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Nitrogen addition stimulates litter decomposition rate: From the perspective of the combined effect of soil environment and litter quality

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A R T I C L E I N F O

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A B S T R A C T

Despite the essential role of litter decomposition in carbon (C) and nutrient cycle in terrestrial ecosystems, some uncertainties remain about how this fundamental process is affected by increasing nitrogen (N) deposition. Based on a large dataset comprising 1108 observations from 162 studies, we conducted a meta-analysis to explore the effect of N addition on litter decomposition rate under three kinds of litter decomposition experiments (i.e., common litter experiment (litter collected from control plot is decomposed in N addition plots); common site experiment (litter collected from N addition plots is decomposed in control plot); in situ experiment (litter collected from control and N addition plots is decomposed in situ)). In general, N addition significantly decreased litter decomposition rate by 2.3% across the three kinds of litter decomposition experiments. However, litter decomposition rate responded differently to N addition among different kinds of litter decomposition experiments. N addition significantly decreased litter decomposition rate by 5.1% in common litter experiment. In contrast, N addition significantly increased litter decomposition rate by 9.2% and 10.3% in common site and in situ experiments, respectively. The response of litter decomposition rate to N addition was positively correlated with initial N and phosphorous (P) concentrations, but negatively correlated with initial C:N and lignin:N ratios of plant litter in common litter experiment. For common site and in situ experiments, the N-induced increase in litter decomposition rate was attributed to the increased N and P concentrations and decreased C:N and lignin: N ratios of plant litter under N addition. Collectively, our results suggest that common litter experiment might underestimate the positive effect of N addition on litter decomposition. By contrast, the overall stimulatory effect of N addition on litter decomposition rate under in situ experiment should be more realistic, and its adoption could improve the prediction of ecosystem consequences of increased anthropogenic N deposition.

1. Introduction

Litter decomposition is a fundamental process that governs the cycling of carbon (C) and nutrients in terrestrial ecosystems (Gessner et al., 2010; Paul, 2016; Gill et al., 2021). It is known that litter quality and soil biota play vital roles in regulating the decomposition process at the local scales (Strickland et al., 2009; Prescott, 2010; Garcia-Palacios et al., 2016). These control factors of litter decomposition, without exception, are highly sensitive to nitrogen (N) deposition (Treseder, 2008; Niu et al., 2016; Liu et al., 2016; Zhang et al., 2018a). Given the significant increase in the atmospheric deposition of reactive N over the past decades, it is regarded as an important global change driver (Galloway et al., 2008; Niu et al., 2016). Therefore, comprehensive knowledge about the effect of N addition on litter decomposition is crucial for predicting ecosystem consequences of increasing anthropogenic reactive N deposition.

Despite numerous investigations on the effect of N addition on litter decomposition, the research outcomes were inconsistent. Many studies reported the suppression effect of N addition on litter decomposition rate (Magill and Aber, 1998; Tu et al., 2014; Peng et al., 2022). While, several others suggested insignificant (Liu et al., 2010; Jacobson et al., 2011; Xia et al., 2018) or faster litter decomposition rate in response to N addition (Vivanco and Austin, 2011; Schuster, 2016; Hou et al., 2021). The different response of litter decomposition rate to N addition could be partly explained by the different litter decomposition methods that were used in different studies. In general, there are three commonly used

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methods for investigating the effect of N addition on litter decomposition. First, litter collected from control plot is decomposed in N addition plots (common litter experiment). This kind of experiment focuses on how N addition influences litter decomposition through its effect on soil environment or microbial properties (Keeler et al., 2009; Zhang et al., 2016; Peng et al., 2022). Second, litter collected from N addition plots is decomposed in control plot (common site experiment). This experimental design intents to figure out how N addition affects litter decomposition via its effect on litter quality (Henry and Moise, 2014; Li et al., 2020). Third, litter collected from control and N addition plots is decomposed in situ (in situ experiment). Such experiment is conducted to investigate how N addition affects litter decomposition through its integrated effect on soil environment and litter quality (Liu et al., 2010; Hou et al., 2021).

It is widely accepted that N addition could reduce microbial biomass (Treseder, 2008; Zhang et al., 2018a), decrease the abundance of ligninolytic fungi (Entwistle et al., 2018; Moore et al., 2021) and inhibit the activity of ligninolytic enzymes (Jian et al., 2016; Chen et al., 2018). Consequently, the decomposition of lignin-like substrates can be suppressed (Entwistle et al., 2018; Argiroff et al., 2021). Thus, for common litter experiments, N addition usually reduces the litter decomposition rate (Magill and Aber, 1998; Tu et al., 2014; Peng et al., 2022), especially for long-term decomposition experiments (Magill and Aber, 1998; Peng et al., 2022). N addition also affects litter decomposition by altering litter quality. Long-term N addition appears to increase litter N and phosphorus (P) concentration (Li et al., 2017; Hou et al., 2021), but decrease litter lignin and cellulose content (Hou et al., 2018). As a result, the C:N and lignin:N ratios can decline with N addition. Faster decomposition rates are often positively correlated with higher initial litter N and P concentrations and lower C:N and lignin:N ratios (Prescott, 2010; Li et al., 2017). Hence, for common site experiment, N addition can generally increase litter decomposition rate (Liu et al., 2010; Li et al., 2020). However, neither common litter nor common site experiments can reasonably reflect the real effect of N addition on litter decomposition. Since litter decomposition is the result of a complex interaction between litter chemistry and decomposer community (Bhatnagar et al., 2018; Osburn et al., 2022), in situ experiment could be more realistic. However, the effect of in situ experiment on litter decomposition is more complicated. It depends on the trade-off between the negative effect of inhibited microbial activity and the positive effect of improved litter quality. (Liu et al., 2010; Hou et al., 2021). Hou et al. (2021) found that the improved litter quality was the dominant factor in controlling the higher decomposition rate under in situ experiment. Liu et al. (2010) found that N addition had little effect on litter decomposition rate because the positive effect of improved litter quality was offset by the negative effect of increased soil N. Moreover, there were also several meta-analyses had investigated the effect of N addition on litter decomposition rate (Knorr et al., 2005; Zhang et al., 2018b; Su et al., 2021). However, they merged these three kinds of litter decomposition experiments together, the results may not be convincing enough. To compare the effects of these three kinds of litter decomposition experiments on litter decomposition, and also to comprehensively and accurately assess the effect of N addition on litter decomposition, there is a need to summarize the results of these three kinds of litter decomposition experiments, respectively.

