Dear Associate Editor Michael Bahn,

Thank you very much for kindly considering our manuscript (bg-2017-298), “Soil properties determine the elevational patterns of base cations and micronutrients in plant-soil system up to the upper limits of trees and shrubs”. We have carefully considered all the thoughtful and valuable comments and suggestions from you and the reviewers and revised our manuscript accordingly. We believe that we have addressed and answered the major and minor comments and questions and the manuscript is in good shape now. We will be delighted to improve the manuscript further if you and the reviewers get more comments on it.

Below we address the comments point by point. Reference to line numbers is for the revised manuscript with changes marked (bg-2017-298).

**Comments from Editor:**

Reviewer 1 questioned the comparability of your sites, which is a key issue to be considered in your revisions. Furthermore, I ask you to provide the addition information requested and to streamline the manuscript, focusing more strongly on the novel aspects of your study.

**Reply:** Regarding the comparability of our sites, it can be seen from the information provided in Table S1 in terms of climatic conditions, soil parent materials, bedrocks, and soil types, that the three sites were not comparable. We chose distinct study sites (subtropical, dry-temperate and wet-temperate) expecting to find general patterns for the distribution of base cations and micronutrients in plant-soil systems along elevational gradients up to the upper limits of trees and shrubs. The detailed answer can be found in ‘Response to Reviewer #1’ and related information has also mentioned in the text (Lines 116-118).

We have also streamlined the manuscript to present the current knowledge gaps and stressed the novel aspects of our study. For example, in Lines 63-65: ‘However, little attention has been paid to base cation and micronutrient availabilities as well as their inputs and outputs under changing environmental conditions’; in Lines 70-73: ‘Physiological studies of treeline trees have mainly focused on macronutrients (e.g.,
nitrogen (N), phosphorus (P), and Ca, while there are few data available for
micronutrients in plant-soil systems along elevational gradients’; in Lines 83-85:
‘Whether plants growing at high elevations have higher or lower base cation and
micronutrient concentrations is still unclear’; and in lines 89-94: ‘Uncertainties still
exists whether soil properties, plant cover, or environmental factors determine the
base cations and micronutrients in plant-soil systems. We, therefore, studied the base
cation (Ca, Mg, and K) and micronutrient (Fe, Mn, and Zn) concentrations in
plant-soil systems along elevational gradients up to the alpine treeline and shrubline in
sub-tropic, dry temperate and wet temperate climate zones in China’.

Response to Reviewer #1

Comment 1:
It is not clear to me to which extent the different sites of a given elevation gradients
are comparable or not. The flora, soils, parent material seem quite different among
altitudes. It is possible that initial heterogeneities among altitudes are the cause of the
inconsistent relationships between elevation and ecosystem properties.

Reply: Three sites selected were actually not so comparable and showed distinct
climatic conditions and soil parent materials (information provided in Table S1). They
were chosen mainly to investigate if general patterns existed for base cations and
micronutrients along elevational gradients. This information has been added in Lines
116-118.

Initially, we expected to find consistencies and comparability for the distribution
of base cations and micronutrients in plant-soil systems among sites. Therefore, we
collected samples in a similar way under the same and most common tree species and
shrub species and identify their elevational ranges for each site (mentioned in Lines
134-135). Samples were collected at upper limits of treeline and shrubline, middle
elevation and the lowest elevation of tree/ shrub distribution. As suggested by our
results, the elevational distribution of base cations and micronutrients were not that
similar among sites. We now mention that initial differences in soil properties (e.g.,
parent material) may have played a role in the inconsistent relationships between
elevation and ecosystem properties (please see Lines 350-352).

**Comment 2:**
The manuscript is too long. Indeed, it reports results that are already obvious and well-established relationships (for instance: lines 251-257; line 258; lines 262-267; Figure S2; lines 362-364). I recommend to shorten the manuscript and to focus it on what is new (for instance lines 279-281): that is to say, the weak relationship between elevation on the one hand, and base cations and micronutrients on the other hand.

**Reply:** Thanks so much for the constructive comment. We have re-written and shortened the manuscript. The already obvious and well-established relationships have been deleted and replaced by the new findings (Lines 272-277, Lines 281-286).

**Comment 3:**
Lines 29-32: these patterns are not restricted to mountains but are relevant for all soils.

**Reply:** We agree with the reviewer’s comment. Therefore, the statements have been replaced in Lines 29-35 to emphasize the difference between our findings and the well-established relationships.

**Comment 4:**
Lines 43-44: not useful.

**Reply:** This information has been rephrased as ‘exchangeable calcium (Ca) and magnesium (Mg) are predominant base cations responsible in buffering soil acidity’. Please see Lines 46-47.

**Comment 5:**

**Reply:** Thanks so much for the suggestion and valuable references. These studies have proven that limitation of Ca, Mg and K can occur in terrestrial ecosystems, particularly when they are exposed to acid rain. We have revised the text into ‘… and deficiency of these nutrients can occur in terrestrial ecosystems’ and cited these recommended papers. Please see Lines 47-50.

**Comment 6:**
Lines 49-51: This applies also to Mn and Zn (see the book of Marschner, and the book of Graham et al.; both cited by the authors).

Reply: Thanks for the suggestion. We have rephrased the statement and cited the mentioned references here (Lines 54-55).

Comment 7:
Lines 54-59: these relationships are well-known.

Reply: We agree with this and have deleted the statement of “Both soil pH and soil organic matter are fundamental controllers over base cation and micronutrient availability and subsequently their concentrations in plant tissues”.

Comment 8:
Line 148: this kind of analysis should be made on fresh samples (not dried samples).

Reply: Indeed, we extracted available nitrogen from fresh soils. Therefore, we have revised the text to make it clearer (Lines 152-153 and Line 159).

