Temperature and soil nutrients drive the spatial distributions of soil macroinvertebrates on the eastern Tibetan Plateau

YULIAN YANG,1,2 QINGGUI WU,2 WANQIN YANG,1 FUZHONG WU,1 LI ZHANG,1 ZHENFENG XU,1 YANG LIU,1 BO TAN,1† HAN LI,1 AND WEI ZHOU3

1Long-Term Research Station of Alpine Forest Ecosystems, Key Laboratory of Ecological Forestry Engineering, Institute of Ecology and Forestry, Sichuan Agricultural University, Chengdu 611130 China
2Ecological Security and Protection Key Laboratory of Sichuan Province, Mianyang Normal University, Mianyang 621000 China
3College of Resources, Sichuan Agricultural University, Chengdu 611130 China

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Abstract. Improved knowledge of biological diversity patterns associated with elevation and their driving factors is indispensable for developing ecological theories. However, the results for the elevational distribution patterns of soil fauna are not consistent due to differing climates and vegetation. Here, we present a comprehensive analysis of soil macroinvertebrate composition and structure among different forests at three elevations on the eastern Tibetan Plateau, China. A total of 16,559 individuals belonging to 24 orders and 100 families were collected, and the macroinvertebrate individual abundance, family richness, and diversity apparently increased with increasing elevation. Moreover, remarkable seasonal dynamics were observed for both the composition and functional structure of soil macroinvertebrates among forest types and were inconsistently affected by different environmental factors. The structural equation model suggested that elevation indirectly affected soil macroinvertebrate abundance by modulating climate (e.g., temperature) and soil quality (e.g., soil organic carbon and total nitrogen). Additionally, although vegetation had minor direct effects on soil macroinvertebrate abundance, it might indirectly influence soil macroinvertebrate abundance by regulating plant litter input. Our results indicate that temperature and soil nutrients are critical factors of soil macroinvertebrate elevational distributions and highlight the importance of plant litter input in determining the composition and structure of soil macroinvertebrates at different elevations.

Key words: community structure; elevational pattern; environmental factors; forest ecosystems; functional group; soil macroinvertebrate.

INTRODUCTION

Soil macroinvertebrates, ranging from relatively large animals to prokaryotes, contribute to organic matter decomposition, nutrient cycles, and soil physicochemical properties (Brussaard et al. 1997, Lavelle et al. 2006). Therefore, they are indispensable for the functioning of terrestrial ecosystems at any elevation gradient. Although the distribution patterns of soil macroinvertebrates along elevation gradients have been studied previously (Sadaka and Ponge 2003, Wu et al. 2012, Yin et al. 2017b, Karungi et al. 2018), knowledge of the direct or indirect correlation between biodiversity and elevation is unclear. It has been reported that abiotic factors
such as hydrothermal conditions, plant community, and soil physicochemical properties can directly influence the macroinvertebrate distribution (Blankinship et al. 2011, Faly and Brygadyrenko 2018, Wang et al. 2019). Furthermore, these factors can vary with elevation and subsequently have profound repercussions for soil macroinvertebrates (Tang 2006, Wang et al. 2012, Wu et al. 2012), but the understanding of such effects is currently incomplete. Therefore, improved knowledge of the effects of elevation on the structure and diversity of the soil macroinvertebrate community and the related mechanisms driving such differences is indispensable for developing ecological theories (Malhi et al. 2010, Sanders and Rahbek 2012).

Numerous studies have found different results related to the elevational patterns of macroinvertebrate communities, indicating a monotonic decrease (Li et al. 2015, Yin et al. 2017) and increase (Sadaka and Ponge 2003), a hump-shaped pattern of abundance (Xiao et al. 2009) or no trend with increasing elevation (Wu et al. 2012). The combined effects of climate, soil, and vegetation (Morales and Sarmiento 2002, García-Palacios et al. 2013, Gholami et al. 2016, Faly and Brygadyrenko 2018) are considered to be the primary explanations for the inconsistent patterns of macroinvertebrate distribution. On the one hand, changes in hydrothermal conditions along elevational gradients not only directly alter soil macroinvertebrate survival but also affect the composition and production of litter and the soil physicochemical properties associated with plant communities (Carrera et al. 2010, Coyle et al. 2017), thereby altering the soil macroinvertebrate community structure and diversity. On the other hand, variations in plant communities at different elevations provide various food sources in the form of plants and litter and create diversified habitats, thereby varying in microclimatic conditions and soil nutrients (Ayres et al. 2009, Ushio et al. 2010, Sauvadet et al. 2017) and further affecting the soil macroinvertebrate community and its functional roles. Additionally, soil physicochemical properties could influence the plant community, resulting in the existence of a complicated plant–soil interaction (Ushio et al. 2010, Coyle et al. 2017). Nevertheless, seasonal changes in climate, plant community, and litter production can strongly affect the soil microclimatic conditions (Villegas et al. 2010, Thomas et al. 2018) among different elevations and in turn make the mechanisms underlying the vertical differentiation of macroinvertebrate even more complex. Thus, additional studies related to the mechanisms underlying the vertical differentiation of macroinvertebrates in separate seasons are needed.

