

Article

Nitrogen Deposition Reduces the Rate of Leaf Litter Decomposition: A Global Study

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Abstract: The litter decomposition of plant leaves is a vital process in carbon (C) and nitrogen (N) cycling in global terrestrial ecosystems. However, previous assessments of the key determinants of the N deposition effects of litter decomposition have been more controversial. In this meta-analysis, we compared the overall effects of N addition on the litter decomposition rates, litter nutrient content (C and N), and litter constituent (lignin and cellulose) residual rates using a log response ratio approach. Our results showed that exogenous N addition increased the N content and inhibited lignin degradation in litter. N deposition decreased the leaf litter decomposition rate by increasing the lignin and N residues and decreasing the litter C content and soil pH. The analysis also concluded that the initial litter C/N ratio, lignin content, and soil pH were main factors in mediating the effect of N deposition on litter decomposition rate. Overall, the results of this study indicate that N deposition can slow decomposition rates by inhibiting N release and lignin degradation of litter. Notably, these results emphasize that the effect of N deposition on litter decomposition mainly depends on the endogenous quality of the litter and soil pH in the decomposition environment.

Keywords: nitrogen addition; decomposition rate; nutrient release; initial litter C/N ratio; lignin residue; soil pH



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1. Introduction

Litter decomposition is a vital process in nutrient cycling and substance exchange in soil ecosystems [1,2]. Small changes in litter decomposition and nutrient release may affect carbon (C) sequestration in global terrestrial ecosystems [3]. The application of exogenous nitrogen (N) has been shown to affect litter decomposition rates and nutrient release rates [4–6]. Some studies have also reported the relationship between litter properties and decomposition rates under N addition [7,8]. Furthermore, N addition may affect the degradation of refractory macromolecular substances during litter decomposition by mediating the secretion of enzymes related to the late decomposition stage of litter [9]. Therefore, understanding the effects of N deposition on both nutrient depletion and substance degradation during litter decomposition is helpful for evaluating the internal mechanism of N-induced litter decomposition.

The litter decomposition rate is affected by the climate environment, biological activities, endogenous litter quality, and other factors [7,10]. Most studies have confirmed that the decomposition process of litter follows an exponential decay model, which may be restricted by the combined effects of external and internal factors [7,11]. Temperature and precipitation are recognized as the primary factors driving litter decomposition rates [12,13]. High-quality litter, characterized by a low C/N ratio, decomposes relatively quickly [14]. Microbial activity and extracellular enzymes regulate nutrient release and lignin degradation during decomposition [15,16]. However, the responses of nutrient release and substance degradation to biotic and abiotic factors vary depending on the litter's species of

origin and the climatic environment [3]. Despite extensive research, the key factors driving litter decomposition rates remain debated [17].

While some studies show that the deposition of exogenous N affects litter decomposition, nutrient release, and substance degradation [14], the influence of N deposition on leaf decomposition remains controversial [7,18]. Global meta-analyses have reported that the effects of N deposition on leaf decomposition vary, with positive, neutral, and negative impacts observed across different studies [14,19]. For example, it has been shown that N addition increases the solubility of litter and the release of polysaccharides (cellulose, hemicellulose, pectin, etc.), thereby increasing the decomposition rate of litter [20,21]. Other ecologists have revealed that N addition reduces the enzymatic activity in the breakdown of lignin, increasing the litter lignin/N ratio and slowing the decomposition rate of litter [10]. Some studies found that N deposition has no significant effect on the overall litter decomposition rate, although it was found to affect the early stages of litter decomposition [4]. In addition, some models used to evaluate the decomposition rate of litter, such as single-pool exponential decay, double-pool, and asymptotic exponential models, have different results in fitting key constraint parameters to provide insight into the decomposition process [7,18]. Therefore, it is urgent to screen decomposition models and explore the influence and key drivers of N deposition on the nutrient release and substance degradation of decomposition using meta-analytic methods.

We developed a global database of 63 published studies to assess the effect of N deposition on the decomposition of leaves in terrestrial ecosystems. The objectives of this meta-analysis were to (1) assess the effects of N addition on the decomposition rates and chemical properties in litter decomposition processes and (2) identify key drivers affecting litter decomposition rates under N addition. Furthermore, we speculated that N addition would inhibit the release of N and the degradation of lignin during leaf litter decomposition, which could be attributed to the fact that N deposition promotes ecosystem N enrichment and the accumulation of litter macromolecular substances [7,11].