Given the diversity of biome types, litter quality and edaphic conditions across individual site-based studies, it is necessary to summarize the responses of litter decomposition to N addition in these three kinds of litter decomposition experiments on a global scale to reach general conclusions. To this end, we conducted a meta-analysis using 1108 paired observations from 162 individual studies to investigate the response of litter decomposition rate to N addition. The main objectives of this study are to (1) quantify the direction and magnitude of the effect of N addition on litter decomposition in three kinds of litter decomposition experiments (i.e., common litter, common site and in situ experiments); (2) explore the drivers of the response of litter decomposition rate to N addition in these three kinds of litter decomposition experiments. We hypothesize that: (1) N addition would reduce litter decomposition rate in experiments that only considered how N addition affected litter decomposition via its effect on soil or microbial properties (common litter experiments) because of the decrease in microbial biomass and activity under N addition (Jian et al., 2016; Zhang et al., 2018a; Entwistle et al., 2018); (2) N addition would increase litter decomposition rate in experiments that only explored how N addition affected litter decomposition through its effect on litter quality (common site experiment) because of the improved litter quality under N addition (Niu et al., 2016; Hou et al., 2021); (3) N addition would have little effect on litter decomposition rate in experiments that considered the combined effect of litter quality and soil environment (in situ experiment) because the negative effect of inhibited microbial activity may offset the positive effect of improved litter quality.

2. Materials and methods

2.1. Data collection and extraction

In this study, we used two databases: Web of Science (https://www.webofscience.com/) and China National Knowledge Infrastructure (CNKI) (https://www.cnki.net/) to search for the pre-reviewed articles published before May 31, 2022. To investigate the effect of N addition on litter decomposition rate, we set the search terms as follow: ("nitrogen deposition" OR "nitrogen addition" OR "nitrogen enrichment" OR "nitrogen loading" OR "nitrogen fertilization" OR "nitrogen application" OR "nitrogen elevated" OR "nitrogen supply") AND (litter OR leaf OR foliar OR aboveground) AND (decomposition OR decay OR breakdown). Appropriate studies were selected according to the following criteria: (1) litter decomposition rate was measured through litterbag method; (2) only field experiments were included and laboratory studies were excluded; (3) litter decomposition rate (*k* value) were calculated by the single-pool exponential decay model (Olson, 1963); (4) for studies that didn't reported the decomposition rate directly, the percent litter mass remaining or loss for at least three time points throughout the litter decomposition period must be reported; (5) the experiment designed must be side-by-side paired-plot treatments including N addition and control treatment at the same time; (6) for multifactorial studies, we only selected data from the N addition and control treatment to avoid the influence of interaction from other factors; (7) studies should report the mean, sample size and standard deviation (SD). If the SD was not reported, SD was calculated from SE ($SD = SE\ \sqrt{N}$). When neither SD nor SE was reported, SD was estimated based on the average coefficient of variation (CV) of the datasets with known SD (Zuber and Villamil, 2016; Dai et al., 2018). Based on the abovementioned criteria, a total of 162 individual studies with 1108 paired observations were obtained for further analysis. PRISMA Flow Diagram (Fig. S1) was drawn to show the procedure of the article selection.

Except for the decomposition rate value (*k*), we also collected the related information from the original case studies or relevant studies. The information included: (1) environmental variables: latitude and longitude, mean annual temperature (MAT) and mean annual precipitation (MAP); (2) N addition regime: N addition amount (kg ha^{-1} $year^{-1}$), N form, duration of N addition (year); (3) Initial litter quality: the concentration of C, N, P, cellulose, hemicellulose and lignin (g kg^{-1}), C:N and lignin:N; (4) other information: litter decomposition time (year), number of species (single and mixture), litter source (grass, shrub and tree) and mycorrhizal type (arbuscular mycorrhizal (AM), ectomycorrhizal (EM)). The mycorrhizal type of plant was confirmed according to the published plant-specific mycorrhizal associations (Wang and Qiu, 2006; Soudzilovskaia et al., 2020). Data was directly obtained from the tables or extracted from the graphs by using the GetData Graph Digitizer (version 2.24, http://getdata-graph-digitizer.com, Russian Federation).

2.2. Meta-analysis

We used a natural log response ratio (RR) (Hedges et al., 1999) to evaluate the magnitude the direction of the N addition effect on decomposition rate and other variables. The RR was calculated as follows:

$$RR = \ln\left(\frac{\overline{X_t}}{\overline{X_c}}\right) = \ln(\overline{X_t}) - \ln(\overline{X_c}) \quad (1)$$

where $\overline{X_t}$ and $\overline{X_c}$ are the mean values of each variable for the N addition treatment and the control treatment, respectively. Its variance (ν) is calculated as:

$$\nu = \frac{S_t^2}{n_t\overline{X_t^2}} + \frac{S_c^2}{n_c\overline{X_c^2}} \quad (2)$$

where S_t and S_c are the SD of the concerned variable for the N addition treatment and the control treatment, respectively. n_t and n_c are the sample sizes of the concerned variable for the N addition and the control treatment, respectively.

The weighting factor (ω) of each observation was calculated as the inverse of the variance:

$$\omega = 1 / \nu \quad (3)$$

Because some studies contained two or more observations, in order to eliminate or reduce the disproportionate effect of individual studies with large numbers of observation on global means, we adjusted the weights on the basis of the total number (n) of the observations per study (Bai et al., 2013; McDaniel et al., 2019). The final weight (ω′) used in the analyses was:

$$\omega' = \omega / n \quad (4)$$

The weighted response ratio RR' was calculated as:

$$RR' = \omega' \times RR \quad (5)$$

The overall weighted response ratio $\overline{RR'}$ for all observation was calculated as:

$$\overline{RR'} = \frac{\sum_i RR_i'}{\sum_i \omega_i'} \quad (6)$$

where RR_i' and ω_i' are weighted response ratio and adjusted weighting factor of the *i*th observation, respectively.