The forests on the eastern Tibetan Plateau range in elevation from 600 to 4500 m and differ in climate, vegetation, and decomposer communities. Previous studies have described the spatiotemporal distribution of soil macroinvertebrates in this region (Wu et al. 2012, Tan et al. 2013), whereas little attention has been paid to the mechanism influencing the vertical differentiation of macroinvertebrates, especially among different seasons. Therefore, a two-year study was carried out in forests at 960, 1870, and 3058 m on the eastern Tibetan Plateau. We investigated the soil macroinvertebrate community and ecological factors, including climate, vegetation, and soil properties, to reveal the comprehensive factors driving the elevational patterns of soil macroinvertebrates. Our objectives were to determine the characteristics of the taxonomic and trophic groups of soil macroinvertebrates communities over elevational gradients and seasons and to explore the seasonal mechanisms driving the investigated factors of the soil macroinvertebrate community across an elevational gradient. Specifically, we hypothesized that (1) the abundance and diversity of soil macroinvertebrates would decrease from lower to higher elevations since temperature at higher elevations would constrain soil fauna activity and (2) elevations would indirectly affect soil macroinvertebrate abundance not only by temperature but also by soil quality and plant community structure.

**Materials and Methods**

**Study site**

This study was conducted on the eastern edge of the Qinghai-Tibetan Plateau, situated in western Sichuan, China. This region encompasses a wide range of elevation gradients, environmental conditions, and vegetation types, extending from lowland plains at under 1000 m to mountain peaks above 3000 m. Along the increasing
altitudinal gradient from 960 to 3058 m, the mean annual temperature and precipitation decrease from 15.2°C to 5.9°C and from 1243 to 850 mm, respectively. The unique vertical distribution of vegetation on the eastern edge of the Qinghai-Tibetan Plateau changes very distinctly from evergreen broadleaved forest at low elevations to alpine/subalpine dark coniferous forests at high elevations. All the aforementioned studies indicate that this region provides an optimal environment for investigating soil macroinvertebrate elevational patterns.

**Experimental design**

Three elevations were selected to cover a vertical nearly 2100 m transition zone at elevations of 960, 1870, and 3058 m. The environmental characteristics and plant community of each elevation are described in Table 1. Each elevation included an artificial forest and a secondary forest, specifically artificial forests of zhennan (*Phoebe zhennan*), cedar (*Cryptomeria fortunei*), and spruce (*Picea asperata*) as well as secondary forests of oak (*Quercus acutissima*), dove tree (*Davidia involucrata*), and birch (*Betula albosinensis*) at 960, 1870, and 3058 m, respectively. In each forest, five 20 × 20 m plots with similar environmental factors were randomly established for soil sampling and vegetation investigation.

**Sampling and analysis**

Soil samples were collected from the six forests in August, November, January, and April from 2014 to 2016, which corresponded to the main periods of soil macroinvertebrate activity at the study sites. In each plot, an area of 50 × 50 cm was selected to sample soil macroinvertebrates by hand sorting from the litter layer to the soil layer at a 15 cm soil depth. A total of 240 soil macroinvertebrate samples were collected (6 forests × 5 plots × 8 sampling periods), and the collected samples were stored in soil fauna sealing bags and then transported to the laboratory within 12 h. Subsequently, the soil macroinvertebrates were identified at the order or family level and counted under a stereoscopic microscope (Olympus SZX16) following the protocols by Yin et al. (1998) and Li et al. (1987). The adults and larvae were counted separately owing to their functional differences. In addition, considering that the functional groups of soil macroinvertebrates are highly dependent on

