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Soil and plant $\delta^{15}N$ have a different response to experimental warming: A global meta-analysis

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Abstract. The ^{15}N natural abundance composition ($\delta^{15}N$) in soils or plants is a useful tool to indicate the openness of ecosystem N cycling. This study was aimed to evaluate the influence of the global warming on soil and plant $\delta^{15}N$. We applied a global meta-analysis method to synthesize 79 and 76 paired observations for soil and plant $\delta^{15}N$ from 20 published studies, respectively. Results showed that the mean effect sizes of the soil and plant $\delta^{15}N$ under experimental warming were -0.524 (95% CI: -0.987 to -0.162) and 0.189 (95% CI: -0.210 to 0.569), respectively. This indicated that soil and plant $\delta^{15}N$ had negative and positive responses to warming at the global scale, respectively. Experimental warming significantly ($p < 0.05$) decreased soil $\delta^{15}N$ in Alkali soil, grassland/meadow, and under air warming, whereas it significantly ($p < 0.05$) increased soil $\delta^{15}N$ in neutral soil. Plant $\delta^{15}N$ significantly ($p < 0.05$) increased with increasing temperature in neutral soil and significantly ($p < 0.05$) decreased in alkali soil. Latitude did not affect the warming effects on both soil and plant $\delta^{15}N$. However, the warming effect on soil $\delta^{15}N$ was positively controlled by the mean annual temperature, which is related to the fact that the higher temperature can strengthen the activity of soil microbes. The effect of warming on plant $\delta^{15}N$ had weaker relationships with environmental variables compared with that on soil $\delta^{15}N$. This implied that soil $\delta^{15}N$ tended to be more efficient in indicating the openness of global ecosystem N cycling than plant $\delta^{15}N$.

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1 Introduction

Nitrogen (N) is one of the most important nutrient elements for plant growth and the key limiting factors for vegetation productivity (McLay et al., 2001; Zhu et al., 2018; Lu et al., 2020). On the one hand, if the available N in the soil is insufficient, it will damage and weaken the ecosystem service function, including the supply of primary material products, water conservation, climate regulation, etc. (Averill and Waring, 2018). On the other hand, if the available N in the soil is over supplied, it will also damage the structure and function of the ecosystem, resulting in a series of environmental problems such as soil acidification and imbalance of ecosystem nutrient (Schrijver et al., 2008). The intermediate products of the N cycle process, such as nitrate nitrogen ($NO_3^- - N$), nitrous oxide (N_2O) and nitric oxide (NO), may also cause eco-environmental problems such as eutrophication of water body and aggravation of greenhouse effect (Liao et al., 2019). Therefore, it is of great significance to reveal the openness of the ecosystem N cycle process for understanding the plant N fixation and long-term trend of N cycling and protecting the eco-environment (Wang et al., 2014; Wu et al., 2019).

The ^{15}N natural abundance composition ($\delta^{15}N$) in soils or plants (leaves, shoots, fine roots and litter) becomes a useful tool to indicate the openness of ecosystem N cycling (Robinson, 2001). This is because the lighter ^{14}N always preferentially loses from the ecosystem. Thus, the heavier ^{15}N gradually enriches in the ecosystem, resulting in the isotopic fractionation effect (Aranibar et al., 2004). The larger the $\delta^{15}N$ value, the higher degree of openness of N cycling. A large number of studies