Comment 9:
Line 159: replace “slurry” by “soil-solution suspension”.

Reply: This has been replaced (Line 169).

Comment 10:
Line 293-297: It depends on the range of pH values in each site (small ranges are unable to put such relationships into evidence). I recommend to use different symbols in the Figure S2 (one symbol per study area).

Reply: We agree with this point that small pH ranges are unable to put such relationships into evidence. In our study, soil pH ranged from 4.5 to 4.8 for Changbai (wet-temperate Mt.), from 5.0 to 6.2 for Balang (subtropical Mt.), and from 7.2 to 8.1 for Qilian site (dry-temperate Mt.). Across the three sites, the relatively large soil pH range would be enough to analyze such relationships. Also, we have used different symbols in the Figure S2 (one symbol for each study area).

Comment 11:
Line 300: replace “decomposed” by “decomposable”.

Reply: Thanks for pointing this out but we disagree with this comment. In our opinion it should be “decomposed”. “Decomposable” refers to the recalcitrance of
SOM, but that is not what we mean here. What we mean is that SOM that is more decomposed tends to have a lower C:N ratio (because the C is burned off) and tends to have more functional groups that are negatively charged (Line 313).

**Comment 12:**
Lines 302-303: This reference is about croplands. It seems to be not relevant.

**Reply:** The reference has been replaced by a study conducted in forest ecosystems (Haberhauer et al., 1998) (Lines 315-316).

**Comment 12:**
Lines 333-336 and 343-345: another explanation could be that initial differences in biogeochemical properties among elevation positions were larger than the effects of elevation. In other words, an elevation effect might exist, but it is of a too small magnitude to be detected with this study design.

**Reply:** Thanks so much for the suggestion. We agree with the view that an elevation effect might exist but is too small to be detected in this study. Related information has been added in Lines 350-352.

**Comment 13:**
Lines 353-354: I disagree. See for instance the compilation in Marschner’s book.

**Reply:** Thanks for the comment. We have deleted the statement of “Very limited progress has been made towards base cation and micronutrient translocation among plant tissues”.

**Comment 14:**
Table 1 should be merged with Table 2.

**Reply:** As suggested, Table 1 and Table 2 have been merged.

**Comment 15:**
Table 4: these relationships are not new. Please move this table to supplementary materials.

**Reply:** Table 4 has been moved to supplementary materials as Table S3.

**Comment 15:**
Table S1: MAP values are probably along the elevation gradient in Balang and in Qilian (such as in Changbai). Therefore, please indicate the range of MAP values for
all sites. –MAT: please indicate range of values for temperature. –Soil parent materials are important drivers of soil biogeochemistry (Castle & Neff, 2009; Augusto et al., 2017). This information should be provided.

Reply: The range values of MAP and MAT have been provided in Table S1. We agree that soil parent materials are important drivers of soil biogeochemistry. Thus, information about soil parent materials and mother rock has been added in Table S1.

Comment 16:
Figure S2: in panels c and e, the relationships are clearly non-linear. Hence, why using a linear fitting?

Reply: Thanks so much for pointing this out. The relationships in panels c and e have been changed to fit using a power function curve.

Comment 17:
I suggest to change site names. For instance, “Balang” by “Subtropical mountain”.

Reply: We have changed the site names of “Balang”, “Qilian” and “Changbai” into “subtropical Mt.”, “dry-temperate Mt.” and “wet-temperate Mt.” in both text and figures.

Response to Reviewer #2

Comment 1:
My main concern is the lack of information from the study systems and sampling design which currently limits the ability to fully interpret the results. Information of the elevations studied at each location – which should automatically provide elevational ranges studied – is needed to provide information on, and assess, the comparability among sites studied.

Reply: We have provided the information of elevational ranges including soil parent materials, bedrock and ranges of both MAP and MAT in Table S1. This has also been mentioned in Lines 148-149 of main text.

Comment 2:
Other relevant information to include would have been MAT and MAP along the studied elevational ranges at each gradient. Water movement is important for the
movement and concentrations of soil base cations and nutrients, and is influenced by slope and inclination (local topography at each elevation). So if available, this information would be valuable to include. Another factor that can influence soil properties and processes is the underlying bedrock, and it should be particularly relevant here.

Reply: Thanks for the comments. We have provided ranges of MAT and MAP along elevational gradients for each site in Table S1. Unfortunately, we do not have data of local topography at each elevation. The information about soil parent material and bedrock was also added for each study site in Table S1.

Comment 3:
The approach used – sampling soil and plant tissues from/under trees and shrubs – can be valuable to address how plant-soil linkages changes along environmental gradients. The species elevational range is provided in the methods, but it is not clear which part of their range was sampled or why these specific plant species were targeted for this study. For instance, are they species that are well adapted to certain environmental conditions represented by each location? And/or are they the commonest species of these growth forms at each location? This kind of information is relevant in describing the context of the study and study systems.

Reply: Thanks so much for the observation. We agree with the point that sampling soil and plant tissues from/under trees and shrubs can be valuable to address how plant-soil linkages changes along environmental gradients. This kind of linkages has been discussed in section 4.2 from Lines 352 to 368. Indeed, the targeted plant species in this study are well adapted and commonest species of the elevational ranges acting as treeline trees or shrubline shrubs. This kind of relevant information has been added in the main text in Lines 134-135.

Comment 4:
Additionally, the species chosen are functionally rather different which consequently could influence soil properties in different ways. While this is explicitly addressed, given that SOC and pH are important drivers for many patterns, the identity of the species may be an important factor influencing the results (which the authors also
briefly mention in the discussion on lines 350-352). Although site is a random factor in the analysis across site effects, I wonder if treating them as main factors (trees versus shrubs) without accounting for the differences among species within these growth forms may mask some important information that seems central to the study question of plant-soil linkages and how they may change with elevation.

