

Review

# Exploring the Factors Affecting Terrestrial Soil Respiration in Global Warming Manipulation Experiments Based on Meta-Analysis

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**Abstract:** Warming significantly impacts soil respiration in terrestrial ecosystems, thereby altering global carbon cycle processes. Numerous field experiments have investigated the effects of warming on soil respiration (Rs), but the results have been inconsistent due to various factors such as ecosystem type, soil warming amplitude, duration, and environmental conditions. In this study, we conducted a meta-analysis of 1339 cases from 70 studies in terrestrial ecosystems to evaluate the response of Rs, heterotrophic respiration (Rh), and autotrophic respiration (Ra) to global warming. The results indicated that Rs, Rh, and Ra increased by 13.88%, 15.03%, and 19.72%, respectively, with a significant rise observed across different ecosystems. Generally, Rs increased with rising temperatures within a specific range (0–4 °C), whereas higher temperatures (>4 °C) did not significantly affect Rs. Moreover, Rs, Rh, and Ra exhibited an initial increase followed by a decrease with prolonged duration, indicating an adaptive response to climate warming. Additionally, Rs and Rh exhibit significant seasonal variations, with levels in winter being markedly higher than in summer. Furthermore, environmental factors exerted direct or indirect effects on soil respiration components. The factors' importance for Rs was ranked as microbial biomass carbon (MBC) > mean annual temperature (MAT) > mean annual precipitation (MAP), for Rh as soil organic carbon (SOC) > MBC > MAT > MAP, and for Ra as belowground biomass (BGB) > aboveground biomass (AGB) > SOC. Future research should focus on the interactions among explanatory factors to elucidate the response mechanisms of soil respiration under global warming conditions.

**Keywords:** soil respiration; heterotrophic respiration; autotrophic respiration; global change; warming amplitude; ecosystems



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## 1. Introduction

Since the Industrial Revolution, human activities have intensified the concentration of greenhouse gases in the atmosphere, resulting in global warming. According to the sixth assessment report of the IPCC, the global average surface temperature is projected to increase by 3.3–5.7 °C by the end of the 21st century [1]. Climate warming will directly affect the structure and function of terrestrial ecosystems, thereby altering various processes of the ecosystem carbon cycle, such as soil respiration [2], fine root dynamics [3], litter decomposition [4,5], photosynthesis [6], plant productivity [7], etc. Soil respiration (Rs) is a complex ecological process that includes heterotrophic respiration (Rh) and autotrophic respiration (Ra) [8]. Specifically, Rs represents the gaseous export from the soil carbon pool, Rh is mainly derived from the decomposition process of soil organic matter (SOM) and litter, and Ra includes the respiration of living roots and root symbionts [9,10]. As a major pathway for the release of carbon stocks from terrestrial ecosystems into the atmosphere,

small changes in the rate of Rs can significantly impact on the atmospheric carbon dioxide (CO<sub>2</sub>) concentrations and associated climate change [11]. Therefore, understanding the changes in soil respiration components (Rs, Rh, Ra) under warming conditions can provide a theoretical basis for predicting the effects of global climate change on the soil carbon cycle (C) and exploring the acclimation mechanisms of ecosystems.

The effect of global warming on soil respiration components in terrestrial ecosystems is a complex and long-term ecological process [12,13]. Numerous studies have indicated that increased temperature enhances soil respiration intensity [14,15]. However, some studies have not detected a facilitating effect of increased temperature on Rs [16,17]. This discrepancy may be due to various factors such as ecosystem type, warming amplitude, warming duration, and soil properties [18–20]. Therefore, it is important to integrate data from different sources to elucidate the effects of climate warming on soil respiration components in terrestrial ecosystems and their mechanisms of action from a unified perspective.

Meta-analysis is a good quantitative system evaluation method, which can evaluate the contradictions of various research results and quantitatively evaluate the size of the effect [21]. This method has been widely applied in the field of ecological environment research in recent decades [22,23]. Chen et al. [24] focused on a single ecosystem in their study of the effects of climate warming on Rs, which limits the generalizability of their findings to other ecosystems; Zhou et al. [8] and Feng et al. [25] quantified the response of soil respiration components to global climate change, including simulated warming, nitrogen additions, increased precipitation, and acid rain. However, the contribution of environmental factors remains inadequately studied; Ngaba et al. [26] assessed the simultaneous effects of mean annual temperature (MAT), mean annual precipitation (MAP), and soil pH on Rs, but neglected changes in its components (Rh and Ra). Therefore, the response mechanisms of soil respiration components to climate warming in terrestrial ecosystems worldwide require further study.

In this study, we conducted a meta-analysis of global manipulative experiments performed in outdoor environments across various terrestrial ecosystems, including forests, grasslands, farmlands, wetlands, and deserts, to address existing knowledge gaps. Our analysis is distinctive in soil respiration studies, as it extracts Rs, Rh, and Ra observations for each month of the cases and synthesizes data from 1339 cases on the effects of warming on soil respiration components. The objective was to enhance our understanding of Rs responses to these drivers. We examined (1) the effects of climate warming on Rs, Rh, and Ra, and their magnitudes in different terrestrial ecosystems; (2) the effects of categorical factors such as warming amplitude, warming duration, sampling month, and sampling season on Rs, Rh, and Ra; and (3) the influences of climatic factors, plant pools, and soil properties on Rs, Rh, and Ra, as well as their contribution characteristics.

Specifically, we used a meta-analysis to evaluate the response of Rs components to climate warming and employed model selection techniques to identify the primary drivers influencing these responses. The findings of this research will contribute to the theoretical framework of the ecosystem cycle under changing conditions, which is crucial for predicting soil carbon emissions in the context of future global environmental changes.