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have confirmed that climate was the main factor regulating the soil and plant $\delta^{15}N$ (Craine et al., 2015; Soper et al., 2015). Previous studies have demonstrated that precipitation had a negative effect on soil and plant $\delta^{15}N$ from in-situ evidences to cross-sites syntheses (Swap et al., 2004; Soper et al., 2015). However, the influence of temperature on soil and plant $\delta^{15}N$ remained controversial. Some studies have showed that soil and plant $\delta^{15}N$ increased with temperature (Amundson et al., 2003; Craine et al., 2015), while others have indicated that $\delta^{15}N$ decreased with temperature (Cheng et al., 2009; Sheng et al., 2014) or even there was no correlation between them (Yang et al., 2013). The various studies suggested that the responses of soil and plant $\delta^{15}N$ to warming were very complex and not well understood. In addition to climate factor, soil and plant $\delta^{15}N$ are affected by a variety of other environmental factors, such as vegetation type, topography, soil properties and management practices (Gurmesa et al., 2017; Wang et al., 2019). However, we know little about the influences of environmental factors on the warming effect on ecosystem N cycling, in terms of soil and plant $\delta^{15}N$.

Soil warming experiment was often conducted to study the effect of warming on the ecosystem N cycling at site scale (Schindlbacher et al., 2009). At present, the effect of experimental warming on soil and plant $\delta^{15}N$ has not been studied on a global scale. The objectives of this study were to: (i) detect the effect of experimental warming on the soil and plant $\delta^{15}N$ based on a global meta-analysis of 20 studies; and (ii) identify the main factors influencing the warming effect on the soil and plant $\delta^{15}N$. Specifically, we hypothesized that soil and plant $\delta^{15}N$ have a different response to

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experimental warming.

2 Materials and methods

2.1 Source of data and selection criteria

Peer-reviewed journal articles and dissertations related to soil and plant $\delta^{15}N$ under experimental warming were searched using Web of Science and China National Knowledge Infrastructure (CNKI, http://www.cnki.net) until March 31, 2020 (Tab. 1). The keywords used for the literature search were related to: "nitrogen isotope composition", "experimental warming" and "ecosystems nitrogen cycling".

Our criteria were as follows: at least one of the target variables must be contained, including soils (different fractions, e.g., sand, silt, clay, aggregate and bulk soil) and plants (leaves, shoots, roots and litters) $\delta^{15}N$; studies with temperature gradients were excluded and only field warming experimental studies were included; only data from control and warming treatments were applied for multifactor experiments; means, standard deviations (SD) (or standard errors (SE)) and sample sizes were directly provided or could be calculated from the studies; if one article contained soil or plant $\delta^{15}N$ in multiple years, only the latest results were applied since the observations should be independent in the meta-analysis (Hedges et al., 1999).

2.2 Data extraction and statistical analysis

In total, 20 published papers were selected from more than 50 published papers. The locations of warming experiments were presented and their site information is listed in Tab. 1. For each study, the means, the statistical variation (SE or SD) and the sample size values for treatment and control groups were extracted for each response

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variable ($\delta^{15}N$). In addition to $\delta^{15}N$, the latitude, longitude, altitude, soil pH, vegetation type, mean annual precipitation (MAP) and mean annual temperature (MAT) were also extracted if they can be obtained (Tab. 1). All data were extracted from tables or digitized from graphs with the software GetData v2.2.4 (http://www.getdata-graph-digitizer.com). A total of 79 and 76 paired observations for soil and plant $\delta^{15}N$ were obtained, respectively.

The METAWIN 2.1 software (Sinauer Associates Inc., Sunderland, MA, USA) (Rosenberg et al., 2000) was used to perform meta-analysis in this study. The Hedges' *d* value was used as the effect size (Hedges et al., 1999). The absolute *d* value indicated the magnitude of the treatment impact. Positive or negative *d* values represented an increase or decrease effect of the treatment, respectively. Zero meant no difference between treatment and control groups. The mean effect size and 95% bootstrap confidence intervals (CI) were then generated. If the 95% CI values of *d* did not overlap zero, the effects of experimental warming on $\delta^{15}N$ were considered significant at $p < 0.05$. We used a random effects model to test whether warming had a significant effect on $\delta^{15}N$. To examine whether experimental conditions alter the response direction and magnitude of soil and plant $\delta^{15}N$, observations were further divided into subgroups according to the soil acidity-alkalinity (acid (pH < 6.5), neutral (6.5 < pH < 7.5), and alkali (pH > 7.5)), vegetation types (forest/shrub, moss/lichen, and grassland/meadow), and warming treatments (soil warming, air warming, and both soil and air warming). A random effects model with a grouping variable was used to compare responses among different subgroups. Linear regression

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analyses were applied to assess the relationships between the Hedges' *d* values and environmental factors (i.e., latitude, altitude, MAT and MAP).

