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Soil δ^{15}N is a better indicator of ecosystem nitrogen cycling than plant δ^{15}N: A global meta-analysis

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Abstract. The nitrogen-15 (^{15}N) natural abundance composition (δ^{15}N) in soils or plants is a useful tool to indicate the openness of ecosystem N cycling. This study aimed to evaluate the influence of the experimental warming on soil and plant δ^{15}N. We applied a global meta-analysis method to synthesize 79 and 76 paired observations of soil and plant δ^{15}N from 20 published studies, respectively. Results showed that the mean effect sizes of the soil and plant δ^{15}N under experimental warming were −0.524 (95 % CI (confidence interval): −0.987 to −0.162) and 0.189 (95 % CI: −0.210 to 0.569), respectively. This indicated that soil δ^{15}N had negative response to warming at the global scale, where warming had no significant effect on plant δ^{15}N. Experimental warming significantly ($p < 0.05$) decreased soil δ^{15}N in Alkali and medium-textured soils, in grassland/meadow, under air warming, for a 4–10-year warming period and for an increase of > 3 °C in temperature, whereas it significantly ($p < 0.05$) increased soil δ^{15}N in neutral and fine-textured soils and for an increase of 1.5–3 °C in temperature. Plant δ^{15}N significantly ($p < 0.05$) increased with increasing temperature in neutral and fine-textured soils and significantly ($p < 0.05$) decreased in alkali soil. Latitude did not affect the warming effects on both soil and plant δ^{15}N. However, the warming effect on soil δ^{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 δ^{15}N had weaker relationships with environmental variables compared with that on soil δ^{15}N. This implied that soil δ^{15}N was more effective than plant δ^{15}N in indicating the openness of global ecosystem N cycling.

1 Introduction

Nitrogen (N) is one of the most important nutrient elements for plant growth and the key limiting factor 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 cycling processes, such as nitrate nitrogen (NO_3^--N), nitrous oxide (N_2O) and nitric oxide (NO), may also cause eco-environmental pollution such as eutrophication of water bodies and aggravation of climate-related issues (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). Openness is a measure of both N inputs and outputs relative to internal cycling and determines both the potential rate of N accumulation in the ecosystem and the potential for N losses following a disturbance (Rastetter et al., 2021).

The ^{15}N natural abundance composition ($\delta^{15}N$) in soils or plants (leaves, shoots, fine roots, and litter) is often used to indicate the openness of ecosystem N cycling (Robinson, 2001). This is because the lighter isotope of ^{14}N is always preferentially lost from the ecosystem. Thus, the isotopic fractionation effect results in gradual ^{15}N enrichment in the ecosystem (Aranibar et al., 2004). The larger the $\delta^{15}N$ value, the higher degree of openness of N cycling. In addition, soil $\delta^{15}N$ also appears to reflect the degree of decomposition of the organic matter, showing that $\delta^{15}N$ increases with processing (Craine et al., 2015). A large number of studies 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 evidence to cross-site syntheses (Swap et al., 2004; Soper et al., 2015). However, the influence of temperature on soil and plant $\delta^{15}N$ remains controversial. Some studies have shown 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 that they were not correlated (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 and air warming experiments have often been conducted to study the effect of warming on the ecosystem N cycling at the 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 $\delta^{15}N$. In addition, previous studies (e.g., Liu and Wang, 2009; Wang et al., 2014) have found that the correlation between soil $\delta^{15}N$ and environmental factors was stronger than that for plant, which may be due to the fact that soil samples represented a long-term average for a given location, while plant samples were affected by the microenvironment or the short-term environmental fluctuations. Therefore, we specifically hypothesized that soil $\delta^{15}N$ is a better indicator of ecosystem N cycling than plant $\delta^{15}N$.

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) last access: 31 March 2020 (Table 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 was contained, including soil (different fractions, e.g., sand, silt, clay, aggregate, and bulk soil) and plant (leaves, shoots, roots, and litter) $\delta^{15}N$; studies with climate gradients (space-time substitution) were excluded and only field warming experimental studies were included; only data from control and warming treatments were applied for multifactor experiments; means, standard deviation (SD) (or standard error (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 54 published papers. The locations of warming experiments were presented, and their site information is listed in Table 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 variable ($\delta^{15}N$). In addition to $\delta^{15}N$, the latitude, longitude, altitude, soil pH, organic matter content, vegetation type, mean annual precipitation (MAP), and mean annual temperature (MAT) were also extracted if they were provided (Table 1). All data were extracted from tables or digitized from graphs with the software GetData v2.2.4 (http://www.getdata-graph-digitizer.com, last access: 17 October 2020). 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. Resampling tests were incorporated into our meta-analysis using the bootstrap method (999 random replicates). The mean effect size (calculated from 999 iterations) and 95 % bootstrap confidence interval (CI) were then generated. If the 95 % CI values of d did not overlap zero, the effects of experimental warming