## 2. Materials and Methods

### 2.1. Search Strategy and Exclusion Criteria

Peer-reviewed journal articles related to terrestrial soil respiration variables were searched using the Web of Science and China National Knowledge Infrastructure (CNKI) search engines. The keywords used for the literature search were (“climate change” or warming or temperature) and (“soil respiration” or “heterotrophic respiration” or “autotrophic respiration”). Also, previously published meta-analysis of soil respiration components under warming treatment were also selected for additional study [24–26]. In addition, the reference section of the article was used as a guide for further potential publications. We then screened the studies based on the following criteria:

- (1) Studies reported results of manipulative experiments conducted in the outdoor environment and having both control and treatment groups. Each group had at least three plots as replicates. In addition, the area of each plot was larger than 1 m<sup>2</sup>. The treatment groups were manipulated artificially to simulate global warming drivers.
- (2) Experiments were conducted in the field, while lab incubation, growth chamber, and translocation studies were not included in this synthesis.
- (3) Studies examined effects of simulated global warming drivers on soil respiration components, including Rs, Rh, and Ra. In a multi-factorial study, only control and changed warming treatment data were extracted, and interactions were excluded.

## 2.2. Data Extraction

We extracted and stored the following data: the mean values of Rs, Rh, and Ra, the sample sizes ( $n$ ), and, depending on the study, the standard deviation (SD) or standard error (SE) of each response variable (Rs, Rh, and Ra) in control and treatment groups. If SE was extracted, it had to be converted to SD by multiplying the SE by the square root of the sample size ( $SD = SE \times \sqrt{n}$ ) [27]. These data were extracted directly from tables and text or indirectly extracted from figures using WebPlotDigitizer (<https://automeris.io/WebPlotDigitizer/>, accessed on 1 July 2023) [28]. Data extracted from graphs were plotted and visually inspected to verify that there were no errors during data extraction. In these studies, the frequency, time interval, and unit of data collection were different. Therefore, the unit of the variable in each report was converted into the same unit. If multiple sampling dates per month of the variable were given, only the monthly mean was extracted.

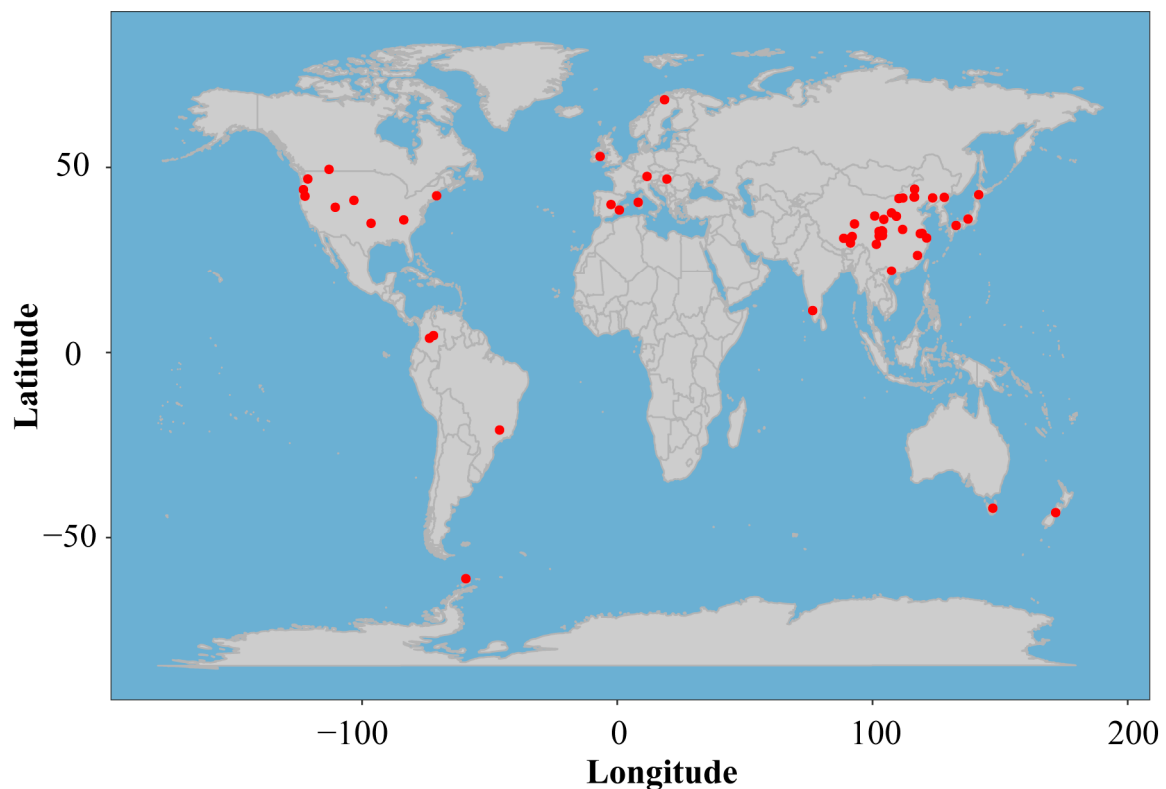
We also recorded data on the study characteristics: geographic coordinates (latitude and longitude), ecosystem type (forests, farmlands, grasslands, wetlands and tundra), soil warming amplitude ( $\leq 1$ , 1–2, 2–4,  $> 4$  °C), warming duration ( $\leq 1$ , 1–3, 3–5,  $\geq 5$  year), sampling season (spring, summer, autumn, winter), MAT, MAP, plant biomass above- and belowground parts (AGB and BGB), litter mass (LM), soil pH, soil moisture (SM), organic carbon (SOC), dissolved organic carbon (DOC), and microbial biomass carbon (MBC). If coordinates were not available, we retrieved them by geo-referencing maps in the papers using ArcGIS 10.3 (ESRI). For data on environmental variables missing from the original literature, they were obtained from their references or from the global database (<https://www.worldclim.org/>, accessed on 5 July 2023).

## 2.3. Data Structure

The data were structured into Study and Case [ $\text{random} < -\text{list}(\sim 1 \mid \text{Study/Case})$ ]. Meta-analysis assumes that individual studies are statistically independent; thus, obtaining several observations (e.g., cases in different experimental sites) from one publication could violate the assumption of independence and create a hierarchical dependence structure among the effect size estimates [29]. Therefore, we also accounted for this hierarchical structure in the model by modeling variance with both among-study and within-study (among-case) components.

## 2.4. Data Availability

After the exclusion criteria, we selected 70 studies (peer-reviewed articles) published from 2005 to 2022. Our meta-analysis spanned 16 countries, mainly distributed in Europe (7), Asia (3), and North America (2), South America (2), and Oceania (2, Figure 1). In the 70 studies, we extracted a total of 1339 cases, of which 833 were Rs, 283 were Ra and 223 were Rh.