3 Results

Across all sites, the mean effect sizes of the soil and plant $\delta^{15}N$ under experimental warming were -0.524 (95% CI: -0.987 to -0.162) and 0.189 (95% CI: -0.210 to 0.569), respectively (Fig. 1). Experimental warming significantly ($p < 0.05$) decreased soil $\delta^{15}N$ in Alkali soil (mean effect size = -2.484; 95% CI: -2.931 to -2.060), grassland/meadow (mean effect size = -0.609; 95% CI: -1.076 to -0.190), and under air warming (mean effect size = -0.652; 95% CI: -1.081 to -0.273), whereas it significantly ($p < 0.05$) increased soil $\delta^{15}N$ in neutral soil (mean effect size = 0.359; 95% CI: 0.078 to 0.620) (Fig. 2). However, experimental warming did not significantly ($p > 0.05$) change soil $\delta^{15}N$ in acid soil (mean effect size = -1.084; 95% CI: -3.588 to 9.211), forest/shrub (mean effect size = -0.179; 95% CI: -1.619 to 1.641), and under soil warming (mean effect size = 0.189; 95% CI: -1.304 to 2.041). In addition, experimental warming significantly ($p < 0.05$) increased plant $\delta^{15}N$ in neutral soil (mean effect size = 3.157; 95% CI: 1.529 to 6.967), whereas it significantly ($p < 0.05$) decreased plant $\delta^{15}N$ in alkali soil (mean effect size = -1.930; 95% CI: -2.325 to -1.573). However, experimental warming did not significantly ($p >$ 0.05) change plant $\delta^{15}N$ under other experimental conditions.

For soil and plant $\delta^{15}N$, their responses to experimental warming did not correlate well with latitude ($p = 0.268$ and $p = 0.160$, respectively) (Fig. 3ab). However, the Hedges' *d* values of soil $\delta^{15}N$ decreased significantly with altitude ($p < 0.001$) (Fig. 3c)

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and increased significantly with MAT (p < 0.001) and MAP (p < 0.001) (Fig. 3eg). In addition, the Hedges' d values of plant $\delta^{15}N$ were also found to increase significantly with MAP (p < 0.001) (Fig. 3h). However, the responses of plant $\delta^{15}N$ to experimental warming did not correlate well with altitude (p = 0.109) and MAT (p = 0.002) (Fig. 3df).

4 Discussion

Soil and plant $\delta^{15}N$ showed a different pattern under experimental warming at the global scale, with a significant decreasing trend in soil $\delta^{15}N$ and an increasing trend in plant $\delta^{15}N$. This is somewhat inconsistent with previous findings. Chang et al. (2017) observed that soil and plant $\delta^{15}N$ values decreased under warming in the Tibetan permafrost. However, Zhang et al. (2019) found that the warming treatment significantly increased soil and plant $\delta^{15}N$ in a subtropical forest. The various studies suggest that soil and plant $\delta^{15}N$ are controlled by interactive effects of N fixation and mineralization. At the global scale, $\delta^{15}N$ of N input (~ 0) is generally lower than that of soil, so greater N fixation or higher N input (deposition and fertilization) under warming can result in a lower soil $\delta^{15}N$ (Rousk and Michelsen, 2017). Plants mainly absorb the inorganic nitrogen in the soil, while increasing temperature can cause higher N mineralization rates and a subsequent increase in plant $\delta^{15}N$ (Swap et al., 2004).