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Table 1. General characteristics of the physical environments of the three elevational zones.

| Zone | Position | Elevation (m) | Annual mean temperature (°C) | Annual mean precipitation (mm) | Soil type | Tree layer | Shrub layer | Herb layer |
|------|----------|--------------|------------------------------|-------------------------------|----------|------------|-------------|-----------|
| A    | 31°18’ N, 102°56’ E | A1 (3058) | 5.9                          | 850                           | Brown soil and dark brown soil | *Picea purpurea*, *Betula albosinensis* | *Fargesia spathacca*, *Berberis juliana*, *Hippophae rhamnoides* | *Cacalia auriculata*, *Cystopteris montana*, *Cyperus rotundus* |
|      |          | A2 (1870) | 13.1                         | 980                           | Brown soil and yellow brown soil | *Davidia involucrata*, *Cryptomeria fortunei*, *Cyclobalanopsis oxyodon* | *Rubus pungens*, *Loniceratatisiensis*, *Berberis henryana* | *Iris japonica*, *Ophiopogon japonicas*, *Cyperus papyrus* |
|      |          | A3 (960)  | 15.2                         | 1243                          | Brown soil | *Quercus acutissima*, *Phoebe zhennan*, *Ginkgo biloba* | *Pittosporum glabratum*, *Lepedea bicolor*, *Zanthoxylum simulans*, *Mahonia fortunei* | *Iris confusa*, *Pteridium aquilinum*, *Ophiopogon japonicas*, *Cyperus papyrus*, *Dranceoptes dichotome* |

Notes: Zones are as follows: A, Bipenggou Nature Reserve, located in Li county, Sichuan Province, China; B, Wolong Nature Reserve, located in Wenchuan county, Sichuan Province, China; and C, Lingyan Mountain, located in Dujiangyan city, Sichuan Province, China.
macr oinvertebrate ecological functions (Ding et al. 2017), soil macroinvertebrates were further classified into fungivores, herbivores, predators, and omnivores based on their known feeding behaviors (Li et al. 1987, Yin et al. 1998).

The atmospheric and soil temperatures were measured every 2 h using iButton automatic recorders (iButton DS1923-F5, Maxim/Dallas Semiconductor, Sunnyvale, California, USA) at each of the three altitudes during the study period. Meanwhile, vegetation and soil properties were measured during each sampling event. The plant species richness was measured in the five 20 x 20 m sampling plots. After the soil macroinvertebrates were hand sorted, the litter from each subplot was transported to the laboratory, oven dried to a constant weight at 70°C, and weighed. The soil properties were measured based on the three layers of mixed soil from each subplot. The soil pH was determined using a 1/2.5 soil/water mix; soil organic carbon (SOC) concentrations were determined using the dichromate oxidation-sulfate-ferrous titration method; soil total nitrogen (STN) was determined by the acid molybdenum stibium anticolor method (Zhang 2000). The average monthly air and soil temperatures and the vegetation and soil properties over the four seasons in the six forests along an elevation gradient are listed in Table 2.

**Data analysis**

The abundance (the total number of soil macroinvertebrates per plot converted to individuals/m²), the taxonomic richness (the number of taxonomic groups per plot), the Shannon index \( H' = -\sum_{i=1}^{n} P_i \ln P_i \), where \( P_i \) is the proportion of individuals in the ith taxon), and the Pielou index \( J = H'/\ln S \), where \( H' \) is the Shannon index and \( S \) is the total number of taxa identified) were calculated for each sampling time. A species was regarded as a dominant species, ordinary species, or infrequent species if the proportion of individuals was greater than 10%, 1.0–10%, or below 1.0%, respectively.

One-way analysis of variance (ANOVA) was conducted to test for significant differences in all variables between the same sampling times or forest types, and if significant differences were identified, multicomparisons were performed using Tukey’s honestly significant difference (HSD) post hoc test. A general linear model (GLM) repeated-measures ANOVA was conducted to test the main effects of elevation, forest type, and sampling season (forest type was treated as a nested factor) on the taxonomic and trophic group levels of soil macroinvertebrate. ANOVAs were performed using SPSS 20.0 (IBM SPP Statistics, Chicago, Illinois, USA). Moreover, principal component analysis (PCA) was performed using CANOCO (version 5.0) to evaluate the effects of forest and sampling period on the soil macroinvertebrate community composition.