**Figure 1.** Global distribution of soil respiration experiments used in this analysis.

### 2.5. Effect Size Metrics

The natural log-transformed response ratio (lnRR) was used to measure the effect size [30] as follows:

$$\ln\text{RR} = \ln(\bar{X}_t / \bar{X}_c)$$

with a variance of:

$$\text{var}(\text{RR}) = \frac{S_t^2}{n_t \bar{X}_t^2} + \frac{S_c^2}{n_c \bar{X}_c^2}$$

where  $\bar{X}_t$ ,  $n_t$ , and  $S_t$  are mean value, sample sizes and standard deviations of the treatment group, respectively, and  $\bar{X}_c$ ,  $n_c$ , and  $S_c$  are mean value, sample sizes and standard deviations of the control group, respectively. Not all studies have reported estimates of SD or SE. In such cases, we used the “Bracken 1992” approach [31] in the “metagear” package [32] to impute missing SD using the coefficient of variation from all complete cases.

For each observation, we calculated the effect size using the “escalc” function in the “metafor” package [33] of R 4.2.3 software. The weighted effect size was transformed back to the percentage change (%), which was evaluated as follows:

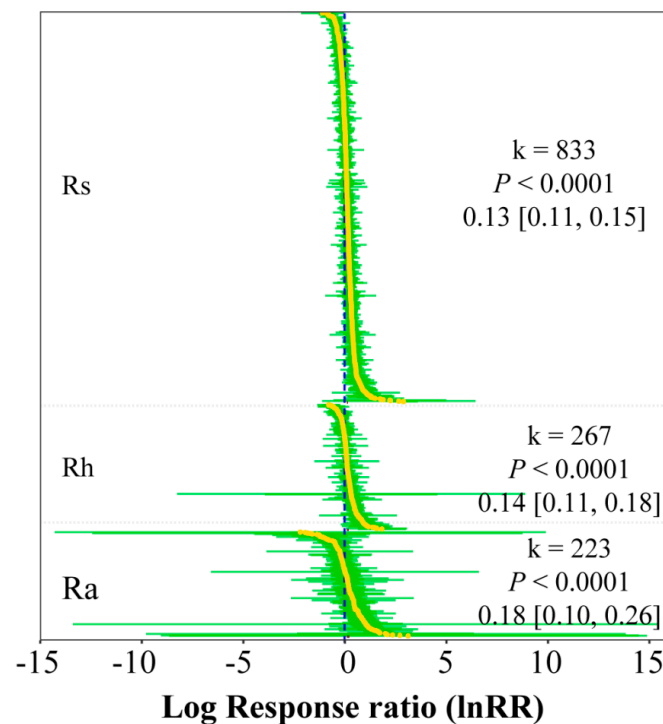
$$\text{Percentage change (\%)} = \left( e^{\ln\text{RR}} - 1 \right) \times 100$$

### 2.6. Data Analyses

Our analyses were separated in three steps: random-effects meta-analysis, single mixed effects meta-regression models, and optimal model selection. With the multilevel random-effects meta-analysis, we assessed overall variation in  $R_s$ ,  $R_a$  and  $R_h$  under the warmed and control treatments. We also checked profile likelihood plots to ensure the identifiability of the variance components in the model ( $\tau^2$ ) and to test whether our more complex models were overparameterized (Figure S1).

We evaluated the heterogeneity of effect sizes with the Q-statistic to determine whether the models could explain a significant amount of variation. For meta-regressions, total

heterogeneity ( $Q_t$ ) can be divided into the variance explained by the moderators ( $Q_m$ ,  $Q$ -statistic which provides information on whether the moderator explains any significant heterogeneity in the data) and the residual error variance ( $Q_e$ ). The  $Q_m$ -statistic is a Wald-type test of model coefficients, and a significant  $Q_m$ -statistic indicates that the moderators contribute to the heterogeneity in effect sizes [33]. In the current study (Figure 2), there was significant residual heterogeneity in the random-effects meta-analysis for the Rs dataset ( $Q_t = 5048.14$ ,  $p < 0.0001$ ), for the Rh dataset ( $Q_t = 889.89$ ,  $p < 0.0001$ ), and for the Rh dataset ( $Q_t = 1382.35$ ,  $p < 0.0001$ ), which we tried to explain with different moderators (Table S1).



**Figure 2.** Responses of Rs, Rh, and Ra to the top-down effects of global warming. Effect sizes (log response ratio) and 95% confidence intervals (CI) for each sample are given in order.  $\ln RR = 0$ , dashed blue line.

We ran multilevel mixed effects meta-analyses in “metafor” (rma.mv) [33] to control for non-independence in the data due to multiple effect sizes per study and cases. Subsequently, we evaluated the relationship between  $\ln RR$  and several explanatory variables, including categorical factors and continuous moderators (Table S1). Continuous variables were log-transformed and fitted as quadratic polynomials to account for non-linear relationships. Models with categorical factors were also run without the intercept to obtain the parameter estimates (mean effect sizes) of each level, and the weighted average effect sizes were significant if the 95% CIs did not contain zero.

For each response variable (Rs, Rh, and Ra), we ranked a set of models according to the small-sample-size corrected Akaike information criterion (AICc) using the “glmulti” package [34]. This method conducts model selection by fitting all possible combinations based on AICc (confesetsize =  $2^n$ ). The importance of a particular factor was expressed as the sum of the weights for the models in which the candidate factor is included. All parameters were estimated using the restricted maximum likelihood method (REML), while the maximum likelihood method (ML) was used when model selection is involved.