Reply: Thanks so much for mentioning this. For each site, the targeted tree species were the dominant species and the shrubs were the commonest species within each chosen elevational range, serving as the treeline tree or shrubline shrub. Thus, we grouped them into different life forms of tree and shrub. If we replace site as a random factor with life form as a main factor, it seems we would no longer make a distinction between sites, which we believe is necessary. However, we initially expected to find consistent elevational patterns of base cations and micronutrients across sites instead of considering differences caused by sites and life form (please see the hypotheses in Lines 97-103). Additionally, we analyzed soil base cations and micronutrients under tree and shrub canopies separately at each site (please see Table S2).

Specific comments:

Comment 5:
Line 117-123: Is the MAP values reported relevant for the study locations/gradients? Does MAP change with elevation along the range studied at the three gradients, or only from the Changbai mountain?

Reply: Indeed, MAP changes with elevation along the range. We have provided ranges of MAP and MAT along the elevational range in Table S1.

Comment 6:
Line 125-130: Why were these specific plant species studied?

Reply: These studied species are the commonest species of the elevational ranges acting as treeline tree or shrubline shrubs. This has been mentioned in Line 134-135.

Comment 6:
Line 135-140: More information on sample handling prior to analysis would be valuable here. Were the samples for each species/below each species bulked?

Reply: The samples were not bulked for each species/below each species. At each
elevation, we selected 6 plots to serve as 6 replicates. And within each plot, 6-10 samples were collected and composited. The related information has been presented in Line 141-146.

**Comment 7:**
Line 143-154: Was all soil dried? A number of these analyses should be done on wet soils (e.g. lines 150-153).

**Reply:** Not all the soil was dried. We separated soil samples into two parts with one of them being air-dried and the other stored at 4 °C for further analyses (see Lines 152-153). Soil nitrate and ammonium concentration were determined on fresh soil samples. This information has been incorporated in Line 159.

**Comment 8:**
Line 170-185: The abstract and results mention results from a multiple regression but this analysis is not mentioned in the methods section.

**Reply:** The multiple regression analysis has been removed in both abstract and results as it contributes little to our discussion and makes our manuscript too long (as commented by Reviewer #1).

**Comment 9:**
Line 185-190: Soil pH under tree canopies decreased with elevation, but increased with elevation under some shrubs. Are there any understory species growing under trees, or was the ground more or less open, or covered with litter from the target tree only? Sampling soil specifically under a tree and specifically under a shrub may be very different in terms of targeting the influence of the actual species on soils.

**Reply:** We agree with the point that large differences exist between soil samples under tree canopy and under shrub canopy. Indeed, soils were covered with more litter from targeted trees than that from shrubs.

**Comment 10:**
Line 279-295: Or could it indicate species specific responses and effects on soil properties?

**Reply:** Thanks so much for pointing this out. We agree with this view and incorporated this in Lines 309-310.
Comment 11:
Lines 337-341, 350-352: It seems plausible that the concentrations of nutrients in the soil are important to determine plant tissue nutrient concentrations and also vice versa, but it is not clear how the final conclusion (referring to Hobbie 1992, lines 350-352) can be drawn from the data or the discussion in this same paragraph.
Reply: Thanks for the nice comment. We have rephrased the sentence into “Inconsistent elevational patterns of plant nutrient concentrations could also be derived from the fact that individual plant species reinforced patterns of soil nutrient availabilities in their vicinity causing a positive feedback between plant and soil” (Lines 365-368).

Comment 12:
Reply: This reference has been cited in the manuscript (Line 350).

Comment 13:
Technical corrections: Line 70—There is a word missing to connect the first part with the second part of the sentence.
Line 365: Word missing: “one of (the) main…”
Reply: We thank the reviewer for the observation and apologize for the oversight. These have been corrected in Line 72 and 379.

With above corrections, the manuscript is hereby resubmitted to the journal. We are thankful for the reviewers’ work and glad to respond any further questions that you have. We look forward to a positive response from you.
Thanking you,

Yong Jiang
Soil properties determine the elevational patterns of base cations and micronutrients in plant-soil system up to the upper limits of trees and shrubs

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Abstract

To understand whether base cations and micronutrients in the plant-soil system change with elevation, we investigated the patterns of base cations and micronutrients in both soils and plant tissues along three elevational gradients in three climate zones in China. Base cations (Ca, Mg and K) and micronutrients (Fe, Mn and Zn) were determined in soils, trees and shrubs growing at lower and middle elevations as well as at their upper limits on Balang (subtropical, SW China), Qilian (dry-temperate, NW China) and Changbai (wet-temperate, NE China) mountains. No consistent elevational patterns were found for base cation and micronutrient concentrations in both soils and plant tissues (leaves, roots, shoots and stem sapwood). Soil pH, soil organic carbon (SOC), total soil nitrogen (TN), the SOC to TN ratio (C:N), and soil extractable nitrogen ($\text{NO}_3^-$ and $\text{NH}_4^+$) determined the elevational patterns of soil exchangeable Ca and Mg and available Fe, Mn and Zn. However, the controlling role of soil pH and SOC was not universal as revealed by their weak correlations with soil base cations under tree canopies at the wet-temperate mountain and with micronutrients under both tree and shrub canopies at the dry-temperate mountain. In most cases, soil base cation and micronutrient availabilities played fundamental roles in determining the base cation and micronutrient concentrations in plant tissues. An exceptional case existed for the decoupling of leaf K and Fe with their availabilities in the soil. Our results highlight the importance of soil physicochemical properties (mainly SOC, C:N and pH) rather than elevation (i.e., canopy cover and environmental factors, especially temperature), in determining base cation and micronutrient availabilities in soils and...
subsequently their concentrations in plant tissues.