2. Materials and Methods

2.1. Data Collection and Inclusion Criteria

The data used in this integrative analysis were derived from the scientific literature and peer-reviewed articles (all data are provided in the Supplementary Materials). Google Scholar (<https://scholar.google.com>) (accessed on 15 May 2021), Web of Science (<http://isiknowledge.com>) (accessed on 10 May 2021), and China Knowledge (<http://www.cnki.net>) (accessed on 21 May 2021) all provided closely relevant data. The search terms were “(litter decomposition) AND (nitrogen deposition OR nitrogen addition OR nitrogen fertilization OR nitrogen application OR nitrogen input).” We reviewed and organized all of the collected literature to target the specific limiting elements: (1) the study had to have measured mass loss during litter decomposition for both N applications and controls, and (2) the residual mass had to be measured at at least three different decomposition time points in each litter decomposition process. To reduce human selection bias, we collected all available data in this analysis (Table S1), regardless of the mesh size, to generate the most comprehensive data set possible. Specific literature screening and removal processes were documented (Figure S1). Our data come from woody and herbaceous species in terrestrial ecosystems, divided into six species types: evergreen broadleaves and conifers, deciduous broadleaves and conifers, graminoids, and forbs. We collected auxiliary data describing the experimental method, including N application rate, fertilizer type, and decomposition duration, and data describing the experimental site, including regional mean annual precipitation (MAP), mean annual temperature (MAT), dominant species, soil pH, litter type, and litter chemical properties in the early and late stages of decomposition (C, N, lignin, and cellulose in N addition and control treatments). To better analyze the data set, we unified the g kg^{-1} , kg kg^{-1} , and mg kg^{-1} of C, N, lignin, and cellulose into % units. We calculated the nutrient release and substrate degradation rates using the ratio of the proportions of C, N, lignin, and cellulose before and after the decomposition of

litter over the decomposition time. In total, the data for this meta-analysis were collected from 63 published studies, including data from 312 reported samples from 65 study sites. We constructed a map of the distribution of study areas specific to the global database (Figure 1). The range of litter decomposition periods for this data set was 3 months to 4 years, with N application rates ranging from 0.24 to 50 g N m⁻² year⁻¹. Appendix S1 references the data sources.

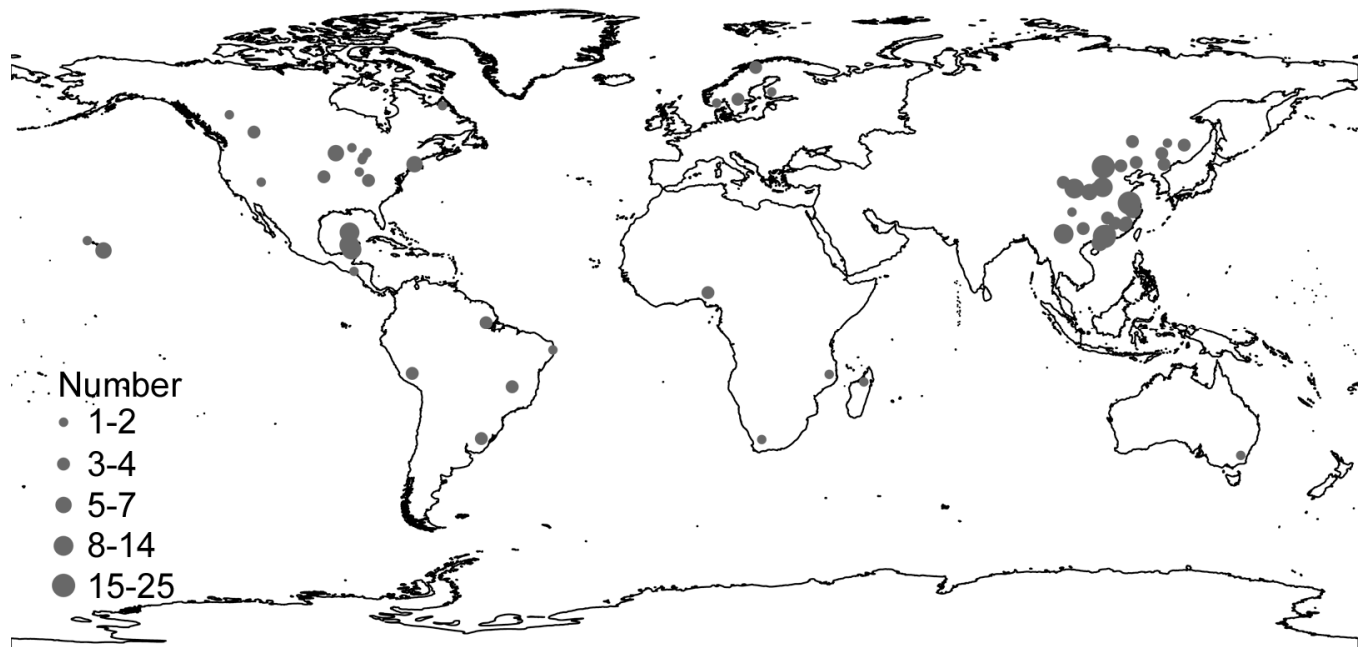


Figure 1. Global distribution of observed sites used in this study.