### 2.7. Potential Publication Bias Analyses

Publication bias was assessed by funnel plots, which indicated no publication bias if studies were symmetrically distributed in a “funnel” shape [35] around the mean effect size. Therefore, we further assessed the potential asymmetry of the funnel plot using Egger’s

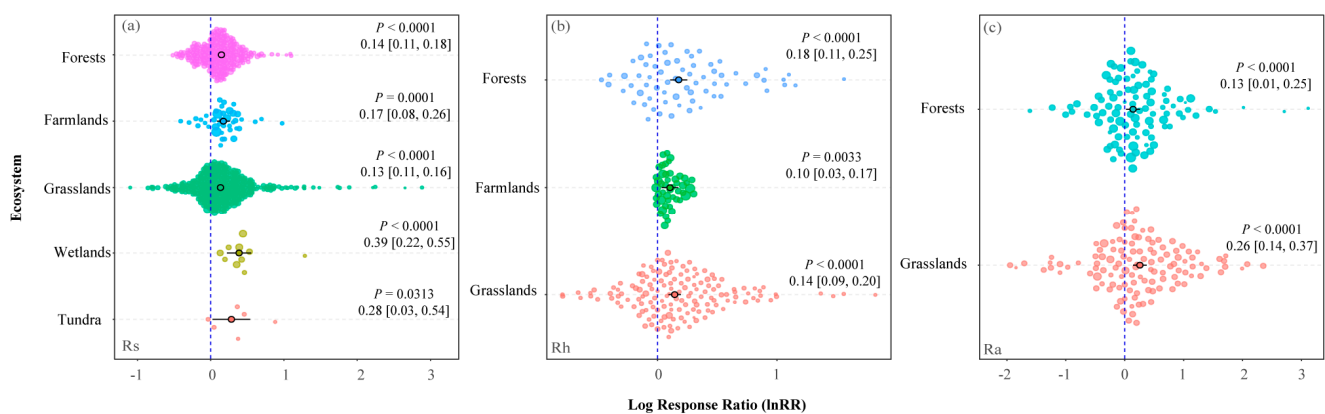


regression [36]. The weighted regression slope is expected to be zero in the absence of publication bias. Trim and fill was also used to both identify and adjust for funnel plot asymmetry from publication bias [37].

### 3. Results

#### 3.1. Response of $R_s$ , $R_h$ , and $R_a$ to Warming in Different Ecosystems

The responses of  $R_s$ ,  $R_h$ , and  $R_a$  to warming were normally distributed throughout the dataset (Figure S2). Meta-analysis of the dataset showed that warming had a significant positive effect on  $R_s$ ,  $R_h$  and  $R_a$  ( $p < 0.0001$ , Figure 2). Compared to the control, warming increased  $R_s$  by 13.88%,  $R_h$  by 15.03%, and  $R_a$  by 19.72%. Ecosystem type significantly affected the response of  $R_s$  to warming ( $p < 0.01$ , Table S2). Under simulated warming,  $R_s$  increased by 15.03% in forests, 18.53% in farmlands, 13.88% in grasslands, 47.70% in wetlands, and 32.31% in tundra (Figure 3a). Under simulated warming,  $R_h$  significantly increased by 19.72%, 10.52%, and 15.03% in forests, farmlands, and grasslands (Figure 3b).  $R_a$  in forests and grasslands were significantly increased by 13.88% and 29.69%, respectively, under the simulated warming treatment (Figure 3c).



**Figure 3.** Orchard plot showing number of cases,  $p$ -values, mean estimate, confidence interval, and individual effect sizes and their precision (inverse variance) of soil respiration ( $R_s$ , (a)), heterotrophic respiration ( $R_h$ , (b)), and autotrophic respiration ( $R_a$ , (c)) in different ecosystems.  $\text{InRR} = 0$ , dashed blue line.

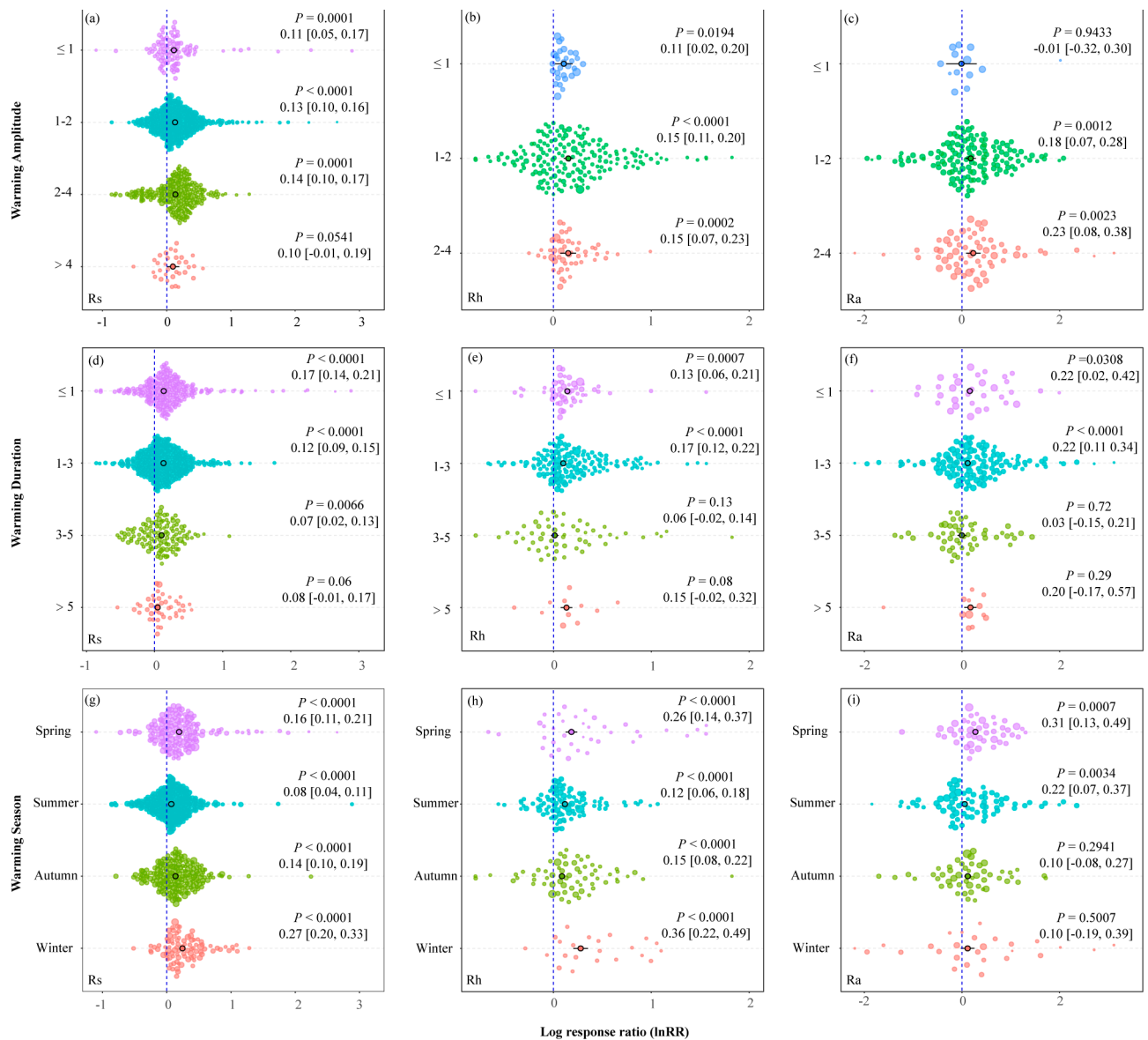
#### 3.2. Soil Warming Amplitude, Warming Duration, and Sampling Season