Soil pH has an important influence on nitrification, denitrification and N_2O emissions from soils (Kyveryga et al., 2004). The results in this study showed that when the soil was acidic or alkaline, the mean effect sizes of soil and plant $\delta^{15}N$ under warming were negative, while when the soil was neutral, they were positive (Fig. 2ab). Compared with acid or alkaline conditions, the near neutral conditions are more suitable for the biological activities of heterotrophic denitrifying bacteria (Simek and Cooper, 2002). Therefore, the denitrification activity is usually higher under neutral conditions, resulting in an enrichment of soil and plant N pools with ^{15}N. Vegetation type has a limited effect on soil and plant $\delta^{15}N$ under warming, showing that the mean effect sizes of $\delta^{15}N$ in forest/shrub were slightly higher than those in moss/lichen and grassland/meadow (Fig. 2cd). This may be related to the differences in altitude, MAP and MAT among the three vegetation types (Tab. 1). Warming treatment was found to have a substantial effect on soil and plant $\delta^{15}N$. The mean effect size of soil $\delta^{15}N$ under soil warming was higher than that under air warming, while the mean effect sizes of plant $\delta^{15}N$ were sequenced as soil warming > air warming > both soil and air warming (Fig. 2ef). Salmon et al. (2016) have found that soil warming can increase N availability by stimulating mineralization of organic matter in the warmed actively layer. However, air warming would only impact aboveground temperatures and has a weak effect on soil and plant N pools which are related to $\delta^{15}N$ (Pardo et al., 2006). In addition, when the two warming treatments were applied together, the inorganic N availability and $\delta^{15}N$ signature of plants decreased due to the negative interaction between air warming and soil warming treatments (Salmon et al., 2016).

The warming effects on soil and plant $\delta^{15}N$ had weak correlations with latitude (Fig. 3), although soil and plant $\delta^{15}N$ were negatively correlated with latitude at the global scale ($p \leq 0.001$) as found in Mayor et al. (2015). However, the warming effect

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on soil $\delta^{15}N$ was significantly influenced by altitude, MAT and MAP. Among these, the strongest correlation was observed for MAT. Temperature has been demonstrated to be a key factor to regulate the soil $\delta^{15}N$ by influencing the processes of N mineralization, nitrification and denitrification. The higher temperature can strengthen the activity of soil microbes and thereafter increase the N uptake for plants and soil N loss from ammonia volatilization and gas N emissions, and thereby more ^{15}N-enriched retains in soils (Wang et al., 2019). High *d* values of soil $\delta^{15}N$ corresponded to MAT of about 20 ^{o}C, which was the most suitable temperature for nitrification and denitrification. However, warming had a substantial negative impact on soil $\delta^{15}N$ when MAT decreased to around -5 ^{o}C. Recently, Rousk et al. (2018) also found that the increase of temperature in the Arctic promoted the biological N fixation, which can decrease the soil $\delta^{15}N$. The decrease of *d* values of soil $\delta^{15}N$ with increasing altitude and decreasing MAP in this study might be caused by the positive response of *d* values to MAT. The relationships between the *d* values and environmental variables for plant $\delta^{15}N$ were weaker than those for soil $\delta^{15}N$ (Fig. 3). The possible reason is that several other factors (e.g., plant N concentrations and species richness) might co-regulate plant $\delta^{15}N$ (Wu et al., 2019). This implied that soil $\delta^{15}N$ was more efficient in indicating the openness of ecosystem N cycling than plant $\delta^{15}N$ at the global scale.

Although the present study provided a global meta-analysis of the responses of $\delta^{15}N$ to experimental warming, the magnitude of these responses might be uncertain. For example, a small number of observations were obtained in moss/lichen under soil

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warming and both soil and air warming treatments, which would affect the results of meta-analysis. In addition, the duration of field exposure to warming and increase in temperature may also have an impact on ecosystem N cycling (Dawes et al., 2017). Future research should take various experimental durations and temperature increases into account when investigating the warming effects on $\delta^{15}N$.