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

References	Country/region	Vegetation types	Soil pH	Soil type	OMC[a] (%)	Latitude	Longitude	Altitude (m a.s.l)	MAT[b] (°C)	MAP[c] (mm)
Anadon-Rosell et al. (2017)	Spain	Subalpine shrub	4.49–4.63	Mineral soil	13.15–14.04	41.39° N	2.17° E	2250	3	1146.4
Zhang et al. (2019)	China	*C. lanceolata* seedlings	5.07	Oxisol	–	26.32° N	117.6° E	300	19.1	1670
Lim et al. (2019)	Sweden	Boreal forests	5.92–6.44	A thin, podzolic, sandy soil	–	64.12° N	19.45° E	310	2.4	600
Deane-Coe et al. (2015)	USA	Tundra mosses	–	Gelisol	–	63.88° N	149.23° W	700	−2.7 to −1	138–228
Bijoor et al. (2008)	USA	Turfgrass lawn	–	Alkaline alo clay	–	33.7° N	117.7° W	30	18.6	352
Chang et al. (2017)	China	Alpine meadow	9.1–9.3	Gelisols	5.5	34.73° N	92.89° E	4750	−5.3	269.7
Gonzalez-Meler et al. (2017)	Brazil	Grasslands	5.0	Dystrophic red Latosols	–	21.17° S	47.86° W	578	21.5	1100
Natali et al. (2012)	USA	Shrubs, sedges, and mosses	–	Gelisol	–	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*	–	Gelisols	–	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	Neutral pH	Nash–Lucien complex	–	34.98° N	97.52° W		16	911.4
Dawes et al. (2017)	Switzerland	Alpine treeline	–	Sandy Ranker and Podzols	–	46.77° N	9.87° E	2180	9.2	444
Schaeffer et al. (2013)	Greenland	Prostrate dwarf-shrub herb tundra	–	Turbic Cryosols	–	76° N	68° W		4–8	< 200
Schnecker et al. (2016)	Austria	Spruce forest	Near-neutral pH	A mosaic of shallow Chromic Cambisols and Rendzic Leptosols	8.55–14.96	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	–	Red soil	2.21	26.32° N	118° E		19.1	1585
Zhao et al. (2016)	China	Alpine meadow	–	Alpine meadow soils	–	37.48° N	101.2° E	3200–3250	−1.7	600
Peng (2017)	China	Alpine meadow	–	Alpine meadow soils	–	34.73° N	92.89° E	3200–4800	−5.03	267.4–426.3

[a] Soil organic matter content; [b] Mean annual temperature; [c] Mean annual precipitation. If the soil organic carbon content was provided in the literature, soil organic matter content was determined by multiplying the organic carbon content by a coefficient of 1.724.

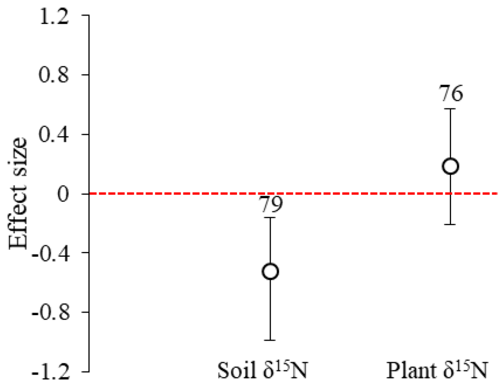

Figure 1. Effect sizes of the experimental warming on soil and plant δ^{15}N from a global meta-analysis of 20 studies. The error bars indicate effect sizes and 95 % bootstrap confidence interval (CI). The warming effect was statistically significant if the 95 % CI did not bracket zero. The sample size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