**Key words** base cation, micronutrient, plant tissue, soil physicochemical property, shrubline, treeline
1 Introduction

Base cations and micronutrients are essential for soil fertility and plant physioecological processes of photosynthesis, metabolism, growth and productivity (Salisbury and Ross, 1992). For instance, exchangeable calcium (Ca) and magnesium (Mg) are predominant base cations responsible in buffering soil acidity, and deficiency of these nutrients can occur in terrestrial ecosystems (Naples and Fisk, 2010; Baribault et al., 2012; Sardans and Peñuelas, 2015), particularly when they are exposed to acid rain. Micronutrient deficiency, on the other hand, occurs more frequently, for instance, when replenishment of micronutrients via litter decomposition do not keep pace with output processes of plant uptake and leaching (White and Zasoski, 1999; Hernandez-Apaolaza, 2014). High soil pH can limit the availability of micronutrients of iron (Fe), manganese (Mn) and zinc (Zn) (Reisenauer, 1988; Lucena, 2000; Rengel, 2007), while low soil pH can induce toxicities of trace metals constraining terrestrial net primary productivity (He et al., 2005; Reisenauer, 1988; Tian et al., 2016). The concentrations of soil base cations and available micronutrients were suggested to be positively and negatively correlated with soil pH, respectively, but both positively correlated with soil organic matter (SOM) concentration (Reisenauer, 1988; Wang et al., 2017). Quantifying base cation and micronutrient concentrations in soils and plant tissues (leaves, roots, shoots, and stems) can help understand the nutritional status and potential deficiencies of micronutrients during plant growth (Richardson, 2004). However, little attention has been paid to base cation and micronutrient availabilities as well as their inputs and outputs under...
changing environmental conditions (Rengel, 2007).

The plant distribution and growth along elevational gradients reflect changes in environmental conditions (Li et al., 2003, 2004, 2006, 2008a,b; Zhu et al., 2012a,b). Plants growing at high elevation, especially close to their upper limits, are expected to be highly sensitive to climate change, in particular to global warming (Noble, 1993).

Physiological studies of treeline trees have mainly focused on macronutrients such as nitrogen (N), phosphorus (P), and Ca (Richardson, 2004; Liptzin et al., 2013; Mayor et al., 2017), while there are few data available for micronutrients in plant-soil systems along elevational gradients (Wang et al., 2009).

Two hypotheses have been proposed to explain nutrient accumulation and/or nutrient deficiency in plant tissues at high elevations (Oleksyn et al., 2002; Richardson, 2004). First, the decrease in temperature with increasing elevation declines soil microbial activity and plant metabolism, and thus constrains soil nutrient cycling and plant uptake processes (Körner & Paulsen, 2004; Thébault et al., 2014). At the alpine treeline, low temperature slows down microbial-mediated litter decomposition and thus reduces nutrient supply to plants (van den Driessche, 1974; Richardson, 2004). Second, another paradigm exists that plants retain higher nutrient concentrations in their tissues to maintain metabolic capacity and to avoid cold injury at higher elevations with cold growth conditions (Oleksyn et al., 2002). Whether plants growing at high elevations have higher or lower base cation and micronutrient concentrations is still unclear.

The change in environmental conditions along elevational gradients, including
temperature and growing season length (Barry, 1981), provides a unique opportunity
to examine the spatial distribution of base cations and micronutrients in plant-soil
systems. Uncertainties still exists whether soil properties, plant cover, or
environmental factors determine the base cations and micronutrients in plant-soil
systems. We, therefore, studied the base cation (Ca, Mg, and K) and micronutrient (Fe,
Mn, and Zn) concentrations in plant-soil systems along elevational gradients up to the
alpine treeline and shrubline in sub-tropic, dry temperate and wet temperate climate
zones in China. Soil base cation and micronutrient concentrations can increase
through soil weathering and decomposition of organic matter, but can decrease with
plant uptake and loss through leaching. At low elevations, forests have closed
canopies and become increasingly more open with elevation. We therefore
hypothesized that soil base cation and micronutrient concentrations increase with
increasing elevation because plant uptake decreases more than the supply through
weathering and decomposition with elevation. We also expected that plants at higher
elevations would have greater base cation and micronutrient concentrations in their
tissues (leaves, roots, shoots, and stem sapwood) to maintain physio-ecological
processes in a colder environment. To test these hypotheses, we collected soil and
plant samples along three elevational gradients from lower elevations up to the alpine
treeline or shrubline in three climate zones in China, and studied the Ca, Mg, K, Fe,
Mn, and Zn concentrations in plant-soil systems.

2 Materials and methods
2.1 Site description and sample collection

Study sites were located in three climate zones (summarized in Table S1): Balang mountain with a subtropical climate located in Wolong Nature Reserve (“subtropical Mt.”, 102°52'-103°24'E, 30°45'-31°25'N) in southwestern China, Qilian mountain located in the dry-temperate climate zone (“dry-temperate Mt.”, 102°58'-103°01'E, 37°14'-37°20'N) in northwestern China, and Changbai mountain with a wet-temperate climate (“wet-temperate Mt.”, 126°55'-129°00'E, 41°23'-42°36'N) located in northeastern China (see Fig. S1). Three distinct sites were chosen to find the general patterns for base cations and micronutrients along elevational gradients across climate scales rather than to investigate the comparability among study sites. The subtropical Mt. is influenced by warm-wet monsoon masses in summer and continental air masses in winter (Li et al., 2012). The mean annual precipitation (MAP) of the subtropical Mt. is about 846 mm monitored by Dengsheng Meteorological Station at 2730 m (Li et al., 2012). For the dry-temperate Mt., the MAP is 435 mm, which is monitored by the Qilian weather station at 2787 m altitude (Qiang et al., 2003). The wet-temperate Mt. is located in a typical continental temperate monsoon climate zone with MAP increasing from 632 to 1154 mm along the elevational gradient from 530 to 2200 m (Shen et al., 2013).

