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# Environmental Conditions Modulate Warming Effects on Plant Litter Decomposition Globally

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## ABSTRACT

Empirical studies worldwide show that warming has variable effects on plant litter decomposition, leaving the overall impact of climate change on decomposition uncertain. We conducted a meta-analysis of 109 experimental warming studies across seven continents, using natural and standardised plant material, to assess the overarching effect of warming on litter decomposition and identify potential moderating factors. We determined that at least 5.2° of warming is required for a significant increase in decomposition. Overall, warming did not have a significant effect on decomposition at a global scale. However, we found that warming reduced decomposition in warmer, low-moisture areas, while it slightly increased decomposition in colder regions, although this increase was not significant. This is particularly relevant given the past decade's global warming trend at higher latitudes where a large proportion of terrestrial carbon is stored. Future changes in vegetation towards plants with lower litter quality, which we show were likely to be more sensitive to warming, could increase carbon release and reduce the amount of organic matter building up in the soil. Our findings highlight how the interplay between warming, environmental conditions,

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and litter characteristics improves predictions of warming's impact on ecosystem processes, emphasising the importance of considering context-specific factors.

## 1 | Introduction

Understanding the temperature sensitivity of plant litter decomposition is a key to predicting future nutrient and carbon cycling, as changes in decomposition may alter nutrient availability, plant growth, and carbon storage in terrestrial ecosystems (Gregorich et al. 2017; Bai et al. 2023). Carbon modelling (e.g., Davidson, Trumbore, and Amundson 2000; Knorr et al. 2005), kinetic theory (e.g., Davidson and Janssens 2006), and laboratory incubations (e.g., Conant, Drijber, et al. 2008; Rey, Pegoraro, and Jarvis 2008) show that decomposition rates increase with increasing temperature. However, site-specific empirical field studies reveal that experimental warming can increase (Li et al. 2022; Zhou et al. 2022), have no effect (Bhuiyan et al. 2023; Bélanger and Chaput-Richard 2023), as well as decrease litter decomposition (Romero-Olivares, Allison, and Treseder 2017; Hong et al. 2021). Results from these site-specific studies pose a challenge to generalisations of the effects of climate change on nutrient and carbon cycling across ecosystems. Here, we synthesise the latest available results from in situ experimental warming studies across terrestrial biomes worldwide that measured decomposition by the mass loss of incubated plant litter. We combine these results with the implementation of a globally distributed, standardised decomposition experiment to improve our understanding of how and where climate warming may affect plant litter decomposition, and to identify potential moderating factors. We use a sixfold larger dataset of 637 paired observations of warmed and non-warmed plots, compared to the recent meta-analysis by Wu et al. (2020). This larger dataset allows us to substantially expand the geographical coverage compared to previous studies in high-latitude systems such as Aerts (2006) and to investigate interactions with both climate and litter quality. That is, previous studies have often focused on a limited set of moderators, primarily temperature and precipitation, while often neglecting more complex interactions, such as those involving litter quality. By including literature data on natural litter as well as a complementary dataset on warming effects on standard litter (i.e., tea bags), we further broadened the geographical and environmental scope of the study. The use of both natural litter and standardised litter allows more reliable comparisons of environmental factors across geographically diverse sites, as well as some assessment of home field effects. The inclusion of two contrasting types of litter (i.e., rapidly decomposing green tea and more slowly decomposing rooibos tea) increased the variety of litter types, allowing us to test for interactions between warming and litter type.

Litter decomposition is a complex process involving the biological (i.e., microbial and soil fauna activity), chemical, and physical transformation and breakdown of organic matter (Bardgett, Freeman, and Ostle 2008; Kirchman 2018; Dai et al. 2020), including leaching of solubles into the soil (Lind et al. 2022). Warming can directly stimulate microbial and enzymatic activity (Xue et al. 2016), as well as leaching (Lind et al. 2022), and thus increase decomposition rates. Global in situ experiments show a strong connection between temperature and precipitation gradients and litter decomposition across biomes and elevations. Projected shifts in temperature and precipitation are expected to significantly impact decomposition rates (Zhang et al. 2008; Conant et al. 2011; Wu et al. 2011; Joly, Scherer-Lorenzen, and Hättenschwiler 2023). However, the exact nature of temperature-precipitation interactions and their combined influence on decomposition remains uncertain. Addressing these complexities requires large-scale datasets that cover diverse environmental conditions and litter types.

Because the type and intensity of climate change vary globally (IPCC 2021), its effects on plant litter decomposition may differ based on environmental settings and litter types, leading to spatial variations in decomposition. For example, cold temperatures tend to inhibit decomposition, creating huge carbon stocks in high-latitude soils (Tarnocai et al. 2009). Concurrently, decomposition in cold environments is particularly sensitive to small changes in temperature (Chen et al. 2015). Therefore, climate warming is expected to increase litter decomposition more strongly in colder high-latitude and high-altitude regions, creating a positive carbon-climate feedback loop. This feedback loop occurs when warming releases greenhouse gases from these carbon-rich soils, further amplifying warming, unless plant growth at higher latitudes and altitudes compensates for the additional release of greenhouse gases (Cox et al. 2000; Fenner and Freeman 2011). In other regions, such as temperate grasslands, climate warming is predicted to increase the frequency and intensity of droughts, which could in turn reduce litter decomposition by limiting the biological activity of decomposer organisms (Vogel et al. 2013; Walter et al. 2013). Therefore, in warmer systems and systems with high variability in precipitation (e.g., savannahs), the warming response is thought to depend strongly on concurrent moisture conditions (Aerts 1997; Seres et al. 2022). Our meta-analysis of 109 experimental warming studies assessing the effect of warming on litter decomposition will improve understanding of the interaction between the prevailing environmental conditions and the warming-induced changes in decomposition. This will enhance our ability to better predict the consequences of these changes for carbon and nutrient cycling in terrestrial ecosystems. Therefore, our study aims to identify recognisable patterns in litter decomposition responses to warming under different macro-environmental conditions.

There is increasing evidence that litter quality (i.e., the chemical characteristics of the decomposing material) may control the temperature sensitivity of litter decomposition (Bosatta and Ågren 1999; Fierer et al. 2005; Davidson and Janssens 2006; Conant, Drijber, et al. 2008; Suseela et al. 2013). Litter with low quality is thought to be more temperature-sensitive, implying that warming could disproportionately accelerate its decomposition compared to that of litter with high quality (Biasi et al. 2005; Davidson and Janssens 2006; Conant, Steinweg, et al. 2008). Given the complex and diverse chemical make-up of plant litter, comparisons across species on a global scale often rely on functional traits or classifications such as carbon

to nitrogen (C:N) ratios (Aerts 1997; Prescott 2010), plant functional types (e.g., trees, shrubs, mosses, graminoids) (Chapin et al. 1996; Dorrepaal et al. 2005), or plant organs (e.g., shoots, leaves, roots) (Freschet, Aerts, and Cornelissen 2012; Xia, Talhelm, and Pregitzer 2015). In addition to these, we used ambient decomposability, quantified as the rate of litter mass loss under ambient conditions (without manipulation), as a proxy for assessing litter quality (Cornelissen et al. 2004; Freschet, Aerts, and Cornelissen 2012). This metric integrates both the inherent chemical composition of the litter, which provides a proxy for how easily decomposers can break it down, and the environmental conditions that affect decomposition rates. Litter with a high C:N ratio (commonly found in trees, shrubs, and roots) has lower decomposability and is considered lower quality due to the presence of more recalcitrant compounds like lignin, tannin, and complex carbohydrates. Conversely, litter with a lower C:N ratio (such as forbs and leaves) is considered high quality with a higher decomposability because it contains less of these recalcitrant materials (Zhang et al. 2008; Prescott 2010; Kirchman 2018). However, understanding how litter quality interacts with warming across large-scale environmental gradients remains a key knowledge gap, crucial for predicting changes in nutrient and carbon cycling under warming. As warming frequently alters plant community composition and thereby litter quality, it is essential to understand how these changes will influence decomposition responses to climate change (Elmendorf et al. 2012; Pearson et al. 2013; Munir et al. 2017).