Final weighted response ratio and 95% bootstrapped confidence interval (CI) were calculated by using MetaWin 2.1 (Rosenberg et al., 2000). All calculation of weighted response ratio and categorical comparisons conducted in MetaWin were set on random-effect model. The 95% bootstrapped CI was calculated with 9999 iterations. If the 95% bootstrapped CI values of weighted response ratio for a variable did not overlap zero, the effect of N addition on this variable was deemed as significant. For a better explanation, the weighted response ratio was transformed back to the percentage change caused by N addition:

$$\text{Change } (\%) = [\exp(\overline{RR'}) - 1] \times 100\% \quad (7)$$

The total heterogeneity (Q_T) between observations was calculated and tested against a χ^2−distribution with n−1 degrees of freedom (Rosenberg et al., 2000). In addition, the heterogeneity between observation was also calculated with the I^2 (Higgins and Thompson, 2002). Our analysis showed that the χ^2 values were significant ($p < 0.05$), and all I^2 indexes were larger than 50% (Table S1). These results revealed that the variability in the observed effect size is larger than one expected based on sampling variability (Rosenberg et al., 2000; Zhang et al., 2022). This may be explained by differences between studies according to one of several factors (i.e., N addition regime, climate), meaning that potential moderator variables can be sought to explain this variability and further investigation with subgroup analysis is appropriate (Higgins and Thompson, 2002).

A categorical meta-analysis was conducted to evaluate the response of decomposition rate to N addition among sub-groups for different conditions. In order to assess whether N addition influences litter decomposition via its effects on soil environment, litter quality or their combined, the litter decomposition experiment was divided into three kinds: common litter experiment, common site experiment and in situ experiment. The following categorical meta-analyses were applied to the three kinds of litter decomposition experiments, respectively.

N addition amount was grouped by < 50, 50−150 and > 150 kg ha^{-1} year^{-1}, which represent low, medium and high N addition levels, respectively (Deng et al., 2020; Chen et al., 2020). N addition form was split into five groups: NH_4^+-N, NO_3^--N, NH_4NO_3, urea (organic N) and a mixture of inorganic N and urea (Deng et al., 2020; Yang et al., 2022). Duration of N addition was divided into two groups: short-term (<5 years) and long-term (≥5 years) N addition experimental durations. The cutoff of 5 years aligned with several previous meta-analyses (Chen et al., 2020; Wu et al., 2022). Given the response of litter decomposition rate to N addition depends on decomposition stage or decomposition time (Gill et al., 2021), in order to more clearly reveal the effect of decomposition time, it was divided into different groups year by year (for instance, decomposition time ≤1 year; 1 year < decomposition time ≤2 years, 2 years < decomposition time ≤3 years and so on). Additionally, the climatic zone was divided into five groups: Tibet plateau, cold temperate, warm temperate, subtropical and tropical zones. Litter species was partitioned into single and mixed species. Litter source was divided into three groups: grass, shrub and tree. Mycorrhizal type was split into two group: AM and EM. Between-group *Q* statistical test (expressed as Q_M value) was applied to compare the heterogeneity of the weighted response ratio of the different groups for each categorical variable listed above. Significant χ^2 values ($p < 0.05$) indicated that the effects within a category were significantly heterogeneous (Table S2).

We assessed publication bias in the studies by funnel plots and Egger's regressions (Rosenberg et al., 2000; Rothstein et al., 2005). The funnel plot showed symmetrical shapes both by visual inspections and Egger's regression tests (Fig. S2; Tables S3 and S4). Thus, the effects of publication bias on our result of meta-analysis were absent, and our calculated effect sizes were robust.

3. Results

3.1. General pattern of the effect of N addition on litter decomposition rate

Across the three kinds of litter decomposition experiments, N addition significantly decreased the litter decomposition rate by 2.3% (95% CI, −3.8− −0.9%) (Fig. 1). Specifically, N addition decreased litter decomposition rate by 5.1% (95% CI, −6.9− −3.4%) in common litter experiment (Fig. 1). In contrast, N addition significantly increased litter decomposition rate by 9.2% (95% CI, 4.4−14.1%) and 10.3% (95% CI, 7.6−12.9%) in common site and in situ experiments, respectively (Fig. 1).

3.2. Effects of different categorical variables on litter decomposition rate under three litter decomposition experiments

The responses of litter decomposition rate to N addition were divergent in the same categorical groups under three different litter decomposition experiments (Figs. 2–4). In particular, the negative effect of N addition on litter decomposition increased with N addition amount in common litter experiment (Fig. 2a). On the contrary, the positive effect of N addition on litter decomposition increased with N addition amount in common site and in situ experiments (Fig. 2b and c). Inorganic N addition significantly decreased litter decomposition rate, while

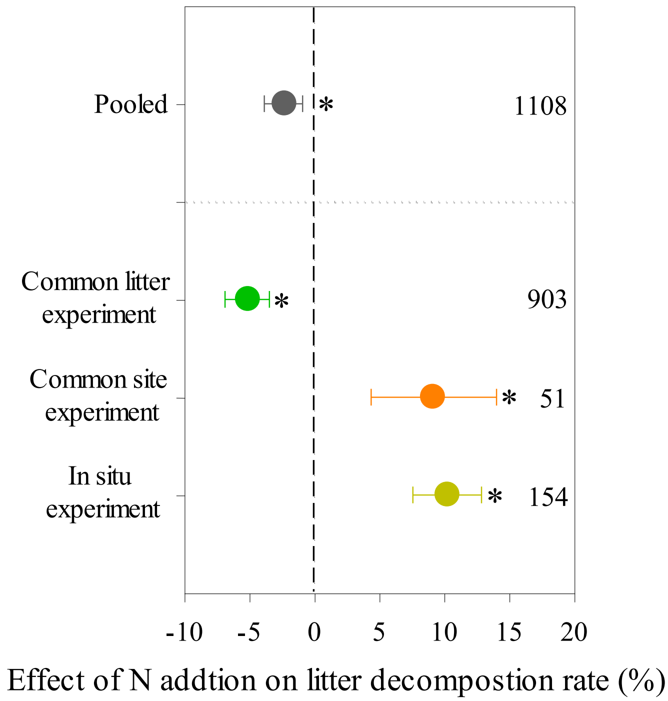

Fig. 1. Effects of N addition on litter decomposition rate in three kinds of litter decomposition experiments. Error bars represent 95% confidence interval (CI). The asterisk indicates a significant difference from zero ($p < 0.05$). The values next to the bars are the corresponding number of observations.

organic and mixture of inorganic and organic N addition increased it in common litter experiment (Fig. 2a). Organic N addition increased litter decomposition rate in common site experiment, and NH_4NO_3 and organic N addition increased litter decomposition rate in in situ experiment, while other types of N addition had no influence on litter decomposition rate in these two experiments (Fig. 2b and c). For all three experiments, the effect of N addition on litter decomposition rate was unrelated to the duration of N addition (Fig. 2).