2.2. Data Analysis

We referenced three decomposition models fitted to the mass of residual litter at each collection site to characterize changes in the mass of litter during decomposition. The corrected Akaike information criterion (AICc) [16] was used to evaluate the degree of fit between the k values (litter decomposition rate) of the single-pool exponential decay model, the double-pool, and asymptotic exponential models, and the actual value of litter mass loss rate (Table S2). We chose the single-pool exponential decay model to calculate and report the decomposition rate of litter after comparison. We applied the following formula:

$$X = e^{-kt} \quad (1)$$

where X represents the ratio of the residual mass/initial mass at time t and k represents the litter constant in the single-pool exponential decay model.

We used the last decomposition time for each collected data set as the time node for calculating the residual rate. We applied the following formula:

$$\text{Residual rate} = (Q_t \times CT_t) / (Q_0 \times CT_0) \times 100\% \quad (2)$$

where t and 0 represent the final and initial decomposition times of litter, respectively. The Q value represents the overall quality of litter, incorporating factors such as nutrient content and structural compounds, while the CT value refers to the specific contents of nutrients, lignin, and cellulose within the litter. The residual rate is calculated based on these values to assess changes over decomposition time.

We used the natural logarithmic response ratio ($\ln RR$) [22] in the statistical analysis to evaluate the litter decomposition rate, nutrient release, and degradation of lignin and

cellulose in response to N addition. The natural logarithmic response ratio was calculated as follows:

$$\ln RR = \ln(X_n/X_c) = \ln(X_n) - \ln(X_c) \quad (3)$$

where X_n and X_c represent the mean values of the samples under N addition and no fertilizer treatments, respectively.

We used MetaWin software (open-source software for meta-analysis) to calculate the natural logarithmic response ratio ($\ln RR$) and 95% confidence interval (CI) for each variable [23]. Significant responses ($p < 0.05$) were detected if the RR and CI did not overlap with zero.

We assessed the litter decomposition rate, the residual rate of nutrients, cellulose, and lignin in different species types in response to N addition. We explored the response of the corresponding variables of litter decomposition to climate factors (MAP and MAT), soil pH, N application rate, and initial litter C/N ratio using a linear regression analysis. An Akaike weight analysis was used to evaluate the relative importance of N application rates, mean annual temperature (MAT), mean annual precipitation (MAP), soil pH, species type, initial litter C/N ratio, and the chemical properties under N addition. The direct and indirect effects of environmental variables on litter decomposition rate were assessed using a structural equation model (SEM) by loading the lavaan package. These analyses were manipulated using R version 4.0.4.

3. Results

3.1. Selection of Litter Decomposition Models

In the N addition and control treatments, the AICc value of single-pool exponential decay was the lowest among the three models, which may better reflect the changes in litter mass loss (Figure S2). In addition, compared with the double-pool and asymptotic exponential models, the single-pool exponential decay model had a better fitting effect for different species types (Table S2). Therefore, we chose the k value of the single-pool exponential decay model to characterize the litter decomposition rate.

3.2. Response of Litter Decomposition Rates and Chemical Properties to N Addition

The results showed that the overall litter decomposition rates after N addition were lower than that of the control treatments (Figure S3). In addition, we calculated the time for decomposition to 50% and 95% of the decomposition mass loss using the single-pool exponential decay model (Figure S4). The decomposition time of leaf litter under N addition was 1.21 times higher than that under the no fertilizer treatments.

We analyzed the k values for litter decomposition and the residual rates of litter C, N, lignin, lignin/N, and cellulose in litter from different species types in response to N addition. The results showed that the N fertilizer significantly reduced the decomposition rate of plant leaf litter (Figure 2). The percentages of lignin, C, and lignin/N residual rates for evergreen conifers and deciduous broadleaf litter under N addition were significantly lower than those in the control treatments. The lignin and N residues in the litter of the overall species under N addition were significantly higher than those in the control treatments. However, there was no significant change in the residual rate of cellulose; that is, it did not respond significantly to N addition. In addition, different N application gradients significantly affected the residual rates of cellulose, C, and N in litter decomposition (Figure 3). The residual rates of litter C and N increased and the residual rate of cellulose decreased with an increase in N application.