6 Conclusions

Our global meta-analysis indicated a significant decreasing trend in soil $\delta^{15}N$ and an increasing trend in plant $\delta^{15}N$ under experimental warming. Latitude did not affect the warming effects on $\delta^{15}N$. However, the warming effect on soil and plant $\delta^{15}N$ was related to soil acidity-alkalinity, vegetation type, warming treatment, altitude, MAT and MAP. The effect of warming on soil $\delta^{15}N$ was better correlated with environmental variables compared with that on plant $\delta^{15}N$. Our findings should be useful for understanding the underlying mechanisms of the response of ecosystem N cycling to global warming.

Data availability. The data that support the findings of this study are available from the corresponding author upon request.

Author contributions. KL and QZ designed this study, KL and XL performed the meta-analysis, KL and QZ obtained funding, and KL and XL wrote the paper with contributions from QZ.

Competing interests. The authors declare that they have no conflict of interest.

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Table 1: Site characteristics from a global meta-analysis of 20 studies.

References	Country/Region	Vegetation types	Latitude	Longitude	Altitude (m a.s.l)	MAT (°C)	MAP (mm)
Anadon-Rosell et al. (2017)	Spain	Subalpine shrub	41.39 °N	2.17 °E	2250	3	1146.4
Zhang et al. (2019)	China	*C. lanceolata* seedlings	26.32 °N	117.6 °E	300	19.1	1670
Lim et al. (2019)	Sweden	Boreal forests	64.12 °N	19.45 °E	310	2.4	600
Deane-Coe et al. (2015)	USA	Tundra mosses	63.88 °N	149.23 °W	700	-2.7~-1	138~228
Bijoor et al. (2008)	USA	Turfgrass lawn	33.7 °N	117.7 °W	30	18.6	352
Chang et al. (2017)	China	Alpine meadow	34.73 °N	92.89 °E	4750	-5.3	269.7
Gonzalez-Meler et al. (2017)	Brazil	Grasslands	21.17 °S	47.86 °W	578	21.5	1100
Natali et al. (2012)	USA	Shrubs, sedges and mosses	63.88 °N	149.23 °W	700	-1	178~250
Munir et al. (2017)	Canada	Shrubs, mosses and trees	55.27 °N	112.47 °W			
Salmon et al. (2016)	USA	*Eriophorum vaginatum*	63.88 °N	149.23 °W	700	-1.45	200
Rui et al. (2011)	China	Alpine meadow	37.62 °N	101.2 °E	3200	-2	500
Aerts et al. (2009)	Sweden	Shrubs, mosses and trees	68.35 °N	18.82 °E	340	0.5	303
Cheng et al. (2011)	USA	Tallgrass prairie	34.98 °N	97.52 °W		16	911.4
Dawes et al. (2017)	Switzerland	Alpine treeline	46.77 °N	9.87 °E	2180	9.2	444
Schaeffer et al. (2013)	Greenland	Prostrate dwarf-shrub herb tundra	76 °N	68 °W		4~8	<200
Schnecker et al. (2016)	Austria	Spruce forest	47.58 °N	11.64 °E	910	6.9	1506
Hudson et al. (2011)	Canada	Heath, willow and meadow	78.88 °N	75.78 °W		8.6~10.4	
Lv et al. (2018)	China	*Cunninghamia lanceolata* juveniles	26.32 °N	118 °E		19.1	1585
Zhao et al. (2016)	China	Alpine meadow	37.48 °N	101.2 °E	3200~3250	-1.7	600

Peng (2017)	China	Alpine meadow	34.73 °N	92.89 °E	3200~4800	-5.03	267.4~426.3

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Figure 1: Effect sizes of the experimental warming on soil and plant $\delta^{15}N$ from a global meta-analysis of 20 studies. The error bars indicate effect sizes and 95% bootstrap confidence intervals (CI). The warming effect was statistically significant if the 95% CI did not bracket zero. The sample size for each variable is shown next to the bar.