on δ^{15}N were considered significant at $p < 0.05$. We used a random effects model to test whether warming had a significant effect on δ^{15}N. To examine whether experimental conditions alter the response direction and magnitude of soil and plant δ^{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), warming treatments (soil warming, air warming, and both soil and air warming), soil texture (fine-, medium-, and coarse-textured soil), length of warming (< 4, 4–10, and > 10 years), and increase in temperature (< 1.5, 1.5–3, and > 3 °C). A random effects model with a grouping variable was used to compare responses among different subgroups. Linear regression 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 δ^{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 δ^{15}N in Alkali (mean effect size = −2.484; 95 % CI: −2.931 to −2.060) and medium-textured (mean effect size = −0.676; 95 % CI: −1.153 to −0.249) soils, in grassland/meadow (mean effect size = −0.609; 95 % CI: −1.076 to −0.190), under air warming (mean effect size = −0.652; 95 % CI: −1.081 to −0.273), for a 4–10-year warming period (mean effect size = −0.652; 95 % CI: −1.081 to −0.273) and for an increase of > 3 °C in temperature (mean effect size = -0.652; 95 % CI: −1.081 to −0.273). However, it significantly ($p < 0.05$) increased soil δ^{15}N in neutral (mean effect size = 0.359; 95 % CI: 0.078 to 0.620) and fine-texture soils (mean effect size = 2.394; 95 % CI: 1.770 to 3.735), and for an increase of 1.5–3 °C in temperature (mean effect size = 0.409; 95 % CI: 0.070 to 0.707) (Fig. 2). Experimental warming did not significantly ($p > 0.05$) change soil δ^{15}N under other experimental conditions.

In addition, experimental warming significantly ($p <$ 0.05) increased plant δ^{15}N in neutral (mean effect size = 3.157; 95 % CI: 1.529 to 6.967) and fine-textured soils (mean effect size = 1.202; 95 % CI: 1.042 to 1.360), whereas it significantly ($p < 0.05$) decreased plant δ^{15}N in alkali soil (mean effect size = −1.930; 95 % CI: −2.325 to −1.573) (Fig. 2). Experimental warming did not significantly ($p > 0.05$) change plant δ^{15}N under other experimental conditions.

For soil and plant δ^{15}N, their responses to experimental warming did not correlate well with latitude ($p = 0.268$ and $p = 0.160$, respectively) (Fig. 3a, b). However, the Hedges' d values of soil δ^{15}N decreased significantly with altitude ($p < 0.001$) (Fig. 3c) and increased significantly with MAT ($p < 0.001$) and MAP ($p < 0.001$) (Fig. 3e, g). In addition, the Hedges' d values of plant δ^{15}N were also found to increase significantly with MAP ($p < 0.001$) (Fig. 3h). However, the responses of plant δ^{15}N to experimental warming did not correlate well with altitude ($p = 0.109$) and MAT ($p = 0.002$) (Fig. 3d, f).

4 Discussion

A significant decreasing trend in soil δ^{15}N and no significant trend in plant δ^{15}N were found in this study. This is somewhat inconsistent with previous findings. Chang et al. (2017) observed that soil and plant δ^{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 δ^{15}N in a subtropical forest. The various studies suggest that soil and plant δ^{15}N are controlled by interactive effects of N fixation and mineralization. At the global scale, δ^{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 δ^{15}N (Sorensen and Michelsen, 2011; Rousk and Michelsen, 2017; Wang et al., 2018).

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 alkaline the mean effect sizes of soil and plant δ^{15}N under warming were negative, and when the soil was neutral they were positive (Fig. 2a, b). Compared with alkaline condition, 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 (Kyveryga