The soil warming amplitude influenced the responses of  $R_s$ ,  $R_h$ , and  $R_a$  to temperature (Table S2).  $R_s$  exhibited a significant positive response at low ( $\leq 1^\circ\text{C}$ ), low-medium ( $1\text{--}2^\circ\text{C}$ ), and high-medium ( $2\text{--}4^\circ\text{C}$ ) temperatures, with increases of 11.63%, 13.88%, and 15.03%, respectively. However, high temperature ( $>4^\circ\text{C}$ ) did not significantly affect  $R_s$  (Figure 4a). In addition,  $R_h$  was significantly increased by 11.63%, 16.18%, 16.18% at low ( $\leq 1^\circ\text{C}$ ), low-medium ( $1\text{--}2^\circ\text{C}$ ), and high-medium ( $2\text{--}4^\circ\text{C}$ ) temperatures (Figure 4b).  $R_a$  increased by 19.72% and 25.86% at low-medium ( $1\text{--}2^\circ\text{C}$ ) and high-medium temperatures ( $2\text{--}4^\circ\text{C}$ ), respectively, but was not significantly affected by low temperatures ( $\leq 1^\circ\text{C}$ ) (Figure 4c).

In addition to warming amplitude, short-term ( $\leq 1$  year), short-medium-term (1–3 years), and long-medium-term (3–5 years) experiments on soil  $R_s$  showed a significant positive increasing trend in effect sizes (18.53%, 12.75%, and 7.25%). In contrast, long-term ( $>5$  years) experiments exhibited non-significant effect sizes (Figure 4d). Furthermore,  $R_h$  and  $R_a$  increased significantly in both short-term ( $\leq 1$  year) and short-medium-term (1–3 years) experiments. However,  $R_h$  and  $R_a$  were not affected by warming in either long-medium-term (3–5 years) or long-term ( $>5$  years) experiments (Figure 4e,f).

The response of  $R_s$ ,  $R_h$ , and  $R_a$  to warming varied considerably across months (Figure S3). The sampling months in this study were categorized into four seasons (spring, summer, autumn, and winter), and it was observed that both  $R_s$  and  $R_h$  increased substantially in different seasons (Figure 4g,h). Specifically,  $R_s$  increased by 17.35%, 8.33%, 15.03%

and 31.00% in spring, summer, autumn, and winter, respectively. Similarly, Rh increased by 29.69%, 12.75%, 16.78%, and 43.33% in spring, summer, autumn, and winter, respectively. Furthermore, Ra increased by 36.34% and 24.61% in spring and summer, respectively, while autumn and winter had less impact on it (Figure 4i).