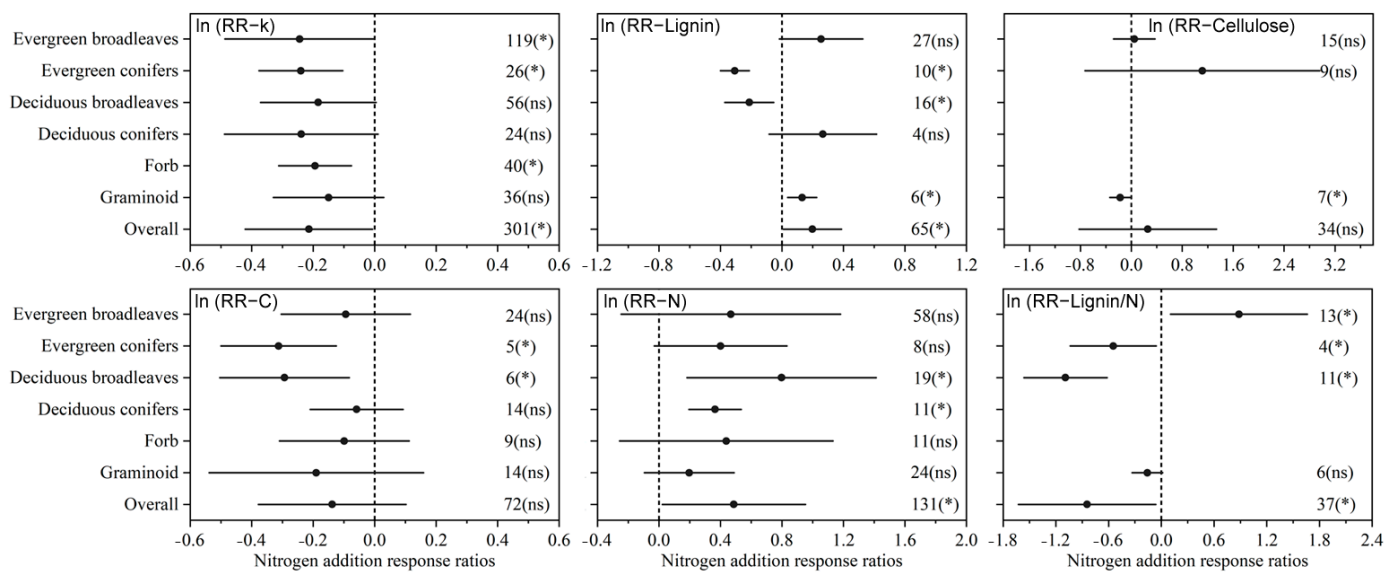


Figure 2. Natural log response ratios ($\ln RR$) of reported litter decomposition rates (k) and chemical property residual rates. Values represent the mean $\pm$ 95% confidence intervals of $\ln RR$ between the N addition and control treatments. Numbers next to each mean indicate the number of observations in the study. Asterisk and ns indicate significant and insignificant responses to N addition, respectively. k , decomposition constant; C, carbon; N, nitrogen.