In this study, we aim to quantify the effect of experimental warming on plant litter decomposition across a wide range of ecosystems and environmental conditions and to identify the contextual dependence of variable warming effects at a global scale. To this end, we assessed whether the effect of warming on litter decomposition varied across (1) macro-environmental regions (i.e., regions derived from map-based environmental variables), (2) experimentally induced changes in microenvironment (i.e., plot-level temperature and moisture changes with warming), and (3) litter quality (i.e., C:N ratio, decomposability under ambient conditions, and plant functional type) within macro-environmental regions. We hypothesize the following:

i. The macro-environmental region is a key determinant of the effect of warming on litter decomposition. In temperature-limited systems, we expect a higher sensitivity and an increase in litter decomposition with warming, whereas in moisture-limited systems, we expect a lower sensitivity to warming and a decrease in decomposition.

ii. A stronger warming will proportionally increase litter decomposition, provided that warming does not limit moisture availability.

iii. Litter quality modulates the effect of warming on litter decomposition, with lower-quality litter being more sensitive to warming than high-quality litter.

To test these hypotheses, we conducted a global meta-analysis examining 109 datasets with experimental setups comprising 637 paired (i.e., warmed and ambient) observations on litter decomposition of plant litter under ambient conditions vs. experimental warming. These datasets were obtained from in situ warming experiments that either decomposed natural local plant species litter (52 paired studies, sourced from published literature) or two standardised plant litter materials, green tea and rooibos (57 paired experiments each, from unpublished primary research). This comprehensive analysis provides a unique opportunity not only to quantify the global effects of warming on litter decomposition, but also to elucidate the interplay between warming, environmental context, and litter quality. Unravelling these complex interactions will be critical for predicting future changes in litter decomposition rates and their associated feedbacks to the global carbon and nutrient cycle.

## 2 | Methods

In this meta-analysis, we combined two global datasets. First, we extracted data from the 52 published studies that measured decomposition responses of natural litter to experimentally imposed higher temperatures. Further, we buried green tea and rooibos as standardised plant litter in 57 warming experiments (Keuskamp et al. 2013). Whereas the natural litter data mainly covers the United States, Western Europe, and China, the standardised plant litter decomposition data ranges from higher latitudes to the Mediterranean and a few sites in the southern hemisphere (Figure 1).

## 3 | Data Collection

### 3.1 | Literature Data on Natural Plant Litter Decomposition

We conducted an extensive literature survey for peer-reviewed publications in the ISI Web of Science database (http://apps.webofknowledge.com/) on September 1st 2023. We used (*warming OR heat* OR OTC OR open-top chamber**) *AND* (*litter* OR litter bag*) *AND* (*decomposition OR mass loss*) as search criteria, which returned 1184 articles (Figure S1). We considered terrestrial field studies that compared litter decomposition (mass loss and decomposition rate of plant material) under experimentally increased temperatures and ambient conditions. Methods found in our search were open-top chambers, heating cables, infrared heaters, sunlit controlled-environment chambers, UVB filter films, open-topped polythene tents, and closed-top chambers. In total, 60 studies met our criteria. We contacted the corresponding authors to obtain access to the raw data for studies that did not report them and had to exclude eight studies due to insufficient reporting. This resulted in 52 studies used for the meta-analysis (Table S1). From these, we extracted mean values, sample sizes, and measures of variation (i.e., standard errors or standard deviations) for litter decomposition (i.e., decomposition rates, absolute and relative mass loss, remaining mass of plant material). Whenever warming was applied in factorial combination with one or more additional treatments (e.g., warming and plant species removal), we only retained the warming vs. ambient contrasts. Each litter bag incubation conducted at different sites, with different plant species, at various time intervals, or using different mesh sizes, was treated as a separate data point.

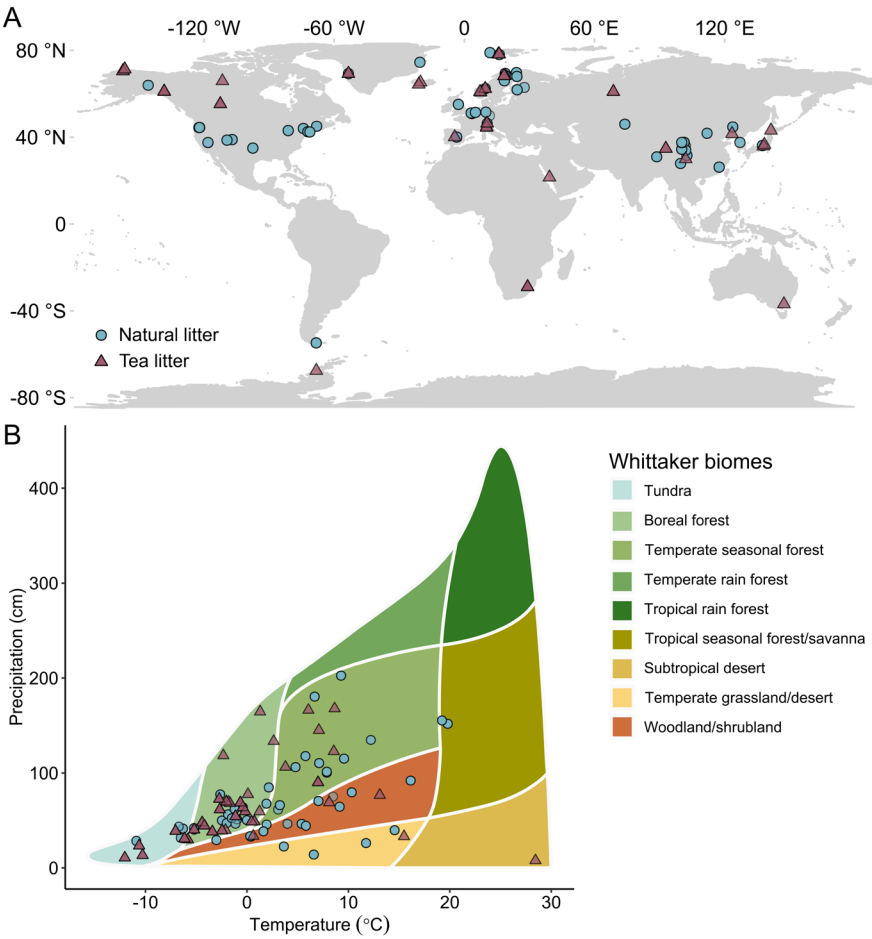


**FIGURE 1** | (A) Map and (B) Whittaker biome diagram showing the location of the 52 published studies of natural litter decomposition in warming experiments (blue circles) and the location of the 57 open-top chamber experiments where we deployed tea as a standardised plant litter to assess decomposition response to experimental warming (purple triangles) used in this meta-analysis. Data availability was limited in temperate and tropical rain forests.

We thus extracted a total of 523 paired (warmed vs. ambient) data points from the 52 studies, either directly from the text or tables or from figures using the software WebPlotDigitizer (v. 4.6, Rohatgi 2021). When litter decomposition was reported as the remaining mass of plant material, this was converted to percentage mass loss:

$$\text{Percentage mass loss} = \frac{\text{Initial mass} - \text{Final mass}}{\text{Initial mass}} \times 100 \quad (1)$$
$$= 100 - \text{percentage mass remaining}$$

We extracted coordinates of each study location (Figure 1A), the incubation duration of the litter (from 14 days to 4.9 years, standardised to days), the mesh size of the litter bags (from 0.02 to 5 mm), the position of incubation (i.e., if litter bags were put on the soil surface or buried below ground), the duration of the warming experiment prior to incubation start (from first year to 23 years), the plant species, the plant functional type (i.e., forb, nonvascular, graminoid, woody species), and the plant organ type (i.e., leaf, shoot, or root). For 32 studies, we also extracted the C:N ratio of the litter reported by the researchers (ranging from 12 to 201). All reported mass losses were from single species incubations, with the only exception being two studies on root decomposition, which included a mixture of grass species. Yet, as all the species in these samples were within the graminoid functional type, we included these studies in the meta-analysis.