In this study, the alpine treeline and shrubline are defined as the upper limit of obvious trees and shrubs, respectively. The trees that were investigated are Abies faxoniana (elevation range 2860-3670 m) for the subtropical Mt., Picea crassifolia (elevation range 2540-3250 m) for the dry-temperate Mt., and Betula ermanii...
(elevation range 1700-2030 m) for the **wet-temperate Mt.**. The shrubs are *Quercus aquifolioides* (elevation range 2840-3590 m) **for the subtropical**, *Salix gilashanica* (elevation range 3020-3540 m) **for the dry-temperate**, and *Vaccinium uliginosum* (elevation range 1430-2380 m) **for the wet-temperate Mt.** The targeted treeline trees, and shrubline shrubs are dominant and common species for each study site. The soils from the three sampling sites of **subtropical**, **dry-temperate**, and **wet-temperate Mts.** were classified as Umbric Cryic Cambisols, Calcaric Ustic Cambisols and Andic Gelic Cambisols, respectively (IUSS Working Group WRB, 2014).

Plant tissue samples of current-year mature leaves, roots (< 2 mm), stem sapwood, and shoots (twigs) from trees and shrubs were collected at lower and middle elevations, as well as at the upper limits. At each elevation, 6 plots (10 m × 10 m) were selected **to serve as 6 replicates** on southern slopes. Within each plot, 6-10 trees or shrubs of similar height were randomly selected for tissue sampling. Soils (0-10 cm) were directly collected under the canopy of trees or shrubs sampled for each plot using a 3-cm diameter corer. **Both plant and soil samples were homogenized and composited within each plot.** Samples were collected at the middle of July for **subtropical Mt.**, at the beginning of August for **dry-temperate Mt.**, and at end of August for **wet-temperate Mt.** in 2014. The main characteristics of the three study sites are summarized in Table S1.

### 2.2 Chemical analysis

The soil samples were **separated into two subsamples with one subsample being**
air-dried to constant weight and the other one stored at 4 °C for further analyses. For subtropical and wet-temperate Mts., soil organic carbon (SOC) and total nitrogen (TN) was determined on ground soils using an elemental analyzer (Vario MACRO Cube, Elementar, Germany). For dry-temperate Mt., the ground soil samples were treated with 12 M HCl according to Wang et al. (2015) to remove inorganic C before organic C determination on the elemental analyzer. Soil NO₃⁻-N and NH₄⁺-N were extracted from fresh soils with a 2 M KCl solution and measured using an AutoAnalyser III continuous Flow Analyzer (Bran & Luebbe, Norderstedt, Germany). Soil total inorganic nitrogen (TIN) was the sum up of extractable NO₃⁻-N and NH₄⁺-N. Soil Olsen phosphorus (P) was quantified by colorimetric analysis after extraction with a 0.5 M NaHCO₃ solution (Olsen et al., 1954).

A subsample of 5 g soil was used to determine soil pH in a 1:5 (w/v) soil-to-water extract. Soil exchangeable base cations were extracted with a 1 M ammonium acetate solution (Wang et al., 2017). Soil available micronutrients were extracted by diethylenetriamine pentaacetic acid (DTPA) according to Lü et al. (2016). Briefly, 10 g of soil was extracted by 20 ml 0.005 M DTPA + 0.01 M CaCl₂ + 0.1 M TEA (triethanolamine) (pH 7.0). The soil-solution suspension was shaken for 2 h at 180 rpm and then filtered through ash-free filter paper. The concentrations of base cations and micronutrients were determined using an atomic absorption spectrometer (AAS, Shimadzu, Japan).

Plant samples of leaves, roots, shoots and stem sapwood were oven-dried and ground for base cation and micronutrient analyses. Root samples were washed prior to
being oven-dried. To determine total base cation and trace element concentrations, 0.2 g plant samples were digested with a mixture of acids of HNO$_3$ and HClO$_4$ (5:1, v/v) on a hot plate. After the mixture turned into clear solution, the digests were decanted into a 50 ml volumetric flasks and the volume was adjusted into 50 ml. The concentrations of Ca, Mg, K, Fe, Mn, and Zn were determined by the AAS (Shimadzu, Japan).

### 2.3 Statistical analyses

Normality of data was determined using the Kolmogorov-Smirnov test, and homogeneity of variances using Levene’s test. Two-way ANOVAs were executed to determine the effects of plant life form (tree or shrub), elevation position and their interactions on soil pH, SOC, soil exchangeable base cations and available micronutrients, and total base cations and micronutrients in plant tissues. We assigned sampling site as a random factor in the statistics, as this study aimed to test the general elevational patterns instead of site-specific heterogeneity of base cations and micronutrients in plant-soil system across three sites. Within each site, the effect of elevation on measured parameters was determined by multiple comparisons with a Tukey design for soils and each life form. Pearson correlation analysis was used to determine the relationships between measured parameters. All statistical analyses were performed in SPSS 16.0 (SPSS, Inc., Chicago, IL, USA) and statistical significance was accepted at $P < 0.05$. 
3 Results

3.1 Soil pH and SOC

Soil pH was significantly different among elevational positions (Table 1). For both subtropical and dry-temperate Mts., soil pH decreased with increasing elevation under tree canopy, while it was the opposite trend under shrub canopy (Fig. 1a). For wet-temperate Mt., the upper limit of shrubs had significantly higher soil pH (Fig. 1a).

For all three sites, SOC concentration showed a hump-shaped trend with the highest value at the middle elevation under tree canopy (Fig. 1b). Under shrubs, SOC concentration significantly increased with increasing elevation for subtropical and wet-temperate Mts., while it was the lowest at the upper limit of shrubs for dry-temperate Mt. (Fig. 1b).