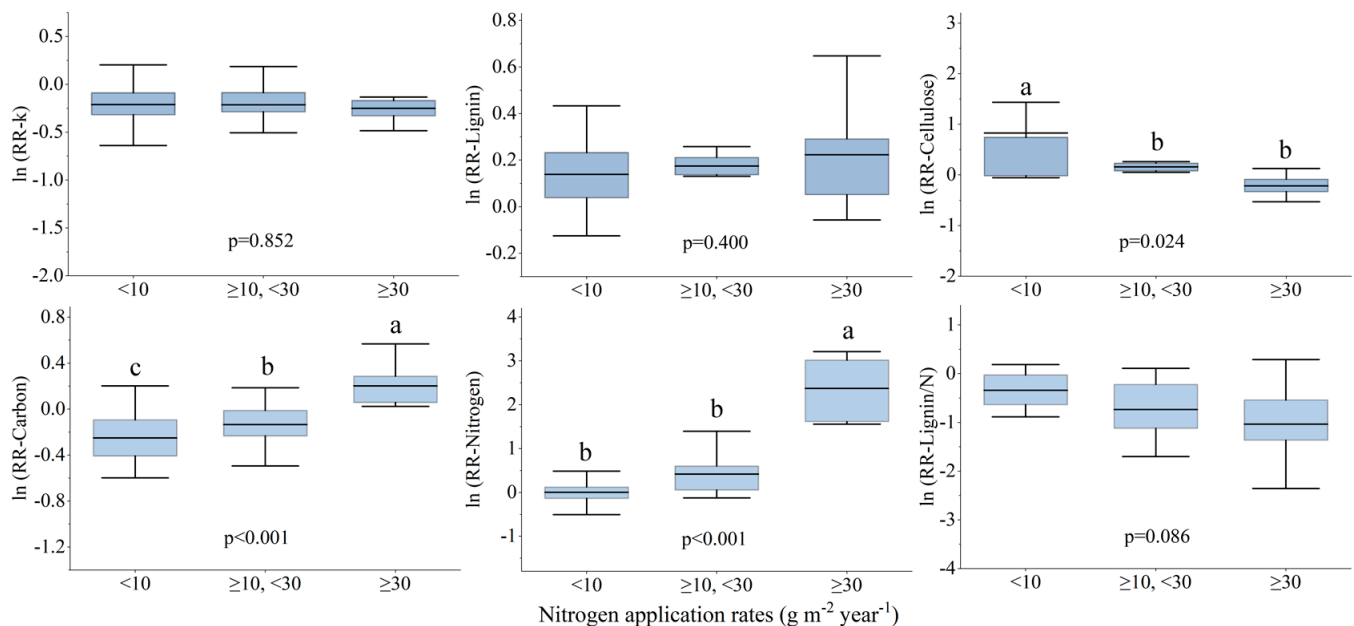


Figure 3. Effect of N application rates on litter decomposition rate and chemical property residual rate. Each box represents the lower and upper quartiles, with the means shown as lines in each box, respectively. Different lowercase letters represent significant differences between different N application rates. The p values represent statistical significance between different N application rates of ANOVA. k , decomposition constant; C, carbon; N, nitrogen.

3.3. Key Factors Affecting Litter Decomposition Rates under N Addition

We used the Akaike weight analysis model to evaluate the relative importance of N application rates, MAT, MAP, soil pH, species type, initial litter C/N ratio, and changes in chemical properties on litter decomposition rates under N deposition (Figure 4). N addition induced a decrease in the litter decomposition rate with an increase in MAP, litter lignin

residue, and the initial litter C/N ratio. However, the litter decomposition rate increased with increasing soil pH and litter lignin/N residue under N addition. The analysis of the optimized model determination using modified Akaike weights emphasized that the best predictive model described the litter decomposition rate as being influenced by N addition, temperature, precipitation, soil pH, species identification, and nutrient residual rates (Figure 4). Soil pH and MAP were important factors influencing litter decomposition rates under N addition, while litter quality (initial C/N ratio and lignin residue) under N addition was still the key driving factor of the litter decomposition rate. Plant species types were included as categorical variables in the Akaike weight analysis model to assess their impact on litter decomposition rates.