The warming method was classified as heating cables (number of studies $n = 11$), infrared heaters ($n = 17$), and open-top chambers ($n = 19$), with 'other methods' including sunlit controlled-environment chambers ($n = 1$), UVB filter films ($n = 1$), open-topped polythene tents ($n = 2$), and closed-top chambers ($n = 1$).

#### 3.1.1 | Standardised Plant Litter Data from Open-Top Chamber Warming Experiments

Following the standard Tea Bag Index protocol (Keuskamp et al. 2013), green (*Camellia sinensis*; EAN no.: 8722700 055525) and rooibos (*Aspalathus linearis*; EAN no.: 8722700 188,438, Lipton, Unilever) tea bags with woven nylon mesh (0.257 mm) were buried at a depth of 8 cm and at a distance of at least 15 cm from each other in open-top chambers (OTCs) and controls under ambient, i.e., non-warmed, conditions at 57 locations (Figure 1 and Table S2). OTCs are commonly used across biomes because they are a cost-effective, robust method

of in situ warming, effectively replicating the natural patterns of interannual variability and latitudinal temperature gradients observed across ecosystems (Hollister et al. 2023). Thus, they are well suited to conduct a global, standardised decomposition experiment. The incubations covered one growing season (82 ± 18 days; mean ± SD), that is, from May/June 2016 to August/September 2016 in the northern hemisphere and from January 2017 to March 2017 in the southern hemisphere. For two sites in Japan (i.e., JPN_1 and JPN_3, Table S2), tea bags were incubated from July to October 2012. Retrieved bags were cleaned of adhering soil and roots, usually by gently brushing the litter bags with a soft brush after air drying to ensure minimal loss of material and avoid damage to the bags. The mass of the remaining tea was determined after drying it in an oven at 60°C–70°C for at least 48 h. To align with the literature data, we calculated treatment means of mass loss (Equation 1), sample sizes, and standard deviations for each experiment location. This resulted in 57 locations with paired (warmed vs. ambient) measurements of both green tea and rooibos (114 data points in total; Figure 1).

### 3.2 | Explanatory Macro-Environmental Drivers

We obtained map-based environmental data based on the geographical locations of the study sites to identify macro-environmental factors that may influence the response of litter decomposition to warming. We used 48 environmental layers reflecting major gradients in climate, soil, vegetation, and topographic variables as covariates in our analysis (Table S3).

Due to the confounding nature of macro-environmental factors, we applied principal component analysis (PCA; Table S3) to scale environmental variables using the R package FACTOMINER (v.2.4; Lê, Josse, and Husson 2008). The first principal component (PC 1) was strongly positively correlated with temperature-associated variables and negatively correlated with soil organic carbon (SOC) and explained 26.9% of the total variance (Figure 3A and Table S3). The second component (PC 2) correlated positively with precipitation-associated variables and explained 18.1% of the total variance (Figure 3A, Table S3). The third PC axis was not considered as it described negligible amounts of the variation (4.2%). In our dataset, the range of mean annual temperature was −12°C–28°C, annual precipitation was 78–2100 mm, and soil saturated water content was 42%–81%.

Based on the origin of the PC1 and PC2 axes, we identified four 'macro-environmental' classes, corresponding to the four PCA quadrants. Positive scores on PC1 represent higher values (warmer conditions), while negative scores indicate lower values (colder conditions). Similarly, positive scores on PC2 indicate wetter conditions, and negative scores denote drier conditions. This classification allowed us to identify four contrasting climates across our study sites (Figure S2 and Table S4). These four 'macro-environmental classes' were described as follows: (1) high temperatures and high precipitation (number of effect sizes $k = 156$), (2) high temperatures and low precipitation ($k = 170$), (3) low temperatures and high precipitation ($k = 156$), and (4) low temperatures and low precipitation ($k = 155$).

### 3.3 | Explanatory Micro-Environmental Drivers Altered by Experimental Warming

For both datasets (i.e., natural and standardised plant litter), we collected available data on the actual degree of warming, that is, the mean absolute temperature difference between warmed and ambient (non-warmed) plots, as well as soil moisture in warmed and ambient plots, when available. We then calculated the degree of warming as the absolute difference between warmed and control plots in air or soil temperature measures, depending on whether the litter was incubated on the soil surface or below ground, respectively. We calculated relative change in soil moisture with warming according to:

$$\text{Relative change in soil moisture} = \left(\frac{\text{Mc}}{\text{MW}} - 1\right) \times 100 \quad (2)$$

where $M_C$ and $M_W$ are soil moisture in ambient (control) and warming treatment, respectively. Positive and negative values indicate respectively drier and wetter conditions under warming than under ambient conditions.

#### 3.3.1 | Litter Quality

We focused on three different, frequently used characterisations of litter qualities: the C:N ratio of the litter before decomposition, which were reported in the original studies and in Keuskamp et al. (2013) for the tea litter; the decomposability measured as decomposition rate under ambient conditions (i.e., standardised to mass loss in % $d^{-1}$) (Cornelissen et al. 2004; Freschet, Aerts, and Cornelissen 2012); and plant functional type (Dorrepaal et al. 2005). We categorised the plant species into four different plant functional types (*sensu* Chapin et al. 1996), forbs (number of studies $n = 7$), graminoids (i.e., grasses and sedges, $n = 28$), woody species (i.e., shrubs and needle-leaved and broad-leaved trees, $n = 27$), and nonvascular (i.e., mosses, $n = 4$; lichens, $n = 1$). For graminoids and woody species, we were able to further specify litter type as above-ground (i.e., shoots and leaves of graminoids, $n = 25$; broadleaves and needles of woody species, $n = 25$) and below-ground plant organs (i.e., roots of graminoids, $n = 6$; and root of woody species, $n = 2$).

### 3.4 | Data Analysis

To evaluate the effect of experimental warming on litter decomposition, we used Hedges'g, which is the standardised mean difference (SMD). This was calculated by dividing the difference between the mean mass loss in the warming treatment and the ambient condition by the pooled standard deviation (Hedges 1981; Supporting Information M1). A SMD greater than zero indicates that experimental warming enhanced decomposition, while a SMD lower than zero indicates that warming decreased decomposition. By using the SMD as a measure of effect size, we were able to synthesise data measured on different scales or units (e.g., mass loss vs. decomposition rate) while still accounting for the precision (variance) of the measurement.

We derived SMDs and corresponding 95% confidence intervals (CI) using the *escalc()* function from the R package METAFOR

(v.4.0–0; Viechtbauer 2010). Pooled average SMDs across all studies were calculated with multivariate linear mixed-effects models using the *rma.mv()* function, which weights effect sizes based on sample sizes, ensuring larger studies contribute more to the overall estimate. A pooled average effect size was considered significant if its 95% CI did not include zero ($\alpha = 0.05$).

To account for spatial autocorrelation between study locations, we included longitude and latitude as random effects based on great-circle distances (WGS84 ellipsoid method). The Test of Moderators ($Q_M$ test) determined how different factors (moderators) influenced the warming effects on litter decomposition (Koricheva, Gurevitch, and Mengersen 2013).

We first tested for differences between natural and standardised plant litter datasets, using data type (i.e., natural litter or standardised plant litter) as a moderator. As no significant differences were found ($Q_M$ (df = 2) = 2.7, $p = 0.26$), we combined these datasets in subsequent analyses.

We tested the impact of the degree of warming and warming-induced changes in soil moisture, along with their interaction, by incorporating them as moderators in multivariate linear mixed-effects models (METAFOR package). To evaluate whether experimentally induced changes in the micro-environment varied amongst the four macro-environmental classes, we included the 'macro-environmental class' as an interacting moderator in the model (Supporting Information M2).

To determine if experimental warming affected temperature and soil moisture, we conducted independent sample *t*-tests to test whether the absolute difference between the warming treatment and the ambient control differed significantly from zero.

We used linear mixed-effects models to test if different warming methods affected micro-environmental conditions (degree of warming, soil moisture). We employed Tukey HSD post hoc tests (R packages MULTCOMP, v. 1.4–19; Hothorn, Bretz, and Westfall 2008, and EMMEANS, v. 1.7.5; Lenth 2019) for significant differences between methods (Supporting Information M3). We also tested for correlations between warming-induced changes in soil moisture and the degree of warming.