**Table 2. Characteristics of environmental factors in four seasons in two types of forests along an elevation gradient (mean ± standard error).**

| Factor group | Specific factors | 960 m | 1870 m | 3058 m |
|--------------|-----------------|-------|--------|--------|
| Climate      |                 | AF    | SF     | AF     | SF     |
| AT (°C)      | 13.30 ± 0.89B   | 13.30 ± 0.89B | 10.88 ± 1.15B | 10.88 ± 1.15B | 3.63 ± 0.97A | 3.63 ± 0.97A |
| ST5 (°C)     | 13.41 ± 0.84B   | 13.41 ± 0.84B | 11.30 ± 0.86B | 11.30 ± 0.86B | 4.37 ± 0.85A | 4.37 ± 0.85A |
| ST10 (°C)    | 12.62 ± 0.66B   | 12.62 ± 0.66B | 11.43 ± 0.84B | 11.43 ± 0.84B | 4.79 ± 0.69A | 4.79 ± 0.69A |
| Vegetation   |                 |       |        |        |        |
| PSR          | 32.10 ± 0.60A   | 45.98 ± 0.69E | 39.50 ± 1.04E | 43.25 ± 0.60C | 33.38 ± 0.81D | 37.05 ± 0.83B |
| LM (t/hm²)   | 4.13 ± 0.17A    | 8.09 ± 0.29B  | 15.73 ± 0.52D | 10.47 ± 0.49C | 20.99 ± 0.91E | 18.45 ± 0.72E |
| Soil quality |                 |       |        |        |        |
| SOC (g/kg)   | 117.14 ± 1.51B  | 109.76 ± 1.82D | 135.90 ± 1.77C | 143.63 ± 1.56D | 173.13 ± 1.76B | 195.49 ± 1.73F |
| STN (g/kg)   | 3.40 ± 0.06A    | 3.29 ± 0.08A  | 5.94 ± 0.10B  | 6.36 ± 0.08C  | 8.92 ± 0.15D  | 9.71 ± 0.10B  |
| STP (g/kg)   | 1.03 ± 0.02A    | 0.91 ± 0.02A  | 1.10 ± 0.02B  | 1.41 ± 0.03D  | 0.91 ± 0.03A  | 1.22 ± 0.05C  |
| SC/N         | 35.07 ± 0.94D   | 34.17 ± 1.13D | 23.75 ± 0.41C | 34.17 ± 1.13D | 19.63 ± 0.38A | 20.24 ± 0.32B |
| SC/P         | 116.13 ± 3.07B  | 127.00 ± 5.52B | 124.55 ± 2.53B | 103.31 ± 1.98B | 196.74 ± 6.72D | 164.64 ± 4.61C |

Notes: AF, artificial forest; SF, secondary forest; AT, air temperature; ST5, soil temperature at 5 cm soil depth; ST10, soil temperature at 10 cm soil depth; PSR, plant species richness; LM, litter mass; SOC, soil organic carbon; STN, soil total nitrogen; and STP, soil total phosphorus. Lowercase letters indicate differences among the three elevations or six forests at the \( P < 0.05 \) level.
The relationships between soil macroinvertebrate composition and environmental factors (climate, soil quality, and vegetation) were determined using Pearson’s correlation coefficients in R (version 3.4.3). Multivariate structural equation models (SEMs) were used in R (version 3.4.3) to analyze the direct and indirect relationships between the soil macroinvertebrate community (abundance) and the factors mentioned above along the elevational gradient in different seasons. The relationship between the multiple variables and the soil macroinvertebrate community in the model was based on previous studies (Carrera et al. 2010, Coyle et al. 2017). Jöreskog’s goodness-of-fit index (GFI), the root mean square error of approximation (RMSEA), and the Bollen-Stine bootstrap test (high P values indicate that the data fit the model well) were used to test the fit of the data to the model (Guo et al. 2015). Models with a GFI value >0.9, an RMSEA <0.05, and P values >0.05 were chosen. To satisfy the assumptions of normality and homogeneity of variance, the abundance data were log (x + 1) transformed, and the environmental factor data were standardized by a 0–1 normalization prior to the statistical analysis.