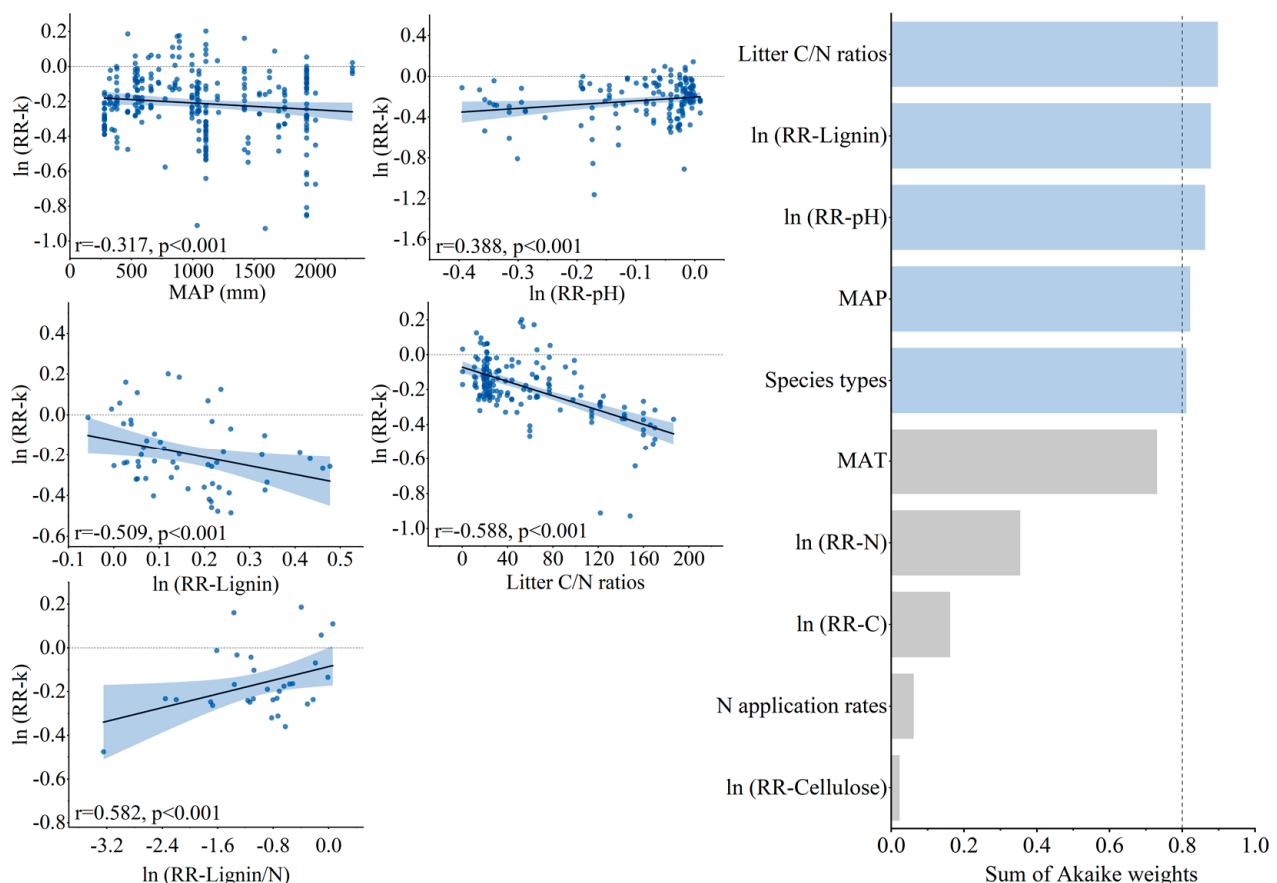


Figure 4. Model-averaged importance of the predictors and partial regression plots of N application rates, mean annual temperature (MAT), mean annual precipitation (MAP), soil pH, species types, litter initial C/N ratios, and chemical property residual rate on litter decomposition rate under N addition. The importance is based on the sum of Akaike weights derived from model selection using corrected Akaike's information criteria. The cutoff was set at 0.8 to differentiate between important and nonessential predictors. k, decomposition constant; C, carbon; N, nitrogen.

Based on the relationship between litter decomposition and environmental factors, we constructed a structural equation model (SEM) to quantify the effects of N deposition (Figure 5). N deposition ultimately reduced the rate of litter decomposition by increasing lignin residues and decreasing litter C/N ratios and soil pH.

Furthermore, we found that N deposition affected the response of the residual rates of litter chemical properties to MAP, MAT, and soil pH (Table S3). The residual rate of lignin/N decreased with an increase in MAP with N deposition. Our results also found that exogenous N deposition induced the residue of litter C to increase with the increase in MAP and MAT. The remaining litter N increased with a decrease in soil pH under N

deposition. Finally, we found that with increasing initial litter C/N ratio, the inhibitory effect of N deposition on the release of litter N was enhanced (Figure S5).

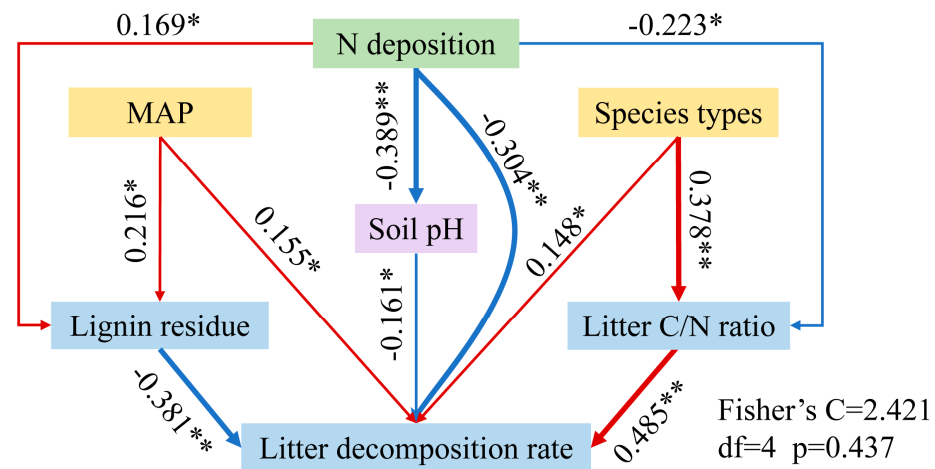


Figure 5. Direct and indirect effects of N deposition on the decomposition rate of litter. N deposition reduced the rate of litter decomposition by mediating environmental and chemical property residual rates on litter decomposition rates under N deposition. Blue arrows indicate a negative relationship, whereas red arrows indicate a positive relationship. The numbers on the arrows are significant standardized path coefficients and proportional to the arrow width. Asterisks denote significant N deposition effects (* $p < 0.05$, ** $p < 0.01$). MAP, mean annual precipitation; C, carbon; N, nitrogen.