To test for differences in litter quality, measured as the C:N ratio or ambient decomposability, between plant functional types across different macro-environments, we used linear mixed-effects models (R package lmerTest, v. 3.1–3; Kuznetsova, Brockhoff, and Christensen 2017). To identify significant differences in C:N ratio and ambient decomposability between plant functional types (including plant organ types) and across the four macro-environmental classes, we performed Tukey HSD post hoc tests. We also tested the hypothesis that lower-quality litter is associated with a stronger positive warming effect on decomposition. For this, we used multivariate linear mixed-effects models, treating each of the three proxies for litter quality (C:N ratio, ambient decomposability, and plant functional type) as moderators in separate models. In these models, 'macro-environmental class' was included as an interactive factor to assess its influence.

We ensured normality and homogeneity of variance for residuals for all models, applying log (C:N ratio) or rank transformations (warming-induced changes in soil moisture) as needed. All analyses were conducted using R version 4.2.3 (R Core Team 2023), with graphical displays produced using the R packages GGPLOT2 (v. 3.3.6, Wickham, Chang, and Wickham 2016) and ORCHARD (v.2.0, Nakagawa et al. 2021).

We assessed publication bias using Egger's regression test (using the *regtest* function, METAFOR package), which indicated no evidence of publication bias (intercept = 0.01, 95% CI: −0.07, 0.08) (Sterne and Egger 2001).

## 4 | Results

### 4.1 | The Effect of Experimental Warming on Natural and Standardised Plant Litter Decomposition

The impact of experimental warming on plant litter decomposition was assessed by comparing treatments with ambient conditions and increased temperatures ranging from –1.6°C–7.5°C. On average, the different warming treatments significantly increased temperatures by 2.1°C ± 0.1°C (mean ± SE, $n = 559$; soil and air combined; *t*-test: $t = 32.30$, $p < 0.001$) and reduced soil moisture by 8.7% ± 0.9% ($n = 317$; *t*-test: $t = -9.23$, $p < 0.001$) compared to ambient conditions. While the effect of experimental warming on decomposition varied amongst studies, overall, experimental warming did not significantly affect plant litter decomposition (SMD = 0.01, $p = 0.84$ [CI95: −0.10, 0.13], $k = 637$, Figure 2). Experimental warming had also no effects on litter decomposition when the natural litter (SMD = −0.04 [CI95: −0.24, 0.10], $p = 0.41$, $k = 523$; Figure 2) and the standardised litter dataset (green tea: SMD = 0.12 [CI95: −0.06, 0.31], $p = 0.17$, $k = 57$; rooibos: SMD = 0.06

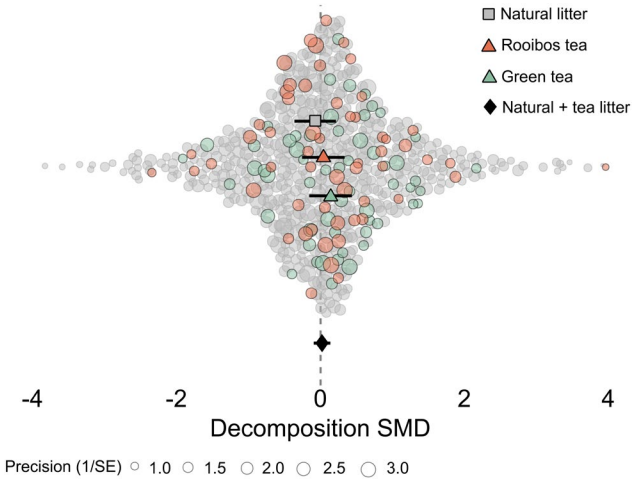


**FIGURE 2** | Effects of experimental warming on plant litter decomposition. The pooled average decomposition standardised mean difference (SMD, Hedges' g; triangles) and 95% confidence intervals (black error bars) resulting from warming. Black diamond, represents the overall mean across natural and standardised plant litter; number of effect sizes ($k = 637$), and separately for the natural litter (grey outlined square, $k = 523$), rooibos (red outlined triangle, $k = 57$) and green tea (green outlined triangle, $k = 57$). Each coloured dot is an individual effect size (non-outlined circles) with dot size representing its precision (i.e., the inverse of the standard error, with larger points having greater influence on the model).

[CI95: −0.12, 0.24], $p = 0.52$, $k = 57$, Figure 2) were analysed independently. The effect of experimental warming on decomposition did not significantly differ between natural and standardised plant litter datasets (moderators' test: $Q_M$ (df = 2) = 2.8, $p = 0.25$).

### 4.2 | The Impact of Macro-Environment on the Warming Effect on Decomposition

Only two of the 48 map-based environmental variables significantly influenced the experimental warming effect on litter decomposition (i.e., precipitation of the coldest month and northness; Table S6). When combined, however, the effect of experimental warming on litter decomposition differed significantly across the four 'macro-environmental classes' identified by the PCA (moderators' test: $Q_M$ (df = 3) = 13.86 $p = 0.003$; Figure 3). In the warm and dry class (high PC1 and low PC2 scores, Figure 3A), we observed a negative warming effect on decomposition (SMD = −0.30 [CI95: −0.52, −0.07], $p = 0.01$, $k = 170$; Figure 3B), driven primarily by a negative effect of experimental warming on natural litter decomposition (SMD = −0.61 [CI 95: −0.94; −0.28], $k = 150$; Figure S3 and Table S7). Despite a trend towards positive effects of experimental warming on litter decomposition in the cold and wet and cold and dry class, which comes with substantial variability, experimental warming did not significantly affect decomposition in any of the other three macro-environmental classes and litter types (Figure 3B, Figure S3 and Table S7).

### 4.3 | The Impact of Experimentally Induced Changes in Micro-Environment on Decomposition and Its Interaction with Macro-Environment

The degree of experimental warming correlated positively with the overall experimental warming effect on litter decomposition (slope = 0.18 SMD/°C warming [CI95: 0.10, 0.26], $p < 0.001$, $k = 315$; Figure S4A). A significant increase in litter decomposition occurred with a degree of warming of 5.2°C or more. However, the relationship between the degree of warming and the experimental warming effect on litter decomposition varied across macro-environmental classes (moderators' test: $Q_M$ (df = 7) = 54.62, $p < 0.001$), with a significantly positive effect on decomposition in relatively warm and wet areas only (slope = 0.20 SMD/°C warming [CI95: 0.09, 0.31], $p < 0.001$, $k = 315$; Figure 4A).

Changes in soil moisture induced by experimental warming had no impact on litter decomposition for any of the four macro-environmental classes (moderators' test: $Q_M$ (df = 7) = 13.66, $p = 0.0$; Figure 4B–H). There was no significant interaction between degree of warming and changes in soil moisture in their impact of the experimental warming effect on litter decomposition (degree warming × soil moisture: $p = 0.89$).

With increasing mesh size, the experimental warming effect on litter decomposition shifted from no effect to a significant negative effect (moderators' test: $Q_M = 4.41$, $p = 0.036$, Figure S4C).

Warming methods significantly affected the experimental warming effect on litter decomposition (moderators' test: $Q_M$ (df = 4) = 12.14, $p = 0.016$). Warming from heating cables resulted in the largest observed temperature increase (4.18 ± 0.1°C, $n = 121$; Table 1), which also increased soil moisture (4.9 ± 4.1%; $n = 48$; Table 1) and significantly increased litter decomposition (SMD = 0.43 [CI95: 0.10, 0.76], $p = 0.010$, $k = 121$). The experimental warming effect of heating cables on litter decomposition differed significantly from the effect of OTCs on decomposition (Tukey HSD, $p = 0.006$, Table 1), but was similar to the experimental warming effect of infrared heaters or other warming methods on decomposition, none of which had a significant experimental warming effect on decomposition (Table 1 and Figure S5).