Figure 2: Factors influencing the effect sizes of the soil and plant $\delta^{15}N$ under experimental warming from a global meta-analysis of 20 studies. The error bars indicate effect sizes and 95% bootstrap confidence intervals (CI). The warming effect was statistically significant if the 95% CI did not bracket zero. The sample size for each variable is shown next to the bar.

Figure 3: Relationships between the Hedges' *d* values of soil and plant $\delta^{15}N$ with the latitude, altitude, mean annual temperature (MAT) and mean annual precipitation (MAP) under experimental warming.

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Figure 1

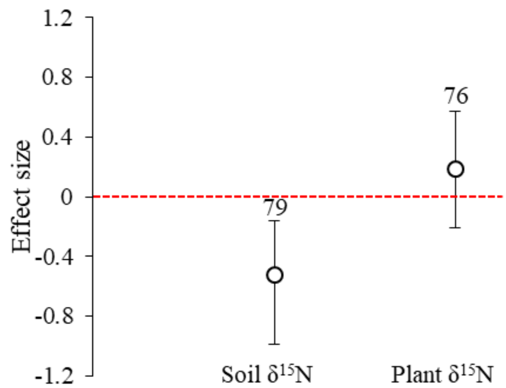

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Figure 2

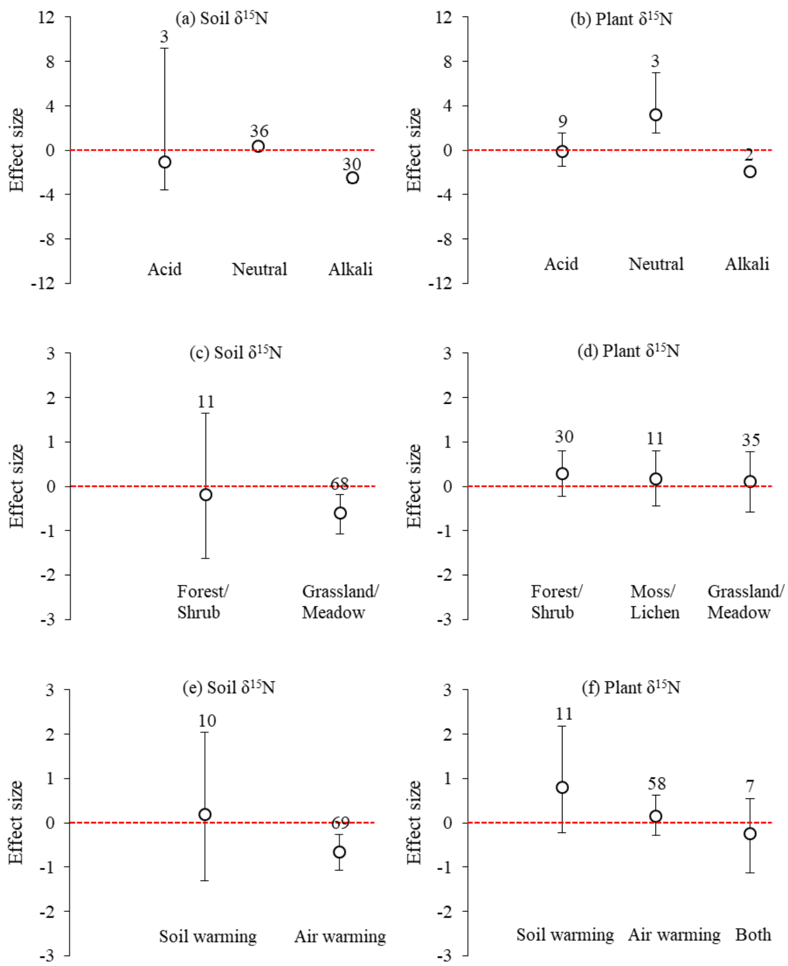

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Figure 3