4. Discussion

Our model fitting results showed that the single-pool exponential decay model best described the vital process of leaf decomposition regardless of species type (Figure S2 and Table S2). This result was consistent with the conclusions of Hobbie [24] and Wang et al. [16], which indicated that the decomposition quality of litter shows a regular decrease. Therefore, for this database, we considered that the k value of the single-pool exponential decay model would be the best to assess the rate of litter decomposition.

The decomposition rates of plant litter negatively responded to N deposition (Figures 2, S3 and S4), which is consistent with the conclusion of Knorr et al. [7]. Previous studies have also reported that N addition increased the loss of soluble C and hemicellulose sugars in litter decomposition but reduced the degradation of lignin and N [18]. Our results showed that N addition has a stronger inhibitory effect on lignin degradation and N release from litter decomposition than the loss of cellulose and C loss. Litter endogenous substrates of different species types were found to have inconsistent responses to N addition. N deposition increased the residue of lignin/N in the leaf decomposition of the high-quality evergreen broadleaves, which emphasized the significant response of the decomposition rate to lignin/N in the litter [10]. In contrast, the residual rates of litter C and lignin in evergreen conifers and deciduous broadleaves under N addition were higher than those under the non-fertilization treatments. This result may be attributable to the N-induced reduction in the enzyme activity of the microbial community related to lignin degradation [7,25]. In addition, the levels of exogenous N application negatively responded to C and N release and lignin degradation during litter decomposition (Figure 4). N addition enhanced the soil C and N enrichment effect in the decomposition of litter [26,27], which indirectly inhibited the decomposition rate of litter. Some studies have also shown that exogenous N input reduces the activity of lignin-degrading enzymes [9,14], which could slow the rate of leaf decomposition. These studies on N deposition effects revealed that the application of exogenous N inhibited nutrient release and lignin degradation during litter decomposition. Therefore, we inferred that N addition slowed the litter decomposition rate by inhibiting the release of C and N and degradation of lignin.

We found that the initial litter C/N ratio and residual rates of litter lignin and N were significant factors influencing decomposition rates under N addition (Figure 4 and Table S3), which was consistent with the conclusion of Apolinario et al. [28]. In general, high-quality litter with a low initial C/N ratio decomposes faster [2]. Exogenous N addition affects the interaction between litter lignin content and N, influencing the decomposition rate [24]. In addition, low-N litter is often accompanied by a high lignin content [25]. Plants with a high initial litter C/N ratio grow in cold temperate regions of terrestrial ecosystems, where the limiting growth factor for plants and soil ecosystems is generally N [29,30]. The input of exogenous N enhances the fixation of soil N [31], which indirectly affects the release of endogenous N from the litter. The introduction of exogenous N stimulates soil microbial activity, enhancing soil nutrient utilization and reducing N loss during litter decomposition [32,33]. Furthermore, the microbial necromass produced in the later stage of decomposition is easily combined with litter compounds to increase the degree of difficulty of decomposition [18,34]. The combination of endogenous N and lignin compounds during N-induced decomposition increases the stability of litter substrates, making them more resistant to further decomposition [14,26]. Therefore, the initial litter endogenous C/N ratio and lignin degradation significantly influence the decomposition rate under N addition.

Environmental factors such as MAP and soil pH play crucial roles in mediating the decomposition rate of litter under N addition (Figure 4 and Table S3). Du et al. [30] conducted a meta-analysis of global patterns of terrestrial N limitation and found that precipitation changes were significantly correlated with litter decomposition rate and N release. Studies of litter decomposition in arid regions have shown that litter slows down its own decomposition rate and nitrogen loss under water deficit conditions due to N limitation [11,21]. Previous studies have also emphasized the relatively high rate of litter decomposition and nutrient release in the tropics due to higher precipitation [7,25]. Litter in low temperature and arid areas has reduced the fixation of endogenous N under N addition [19,31], which in turn increases the rate of litter decomposition. The input of exogenous N increases the utilization of organic N and C in soil by the soil microbes in warm and humid regions, which then weakens the release of endogenous C and N from litter [7,32]. In addition, some studies have suggested that N addition increases the leaching of NO_3^- , which removes a large quantity of alkaline cations (such as Ca^+), resulting in a decrease in soil pH [35,36]. Previous studies have revealed that excessively acidic soil inhibits the activity of microorganisms involved in litter decomposition, especially white rot fungi that degrade lignin, thereby slowing the litter decomposition rate and substrate degradation [18,33]. Therefore, the N deposition effects on litter decomposition are also influenced by precipitation and soil pH, which affect decomposition rates and substrate degradation.