**RESULTS**

**Soil macroinvertebrate taxonomic groups**

Throughout the two-year study, we extracted 16,559 individuals that were included in 24 orders and 100 families of soil macroinvertebrates from the three elevations (Appendix S1: Table S1). The species proportion and taxa composition indicated that Formicidae was the most abundant taxon regardless of elevation and represented 10.97–20.20% of the soil macroinvertebrates. Regardless of forest type, both the individual abundance and family richness of soil macroinvertebrates sharply increased with increasing elevation during the study (Fig. 1a, b). Overall, the PCA results showed that the community composition of soil macroinvertebrates differed significantly among seasons (Fig. 2, Table 3). The individual abundance and family richness of soil macroinvertebrates in the nongrowing season (January) were significantly lower than those in the growing seasons (August, November, and April). The individual abundance and family richness of soil macroinvertebrates in artificial forests were significantly lower than those in secondary forests at 3058 and 960 m, respectively.

Irrespective of forest type, the Shannon-Wiener index of soil macroinvertebrates significantly increased with increasing elevation, but the Pielou index of soil macroinvertebrates showed weak change along the elevational gradient (Fig. 1c, d, Table 3). The Shannon-Wiener index and Pielou index of soil macroinvertebrates varied significantly among forest types and seasons (Table 3). The Shannon-Wiener index of soil macroinvertebrates in the nongrowing season was significantly lower than that in the growing season. Conversely, the opposite results were observed for the Pielou index of soil macroinvertebrates in the secondary forest at 960 m and in the artificial forest at 1870 m, respectively. Compared with the 960 and 1870 m, the Pielou index of soil macroinvertebrates in artificial forests was significantly higher than that in secondary forests at 3058 m.

**Soil macroinvertebrate functional groups**

Regardless of elevation, the fungivores was the most abundant functional group and represented 43.25–65.73% of the soil macroinvertebrates during the entire study period (Fig. 3; Appendix S1: Table S1). The elevational pattern of soil macroinvertebrate functional groups differed significantly with changes in sampling season and forest type (Fig. 3, Table 3). Compared to that in the growing seasons, the relative abundance of fungivores was significantly increased in the nongrowing season, while the opposite result was observed for the abundances of herbivores, predators and omnivores, except for in the artificial forest at 960 m. The relative abundance of fungivores in the artificial forest was significantly higher than that in the secondary forest, while the opposite result was observed for the relative abundances of herbivores and omnivores at 960 m. There was a minor difference in the relative abundance of soil macroinvertebrate functional groups between the artificial forest and secondary forest at both 1870 and 3058 m during the experiment.

**Relationships between the soil macroinvertebrate community and environmental variables**

Regardless of season, the Pearson correlation results showed that the abundance, richness,
Shannon index of soil macroinvertebrates had a significantly positive relationship with elevation, while only the relative abundance of omnivores had a significantly negative relationship with elevation. Air and soil temperatures showed a close relationship with the structure of soil macroinvertebrates, as demonstrated by the Shannon index, Pielou index, and the relative abundance of functional groups. The relative abundance of fungivorous had a significantly negative relationship with plant species richness but had no significant relationship with litter mass. Soil pH, organic carbon, total nitrogen, and the ratio of C/P all had significantly positive relationships with...
the abundance, richness, and Shannon index of soil macroinvertebrates (Table 4).

A significant causal relationship was revealed by the SEM analysis: Soil macroinvertebrate abundances were directly affected by climate and soil quality and were indirectly affected by elevation (Fig. 4). Climate and soil quality were significant, and these parameters showed direct positive and negative correlations with soil macroinvertebrate abundance, respectively. Moreover, the increase in elevation indirectly increased soil macroinvertebrate abundance by increasing the SOC and STN contents and by decreasing soil temperature. Meanwhile, elevation had significant indirect effects on soil quality by affecting vegetation, thereby affecting soil macroinvertebrate abundance. The litter mass showed significantly positive and negative correlations with increasing elevation and SOC and STN, respectively.
DISCUSSION