The decomposition time had significant effect on the responses of litter decomposition rate to N addition under these three kinds of litter decomposition experiments (Fig. 3). Specifically, the inhibitory effect of N addition on litter decomposition rate was more significant when the decomposition time beyond 5 years in common litter experiment (Fig. 3a). The stimulatory effect of N addition on litter decomposition rate disappeared when the decomposition time was longer than 1 year in common site experiment and 2 years under in situ experiment, respectively (Fig. 3b and c). In common litter experiment, N addition decreased litter decomposition rate in subtropical and tropical zones, increased it in Tibetan Plateau and had no effect on it in temperate zone (Fig. 3a). In common site experiment, the litter decomposition rate exhibited positive response to N addition in warm temperate and subtropical zones, but no responses in other climatic zones (Fig. 3b). While for in situ experiment, N addition raised litter decomposition rate in all climatic zones (except for subtropical zone) (Fig. 3c). Litter species also exerted influence on litter decomposition rate under these three kinds of decomposition experiments. In common litter experiment, N addition decreased litter decomposition rate of single species, but had little effect on the decomposition rate of mixed litter (Fig. 3a). While, for common site experiment, the decomposition rate of single species responded positively to N addition, but the decomposition rate of mixed litter showed no response (Fig. 3b). For in situ experiment, N addition increased the decomposition rate of mixed litter to a greater extent, compared with the effect of N addition on the decomposition rate of single species (Fig. 3c).

In common litter experiment, N addition increased the decomposition rate of grass litter, but had no effect and decreased the decomposition rate of shrub and tree litter, respectively, (Fig. 4a). Similarly, the decomposition rate of grass litter showed positive response to N addition, but the decomposition rate of tree litter showed no response in common site experiment (Fig. 4b). For in situ experiment, N addition increased the decomposition rate of grass litter to a greater extent ($Q_M = 12.59$, $p < 0.01$), compared with the effect of N addition on the decomposition rate of tree litter (Fig. 4c). For all these experiments, the effect of N addition on litter decomposition rate was unrelated to mycorrhizal type (Fig. 4).

3.3. *Factors driving the responses of litter decomposition rate to N addition under three decomposition experiment*

N addition significantly increased N and P concentrations of plant litter, but decreased C:N and lignin:N ratios of plant litter in common site and in situ experiments (Fig. 5a and b).

In common litter experiment, the response of litter decomposition

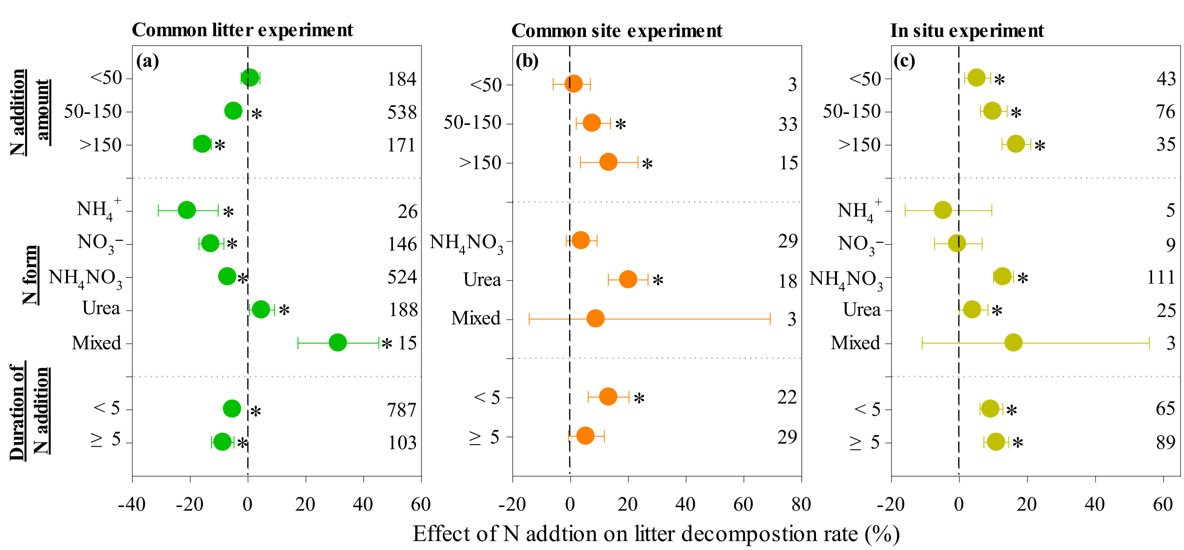

Fig. 2. Effects of N addition amount, form and duration on litter decomposition rate in (a) common litter experiment, (b) common site experiment and (c) in situ experiment. Error bars represent 95% confidence interval (CI). The asterisk indicates a significant difference from zero ($p < 0.05$). The values next to the bars are the corresponding number of observations.