The question of what determines the effect of N deposition on litter decomposition remains. The Akaike weight model analysis showed that the main determinant of N deposition effects on litter decomposition was the initial litter C/N ratio, followed by the lignin residual rate and soil pH (Figure 5). Thus, the inconsistent effect of N addition on litter decomposition rates may be due to the differences in the endogenous substances of the litter, based on the plant species. Plants growing in high-N areas often have high-quality litter (low initial C/N ratio) and consequently a high decomposition rate, while N addition, in turn, reduces the release of endogenous N from plants [26,32]. N addition increases the fixation of exogenous N in the soil, resulting in litter with low N content, which reduces the loss rate of endogenous N [20]. Yan et al. [3] found that the effect of N deposition on litter decomposition rate varied with plant species. Plant species differ significantly in the C/N ratio or lignin content of decomposing organs in different climate conditions [25]. The litter of evergreen broadleaves has a high initial C/N ratio compared to that of other plants that are easily decomposed [37,38]. The lignin content of coniferous species is higher than that of broadleaves [39], which restricts the decomposition rate of litter. In addition, the decrease in soil pH induced by N addition weakens the secretion of lignin-degrading enzymes by microorganisms, inhibiting the degradation of lignin [7,25]. Overall, we concluded that

the effect of N deposition on plant leaf decomposition mainly depends on the endogenous quality of the litter and soil pH. Ultimately, we incorporated these factors into a structural equation model (SEM) to reveal the key factors and pathways of influence by which N deposition inhibits litter decomposition (Figure 5).

Our findings provide new evidence for understanding the effect of N deposition on litter decomposition, but the meta-analysis has some shortcomings. In this study, the influence of certain elements (such as Mn and Fe) in litter on the decomposition rate was ignored. We also did not discuss the type of fertilization, the mesh size of the decomposition bags, and the mixing effect of litter, which may have led to some unexplained variation in results. Additionally, most of the decomposition completion time was calculated using the single-pool exponential decay model, which may differ from actual decomposition rates in terrestrial ecosystems.

5. Conclusions

This meta-analysis found that exogenous N addition slowed the release of N and the degradation of lignin during litter decomposition. Changes in external biological and non-biological factors affect the decomposition dynamics of endogenous substances in litter. Specifically, the addition of exogenous N slowed down the decomposition rate of litter. The addition of exogenous N increased the N content and inhibited lignin degradation in litter. N addition slowed the rate of litter decomposition by inhibiting the initial litter C/N ratio and the residue of lignin in litter decomposition and decreasing soil pH. The quality of endogenous substances in the litter and soil pH are the key drivers in determining litter decomposition rates. Our findings provide insights into how N deposition affects litter decomposition through changes in litter quality and environmental conditions.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/f15091492/s1>, Figure S1: Flow diagram for searching literature against databases and registers; Figure S2: Proportion best model of litter decomposition under N addition and control treatments; Figure S3: Histograms showing the frequency distributions of site-averaged litter decomposition rate in the N addition and control treatments; Figure S4: Histograms showing the frequency distributions of site-averaged litter decomposition time (the mass of litter remains 50% and 95%, respectively) in the N addition and control treatments; Figure S5: Effect of litter initial C/N ratio on N residual rate of litter decomposition under N addition; Table S1: Leaf litter decomposition data and its location and references on a global scale; Table S2: Percent of decomposition curves in which model AICc was lower than that of all alternative models across species types; Table S3: The effect of mean annual precipitation (MAP), mean annual temperature (MAT), and soil pH on natural log response ratios of studied chemical property residual rates in litter decomposition under N addition.

Author Contributions: All authors contributed intellectual input and assistance to this study and manuscript. J.X.: Formal analysis; Investigation; Original draft preparation; Writing—review and editing. J.W.: Writing—review and editing. Y.Z.: Conceptualization; Writing—review and editing. M.X.: Methodology; Funding acquisition; Writing—review and editing. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: Databases from this paper are available from the online supplementary files.

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