3.2 Changes in soil base cations and available micronutrients

Soil exchangeable Ca and Mg decreased with increasing elevation under tree canopy of subtropical and wet-temperate Mts, and under shrubs of dry-temperate Mt. (not for Mg) (Fig. 2a,b). However, they showed the opposite trend under shrubs of subtropical (not for Mg) and wet-temperate Mts. and under trees of dry-temperate Mt. (Fig. 2a,b). Soil exchangeable K decreased with increasing elevation under tree and shrub canopies at subtropical Mt. and under trees at dry-temperate Mt. (Fig. 2c).

Soil available Fe was significantly affected by elevation position (Table 1, Fig. 2d). The upper limit had the lowest concentration under both tree and shrub canopies for subtropical Mt. and under shrub canopy for wet-temperate Mt. (Fig. 2d). For
For subtropical Mt., soil available Fe significantly increased with increasing elevation under both tree and shrub canopies (Fig. 2a). For subtropical Mt., soil available Mn was significantly higher at the middle elevation under tree canopies. Soil available Mn decreased with increasing elevation under shrub and tree canopies for subtropical and wet-temperate Mts., respectively, while it showed the opposite trend under both tree and shrub canopies of dry-temperate Mt, and under shrubs of wet-temperate Mt. (Fig. 2e). Soil available Zn was significantly affected by plant life form and the interactive effect between life form and elevation position (Table 1). Specifically, soils at the upper limit had the highest available Zn under shrubs at wet-temperate Mt.

3.3 Base cations in plants

For subtropical Mt., a significant decrease of Ca concentration was detected in the leaves of trees and shrubs (Fig. 3a), roots and shoots of trees (Fig. 3b,c), and stem sapwood of shrubs (Fig. 3d). For dry-temperate Mt., Ca concentration decreased with increasing elevation in roots, shoots and stem sapwood of trees (Fig. 3b,c,d), and in shoots and stem sapwood of shrubs (Fig. 3c,d). For wet-temperate Mt., shoot Ca concentration decreased with increasing elevation for trees (Fig. 3c). Along with increasing elevation, a significant decrease of Mg was found in shrub leaves, tree roots, shrub shoots and stem sapwood at sub-tropical Mt. (Fig. 3e,f,g,h), and in roots, shoots and stem sapwood of trees at dry-temperate Mt. (Fig. 3f,g,h), and in leaves and shoots of both trees and shrubs at wet-temperate Mt. (Fig. 3e,g). With the increase in elevation, K concentration significantly decreased in leaves of trees, roots and stem sapwood.
sapwood of both trees and shrubs at **subtropical Mt.** (Fig. 3i,j,l), in tree shoots of **dry-temperate Mt.** (Fig. 3k), and in leaves of both trees and shrubs at **wet-temperate Mt.** (Fig. 3i).

### 3.4 Micronutrients in plants

For **subtropical Mt.**, Fe concentrations in leaves (Fig. 4a) and roots (Fig. 4b) showed a similar trend with soil available Fe, with the highest values at the middle elevation for both trees and shrubs. For **dry-temperate Mt.**, the highest Fe concentrations were found at the lower elevation in leaves (Fig. 4a), roots (Fig. 4b), shoots (Fig. 4c) and stem sapwood (Fig. 4d) for trees and in shoots (Fig. 4c) and stem sapwood (Fig. 4d) for shrubs. For **wet-temperate Mt.**, Fe concentration was the highest in tree shoots at the middle elevation (Fig. 4c), in shrub leaves at lower elevation (Fig. 4a), and in roots, shoots and stem sapwood of shrubs at the upper limit of trees (Fig. 4b,c,d).

The Mn concentration decreased with increasing elevation in leaves and shoots of both trees and shrubs at **subtropical Mt.** (Fig. 4e,g), in stem sapwood of shrubs at both **subtropical** and **dry-temperate Mts.** (Fig. 4h). The Mn concentration increased with increasing elevation in leaves of trees at **dry-temperate Mt.** (Fig. 4e), in roots of both trees and shrubs at **wet-temperate Mt.** (Fig. 4f), in shoots of shrubs and stem sapwood of trees and shrubs at **wet-temperate Mt.** (Fig. 4g,h).

The Zn concentration was the highest at middle elevation for trees in leaves at **wet-temperate Mt.** (Fig. 4i), in roots at **dry-temperate Mt.** (Fig. 4j), in shoots at **wet-temperate Mt.** (Fig. 4k) and in stem sapwood at **subtropical Mt.** (Fig. 4l). With the
increase in elevation, a decrease of Zn concentration was found in roots of trees at **subtropical Mt.** (Fig. 4j) and in stem sapwood of shrubs at **dry-temperate Mt.** (Fig. 4l); however, an increase of Zn was found in shrub roots at **wet-temperate Mt.**, in shoots of trees at **dry-temperate Mt.** and shrubs at **wet-temperate Mt.** (Fig. 4k), and in stem sapwood of trees at **dry-temperate Mt.** and shrubs at **wet-temperate Mt.** (Fig. 4l).

### 3.5 Correlations

Across all sampling sites and plant life forms, both soil exchangeable Ca and Mg were positively correlated with soil pH (Fig. S2a,b) and TN (Table 2), while they were negatively correlated with soil C:N, NO$_3^-$, and NH$_4^+$ (Table 2). For **wet-temperate Mt.**, both soil pH and SOC showed no relationship with soil exchangeable Ca and Mg under tree canopies, although SOC was positively related to exchangeable K (Table S2). Negative correlations were found for both Mg and K concentrations between stems and leaves (both $p < 0.01$; Table S3). However, Mg and K concentrations in roots showed no correlation with that in leaves (Table S3).

