**Title:** Direct and indirect interactions among warming, water, and growing condition slow decomposition rates of temperate-boreal tree litter

**Authors:** Rachel A. King[1]*, Samuel P. Reed[2,3]*♦, Habacuc Flores-Moreno[3,4], Raimundo Bermudez[3], Artur Stefanski[3,5], Laura J. Williams[6], Sarah E. Hobbie[7], Peter G. Kennedy[8], Peter B. Reich[3,6,9]

*Rachel A. King and Samuel P. Reed should be considered joint first author
♦Corresponding Author (email: reed0632@umn.edu)

**Affiliations:**
[1] National Center for Ecological Analysis and Synthesis, Santa Barbara, CA. USA
[2] Institute on the Environment, University of Minnesota, St. Paul, MN. USA
[3] Department of Forest Resources, University of Minnesota, St. Paul, MN. USA
[4] Commonwealth Scientific and Research Organization, Brisbane, QLD. AU
[5] College of Natural Resources, University of Wisconsin Stevens Point, Stevens Point, WI. USA
[6] Hawkesbury Institute for the Environment, Western Sydney University, Richmond, NSW. AU
[7] Dept. of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, MN. USA
[8] Dept. of Plant & Microbial Ecology, University of Minnesota, St. Paul, MN. USA
[9] Institute for Global Change Biology, University of Michigan, Ann Arbor, MI. USA

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## Abstract (300 words)

Plant litter decomposition is a primary control on carbon fluxes in terrestrial ecosystems around the world. Individually, the key mediators of decomposition rates—litter traits, temperature, and moisture—are relatively well understood. However, our understanding of how combined drivers influence decomposition remains limited. To test how multiple, interactive climate change factors directly alter decomposition rates and indirectly influence leaf litter decomposition rates by altering substrate chemistry, we conducted two decomposition experiments within the Boreal Forest Warming at an Ecotone in Danger (B4WarmED) study in Minnesota, USA. Our first experiment decomposed ambient-grown leaf litter from eight common tree species under a factorial combination of warming and rainfall reduction treatments. We found that the direct effects of combined warming and rainfall reduction increased litter half-life by 42% ± 11% in comparison to ambient plots with no warming or rainfall reduction. In contrast, only rainfall reduction influenced litter mean residence time, which increased by 37% ± 18% in comparison to ambient rainfall plots. Our second experiment decomposed ambient- and warm-grown leaf litter from the same eight species under ambient and warmed conditions. We found that warming slowed decomposition of both litter types, but warm-grown litter had a 22% ± 6.5% shorter half-life than ambient-grown leaf tissue under ambient environmental conditions. Warm grown litter half-life then increased by 36% ± 11% with warmed environmental conditions. Our results highlight that climate change could slow carbon and nutrient cycling in systems where moisture becomes a limiting factor. In addition, our study demonstrates that there may be an overlooked relationship between the growth conditions of plants and the temperature of decomposition. This nuanced understanding of decomposition can then support carbon cycling models and more effective nature-based climate mitigation efforts.

## Introduction

Plant litter decomposition mediates substantial carbon flows through terrestrial ecosystems, with estimates of 50 to 70% of NPP moving into the litter pool annually and between 53 and 66% of soil mineral-associated organic material, or stable soil carbon, being contributed by plants (Wardle *et al.* 2004; Butenschoen *et al.* 2011; Chang *et al.* 2024). The balance of litter decomposition rates and litterfall determines litter layer depth, which can influence a wide variety of ecosystem biotic and abiotic factors, such as seed germination, soil temperature, pH, moisture, fire potential, soil micro- and macrofauna, and soil carbon storage (Molofsky and Augspurger 1992; Sayer 2006; Cornelissen *et al.* 2017; Briones 2018; Nave *et al.* 2024). Temperature, moisture, and plant traits are primary controls on litter decomposition and given the importance of litter decomposition in ecosystem carbon cycling (Prescott 2010), the effects of each are relatively well understood individually. Increasing $CO_2$ and climate change will have both direct (changes in ambient temperature and precipitation) and indirect (changes in plant traits) impacts on decomposition rates (Aerts 1997; Cornwell *et al.* 2008). However, our understanding of how multiple, interacting global change factors influence decomposition rates is limited.