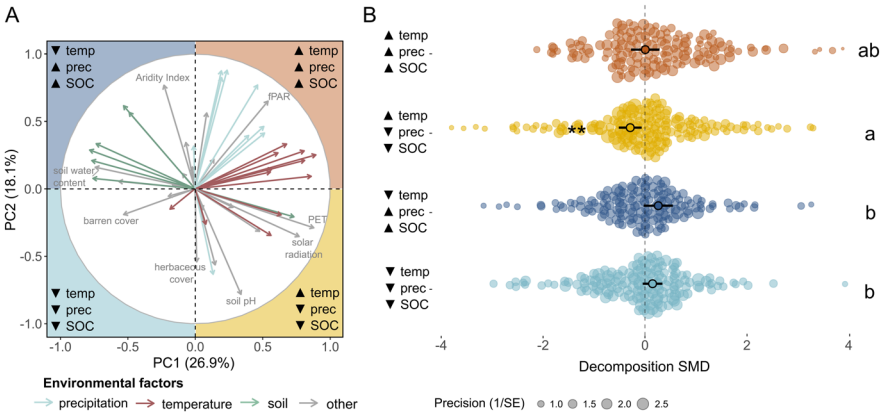


**FIGURE 3** | Impacts of macro-environment on litter decomposition responses to experimental warming. (A) Principal component analysis (PCA) of the variation in macro-environmental factors in our dataset. The arrows are coloured according to the components, which are grouped into temperature, precipitation, soil and other factors (Table S3). The first two axes represent temperature and soil organic carbon-related variables (PC1), and precipitation (PC2). Full list of the macro-environmental factors, their scores on PC1 and PC2 and their mean in every class is presented in Tables S3 and S4A. Colours indicate the four macro-environmental classes distinguished by different combinations of high (▲) or low (▼) temperature (temp), precipitation (prec) and soil organic carbon (SOC). (B) Pooled average decomposition SMD per macro-environmental class of natural litter (outlined diamonds), rooibos tea (outlines squares), and green tea (outlined circles) ±95% confidence intervals (error bars). Each coloured dot is an individual effect size (non-outlined circles) with dot size representing its precision (the inverse of the standard error, with larger points having greater influence on the model). Asterisks indicate that the overall pooled average SMD is significantly different from zero (**$p < 0.01$), whereas different letters denote overall significant differences in the pooled average SMD between macro-environmental classes, averaged over data type.

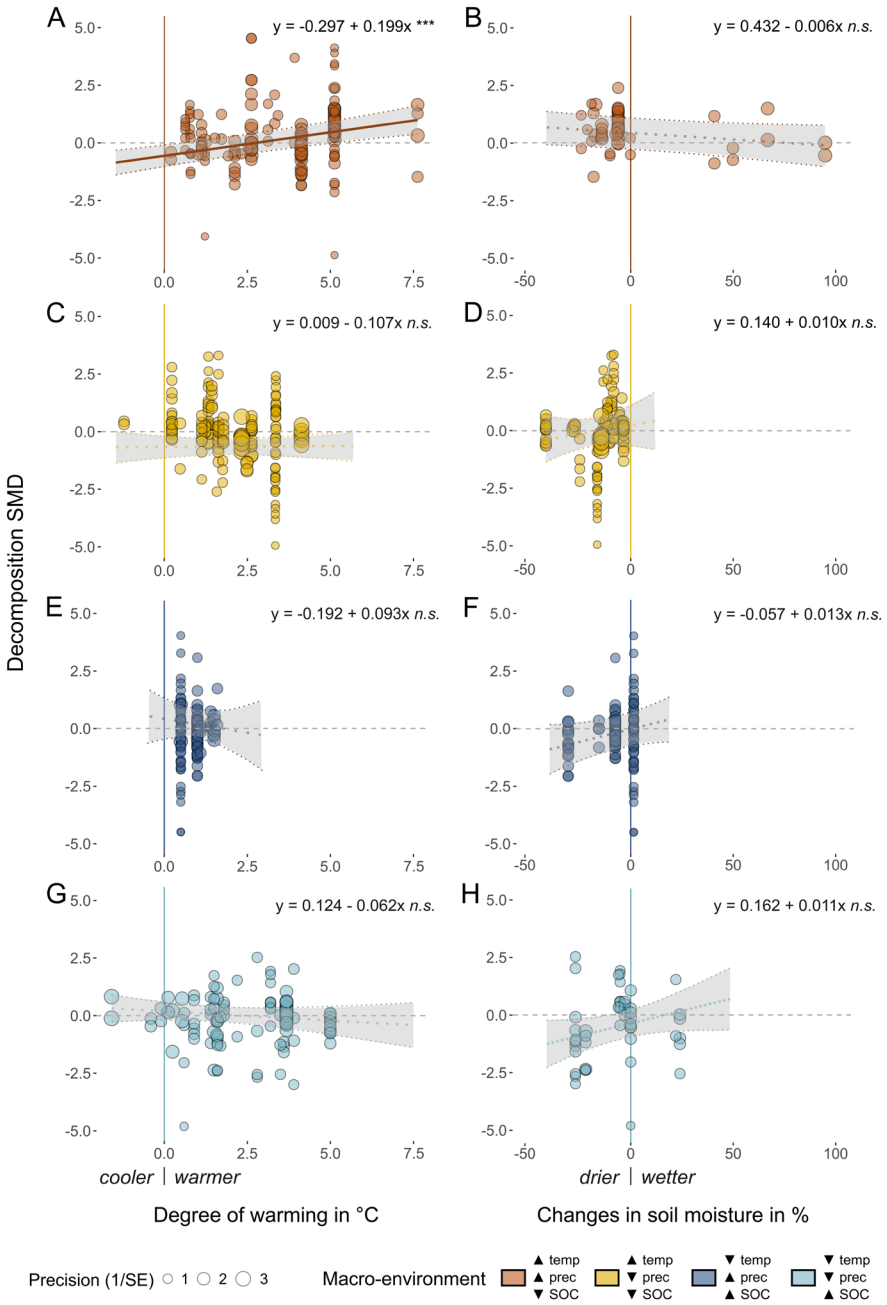


**FIGURE 4** | Relationships between the effect of experimental warming on litter decomposition (SMD) and either (A, C, E, G) the degree of warming (i.e., absolute temperature difference between warmed and ambient plots) or (B, D, F, H) warming-induced changes in soil moisture (i.e., difference between warmed and ambient plots) separately for the four macro-environmental classes (different panels). Colours indicate the four macro-environmental classes distinguished by different combinations of high (▲) or low (▼) temperature (temp), precipitation (prec) and soil organic carbon (SOC), consistent with Figure 3. Each coloured dot is an individual effect size (non-outlined circles) with dot size representing its precision (the inverse of the standard error, with larger points having greater influence on the model). Solid lines indicate regression lines with shaded areas representing the 95% confidence intervals (***$p < 0.001$). Dashed lines indicate no significant relationship (n.s. = not significant).

### 4.4 | The Relationship between Litter Quality Proxies and the Warming Effect on Decomposition

Plant functional types (including green and rooibos tea) and plant organ types differed significantly in their C:N ratio (ANOVA: $F(9, 72) = 417.9$, $p < 0.001$, $n = 72$; Figure S6A).

While the C:N ratio was not significantly related to the experimental warming effect on litter decomposition (slope = −0.001 SMD/C:N ratio [CI: −0.003, 0.001], $p = 0.33$, $k = 428$), plant functional and organ types differed in their warming effect on decomposition (moderators' test: $Q_M$ (df = 8) = 47.92, $p < 0.001$). Experimental warming increased decomposition of graminoid roots (SMD = 0.55 [CI: 0.27, 0.84], $p < 0.001$, $k = 49$) and decreased decomposition of graminoid shoots and leaves (SMD = −0.25 [CI: −0.43, −0.06], $p = 0.010$, $k = 151$). While experimental warming did not significantly affect the decomposition of broadleaves or roots of woody species, it did significantly

**TABLE 1** | The impact of warming methods (i.e., Heating cables, Infrared heaters, Open-top chambers, other methods) on the degree of warming, the relative change in percent soil moisture (mean ± SE), and the effect of warming on litter decomposition (SMD).

| Warming method | Warming degree [°C] | | Soil moisture changes [%] | | SMD estimate | *k* | SMD *p*-value | 95% CI |
|---|---|---|---|---|---|---|---|---|
| Heating cables | $4.18_{a}$ | ±0.1 | $4.88_{a}$ | ±4.1 | $0.41_{a}$ | 121 | **0.021** | **[0.06; 0.76]** |
| Infrared heaters | $1.91_{a}$ | ±0.1 | $-9.46_{ab}$ | ±0.9 | $0.06_{ab}$ | 120 | 0.691 | [−0.26; 0.39] |
| Open-top chambers | $1.33_{a}$ | ±0.1 | $-11.88_{b}$ | ±0.9 | $-0.07_{b}$ | 366 | 0.594 | [−0.33; 0.19] |
| Other methods | $2.51_{a}$ | ±0.2 | $-13.25_{ab}$ | ±5.0 | $-0.25_{ab}$ | 30 | 0.353 | [−0.77; 0.27] |

*Note:* Different letters indicate significant differences in the degree of warming, the soil moisture changes, and the pooled average SMD across warming methods. Bold values indicate a significant effect of the warming method on SMD ($p \leq 0.05$ or CI ≠ 0). Number of effect sizes (*k*), *p*-values for SMD estimates, and 95%-confidence interval are shown.