When analyzing data across sampling sites and plant life forms, soil available Fe, Mn and Zn were negatively correlated with soil pH ($p < 0.01$; Table 2, Fig. S2c,d,e), and soil available Fe and Zn were positively correlated with SOC ($p < 0.01$; Table 2).

However, available micronutrients had no relationships with both soil pH and SOC at **dry-temperate Mt.**, except for a positive correlation between soil pH and available Mn under shrub canopies (Table S2). For both Mn and Zn concentrations, significant and positive correlations were found between soil and plant tissues (Table S3).
available Fe was negatively correlated with Fe concentrations in shoots and stems (both $p < 0.01$; Table S3).

4 Discussion

4.1 Elevational patterns of base cations and available micronutrients in soils and relationships with pH and SOC

Contrary to our first hypothesis, no consistent elevational patterns were detected for soil exchangeable base cations and available micronutrients under either trees or shrubs. Inconsistent elevational patterns of soil base cations and available micronutrients indicated that plant uptake of these nutrients did not necessarily decrease more than nutrient supply at higher elevation due to more open canopies.

Our results suggest that soil physiochemical parameters were the dominant contributors and more important than environmental gradients affecting elevational patterns of soil exchangeable base cations and available micronutrients (Fig. S2, Table 2). For instance, soil available Fe, Mn and Zn followed patterns of SOC under trees along the elevational gradient at subtropical Mt. (Table S2), while for shrubs at subtropical Mt., soil pH, instead of SOC, regulated elevational patterns of soil available Fe, Mn and Zn (Table S2). Our findings are consistent with a vast amount of previous studies confirming the pivotal role of soil pH and SOC concentration in determining soil base cation and micronutrient availabilities (Sharma et al., 2004; Lü et al., 2016; Wang et al., 2017). However, the fundamental roles of SOC and soil pH in controlling soil base cation and micronutrient availabilities, was not universal as
suggested by the relatively weak relationships of soil pH and SOC with soil base
cations under tree canopies at wet-temperate Mt. and with micronutrients under both
tree and shrub canopies at dry-temperate Mt. (Table S2). This could indicate species-
and life form-specific effects on soil base cation and micronutrient availabilities.

Other soil parameters, such as C:N and extractable NO$_3^-$ and NH$_4^+$ also
influenced the availability of base cations (Table 2). Soil C:N ratio serves as an
indicator of SOM decomposition status where more decomposed SOM possesses a
lower C:N ratio (Sollins et al., 2009) and a higher content of negatively charged
functional groups (i.e. phenolic, carboxyl, and hydroxyl groups) (Haberhauer et al.,
1998). In this study, negative correlations between soil C:N and base cations (Table 2)
suggest that more decomposed SOM is beneficial for the retention of soil base cations.
Furthermore, soil with a higher level of extractable NO$_3^-$ predisposes cations to leach
accompanied by loss of NO$_3^-$ (Cremer and Prietzel, 2017). Therefore, significant
negative correlations were detected between soil NO$_3^-$ and base cations in this study
(Table 2). Soil extractable NH$_4^+$ was also negatively correlated to exchange with Ca
and Mg, possibly because NH$_4^+$ can exchange with base cations on surface soil
colloids into soil solution thereby enhancing their loss (Wang et al., 2015; Cusack et
al., 2016).

A negative correlation between soil pH and soil available micronutrients (Table 2)
might be due to precipitation of micronutrient cations at higher soil pH (Rengel, 2007).
Indeed, solubility of micronutrients was suggested to decrease from 100-fold (for Mn
and Zn) to 1000-fold (for Fe) with one-unit increase of soil pH (Rengel, 2001). Soil
organic matter plays an important role in micronutrient retention due to its negative charge (He et al., 2005; Wang et al., 2015, 2017). This may be a reason for the positive relationships between SOC and micronutrients (although not always significant, Table 2). While no general patterns were found for distribution of micronutrients under both tree and shrub canopies with elevation, our results suggest that the determinants of soil micronutrient availabilities were soil pH and SOC concentration, which are reflections of long-term climatic conditions, plant-soil interactions, and biogeochemical processes (Sinsabaugh et al., 2008).

4.2 Elevational patterns of base cations and micronutrients in plants and plant-soil system

In contrast to our second hypothesis, both trees and shrubs at higher elevation did not necessarily contain higher base cation and micronutrient concentrations in their tissues. No general patterns were found for base cations and micronutrients in both trees and shrubs along elevational gradients across the three sites (Fig. 3,4). Even normalizing the data to per unit concentration of soil available nutrients, there were still no consistent elevational patterns for both base cations and micronutrients in plant tissues (Fig. S3). This suggests that base cation and micronutrient concentrations in plants are influenced by other factors besides elevation-induced changes in temperature, precipitation, specific nutrient absorption characteristics of different tissues, soil base cation and micronutrient availabilities and other edaphic properties (Campo-Alves, 2003; Richardson, 2004). Another explanation could be that initial
differences in soil properties (e.g., parent material) among climate zones were larger than the effects of elevation. Soil base cation and micronutrient availabilities were an important factor influencing their concentrations in plant tissues across all plant species and sampling sites (Table S3). Similar results were found for macronutrients (i.e. nitrogen and phosphorus) suggesting that “plants are what they root in” (Elser et al., 2010; Han et al., 2014). However, plant nutrients did not covary with soil nutrients along a 2200 km-long climatic gradient in grasslands of northern China (Luo et al., 2015, 2016). The discrepancy of our study with Luo et al. (2015, 2016) might be driven by different ecosystem types (forest vs. grassland), dominant climatic factor gradients (temperature vs. precipitation), and different soil properties. The studies of Luo et al. (2015, 2016) were conducted in grassland ecosystems where precipitation played an essential role in nutrient concentrations in plant-soil systems. Moreover, base cation and micronutrient cycling processes are likely to be different between high-organic and fine-grained forest soils in our study versus low-organic and sandy grassland soils in Luo et al. (2016). Inconsistently elevational patterns in plant nutrient concentrations could also be derived from the fact that individual plant species reinforced patterns of soil nutrient availabilities in their vicinity causing a positive feedback between plant and soil (Hobbie, 1992).