Ecologists have long predicted that a warming climate will increase litter decomposition rates, particularly within colder regions, as microbial decomposer activity will increase (Waksman and Gerretsen 1931; Kirschbaum 1995). Climate variables such as temperature and precipitation are considered to be the strongest direct drivers of litter decomposition in terrestrial ecosystems (Lavelle *et al.* 1993; Aerts 1997). However, there have been mixed results regarding how warming alone influences decomposition, with many studies showing either negligible or reduced decomposition rates with warming (Cornelissen *et al.* 2007; Lu *et al.* 2013; Ward *et al.*

2015; Chuckran *et al.* 2020; Krna *et al.* 2023; Liu *et al.* 2024). (Aerts 2006) theorized that warming does not have a positive effect on cold biome decomposition because moisture becomes the limiting factor. Similarly, plant performance in northern latitudes under shifting temperatures has been shown to depend on concurrent soil moisture levels (Reich *et al.* 2018), but how warming and precipitation influence decomposition rates in combination is less understood. Thus, it may be particularly informative to assess if and how altered warming and moisture interact to alter litter decomposition, although few studies have tested both of these factors within a robust experimental framework.

Climate can also have an indirect effect on litter decomposition by changing plant traits and resulting litter quality (Chapin 2003; Cornwell *et al.* 2008). Warming may delay leaf senescence and reduce nutrient resorption, which would reduce leaf litter quality and likely slow decomposition (Yuan and Chen 2009; Estiarte and Peñuelas 2015; Zani *et al.* 2020). In addition, warming has been shown to increase forest litter C:N by ≈10% on average potentially due to increasing leaf structural compounds (Wan *et al.* 2023), while precipitation has been shown to have no consistent effect on litter C:N (Sun *et al.* 2021), highlighting the uncertainty of how climate change may affect future litter stoichiometry and resulting decomposition (Zhang *et al.* 2008; Elser *et al.* 2010). Despite these potential changes in plant traits and chemistry, few decomposition studies use plant material grown under both ambient and warmed conditions to test the effects of global change on decomposition (Krna *et al.* 2023). By testing only how ambient litter decomposes in warmed environments, we may be overlooking a key interaction between climate and plant traits, thereby hindering our ability to predict how litter quality and decomposition rates are altered by global change factors.

To test how global change factors directly alter decomposition rates and indirectly influence leaf litter decomposition rates by altering substrate chemistry, we conducted two decomposition experiments within the Boreal Forest Warming at an Ecotone in Danger (B4WarmED) project (Fig. 1). B4WarmED is rare among global climate change experiments in manipulating temperatures both aboveground and belowground without the use of chambers (Rich *et al.* 2015). The first experiment (hereafter "Climate of Decomposition") was designed to assess the direct effect of climate (temperature and precipitation) on decomposition by decomposing ambient-grown leaf litter in all factorial combinations of ambient or elevated temperature (+3.4 ºC) and ambient or reduced rainfall (-40% ambient rainfall). We hypothesized that combined warming and rainfall reduction would lead to the slowest decomposition rates, while warming alone would accelerate decomposition relative to combined warming and rainfall reduction (**H1**). The second experiment (hereafter "Climate of Plant Growth") was designed to assess the effect of warming on decomposition via its effects on substrate chemistry by decomposing leaf litter from each species grown in ambient or elevated temperatures. Specifically, we hypothesized that warm-grown litter would have reduced litter quality (e.g. higher CN or Lignin:N ratios) because of prolonged nutrient resorption, leading to slower leaf decomposition in both ambient and warmed environments (**H2**).