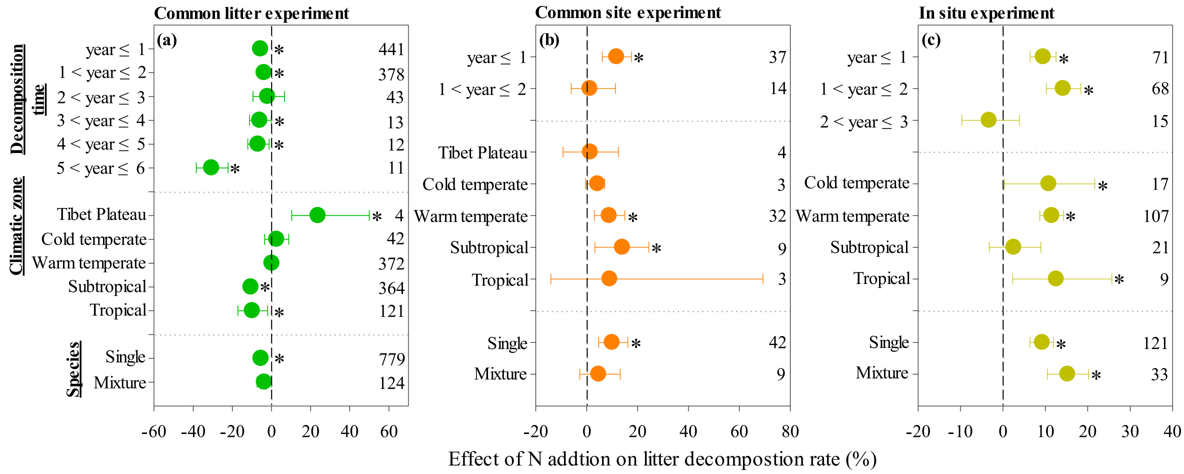

Fig. 3. Effects of N addition on litter decomposition rate in (a) common litter experiment, (b) common site experiment and (c) in situ experiment as related to decomposition time, climatic zone and number of species. Error bars represent 95% confidence interval (CI). The asterisk indicates a significant difference from zero ($p < 0.05$). The values next to the bars are the corresponding number of observations.

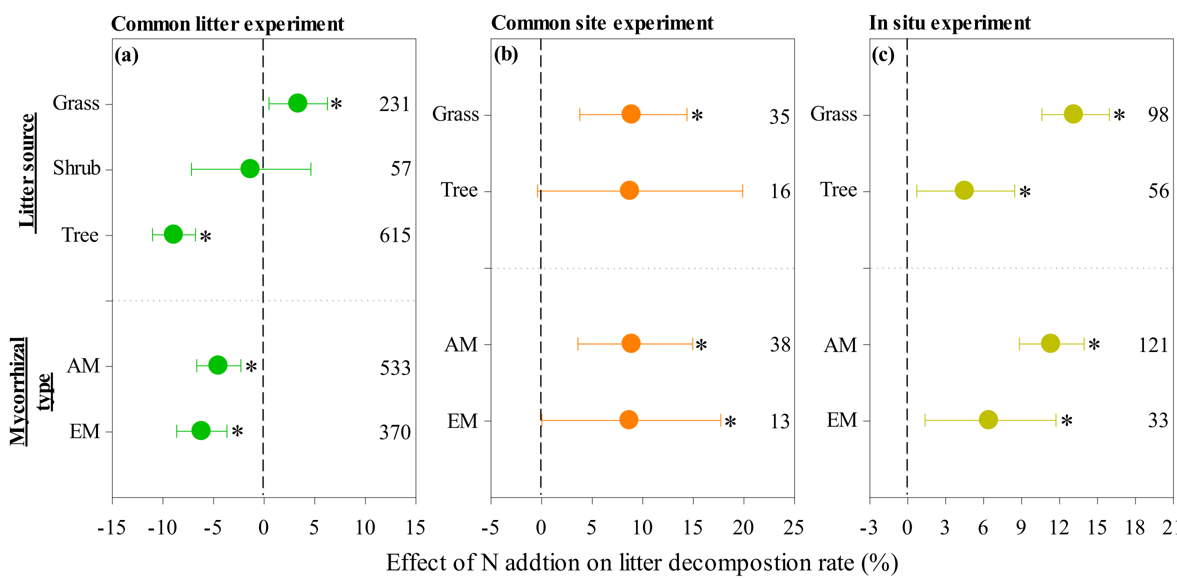

Fig. 4. Effects of N addition on litter decomposition rate in (a) common litter experiment, (b) common site experiment and (c) in situ experiment as related to litter source and mycorrhizal type. Error bars represent 95% confidence interval (CI). The asterisk indicates a significant difference from zero ($p < 0.05$). The values next to the bars are the corresponding number of observations. Abbreviations: AM, arbuscular mycorrhizal; EM, ectomycorrhizal.

rate to N addition was positively correlated with the initial C, N, P and hemicellulose concentrations of plant litter, but negatively correlated with the initial C:N and lignin:N ratios of plant litter (Table 1). For common site and in situ experiments, the response of litter decomposition rate to N addition was positively correlated with the responses of N and P concentrations of plant litter to N addition, but negatively correlated with the responses of C:N and lignin:N ratios of plant litter to N addition (Table 2).

4. Discussion

Although numerous studies have investigated the effect of N addition on litter decomposition, the results varied widely (Vivanco and Austin, 2011; Hou et al., 2021; Peng et al., 2022; Su et al., 2022). Litter quality (Knorr et al., 2005), different decomposition stage (Gill et al., 2021) and N addition regime (i.e., N addition amount and form) (Dong et al., 2019; Fu et al., 2022) were found could regulate the effect of N addition on litter decomposition. However, the underlying mechanisms need further study. Based on 1108 observations (903, 51 and 154 observations for common litter, common site and in situ experiments, respectively), our meta-analysis conducted the first systematic assessment of the response of litter decomposition rate to N addition under these three kinds of litter decomposition experiments (Fig. 6). Our results clearly demonstrated that different litter decomposition methods could also affect the results of N addition on litter decomposition: N addition significantly decreased litter decomposition rate in common litter experiment, but significantly increased it in common site and in situ experiments. These findings provided new insight into the understanding of N addition on litter decomposition. Next, we discussed the possible underlying mechanisms for the observed patterns of the response of litter decomposition rate to N addition under the three litter decomposition experiments.