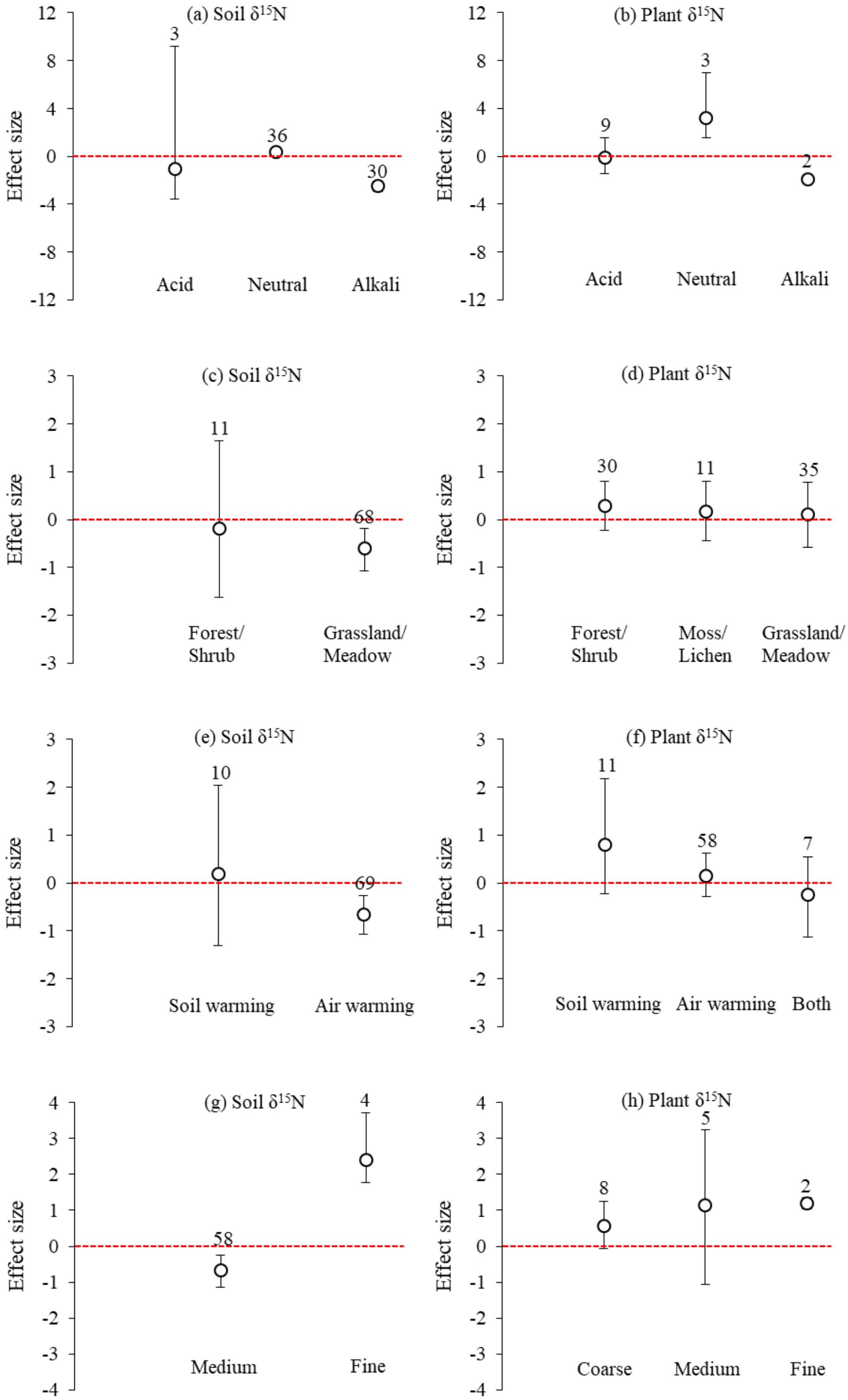

Figure 2. Continued.