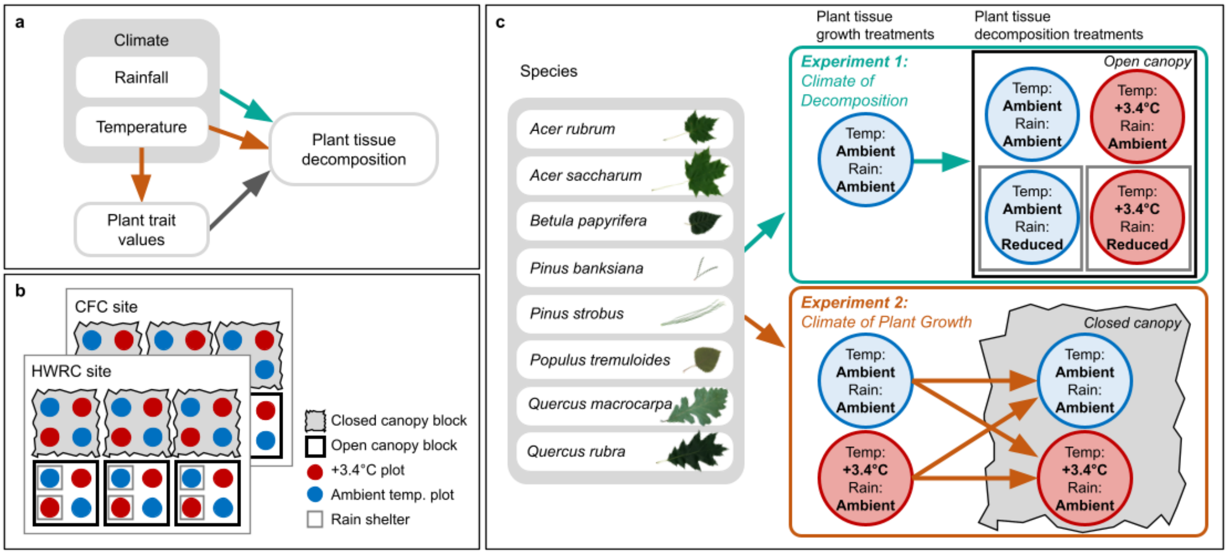

**Figure 1** Conceptual framework and design of the two experiments that examine the effects of climate (temperature and rainfall) on plant leaf litter decomposition. (a) We hypothesized that climatic conditions directly affect decomposition as well as affect decomposition via effects on substrate chemistry. (b) We tested these hypotheses at the B4WarmED climate change experiment. The experiment consists of two sites (Cloquet Forestry Center, CFC, and Hubachek Wilderness Research Center, HWRC) each with 6 experimental blocks: three with an overtopping tree canopy and three with no canopy overhead. Each block contains four, circular research plots each 3 m in diameter. Colored circles indicate ambient (blue) or warmed (red) plots. Grey boxes indicate the rain shelters found in open canopy plots. (c) The hypotheses were tested with two decomposition experiments. The Climate of Decomposition experiment (top) used litter from the eight species grown in ambient climatic conditions and assessed rates of decomposition under each of the four climate treatments (the combinations of ambient or elevated temperature and ambient or reduced rainfall) in open canopy plots. The Climate of Plant Growth experiment (bottom) used two different litter sources for each species – tissue grown under elevated or ambient temperature – and assessed rates of decomposition of each source under the two temperature treatments in closed canopy plots.

## Methods

### *Study Sites & B4WarmED Design*

This research was conducted at B4WarmED, a long-running free-air warming and rainfall reduction experiment in northern Minnesota, USA (Fig. 1). For details of the experimental design and treatments see Rich *et al.* 2015 and Stefanski *et al.* 2020. In brief, the experiment was established in 2008 at two sites along the boreal-temperate forest ecotone: one at the Cloquet Forestry Center (CFC, 46°40’46” N, 92°31’12” W, 382 m a.s.l.) near Cloquet, MN and the other at the Hubachek Wilderness Research Center (HWRC, 47°56’42” N, 91°45’29” W, 415 m a.s.l.) near Ely, MN. At CFC and HWRC, the study period mean annual precipitation was 827 mm and 667 mm, respectively, and mean annual temperature was 4.0 °C and 3.6 °C (averaged from 2018-2020 from nearby weather stations). Both sites are situated on coarse-textured upland soil (CFC: Cloquet Series - coarse-loamy over sandy or sandy-skeletal, isotic, frigid Typic Dystrudepts; HWRC: Rollins Series - sandy-skeletal, isotic, frigid Typic Dystrudepts (Web Soil Survey 2025) and, prior to the experiment, were forested with approximately 70-year-old mixed aspen, pine and birch forest.