Changes in elevation usually cause substantial variations in climatic conditions, vegetation compositions, and soil properties (McCain 2005, Guo et al. 2013, 2015). Previous studies have suggested that the composition and diversity of soil fauna vary significantly among sites with different prevailing climatic conditions and generally decrease with increasing altitude and latitude (Li et al. 2015, Yin et al. 2017). Contrary to our first hypothesis, the individual abundance, family richness, and diversity of soil macroinvertebrates increased with increasing elevation on the eastern Tibetan Plateau in our study (Fig. 1). This is inconsistent with the results in temperate forests in the Changbai Mountains (Yin et al. 2017b) and tropical forests in the Gaoligong Mountains (Xiao et al. 2009). However, our results are consistent with the findings that greater macroinvertebrate abundance and family richness were present at higher elevations in the holm oak forests in the Mediterranean region (Sadaka and Ponge 2003). The disparate results can be explained mainly as follows: (1) Soil macroinvertebrates are suggested to have a diverse adaptation strategy and a high tolerance to extreme climatic conditions (i.e., temperature and precipitation; Izadi et al. 2017), which may conceal the negative impacts of climate with increasing elevation; (2) the fallen litter on the forest floor is an important food source and habitat for soil fauna (Wardle et al. 2004, Izadi et al. 2017, Yue et al. 2018), and the higher litter input (Table 2) may favor the colonization of more soil fauna in the soil, subsequently resulting in a higher abundance and diversity of soil macroinvertebrates at 3058 m (Fig. 1); (3) the increased soil organic matter content along the elevational gradient can also provide the adequately available nutrients to soil organisms (fauna and microbe; Wardle et al. 2004, Huhta 2007), which then leads to increases in the abundance and diversity of soil macroinvertebrates with increasing elevation; and (4) the differences in microclimate, forest vegetation, and elevation may also cause the opposite findings among different sites (Ayres et al. 2009, Zhukov et al. 2018). Thus, these results suggest that the distribution pattern of soil macroinvertebrates varies significantly in heterogeneous environmental conditions along elevational gradients.

The functional structure of soil fauna has been suggested to be tightly linked to abiotic environments, vegetation composition, and food availability in various ecosystems (Ding et al. 2017). In this study, fungivorous soil macroinvertebrates were the dominant group at the three elevations regardless of the forest type and season (Fig. 3). This is in accordance with earlier studies of many forest ecosystems (Huang and Zhang 2008, Li et al. 2015). The decomposed animal and plant residuals are the main food source for fungivorous soil fauna (Brussaard 1998, Wardle et al. 2004), so the continuous input of abundant forest litter (above and below ground) could provide sufficient conditions for the survival and reproduction of this group. Moreover, the
relative abundance of the four functional groups fluctuated significantly among the sampling seasons at different elevations (Fig. 3). The herbivorous, predatory, and omnivorous soil macroinvertebrates were more abundant in the growing seasons (Fig. 3) and less abundant in the nongrowing seasons. A likely explanation is that the greater diversity of plant communities and food resources in the growing seasons can maintain the more complex functional composition of soil macroinvertebrates under warmer and wetter climatic conditions. Conversely, in the nongrowing season, low temperature, food availability, and decomposer activity can result in the migration or dormancy of some soil macroinvertebrates and then decrease the complexity of these functional groups. However, it should be noted that the fungivorous soil fauna maintained a
relatively high proportion in the nongrowing season, especially at high elevations. The possible reason is that the litter input during autumn may provide numerous foods for soil microorganisms and macroinvertebrates in the nongrowing season (Brussaard 1998, Izadi et al. 2017, Yue et al. 2018). In addition, the survival microorganisms during the nongrowing season also consist of the food resources for the fungivorous soil fauna (Steinwandter et al. 2018). As a result, these findings indicate that the functional composition of soil macroinvertebrates differs significantly among seasons in heterogeneous environmental conditions at different elevations.

Environmental factors, including temperature, vegetation, and soil quality, usually vary with changes in elevation and exhibit complicated interactional effects on the composition and diversity of soil fauna (Blankinship et al. 2011, Sanders and Rahbek 2012, Coyle et al. 2017, Zhukov et al. 2018).