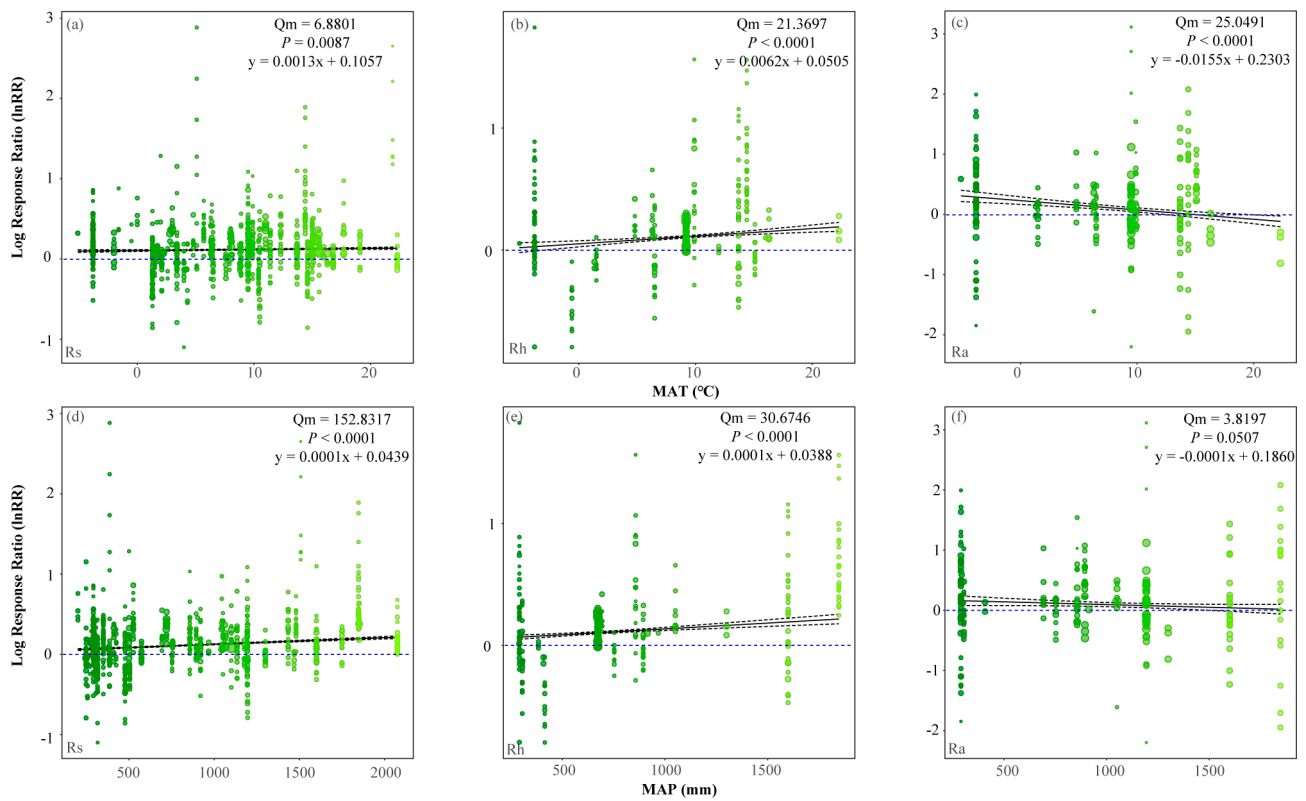


**Figure 4.** Orchard plot showing number of cases,  $p$ -values, mean estimate, confidence interval, and individual effect sizes and their precision (inverse variance) of soil respiration (Rs, (a,d,g)), heterotrophic respiration (Rh, (b,e,h)), and autotrophic respiration (Ra, (c,f,i)) in different warming amplitude, warming duration, and warming season.  $\ln\text{RR} = 0$ , dashed blue line.

### 3.3. Environmental Factors Affecting the Response of Rs, Rh, and Ra to Warming

#### 3.3.1. Climate Factors

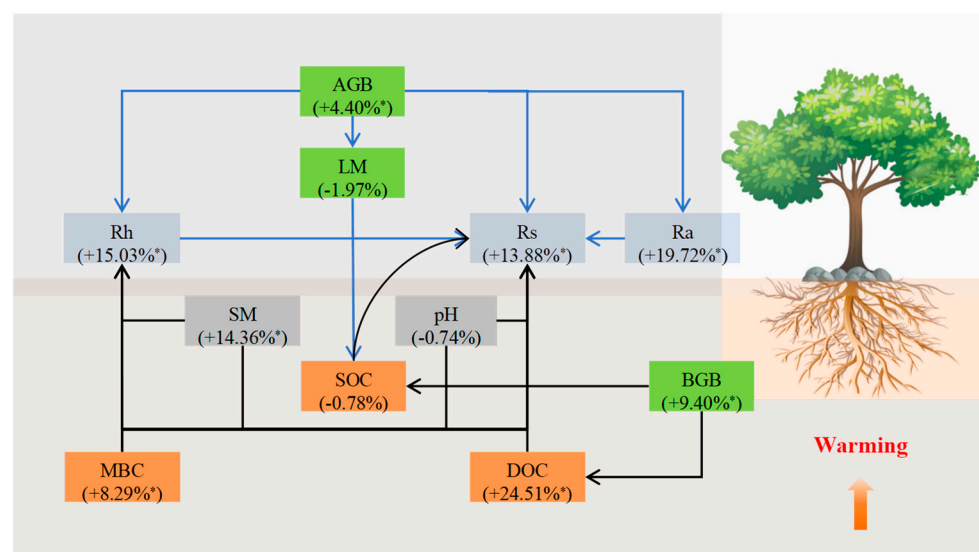
Climate factors (MAT and MAP) played an important role in warming affecting soil respiration. Meta-regression analysis revealed that the effect sizes of warming on Rs and Rh were both significantly and positively correlated with MAT and MAP (Figure 5). In contrast, the effect size of warming on Ra was significantly negatively correlated with MAT and not significantly correlated with MAP (Figure 5c,f).



**Figure 5.** Relationships between soil respiration ( $R_s$ , (a,d)), heterotrophic respiration ( $R_h$ , (b,e)), and autotrophic respiration ( $R_a$ , (c,f)) responses to climate warming treatment for mean annual temperature (MAT) and mean annual precipitation (MAP).

### 3.3.2. Plant Pools

Warming prominently increased soil’s aboveground biomass (AGB, 4.40%) and belowground biomass (BGB, 9.40%) (Table S3, Figure 6). Linear regression analysis showed that  $R_s$ ,  $R_h$ , and  $R_a$  were significantly positively correlated with AGB, while no significant correlation was found with BGB (Table S4, Figure 6).



**Figure 6.** The response of  $R_s$ ,  $R_h$ , and  $R_a$  to experimental warming with the changes of plant carbon pool and soil properties. \* indicates statistical significance ( $p < 0.05$ ). Numbers indicate the effect size (percentage change).



### 3.3.3. Soil Property

Warming significantly reduced soil's SM by 14.36% and significantly increased soil's DOC by 24.51% and MBC by 8.29% (Table S3, Figure 6). Linear regression analysis showed that the effect sizes of Rs were significantly positively correlated with all soil properties (pH, SM, SOC, DOC, MBC) (Table S4). The effect size of Rh was significantly negatively correlated with pH and significantly positively correlated with SM and MBC. However, no significant relationship was found between the effect size of Ra and soil properties.

### 3.4. Optimal Model Selection

The environmental factors mentioned above were incorporated into the models for Rs, Rh, and Ra for model selection, excluding LM and DOC due to insufficient data. In the optimal model for Rs, the order of importance of environmental factors was MBC > MAP > MAT > pH > SOC > BGB > AGB, with MBC, MAP, and MAT meeting the significance criteria (Figure 7). For the best Rh model, the importance order was SOC > MBC > MAP > MAT > AGB > BGB > pH, where SOC, MBC, MAP, and MAT met the significance criteria. For Ra, the factors ranked by importance were BGB > AGB > SOC > MBC > pH > MAT > MAP, with BGB, AGB, and SOC meeting the significance criteria.