4.1. N addition decreased litter decomposition rate in common litter experiment

Consistent with the first hypothesis, N addition lowered the litter

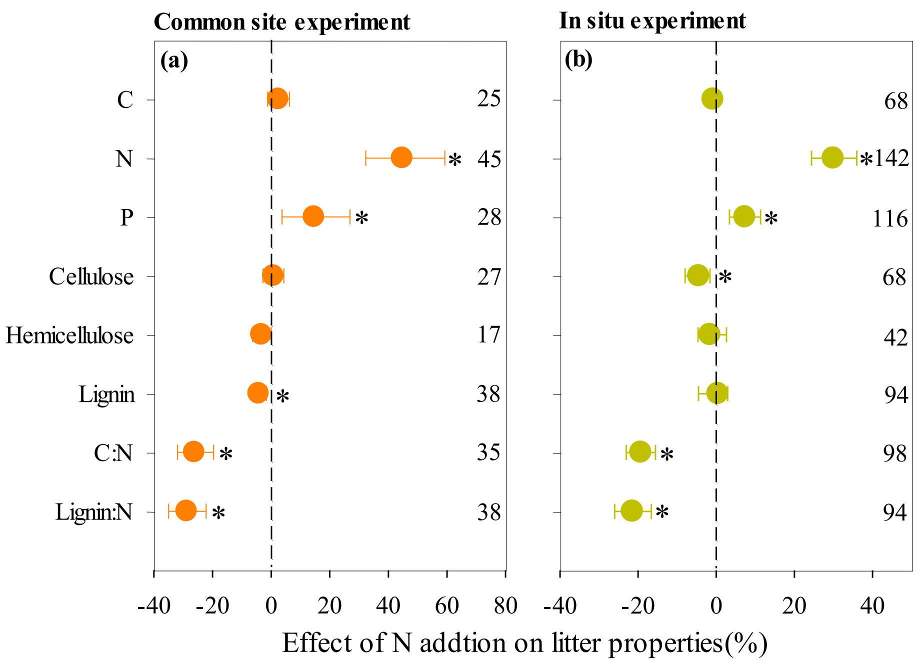

Fig. 5. Effects of N addition on several litter properties in (a) common site and (b) in situ experiments. Error bars represent 95% confidence interval (CI). The asterisk indicates a significant difference from zero ($p < 0.05$). The values next to the bars are the corresponding number of observations. Abbreviations: C, carbon concentration of plant litter; N, nitrogen concentration of plant litter; P, phosphorus concentration of plant litter; C:N, the carbon to nitrogen ratio of plant litter; Lignin:N, the lignin to nitrogen of plant litter.

Table 1
Pearson's correlation coefficients (r) between the response ratios of decomposition rate to N addition and the initial litter quality in common litter experiment.

Decomposition rate	Initial litter quality	Correlation coefficient (r)	Significance (p)	Number of observations (n)
RR(*k*)	C	**0.20****	**< 0.01**	581
	N	**0.18****	**< 0.01**	654
	P	**0.30****	**< 0.01**	499
	Cellulose	0.04	0.39	411
	Hemicellulose	**0.24****	**< 0.01**	188
	Lignin	0.06	0.18	496
	C:N	**−0.22****	**< 0.01**	603
	Lignin:N	**−0.10***	**< 0.05**	497

Abbreviations: C, carbon concentration of plant litter; N, nitrogen concentration of plant litter; P, phosphorus concentration of plant litter; C:N, the carbon to nitrogen ratio of plant litter; Lignin:N, the lignin to nitrogen ratio of plant litter.

decomposition rate in common litter experiment (Fig. 1). In most ecosystems, litter decomposition is primarily regulated by the activities of microorganisms and animals which breakdown the organic matter into simpler forms, so as to gain energy and matter to build and maintain their own biomass (Bradford et al., 2016). In common litter experiments, previous studies mainly examined the influence of N addition on litter decomposition via its effect on soil microorganisms. A number of microbial mechanisms have been proposed to explain the decline in litter decomposition rate in response to N addition. First, N addition might reduce litter decomposition rate by reducing the biomass of the decomposing microbes. It is known that N addition could decrease microbial biomass (Treseder, 2008; Zhang et al., 2018a). N addition could cause soil acidification, loss of base cations and increased solubility of hydrolyzing cations, which could in turn result in microbial base cation limitation and toxic effects of increased Al^{3+} on microbes (Averill and Waring, 2017), and subsequently, reduce microbial biomass and decomposition rate. Second, plenty N supply could stimulate the biosynthesis of hydrolase, but reduce oxidase (i.e., peroxidase, phenol

Table 2
Pearson's correlation coefficients (r) between the response ratios of decomposition rate to N addition and the response ratios of litter quality to N addition in common site and in situ experiments.

Decomposition rate	Variable	Correlation coefficient (r)	Significance (p)	Number of observations (n)
RR(*k*) in common site experiment	RR(C)	**0.51****	**< 0.01**	25
	RR(N)	**0.39****	**< 0.01**	45
	RR(P)	**0.41***	**< 0.05**	28
	RR(Cellulose)	**−0.45****	**< 0.01**	27
	RR(Hemicellulose)	−0.02	0.94	17
	RR(Lignin)	−0.11	0.50	38
	RR(C:N)	**−0.35***	**< 0.05**	35
	RR(Lignin:N)	**−0.36***	**< 0.05**	38
RR(*k*) in in situ experiment	RR(C)	**−0.33****	**< 0.01**	68
	RR(N)	**0.18***	**< 0.05**	142
	RR(P)	**0.19***	**< 0.05**	116
	RR(Cellulose)	−0.19	0.11	68
	RR(Hemicellulose)	−0.01	0.99	42
	RR(Lignin)	0.03	0.81	94
	RR(C:N)	**−0.22***	**< 0.05**	98
	RR(Lignin:N)	**−0.30***	**< 0.05**	94

Abbreviations: C, carbon concentration of plant litter; N, nitrogen concentration of plant litter; P, phosphorus concentration of plant litter; C:N, the carbon to nitrogen ratio of plant litter; Lignin:N, the lignin to nitrogen ratio of plant litter.