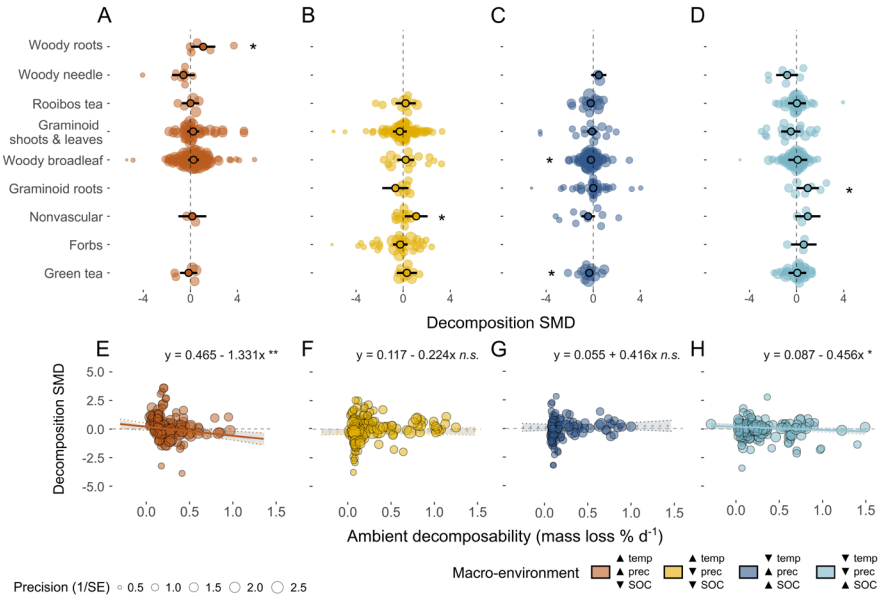


**FIGURE 5** | Relationship between plant functional types, ambient decomposability and the experimental warming effect on litter decomposition across the four macro-environmental classes. (A, B, C, D) The pooled average decomposition standardised mean difference (SMD, Hedges' g, black outlined circles) and 95% confidence intervals (black error bars) for different plant functional types (when data was available; see methods) in each of the four macro-environmental classes. (E, F, G, H) Relationship between ambient decomposability (ambient mass loss rate in % $d^{-1}$) and the warming effect on decomposition for each of the four macro-environmental classes (see also Figure S7). Colours indicate the four macro-environmental classes distinguished by different combinations of high (▲) or low (▼) temperature (temp), precipitation (prec) and soil organic carbon (SOC), consistent with Figure 3. Each coloured dot is an individual effect size (non-outlined circles) with dot size representing its precision (i.e., the inverse of the standard error, with larger points having greater influence on the model). Solid lines indicate regression lines with shaded areas representing the 95% CI. Asterisks, located in association to the direction of the effect, indicate that the overall pooled average SMD is significantly different from zero (*$p < 0.05$, **$p < 0.01$). Dashed lines indicate no significant relationship (n.s. = not significant).

reduce the decomposition of needle-leaf litter (SMD = −0.44 [CI: −0.82, −0.07], $p = 0.021$, $k = 20$; Figure S6B and Table S8).

Although data were not available for all plant functional types and plant organ types across all four macro-environmental classes, the available data suggest that the macro-environment determined how decomposition of different plant functional types responded to experimental warming (moderators' test: $Q_M$ (df = 28) = 138.82, $p < 0.001$). Data on woody roots were available only for the warm and wet class, where woody roots' decomposition increased with warming (SMD = 1.08 [CI95: 0.05, 2.11], $p = 0.040$, $k = 5$, Figure 5A). In the warm and dry class, only moss and lichen litter decomposition significantly increased with experimental warming (SMD = 1.10 [CI95: 0.13, 2.07], $p = 0.026$, $k = 12$, Figure 5B). In the cold and wet class, experimental warming decreased decomposition of woody broadleaf litter (SMD = −0.20 [CI95: −0.35, −0.05], $p = 0.010$, $k = 66$) and green tea (SMD = 0.34 [CI95: 0.06, 0.61], $p = 0.016$, $k = 15$, Figure 5C). Lastly, in the cold and dry class, only graminoids roots' decomposition significantly increased with experimental warming (SMD = 0.95 [CI95: 0.004, 1.89], $p = 0.049$, $k = 7$, Figure 5D).

Overall, the effect of experimental warming on decomposition was more positive for litter that had lower decomposability under ambient conditions (i.e., mass loss per day in non-warmed conditions) (moderators' test: $Q_M$ (df = 1) = 5.60, $p = 0.018$). Despite similar ambient decomposability across macro-environments (ANOVA: F(3, 124) = 1.21, $p = 0.31$), higher decomposability

significantly reduced the effect of experimental warming on litter decomposition in the warm and wet—(slope = −1.33 SMD/ decomposability [CI95: −2-188, −0.48], $p = 0.002$, $k = 154$; Figure 5E), and cold and dry macro-environmental class (slope = −0.46 SMD/ decomposability [CI95: −0.83, −0.08], $p = 0.018$, $k = 151$; Figure 5H). In these macro-environments, litter that is relatively harder to decompose tends to decompose slower under experimental warming compared to ambient conditions.

## 5 | Discussion

Across 109 datasets and 637 paired observations of plant litter decomposition under experimentally warmed and ambient conditions globally, we found that warming only increased decomposition when it exceeded 5.2°C and moisture was not limited. This estimated threshold is above the global warming predicted for the end of the century (1.4°C–4.4°C; IPCC 2021). The macro-environmental region is a key determinant of the effect of experimental warming on litter decomposition (Figure 6), with our findings showing that warming decreased decomposition in warm and dry macro-environments. Litter quality was an important moderator of the experimental warming effect, and the macro-environmental settings determined which litter characteristics were most important (Figure 6). Overall, the decomposition of litter with low decomposability increased with experimental warming, while the decomposition of litter with high decomposability decreased with warming.

### 5.1 | Contextual Dependence of the Experimental Warming Effect on Decomposition

We found that the prevailing macro-environmental conditions influence whether experimental warming leads to an increase, a decrease, or no change in litter decomposition. As hypothesised, warming reduced litter decomposition at warm and dry sites with limited moisture availability due to low precipitation and high evapotranspiration (Sierra, Malghani, and Loescher 2017). Macro-environmental conditions in warmer regions, such as temperate and subtropical areas, generally favour decomposition processes (Powers et al. 2009). Thus, additional warming is unlikely to further stimulate litter decomposition in these warm ecosystems (Bradford 2013; Crowther and Bradford 2013). Instead, the role of soil moisture becomes a potentially more important limiting factor (Aerts 2006). Accordingly, our observation that warming led to decreased litter decomposition in warm and dry areas, but not in warm and wet areas aligns with both our expectations and previous studies where warming amplified the effects of drought in dry macro-environments but not in wet ones (Wu et al. 2011; Thakur et al. 2018; Schimel 2018). It is noteworthy that warm and dry systems exhibit the lowest soil organic carbon content (Table S4), indicating limited carbon storage