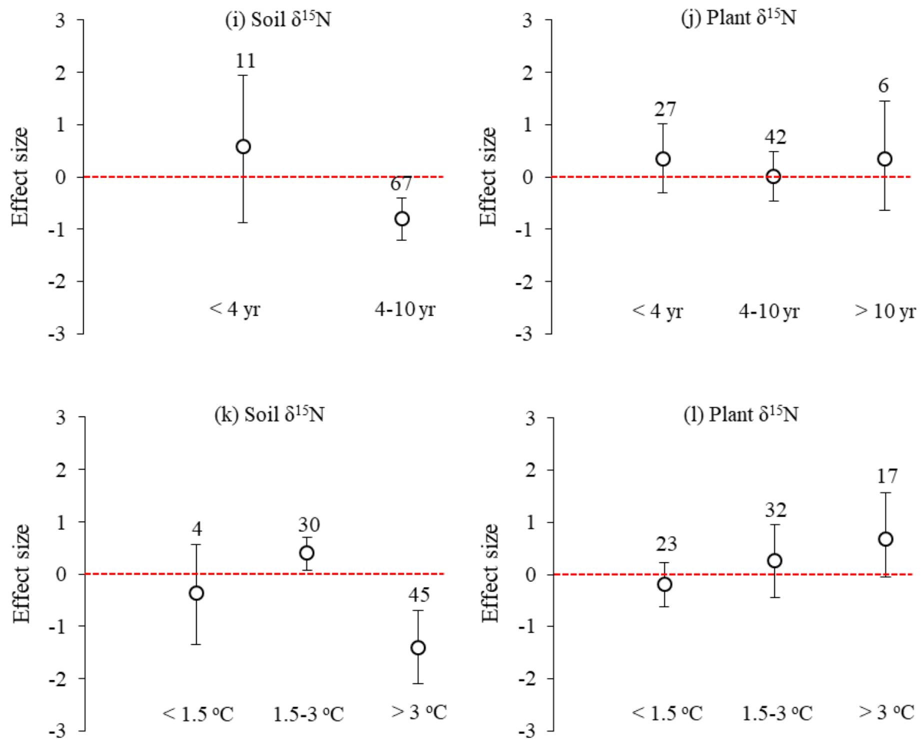

Figure 2. Factors influencing the effect sizes of the soil and plant δ^{15}N under experimental warming from a global meta-analysis of 20 studies, including **(a–b)** soil acidity–alkalinity, **(c–d)** vegetation types, **(e–f)** warming treatments, **(g–h)** soil texture, **(i–j)** length of warming, and **(k–l)** increase in temperature. The error bars indicate effect sizes and 95 % bootstrap confidence interval (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.

et al., 2004). Vegetation type had limited effects on δ^{15}N under warming, except for soil δ^{15}N in grassland/meadow (Fig. 2c, d). This may be related to the differences in altitude, MAP, and MAT among three vegetation types (Table 1). The type of warming treatment was found to have a substantial effect on soil δ^{15}N, showing that the mean effect size of soil δ^{15}N under air warming was negative and less than that under soil warming (Fig. 2e, f). Salmon et al. (2016) have found that soil warming can increase N availability by stimulating mineralization of organic matter in the warmed active layer. In addition, air warming directly impacts aboveground temperatures and has an indirect effect on soil δ^{15}N (Pardo et al., 2006). From Fig. 2g and h, the finer the soil texture, the more significant the positive effect of warming on soil and plant δ^{15}N. One possible reason is that the finer the soil texture, the stronger the adsorption of various ions on the soil and the smaller the leaching loss of the soil, resulting in greater residual amount of ^{15}N in the soil (Webster et al., 1986). In addition, the longer warming period and the greater increase in temperature resulted in a more negative effect of warming on soil δ^{15}N (Fig. 2i, k). Chang et al. (2017) deduced that N fixation was greater under warming and consequently resulted in a lower soil δ^{15}N.

In the study of Mayor et al. (2015), soil and plant δ^{15}N values were significantly ($p < 0.001$) and negatively correlated with latitude at the global scale. However, the Hedges' d values of soil and plant δ^{15}N had weak correlations with latitude in this study (Fig. 3). The warming effect on soil δ^{15}N was significantly ($p < 0.001$) influenced by altitude, MAT and MAP. Among these, the strongest correlation was observed for MAT. It is possible that soil δ^{15}N increased with increasing MAT when the MAT exceeded a certain threshold (e.g., 9.8 °C as proposed by Craine et al., 2015). In this case, the increase in MAT can enhance the positive effect of experimental warming on soil δ^{15}N. In addition, the MAT can also affect ecosystem N cycle by influencing soil texture. Craine et al. (2015) reported that hot sites had greater clay concentrations than cold sites. As depicted in Fig. 2g, the finer the texture of the soil, the more significant the effect of experimental warming on soil δ^{15}N. High d values of soil δ^{15}N corresponded to MAT of about 20 °C, which was the most suitable temperature for nitrification and denitrification. However, warming had a substantial negative impact on soil δ^{15}N when MAT decreased to around −5 °C. Recently, Rousk et al. (2018) also found that the increase in temperature in the Arctic promoted the biological N fixation, which can decrease the soil δ^{15}N. The decrease of d values of soil δ^{15}N with increasing altitude and decreasing MAP in this study might be caused by the positive response of d values to MAT.

