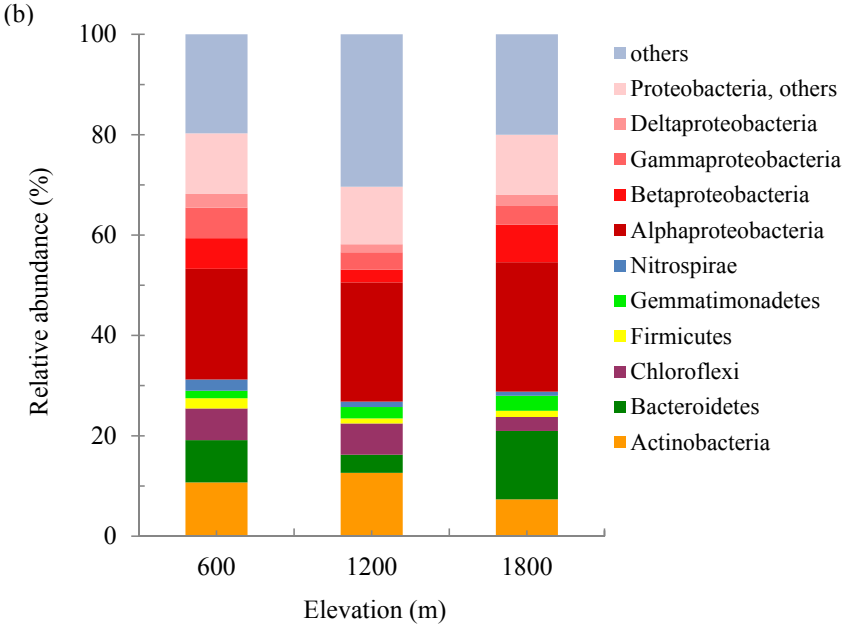
Fig. 4





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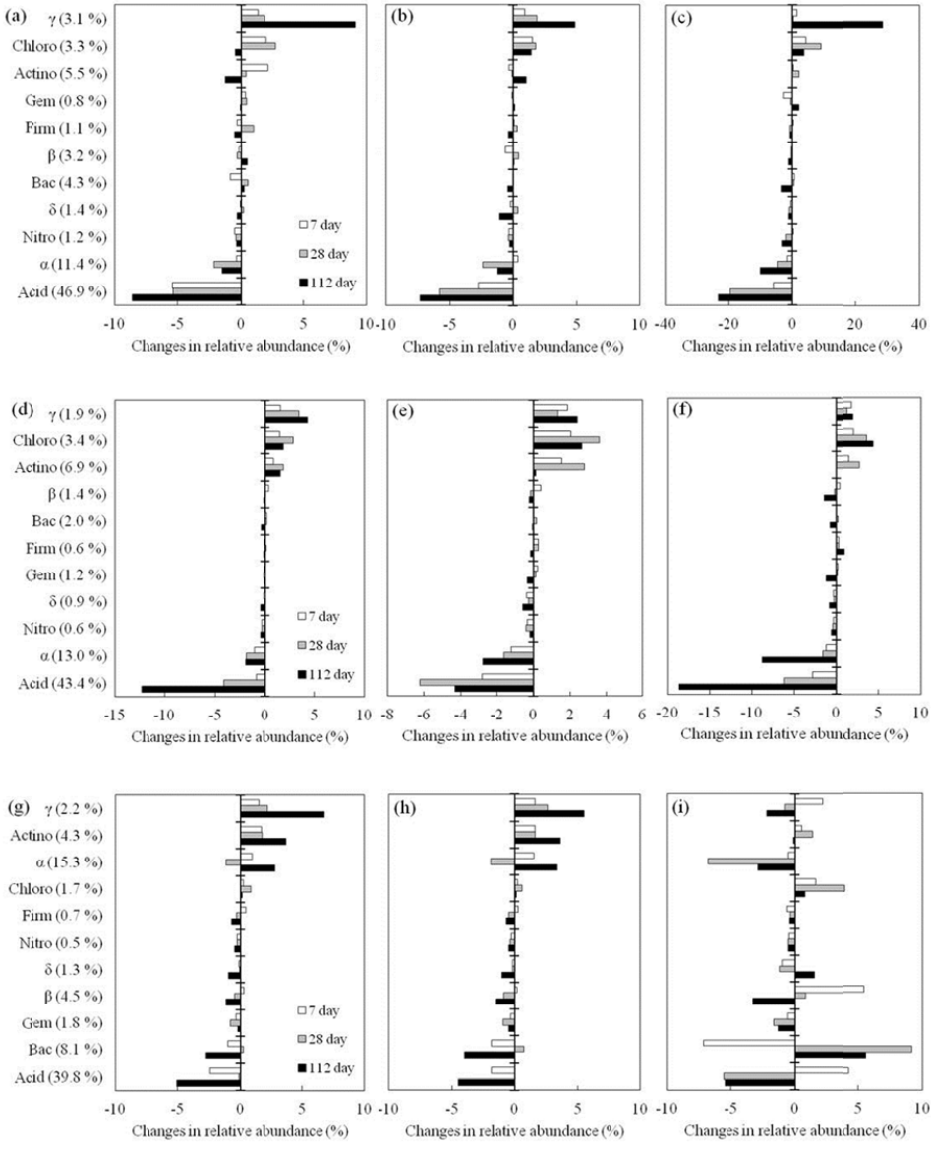

2 **Fig. 5.**

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Fig. 6.

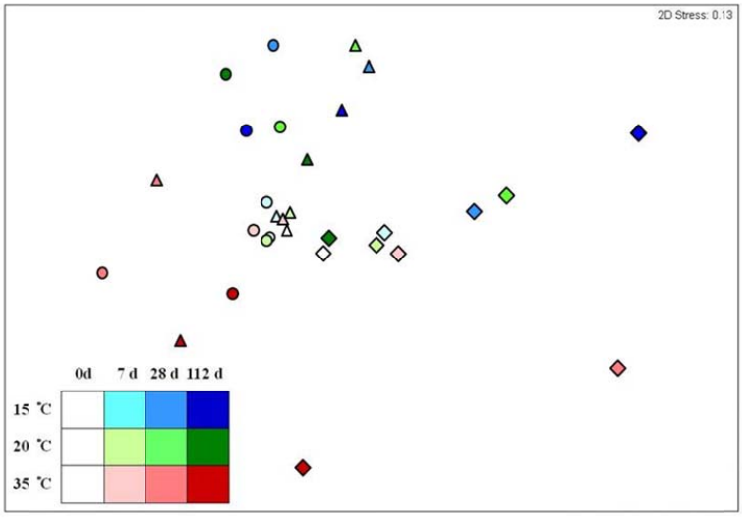

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Fig. 7.