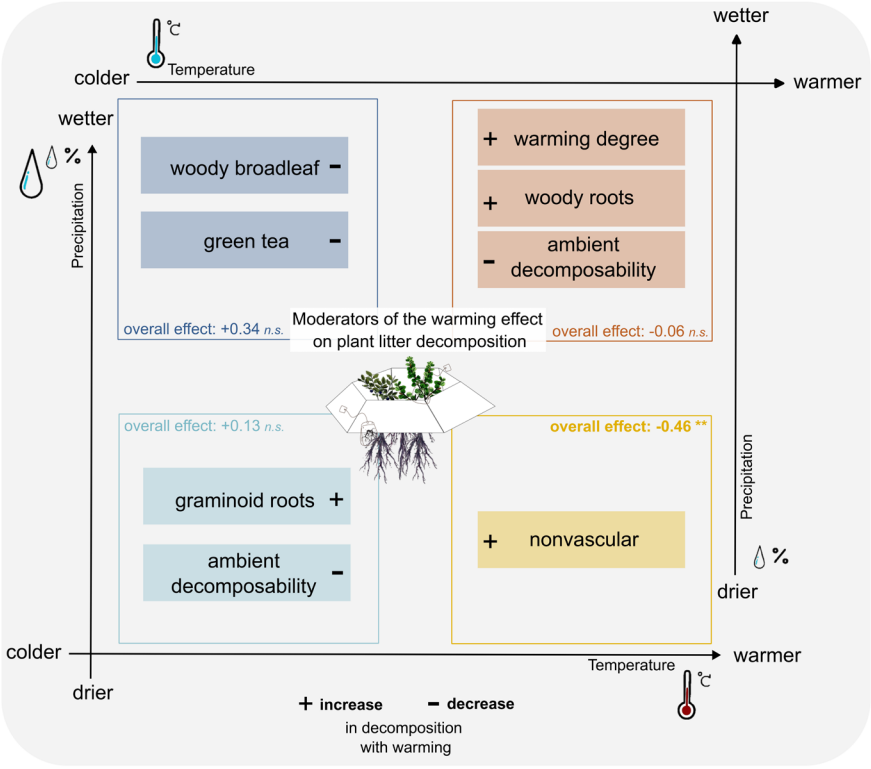


**FIGURE 6** | Conceptual summary of significant moderators of the experimental warming effect on plant litter decomposition across four macro-environmental classes. Main effects of macroenvironmental settings is indicated with large squares, Asterisks denote that the overall pooled average SMD is significantly different from zero (**$p < 0.01$; n.s. = not significant). Moderators within classes are indicated as having an increasing (+) or decreasing (−) effect on decomposition compared to ambient conditions for those moderators that were significant. Colours represent the four classes, defined by combinations of high or low temperature and precipitation, consistent with Figure 3.

potential in these warm and dry sites. This implies that while warming decreases litter decomposition in warm and dry systems, the effectiveness of carbon storage is likely compromised due to warmer temperatures and dry conditions (Yi, Wei, and Hendrey 2014; Hartley et al. 2021). While previous studies have reported clear interactions between increasing temperature and moisture (Aerts 2006; Thomas et al. 2023), our research shows that these interactions manifest differently in various macro-environments. Our results highlight that macro-environmental factors can significantly influence how site-specific factors like the degree of warming affect litter decomposition, especially in warm and wet conditions, which in our dataset had the largest range of degree of warming.

A recent meta-analysis by Sagi and Hawlena (2024) highlights the role of macrofauna (e.g., invertebrates) in regulating litter decomposition, particularly in warm and dry environments. While our dataset on standardised litter (mesh size: 0.257 mm) captured primarily microbial-driven decomposition, studies of natural litter using larger meshes (> 1 mm) likely included macrofaunal effects. We found that the warming effect on litter decomposition was negligible for smaller mesh sizes, where only microbes were included. However, experimental warming significantly reduced litter decomposition in larger mesh sizes, where marcofauna was involved. This suggests that macrofauna may be more negatively impacted by warming than microbes. Sagi and Hawlena (2024) proposed that higher temperatures regulate macrofaunal activity, leading to an increased contribution of macrofauna to decomposition in warm and dry environments. However, in our study, we observed a reduction in decomposition rates with warming in conditions that favoured macrofaunal activity, such as larger mesh sizes and warm, dry macro-environments. This suggests that the activity of macrofauna may be down-regulated by warming, reducing their role in decomposition.

Contrary to our expectations, we did not observe significant overall effects of warming on litter decomposition at colder sites, where temperature is typically the main constraint. Cold ecosystems, such as high latitude and alpine regions with tundra and boreal forests (Figure S2B), are dominated by recalcitrant litter that decomposes relatively slowly and has higher temperature sensitivity (Biasi et al. 2005; Davidson and Janssens 2006; Conant, Steinweg, et al. 2008). In addition, these ecosystems contain a greater proportion of below-ground plant material (Mokany, Raison, and Prokushkin 2006; Poorter et al. 2012; Iversen et al. 2015; Wang et al. 2016). Consequently, these ecosystems were expected to show increased litter decomposition upon warming. However, while there was no statistically significant warming effect for the cold and wet macro-environment class, we observed a tendency towards increased decomposition with experimental warming. Our analysis suggests that a minimum warming threshold of 5.2°C is necessary for a positive effect on litter decomposition. However, the passive methods predominantly used in those cold systems do not achieve this degree of warming. Since warming in high latitude and high-altitude systems has outpaced the global average, with the Arctic warming nearly four times faster over the last four decades (Tingley and Huybers 2013; Rantanen et al. 2022), our predicted temperature threshold could become relevant for these systems in the near future. Hence, the ongoing warming trend may potentially accelerate decomposition in these environments with exceptionally high carbon storage.

### 5.2 | Litter Quality Proxies as Regulators of the Experimental Warming Effect on Decomposition

We found that litter material that decomposes slowly under ambient conditions (i.e., lower decomposability) decomposed faster under warming compared to litter material that decomposes fast under ambient conditions, which was significant under warm and wet as well as cold and dry conditions. As lower decomposability is frequently associated with lower-quality litter (Cornelissen et al. 2004; Freschet, Aerts, and Cornelissen 2012), this supports our hypothesis that lower-quality litter is more sensitive to warming than high-quality litter (Fierer et al. 2005; Conant, Drijber, et al. 2008; Suseela et al. 2013). This finding may have implications for soil organic matter (SOM) formation. That is, warming may accelerate the decomposition of the existing pool of slow-cycling, recalcitrant litter that was previously decomposing very slowly (Davidson and Janssens 2006). This faster decomposition could lead to a short-term carbon release, potentially contributing to a positive feedback loop, accelerating climate change (Cox et al. 2000; Fenner and Freeman 2011). However, it may not necessarily deplete the total SOM pool in the long term, as SOM formation might be primarily driven by the decomposition of fast-cycling, high-quality litter (Cotrufo et al. 2013, 2015), which was less affected by experimental warming in our study.

Surprisingly, the experimental warming effect on decomposition appears to be unrelated to a classic measure of litter quality (C:N ratio). Instead, we observed the strongest correlation of the warming effect on litter decomposition with ambient decomposability, which integrates both litter quality and environmental conditions (Cornelissen et al. 2004; Freschet, Aerts, and Cornelissen 2012). While the quality of the litter material (e.g., C:N ratio) may not strongly drive litter decomposition under experimental warming, our study emphasises the importance of considering the interaction between litter quality and environmental conditions for understanding decomposition dynamics in response to climate change (Joly, Scherer-Lorenzen, and Hättenschwiler 2023). The varying effects of warming on the decomposition of litter from different plant functional types and plant organs suggest that the specific composition of plant species or functional groups within a plant community significantly influences warming responses.