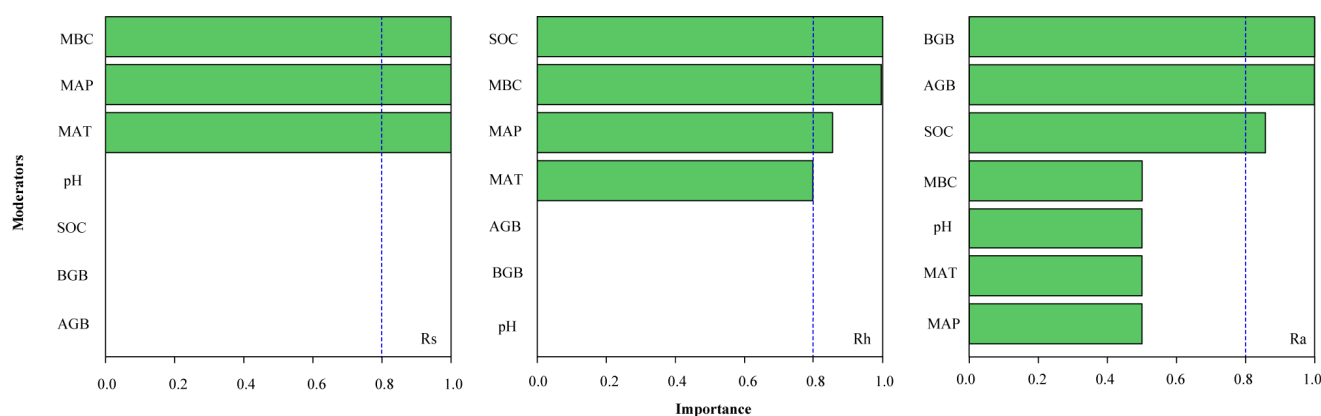


Figure 7. The importance of the factors of significance ( $p < 0.05$ ) for Rs, Rh, and Ra.

## 4. Discussion

Our meta-analysis synthesized global experimental data from diverse geographic regions, providing robust evidence that warming significantly influences all components of soil respiration (Rs, Rh, Ra). With 1339 experimental observations from 70 studies, our work provided a relatively comprehensive assessment of how the effects of simulated warming on soil respiration components are modulated by multiple factors.

### 4.1. Category Moderators Affecting the Response of Rs, Rh, and Ra to Warming

Most field experiments have demonstrated that warming increases soil respiration rates by enhancing the decomposition of soil organic matter and apoplastic material [38,39]. In this study, we observed that soil respiration components in major terrestrial ecosystems exhibited significant positive responses to warming (Figure 3). Lu et al. [40] investigated soil respiration responses to experimental warming across various ecosystems and found that warming significantly increased soil respiration in forests, grasslands, and wetlands, with forest soil respiration rates being significantly higher than those in grasslands. This finding aligns with the observed changes in Rs and Rh in forests and grasslands in our study (Figure 3a,b). The varying effects of warming on different ecosystems can be attributed to differences in the yield and quality of soil organic carbon inputs from these ecosystems [18] and to the differing hydrothermal conditions among ecosystems [41].

A soil respiration temperature sensitivity index (Q10) is commonly used to characterize the response of soil respiration to temperature changes [42], largely influencing the soil carbon cycle's response to climate change. Soil temperature, a key factor affecting

Q10, directly impacts the biochemical processes of soil respiration [43]. The results of meta-analysis in this study showed that Rs increased within a certain temperature range (0–4 °C) (Figure 4a), attributed to the enhanced activities of soil microorganisms and enzymes due to warming [44]. This warming facilitated the consumption of both readily and poorly decomposable components of respiratory substrates and increased soil humus content [45], thereby providing a more abundant carbon supply for plant roots and microorganisms [46,47]. However, further increases in soil temperature did not necessarily favor soil carbon release, as Rs did not significantly change at temperatures above 4 °C (Figure 4a). The reasons for these findings may include (1) sufficiently elevated soil temperatures depleting substrate availability or unstable carbon pools, and (2) elevated soil temperatures reducing soil moisture [48], which limited microbial and enzyme activities and attenuated CO<sub>2</sub> release in the soil.

Numerous studies have demonstrated that soil CO<sub>2</sub> emissions exhibit an initial increase followed by a decrease with prolonged warming [22,49]. Our results also indicated a significant rise in Rs in the short term ( $\leq 1$  year), short-to-medium term (1–3 years), and medium-to-long term (3–5 years), with no notable change in the long term ( $> 5$  years), reaching an experimental inflection point (Figure 4d). Similarly, Rh and Ra, as the primary components of Rs, exhibited an inflection point earlier than Rs and increased significantly in the short term ( $\leq 1$  year) and short-to-medium term (1–3 years). However, they did not change significantly in the medium to long term (3–5 years) or long term ( $> 5$  years, Figure 4e,f). This phenomenon may be attributed to the rapid decomposition of soil organic carbon under short-term warming, which provides ample nutrients for microorganisms [50]. Over time, soil microorganisms undergo a certain degree of acclimatization to the warming conditions [51,52], thereby reducing the positive feedback of soil respiratory components to warming.

Additionally, there were clear seasonal variations in Rs [13]. In the current study, Rs and Rh were higher in winter than in summer (Figure 4g,h), which contradicts some literature reporting “high summer and low winter” Rs under warming conditions [16]. Several reasons may explain this phenomenon: (1) in winter or early spring, temperature is the main limiting factor controlling the metabolic activities of the root systems and soil microorganisms; thus, an increase in temperature leads to significant changes in respiration rates [53]; (2) Q10 varies with temperature, and winter temperatures are cooler, resulting in a relatively high Q10; (3) in some extreme arid and semi-arid regions, increased precipitation in winter and increased soil dryness in summer [54] lead to significant seasonal differences in Rs response to warming.

In conclusion, the dynamic effects of global warming on soil respiration components in terrestrial ecosystems are complex and are synergistically affected by climatic factors, soil properties, and other experimental conditions. Therefore, analyzing the combined effects of climatic warming and other factors has become a focus of future research.

#### 4.2. Continuous Moderators Affecting the Response of Rs, Rh, and Ra to Warming

The results of this study showed that soil Rs and Rh significantly increased with elevated MAT and increased MAP (Figure 5). Differences in MAT lead to variations in soil microbial content and soil pH [55] which regulate the decomposition activity of soil organic matter and indirectly affect Rs. MAP can induce dry and wet alternation processes in arid and semi-arid regions, which promote increased soil microbial activity. Rh is the major contributor [56], so precipitation is usually able to stimulate Rs [57,58]. Conversely, soil Ra decreased significantly with elevated MAT (Figure 5c). This difference may be due to the distinct influences of the two components of soil respiration (Rh and Ra) in response to warming (Figure 5b,c). Rh is regulated by a combination of biotic factors (soil fauna, microbial community structure, etc.) and abiotic factors (temperature, moisture and pH, etc.) [3,13], while Ra's response to warming is primarily dependent on plant biomass [59]. In areas with higher MAT, warming led to a decrease in soil water availability [60], affecting plant photosynthesis and resulting in decreased AGB

and BGB, which in turn weakened the response of soil Ra. Overall, soil CO<sub>2</sub> emissions responded most strongly to warming in areas with relatively favorable temperatures and moderate precipitation.