The topic of base cation and micronutrient translocation in intact plant is important as it deals with the movement of micronutrients from root to the leaves for physiological activities, such as photosynthesis (Welch and Shuman, 1995). Also, it is an important process in determining plant chemical composition and subsequently
litter quality, litter decomposition and nutrient release (Sun et al., 2016). Given earlier findings that transport of base cations from roots to the leaves in woody plants is slow (van der Heijden et al., 2015), we found no significant correlation for both Mg and K between roots and leaves (Table S3). However, negative relationships of stem Mg vs. leaf Mg and stem K vs. leaf K suggest that the plant internal pools of base cations could act as sources of base cation supply for leaves (Weatherall et al., 2006).

Translocation of base cations within plant tissues is one of the main physiological mechanisms buffering low nutrient availabilities in soils (van der Heijden et al., 2015). For instance, supplementation of Mg is a critical process to maintain photosynthesis in forests growing on acid and cation poor soils (Verbruggen and Hermans, 2013). In support of this, we found significantly positive correlations between Mg and soluble sugar concentrations (one of the main photosynthate) in leaves across the three sites (Fig. S4a), while relationships were more pronounced at wet-temperate Mt. (Fig.S4b) where soil pH and exchangeable Mg was the lowest (Fig. 1a, 2b).

Unlike Ca, Mg, Mn and Zn, the concentrations of K and Fe in plant leaves decoupled with their availabilities in the soil (Table S3), which may suggest that not only availability of these nutrients in soils affect their leaf concentrations, but that also other environmental factors (e.g., temperature) played more important roles in affecting plant nutrition (van den Driessche, 1974). We do not know why this decoupling only occurred for K and Fe, but possibly factors such as temperature constrained soil microbial activity and plant metabolism (Körner and Paulsen, 2004) and subsequently uptake of these nutrients by plants. On the other hand, plants often
increase nutrient uptake to compensate for decreased metabolism at low temperature (Reich and Oleksyn, 2004). Thus, these opposite effects of temperature on K and Fe concentrations in plant tissues may have obscured their relationships with K and Fe availability in the soil along the elevational gradients. While plant nutrient concentrations were mainly influenced by nutrient availabilities in the soil and by plant-internal translocation processes, we found no consistent evidence that plants accumulate more base cations and micronutrients in their tissues to better adapt to cold environments at higher elevation.

5 Conclusions

We did not find consistent elevational patterns of base cations and micronutrients in plant-soil systems along three different elevation transects up to the alpine treeline and shrubline in different regions of China. Rather, our results highlight the essential roles of specific edaphic properties of soil pH, SOC and extractable nitrate and ammonium in regulating soil base cation and micronutrient availabilities across climate zones. Soil available base cations and micronutrients were mostly positively correlated with concentrations of base cations and micronutrients in plant tissues, except for K and Fe. Our results suggest that base cation and micronutrient concentrations in plants (trees and shrubs) growing at their upper limits are largely controlled by their availabilities in the soil rather than by plant adaptations to cold environment at higher elevations.
Acknowledgments

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Data Availability

Data sets for this paper can be obtained via personal communication.

Author contributions

Mai-He Li designed the study; Xue Wang, Heyong Liu, Jinfei Yin and Zhan Shi did the plant and soil measurements; Ruzhen Wang and Xue Wang analyzed the data; Ruzhen Wang wrote the manuscript; Mai-He Li, Feike A. Dijkstra and Artemi Cerdà revised the manuscript; Mai-He Li and Yong Jiang provided funding and laboratory facilities for this study.

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Tables

**Table 1** Two-way ANOVAs (F values) of the effect of plant life form (L, tree or shrub), elevation position (E), and their interactions on soil pH, soil organic carbon (SOC), base cations and micronutrients in soils (exchangeable/available form) and plants (total) across sampling sites.

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<th>SOC</th>
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<th>Soil Mg</th>
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* and ** indicate significant level at P < 0.05 and 0.01, respectively.
The TN, C:N, TIN, and Olsen P represent soil total nitrogen, SOC to TN ratio, total inorganic nitrogen, and Olsen phosphorus.

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<th>Fe</th>
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<td>0.19*</td>
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* and ** indicate significant level at $P < 0.05$ and 0.01, respectively.
Fig. 1 Soil pH values (a) and soil organic carbon (SOC) concentration (b) at lower and middle elevations as well as at the upper limit of treelines or shrublines for each of the three sites. Different letters indicate significant differences among three elevations within treeline or shrubline for each site.
Fig. 2 Concentrations of soil exchangeable base cations of Ca (a), Mg (b) and K (c) and available micronutrients of Fe (d), Mn (e) and Zn (f) at lower and middle elevations as well as at the upper limit of trees or shrubs for each of the three sites. Different letters indicate significant differences among three elevations within treeline or shrubline for each site.
Fig. 3 Base cation concentrations of Ca (a, b, c, d), Mg (e, f, g, h) and K (I, j, k, l) in plant tissues of leaf, root, shoot and stem sapwood at lower and middle elevations as well as at the upper limit of trees or shrubs for each of the three sites. Different letters indicate significant differences among three elevations within treeline or shrubline for each site.
Fig. 4 Micronutrient concentrations of Fe (a, b, c, d), Mn (e, f, g, h) and Zn (i, j, k, l) in plant tissues of leaf, root, shoot and stem sapwood at lower and middle elevations as well as at the upper limit of trees or shrubs for each of the three sites. Different letters indicate significant differences among three elevations within treeline or shrubline for each site.