Specifically, we found that warming decreased decomposition for shoots and leaves (including needles), while it increased decomposition for roots (Figure S6B). This contrasting response might be due to inherent traits in roots, such as high lignin, carbon, and dry matter content, making them more resistant to decomposition (Freschet, Aerts, and Cornelissen 2012; Xia, Talhelm, and Pregitzer 2015) and consequently, more temperature-sensitive and responsive to warming (Bosatta and Ågren 1999; Fierer et al. 2005; Conant, Drijber, et al. 2008; Suseela et al. 2013). The distinct responses to warming of shoot/leaves compared to roots might be partly attributed to their incubation position in the soil or on the soil surface (Blok

et al. 2018, Table S8). Needle-leaf litter, while also rich in lignin, is exposed directly to surface-level conditions, where it experiences more extreme temperature fluctuations and drying, which may limit microbial activity compared to roots that decompose in the more buffered, moister soil environment (Wang et al. 2009; Fanin et al. 2020). The specific environmental conditions in which above- and below-ground decomposition occurs likely influence the response to warming. Drier soil surface conditions likely contributed to the negative impact of warming on leaf and shoot decomposition (Blok et al. 2018), whereas wetter soil conditions enhanced decomposition under warming, irrespective of the plant organ type (Hicks Pries et al. 2013). The distinct impact of warming on roots and shoots/leaves is unlikely to be caused by differences in litter quality since the C:N ratio did not differ between roots and shoots/leaves (Figure S6A). This opposite response of plant organ types was exclusive to graminoids and not observed in woody species, indicating an undiscovered potential interaction between warming and plant functional type. This urges further investigation, especially for accurate assessments of carbon and nutrient budgets on a global scale in a warming climate, since root production and turnover account for 20%–80% of the global annual net primary productivity (Jackson, Mooney, and Schulze 1997; McCormack et al. 2015). This knowledge gap is currently posing a challenge for carbon cycle modelling especially in ecosystems with a substantial portion of biomass located below ground.

### 5.3 | Limitations of Specific Warming Methods

Specific warming methods can have limitations, such as their impact on soil moisture and their ability to achieve large temperature changes. Our study found that heating cables, used primarily in the warm and wet macro-environment class, effectively increased temperature with minimal impact on soil moisture, leading to a significant increase in litter decomposition. However, variations in soil moisture effects could be attributed to methodological artefacts or site-specific conditions. The pre-existing moist conditions in the warm and wet environment likely contributed to the effectiveness of the heating cables and allowed them to exceed the 5.2°C warming threshold required for a significant increase in litter decomposition. In other macro-environmental classes where heating cables were not widely used, the temperature increases did not reach the 5.2°C threshold, potentially limiting the impact on decomposition. However, by warming soils rather than air, heating cables may provide less realistic warming conditions. Infrared heaters instead replicate natural warming conditions (Aronson and McNulty 2009), but those had no effect on litter decomposition as their warming capacity was relatively small ($1.91 \pm 0.1$; Table 1). The non-significant effect of passive warming by OTCs on litter decomposition might be explained by confounding factors, such as reduced soil temperatures due to shade or increased radiation absorption in OTCs (Marion et al. 1997). Notably, OTCs were associated with the largest decrease in soil moisture ($-11.88 \pm 0.9\%$) and a modest warming of $+1.33 \pm 0.1$°C (Table 1), in line with the lower end of global warming projections (e.g., SSP1–1.9, IPCC 2021). By combining studies of different warming methods, we were able to demonstrate the contextual dependence of the experimental warming effect with the micro-environment. We found a significant experimental warming effect on litter decomposition only for warming methods (i.e., heating cables) with a high degree of warming, which did not decrease but increased soil moisture (Table 1).

Our dataset covers large parts of the world and most biomes (Figure 1), but notably lacks data from tropical and temperate rain forests, particularly in the Southern Hemisphere. This gap is likely reflecting a global scarcity of experimental in situ warming studies conducted in these biomes rather than their exclusion based on our inclusion criteria. Hence, in our study, the impact of warming on litter decomposition in rain forests remains uncertain, and we suggest it should be a priority for future research (Cavaleri et al. 2015).

### 5.4 | Global Implications

This global meta-analysis integrates all available data from in situ experimental warming studies on litter decomposition across terrestrial ecosystems worldwide. The global approach enabled us to explore contextual dependence amongst warming, environmental factors (e.g., moisture, degree of warming), and litter quality. This represents an advancement over previous research, which often focused on regional scales or the impacts of experimental warming on litter decomposition within a specific environment (Aerts 2006; Blok et al. 2018; Hong et al. 2021). We show that accurate predictions of climate change impacts on key ecosystem processes, such as decomposition, must account for the complex interactions between macro-environmental conditions and litter quality.

In particular, our findings highlight the need for further investigation into below-ground decomposition under warming. Our results indicate an important interaction between experimental warming and below-ground litter decomposition (i.e., roots) that is distinct from the warming effects of above-ground litter (i.e., shoots). This presents a challenge for accurate carbon cycle modelling, especially in regions like tundra, cold deserts, and temperate grasslands, where up to 80% of the plant biomass is located below ground (Mokany, Raison, and Prokushkin 2006; Poorter et al. 2012; Iversen et al. 2015; Wang et al. 2016). This distinction underscores the importance of incorporating both above- and below-ground decomposition responses in carbon models, which could help improve predictions of future carbon storage (Bai et al. 2023).

Furthermore, rapid vegetation shifts in biomes such as tundra, alpine systems, and savannahs, characterised by increasing shrub cover, are likely to introduce harder-to-decompose litter (Harte et al. 1995; Myers-Smith et al. 2011; Elmendorf et al. 2012; Pearson et al. 2013; García Criado et al. 2020). Our results suggest two key changes that could affect carbon storage: (1) the increase in lower-quality plant litter will lead to faster decomposition under warming conditions, and (2) the higher sensitivity of below-ground decomposition to warming, often overlooked, may lead to an underestimation of warming's overall impact on decomposition. Together, these processes could contribute to increased carbon release and reduce carbon storage potential.

Our findings indicate that litter decomposition is likely to increase significantly under more extreme warming scenarios in the range of 3.3°C–5.7°C (SSP5-8.5, IPCC 2021). This is particularly concerning in light of recent record-breaking global temperatures. High-latitude ecosystems, which are warming rapidly, could see substantial shifts in decomposition rates, with an average temperature increase of 0.65°C ± 0.09°C per decade (1979–2022) according to ERA5 (ECMWF Reanalysis v5, European Centre for Medium-Range Weather Forecasts).

In addition, rising drought intensity in Europe, the Mediterranean, and large parts of Asia suggests that additional warming leading to drier soils might increasingly become a limiting factor for litter decomposition (NOAA National Centers for Environmental Information). Our findings suggest that ecosystems in warm and dry regions may experience reduced decomposition rates in the future, which could lead to reduced soil carbon emissions from the soil depending on how drought will affect primary productivity. However, our findings suggest further that this effect is more prominent in ecosystems with inherently lower initial carbon storage potential, which might indicate that warming effects on litter decomposition in these warm and dry systems may play a minor role for worldwide carbon budgets.

Certainly, the net carbon balance of a system is as well determined by carbon uptake, yet decomposition plays a pivotal role in the carbon budget. This study improves our understanding of the contextual dependence of warming sensitivity, contributing to more accurate predictions of climate change impacts on decomposition as a key ecosystem process.

## Author Contributions

J.M.S. conceived the idea and S.S., J.M.S., and E.D. designed the study. J.M.S., E.D., M.P.B., V.V., E.l.R., and M.S. gave extensive feedback on the analyses and manuscript. R.A., E.A., J.A., I.A., K.B., S.B., M.P.B., M.C., A.C., C.T.C., K.C., R. Alonso, N.F., W.G., I.A.H., A.H., R.D.H., I.S.J., E.H.K., K.K., Q.L., J.O.L., A.M., T.M., I.M.S., A.P., M.S., S. Suzuki, T.K., M.t.B., H.T., F.V, V.V., S.V., Y.Y., J. Asplund, and E.l.R. collected the data on standardised plant litter decomposition from open-top-chamber warming experiments. J.v.d.H. and T.W.C. provided the map-based environmental data. All authors excluding S.S., E.D., and J.M.S. contributed data. S.S. and J.M.S. assembled the data for meta-analysis and meta-regression. S.S. analysed the data with feedback from J.M.S. and E.D. S.S. designed the figures and tables and wrote the manuscript.


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### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

The data supporting the results of this study have been published on Dryad and can be accessed here: https://doi.org/10.5061/dryad.p5hqbzkw5

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**Supporting Information**

Additional supporting information can be found online in the Supporting Information section.