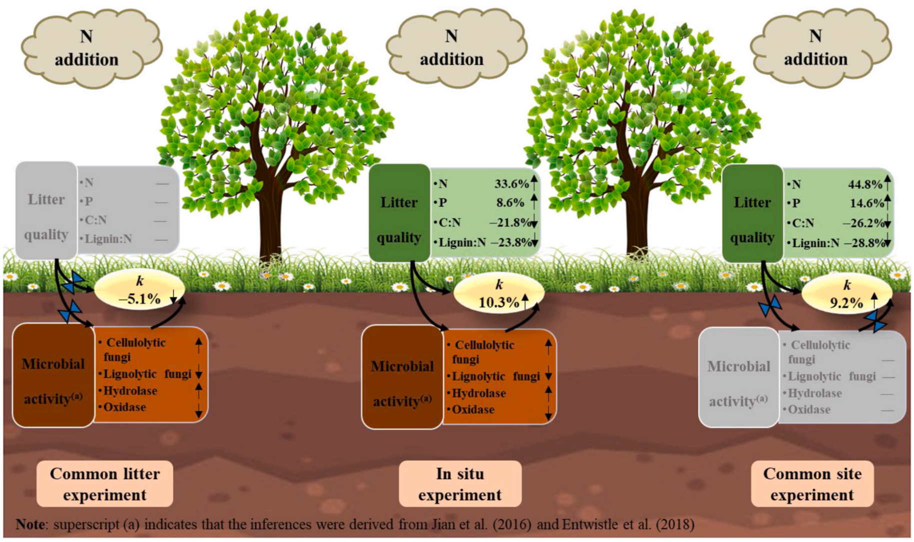

Fig. 6. Conceptual diagram illustrating mechanisms of N addition affecting the decomposition rate in the three experiments. The values behind the variables indicate the percentage changes caused by N addition. The upward and downward arrow indicate positive and negative effect of N addition on the variables, respectively. Abbreviations: *k*, litter decomposition constant; N, nitrogen concentration of plant liter; P, phosphorus concentration of plant liter; C:N, the carbon to nitrogen ratio of plant litter; Lignin:N, the lignin to nitrogen ratio of plant litter.

oxidase) production (Jian et al., 2016; Chen et al., 2018). This is because microorganism does not need to depolymerize recalcitrant substrate such as lignin to mine N, since oxidative enzyme production is high energy cost (Jian et al., 2016). Additionally, N addition could accelerate the release of manganese (Mn) (Peng et al., 2022). Since Mn is an essential element for enhancing ligninolytic enzyme activity and oxidizing lignin (Entwistle et al., 2018; Whalen et al., 2018; Jones et al., 2020), ligninolytic enzyme activity and litter decomposition would be suppressed when Mn is limited. Finally, fungal biomass, richness, especially the abundance of ligninolytic fungi which have the ability to completely decompose lignin could also be reduced by N addition (Entwistle et al., 2018; Moore et al., 2021). The abundance of functional genes involved in the depolymerization of a variety of complex substates was also reduced by N addition (Eisenlord et al., 2013). The reduced abundance of functional microbial groups and genes could also contribute to the decreased litter decomposition rate under N addition.

Nevertheless, N addition might not always reduce litter decomposition rate in common litter experiment. Specifically, N addition had little effect on litter decomposition rate in low amount (<50 kg ha^{-1} $year^{-1}$) of N addition experiment (Fig. 2a), decomposition experiment that conducted in temperate zone and mixed litter decomposition experiment, respectively (Fig. 3a). The low sensitivity of litter decomposition rate to low amount N addition was probably because of insignificant effect of lower amount of N addition on the activity of decomposer (Zhou et al., 2017). The plants and microbes are all N-limited in high latitude and altitude regions, such as cold temperate zone or Tibetan Plateau (Soong et al., 2020; Du et al., 2020). By adding N into N-limited ecosystems, plant uptake can reduce the inhibitory and toxic effects of excessive N on microorganism. Thus, N addition may have little effect on litter decomposition rate or even promote it in N-limited ecosystems. The unchanged litter decomposition rate of mixed litter in response to N addition maybe due to that litter mixtures represent resources of different quality for decomposers. The more diverse litter types could provide more compensatory resources and diverse habitats, and then recruit more diverse decomposers (Gessner et al., 2010). The higher diversity of decomposers might enhance the ability of ecosystem to resist environmental change (Saleem et al., 2019), such as N addition. However, further studies are needed to explore the underlying mechanisms. Moreover, litter decomposition rate was significantly increased by organic and mixture of inorganic and organic N addition (Fig. 2a), and the decomposition rate of grass litter was also enhanced by N addition in common litter experiment (Fig. 4a). Our findings are supported by the regional meta-analysis conducted in China (Su et al., 2021). Since organic N is more readily bioavailable and a preferential N source for microorganisms (Hobbie, 2005), its addition could positively affect microbial activity compared with inorganic N. Moreover, the mixed forms of N addition can offer a broader use of N sources for decomposing microbes to grow on (Dong et al., 2019). The positive response of the decomposition rate of grass litter to N addition was mainly because that grass litter is generally characterized with higher litter quality compared with tree litter (9.9% vs. 22.4% for the percent of lignin in litter; 46.92 vs. 62.21 for C:N ratio, 16.48 vs. 30.40 for lignin:N ratio in this meta-analysis) because of their larger specific leaf area and leaf N concentration (Erdenebileg et al., 2023). Moreover, N addition was found could stimulate the decomposition of high-quality litter (litter with lignin that is less than 10%), but inhibit the decomposition of low-quality litter (litter with lignin that is more than 20%) (Knorr et al., 2005). Since N addition could suppress lignin-degrading metabolism (Entwistle et al., 2018; Moore et al., 2021) and the decomposition of litter with greater lignin contents (Knorr et al., 2005; Xia et al., 2018). They could both verify the finding that N addition imposed inhibitory effect on the decomposition of tree litter. The negative relationships between litter decomposition rate and initial C:N and lignin:N ratios of plant litter in common litter experiment (Table 1) provided further evidence for this explanation.

4.2. N addition increased litter decomposition rate in common site and in situ experiments

Consistent with our second hypothesis, N addition significantly promoted litter decomposition rate in common site experiment. The increased litter decomposition rate was mainly attributed to the improved litter quality under N addition (Hou et al., 2021). Remarkably, both N and P concentrations of plant litter were enhanced by N addition. While the C and lignin concentrations were unchanged, and consequently, the quality of plant litter (i.e., C:N and lignin:N ratios) was improved by N addition (Fig. 5a). Litter with high N and P concentrations could decompose faster than litter with low nutrient contents because high-quality litter can stimulate the growth and activity of decomposer (Fanin and Bertrand, 2016; Bhatnagar et al., 2018). Moreover, C:N ratio, especially lignin:N ratio of plant litter is the dominant regulator of decomposition process (Prescott, 2010). In general, higher decomposition rate is associated with lower C:N and lignin:N ratios (Prescott, 2010; Lin et al., 2020). The response of litter decomposition rate to N addition was positively correlated with the responses of N and P concentrations to N addition, and negatively correlated with the responses of C:N and lignin:N ratios to N addition in common site experiment (Table 2) confirmed the abovementioned mechanisms. Our result confirmed that litter quality is a major determinant of litter decomposition rate (Strickland et al., 2009; Wang et al., 2021).