### Table 4. Pearson correlation coefficient between soil macroinvertebrate composition and environmental factors.

| Variable             | Climate | Vegetation | Soil quality |
|----------------------|---------|------------|--------------|
|                      | AT      | ST5        | ST10         | PSR | LM | pH | SOC | STN | STP | SC/N | SC/P |
| Community Abundance  | 0.16*   | 0.51***    | 0.52***      | 0.61*** | 0.61*** | -0.06 | 0.61*** | -0.45*** | 0.53*** |
| Community Richness   | 0.08    | 0.04       | 0.20***      | 0.52*** | 0.53*** | 0.59*** | 0.63*** | -0.05 | -0.48*** | 0.49*** |
| Shannon index        | 0.15*   | 0.10       | 0.05         | 0.29*** | 0.51*** | 0.51*** | 0.49*** | 0.56*** | -0.04 | -0.49*** | 0.41*** |
| Pielou index         | -0.13*  | -0.15*     | -0.08        | -0.06 | 0.15* | 0.14*   | 0.01   | 0.06 | -0.04 | 0.06   |
| Functional groups    |         |            |              |      |     |      |      |      |      |       |
| Fungivores           | -0.30***| -0.38***   | -0.34***     | -0.53*** | 0.04 | 0.04 | 0.16* | 0.07 | -0.07 | 0.13*   | 0.15*   |
| Herivores            | 0.32*** | 0.31***    | 0.25***      | 0.57*** | 0.15* | 0.07 | -0.01 | 0.06 | -0.07 | -0.13* | 0.07     |
| Predators            | 0.06    | 0.05       | 0.06         | 0.10  | 0.07 | 0.21*** | 0.11  | 0.14* | 0.14* | -0.22*** | 0.02     |
| Omnivores            | 0.33*** | 0.34***    | 0.31***      | 0.34*** | -0.22*** | -0.28*** | -0.32*** | -0.27*** | 0.04 | 0.07 | -0.30*** |

Notes: The statistically significant (P < 0.05) results are in boldface type. See Table 2 for abbreviations. *P < 0.05; **P < 0.01; ***P < 0.001.

Fig. 4. Path diagrams showing the direct and indirect effects of climate, vegetation, and soil quality along the elevational gradient on soil macroinvertebrate abundance. See Table 2 for abbreviations.
Generally, these factors are thought to be important drivers of the elevational distribution pattern for soil fauna (Sanders and Rahbek 2012). Our SEMs were also consistent with those from previous studies (Briones et al. 2010, Yin et al. 2017a, Morales-Márquez et al. 2018), indicating that climate and soil quality had significant direct effects on the abundance of soil macroinvertebrates (Fig. 4). Interestingly, consistent with our expectation, our model revealed the indirect pathway that is linked to alterations in soil macroinvertebrate abundance due to elevation. Specifically, the positive effects were driven by soil quality, especially the soil organic carbon and total nitrogen, increasing with increased elevation. This is most likely the result of the low soil organic matter mineralization rate and high litter accumulation on the forest floor at high elevations (Table 2). Moreover, the close relationship between soil quality and soil fauna abundance is in accord with many previous studies (Izadi et al. 2017, Yin et al. 2017a, Morales-Márquez et al. 2018). Therefore, our results suggest that elevation can have an indirect effect on soil fauna abundance by directly affecting soil quality. In addition, previous studies have verified that plant species richness has direct effects on soil fauna and soil microbes (Scherber et al. 2010, Wu et al. 2012), and the altered litter quantity and quality as well as the root exudates may be the main cause (Brussaard 1998, Srivastava et al. 2009, Eisenhauer et al. 2010). Similarly, we found that plant species richness and litter quantity had significant correlations with soil macroinvertebrate composition and trophic structure (Table 4). However, inconsistent with our expectation, the direct effects of vegetation on soil macroinvertebrate abundance were not significant in the four seasons (Fig. 4). Strikingly, we observed that elevation had significant indirect effects on the soil quality by litter mass, rather than the plant species richness (Fig. 4). This suggests that the litter quantity on the forest floor plays a key role in the elevational distribution of soil macroinvertebrate abundance.

**Conclusions**

This study explored the soil macroinvertebrate composition and structure at different forests along an elevational gradient from 960 to 3058 m on the eastern Tibetan Plateau, China. The individual abundance, family richness, and diversity of soil macroinvertebrates dramatically increased with increasing elevation. Furthermore, the dynamics of the composition and functional structure of soil macroinvertebrate differed significantly among seasons at different forest types. The SEMs suggested that elevation indirectly influenced soil macroinvertebrate abundance by affecting climate (e.g., temperature) and soil quality (e.g., soil organic carbon and total nitrogen). Furthermore, vegetation might indirectly modulate soil macroinvertebrate abundance by controlling plant litter input. Our results suggest that temperature and soil nutrients are crucial regulators of soil macroinvertebrate elevational distributions and highlight the importance of plant litter input in determining the composition and structure of soil macroinvertebrates at different elevations.

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