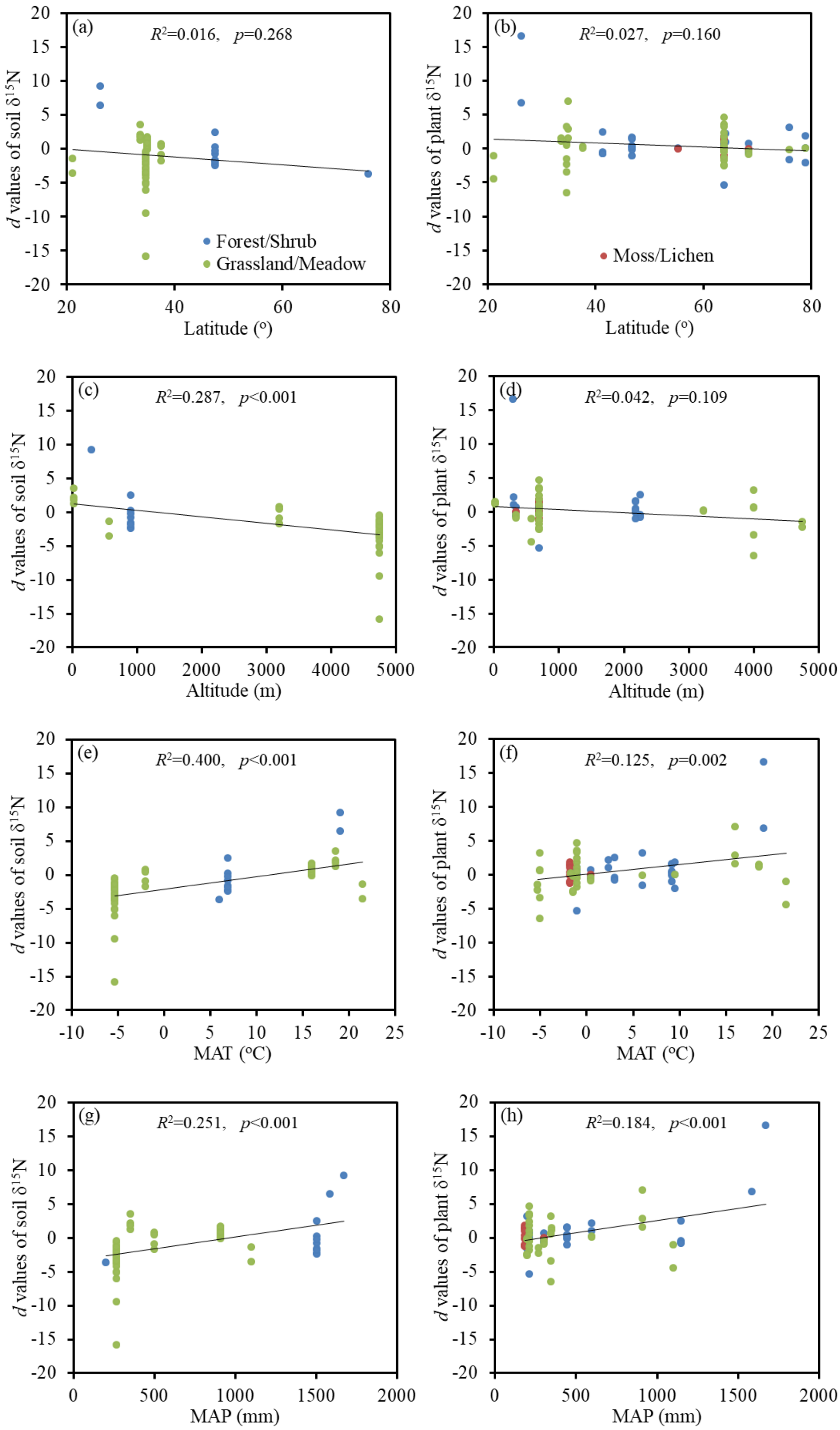

Figure 3. Relationships between the Hedges' d values of soil and plant $\delta^{15}N$ with the latitude, altitude, mean annual temperature (MAT), and mean annual precipitation (MAP) under experimental warming.

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). One 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 is consistent with the study of Craine et al. (2009), who found different inflection points in soil and plant $\delta^{15}N$ relationships with MAT. In addition, plants are generally depleted in ^{15}N relative to soils. Above results 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 warming and both soil and air warming treatments, which would affect the results of the meta-analysis. Future research should take more experimental data into account in order to better investigate the warming effects on $\delta^{15}N$.

5 Conclusions

Our global meta-analysis indicated a significant decreasing trend in soil $\delta^{15}N$ and no significant 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 $\delta^{15}N$ was related to soil acidity–alkalinity; texture; vegetation type; warming treatment and period; and increase in temperature, 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.

Author contributions. The contact author has declared that neither they nor their co-authors have any competing interests.

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