It is intriguing that N addition also significantly increased litter decomposition rate through its integrated effect on soil environment and litter quality (in situ experiment) (Fig. 1), which was inconsistent with our third hypothesis. Litter quality was also significantly improved in in situ experiment (Fig. 5b). However, we lack the information about the influence of N addition on microbial activity in litter decomposition experiment. Tentatively, we propose that the stimulatory effects of improved litter quality on litter decomposition rate out-performed the inhibitory effects of reduced microbial activity on litter decomposition rate under N addition. Nonetheless, a mechanism which could not be neglect was that, owing to long-term N addition, soil microbial communities could adapt to the high N environment and litter quality, which is known as home-field advantage (HFA). The HFA hypothesis states that leaf litter is often decomposed more rapidly in its habitat of origin than in other habitats, suggesting the specialization of home soil communities in decomposing local litter (Freschet et al., 2012; Osburn et al., 2022). Earlier studies on the three kinds of litter decomposition experiments (i.e., common litter, common site and in situ experiments) reported that litter collected from N addition plot decomposed faster in its own soil than litter from control plot decomposed in N addition plot (Liu et al., 2010; Henry and Moise, 2014; Li et al., 2017). These results suggested that the HFA effects may also be applicable to N addition experiments. Furthermore, N addition was found to increase bacteria to fungi ratio (Zhang et al., 2018a; Hou et al., 2021), suggesting that N addition would shift the systems to the bacterial channel of nutrient cycling. As the nutrient demands and metabolic activities of bacteria are higher than those of fungi (Strickland and Rousk, 2010), bacterial dominated decomposer system is characterized by high turnover rates of substrates (Wardle et al., 2004; Zechmeister-Boltenstern et al., 2015). The higher quality of plant litter coupled with the dominance of bacteria could yield higher litter decomposition rate.

It was worth noting that when the decomposition time was longer than 2 years, the litter decomposition rate showed no response to N addition under in situ experiment (Fig. 3c). It is well supported that N addition could accelerate initial stages litter decomposition, but slow later stages litter decomposition (Knorr et al., 2005; Hobbie et al., 2012; Gill et al., 2021, 2022). The decomposition time ($2 \leq$ year <3) that had no effect on the response of litter decomposition rate to N addition could be a balance period between the positive effect of short-term ($\leq$2 years) and negative effect of long-term (>3 years) decomposition time on litter decomposition rate. However, long-term in situ litter decomposition experiments, especially the experiments that are longer than 3 years, are required to confirm whether N addition could decrease litter decomposition rate under in situ experiment. Given that the overall stimulatory effect of N addition on litter decomposition rate was found under in situ experiments, and in situ litter decomposition experiments can reflect the effect of N addition on litter decomposition more realistically, traditional experiments about the effect of N addition on litter decomposition (i.e., common litter experiments) might underestimate the positive effect of N addition on litter decomposition rate.

4.3. Uncertainties and implications

Our analysis highlights three crucial knowledge gaps. First, more than three quarters of studies about the effect of N addition on litter decomposition only paid attention to the influence of N addition on litter decomposition rate through its effect on soil environment (common litter experiment). These previous studies failed to consider the integrated effect of N addition on soil environment and litter quality. To rigorously investigate the effect N addition on litter decomposition, we need to prioritize in situ experiments. Second, the information about the effect of N addition on soil or litter associated microorganisms in common litter and in situ experiments was rare (Hobbie et al., 2012; Hou et al., 2021). The lack of information limited our understanding on the mechanism of N addition on litter decomposition through its effect on microbial characteristics. Future litter decomposition studies should measure litter and microbial properties (microbial functional groups, genes and enzyme activities) simultaneously. Third, as mentioned in Prescott (2010), to sequester more C in soil, we need to consider not how to slow decomposition, but rather how to divert more litter to relative stable soil organic matter (SOM) pools through microbial and chemical processes. Future studies should also explore the formation of SOM via biochemical and physical pathways of litter mass loss under N addition (Cotrufo et al., 2015). However, our finding of the promoting effect of N addition on litter decomposition under in situ experiments has important implications for the process of soil organic matter formation. The acceleration of litter decomposition could favor the dissolved organic matter (DOM)-microbial pathway for the formation of mineral-associated organic C (MAOC) (Cotrufo et al., 2015). Moreover, litter with lower C:N ratio under N addition typically could form mineral-associated organic matter (MAOM) more efficiently through either microbial transformation or direct sorption to mineral surfaces (Cyle et al., 2016; McFarland et al., 2019). As such, the increased litter decomposition following N addition might increase the input of litter-derived C to more stable SOC pool (i.e., MAOC) (Hobbie, 2015).

5. Conclusions

This global meta-analysis clearly demonstrated that litter decomposition rate responded differently to N addition among different kinds of litter decomposition experiments. For instance, N addition decreased litter decomposition rate in common litter experiment, but increased it in common site and in situ experiments. In a sense, studies that only considered the influence of N addition on litter decomposition rate via its effect on soil environment or microbial properties (common litter experiment), or synthesis studies which mixed different kinds of litter decomposition experiments together, might underestimate the promoting effect of N addition on litter decomposition. For in situ experiment, the increased litter decomposition rate in experiments less than 2 years could be partially explained by the positive effects of improved litter quality exceeding the negative effect of inhibited microbial activity. However, more studies would be needed to further clarify how N addition affects litter decomposition through its integrated effects on litter quality and microbial properties under in situ experiment. Collectively, this meta-analysis advances our comprehensive understanding of the effect of N addition on litter decomposition and benefit the ecosystem models in the accurate projection of C and nutrient cycle under increasing N deposition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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