Further analysis revealed that warming indirectly affected soil respiration components by influencing AGB and BGB (Table S3). Significant positive correlations were found between AGB and Rs, Rh, and Ra (Table S4). This aligns with the findings of Melillo et al. [61], who reported that climate warming enhances plant photosynthetic capacity through metabolism or increases the uptake of mineral nutrients via higher decomposition rates, thereby promoting biomass accumulation and CO<sub>2</sub> emissions. In addition, pH was identified as the main driver of Q<sub>10</sub>, significantly affecting changes in Rs and Rh (Table S4). This is because pH influences soil CO<sub>2</sub> emissions by affecting organic matter synthesis and decomposition, as well as microbial community structure [62]. We found that SOC, as the main carbon source of Rs [63], was significantly and positively correlated with Rs (Table S4). This result contrasts with the study by Knorr et al. [64], who found a negative correlation between SOC content and Rs under warming conditions. The discrepancy may be due to SOC responding to warming in different ways: negative feedback promotes SOC decomposition by accelerating soil microbial growth, while positive feedback promotes SOC accumulation by increasing AGB and LM, which counteracts the depletion of active respiratory substrates caused by warming [65,66]. Previous studies have shown that the active component of soil organic carbon primarily contributes to soil respiration [67], which is supported by the significant positive correlations between DOC, MBC, and Rs found in this study (Table S4). Overall, the effects of different indicators on the characterization of soil respiration components in response to warming were also correlated with the complex and diverse environmental conditions of the corresponding sites.

## 5. Limitations and Future Experiments

Our meta-analysis of 1339 experimental results from 70 studies offers insights into the impact of warming on soil respiration components in terrestrial ecosystems. The effects of global warming on these components are likely more complex and uncertain than previously thought, due to inherent methodological limitations. To more accurately estimate the effects of warming on soil respiration fractions and to gain a comprehensive understanding of the response mechanisms, four key questions need to be addressed, as follows:

(1) The compilation databases utilized in this study are predominantly concentrated in subtropical and temperate regions of the Northern Hemisphere, with limited related research in other areas. This uneven distribution of data sources introduces a potential bias in the study's findings. (2) The current methodology for partitioning soil respiration rates into Ra and Rh is flawed and costly [68], resulting in a scarcity of studies that report on Ra and Rh. (3) Research on the effects of warming on soil respiration components in terrestrial ecosystems predominantly focuses on short- and medium-term experiments, with a notable lack of long-term studies, particularly concerning Rh and Ra. (4) Some references did not account for the physical and chemical properties of soil, which limited our ability to further investigate the mechanisms of soil respiration component responses to warming. Therefore, it is imperative to continue exploring more comprehensive experimental data in future studies to conduct global-scale analyses and derive more robust conclusions.

In conclusion, future terrestrial ecosystem warming experiments should extend beyond the Northern Hemisphere to include those in the Southern Hemisphere, focusing on soil Rh and Ra to accurately assess the integrated response mechanisms of soil respiration components to climate warming. Additionally, long-term warming experiments are essential to evaluate the prolonged effects of climate warming on terrestrial ecosystem components, including plants, soils, and soil organisms. Furthermore, the influence of soil physicochemical properties and vegetation productivity on soil respiration components should be thoroughly examined to deepen our understanding of how warming impacts soil respiration mechanisms.

## 6. Conclusions

Our study conducted a global meta-analysis to examine the response of soil respiration components (Rs, Rh, Ra) to climate warming, observing effect size increases of 13.88%, 15.03%, and 19.72%, respectively. However, these effects varied across different ecosystems. Notably, Rs increased with warming within the range of 0–4 °C, while higher temperatures (>4 °C) had no significant impact on Rs. Additionally, Rs, Rh, and Ra all adapted to warming over time, with experimental inflection points occurring earlier for Rh and Ra than for Rs. Our data revealed that Rs and Rh were significantly higher in winter than in summer, indicating clear seasonal variations. Environmental factors such as climatic conditions, plant carbon pools, and soil properties directly or indirectly influence soil respiration components, providing valuable information for modeling Rs, Rh, and Ra under climate warming. The factors' importance ranking for Rs was MBC > MAT > MAP, for Rh it was SOC > MBC > MAT > MAP, and for Ra it was BGB > AGB > SOC. Our research offers new insights into the significance of moderators affecting Rs, Rh, and Ra and presents new models to better understand the carbon cycle's response to global warming. Future research should focus on the interactions of multiple factors affecting soil respiration components, necessitating more empirical studies to elucidate their combined effects.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/agriculture14091581/s1>, Figure S1: Profile likelihood plots of the variance components in the model ( $\tau^2$ , random<-list(~1|Study/Case)) for Rs (a), Rh (b), and Ra (c); Figure S2: Frequency distribution of the log-transformed response ratio (lnRR) of Rs (a), Rh (b), and Ra (c) to experimental warming; Figure S3: Orchard plot showing number of cases, *p*-values, mean estimate, confidence interval, and individual effect sizes and their precision (inverse variance) of Rs, Rh, and Ra in different months; Figure S4: Funnel plots for the Rs data (a), Rh data (b), and Ra data (c). The white area bordered by dashed lines represents the region of 95% pseudo confidence intervals where 95% of studies are expected to fall in the absence of bias and heterogeneity; Table S1: Moderators included in the analyses. For continuous moderators, units and transformations are indicated; for categorical moderators (factors), levels of the factor are indicated; Table S2: Effect of warming on between-group heterogeneity (Qm) of soil respiration (Rs), heterotrophic respiration (Rh), and autotrophic respiration (Ra); Table S3: Effects of simulated warming on soil pH, plant C pools, and soil C pools; Table S4: Relationships between lnRR of Rs, Rh and Ra and lnRR of soil pH, soil carbon pools and plant biomass in response to simulated warming; Table S5: References used for the meta-data.

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