Each site contains six experimental blocks with the preexisting forest overstory retained on three blocks (hereafter “closed canopy”) and removed from the remaining three (“open canopy”) in 2008. Within each block there are four circular research plots of 3 m diameter, two of which were warmed 3.4°C above ambient temperature using infrared ceramic heaters aboveground and resistance-type warming cables belowground while the other two blocks remained at ambient temperature. At the CFC site, only belowground warming remained active in 2019 and 2020 in the closed canopy plots due to concerns about potential fires in the understory. We accounted for this in the analysis by including site as a random effect, though we did not note differences in the warming effect between the two sites. In the open canopy plots, rainfall was also manipulated. Starting in 2012, rainout shelters were periodically deployed to exclude approximately 40% of summer rainfall (i.e. June to September) in half of the plots, one warmed and one ambient temperature plot per block, while the remaining two plots per block received ambient rainfall. Soil moisture, measured as volumetric water content from 0–20 cm depth, was continuously monitored via a 30 cm Campbell Scientific CS-616 probe inserted into the soil at 45°. In each plot, one to two year old tree seedlings of species commonly found in the temperate or boreal region of North America were planted and allowed to grow for four to five years.

*Litter Decomposition Experiments*

We collected leaf litter from 8 species within the experiment: *Acer rubrum* L., *Acer saccharum* Marshall, *Betula papyrifera* Marshall, *Quercus macrocarpa* Michx., *Quercus rubra* L., *Pinus banksiana* Lamb., *Pinus strobus* L., and *Populus tremuloides* Michx. For the Climate of Decomposition experiment, we collected litter from individuals grown in open canopy plots exposed to ambient precipitation and temperature. In our Climate of Plant Growth experiment, we collected leaf litter in closed canopy plots from directly below individuals grown in both the ambient temperature and + 3.4 °C warmed plots (litter source). Our naming convention for the Climate of Plant Growth experiment is either warm-grown or ambient-grown as the litter source (the ambient or warming treatment that litter was retrieved from) and then warmed plots or ambient plots as the litter destination (the ambient or warming treatment where litter was deposited). We are certain that this ambient and warm grown litter came from the planted trees for most species due to the overstory being dominated by aspen with very few nearby like-species. It is possible, however, some aspen leaf litter from the overstory entered our aspen leaf samples. To collect the litter, each experimental plot was visited weekly during the fall of 2011, 2012, and 2013 and recently fallen leaves from planted seedlings were collected, air-dried at room temperature, and stored in paper bags.

Litter bags (100 x 100 mm) were constructed from 1 mm nylon mesh and filled with 2 g of species-specific litter weighed to the nearest milligram. This amount of litter approximates the average litter density resulting from annual litterfall in temperate and boreal systems (Young An *et al.* 2017). We were not able to collect enough litter from experimental plots for either of the two *Pinus* species. Thus, the *Pinus* litter for the Climate of Decomposition experiment (litter from ambient conditions in the open canopy) was collected from *P. banksiana* and *P. strobus* trees growing outside the research plots but within the experimental sites. For the Climate of Plant Growth experiment (litter from ambient temperature and elevated temperature at closed canopy sites), we used *Pinus* litter collected from the experimental plots but deployed bags with a lower mass of tissue (ranging from 0.5 to 1.7 g), with the heavier bags assigned for collection at later time points. For both experiments, litter bags were strung together in groups of four with two strings of four bags (one bag for each species) assigned to be collected per time point per plot. Litter bags were randomly assigned to positions along the strings, and strings were deployed randomly inside plots with some constraints to avoid interfering with the growth of trees in the plots and avoid being stepped on by workers. Litter bags were deployed in the field in late fall 2017 and subsets retrieved in early spring 2018, fall 2018, fall 2019, and fall 2020. For the Climate of Decomposition experiment, ambient litter was placed in each treatment combination (ambient temperature + ambient moisture; ambient temperature + reduced rainfall; warmed temperature + ambient rainfall; warmed temperature + reduced rainfall). For the Climate of Plant Growth experiment, both ambient-sourced litter and warm-sourced litter were placed in ambient and warmed temperature destination treatments (ambient-grown litter + ambient temperature destination; ambient-grown litter + warm temperature destination; warm-grown litter + ambient temperature destination; warm-grown litter + warm temperature destination). Once retrieved, litter was removed from the bags, dried at 60°C for 48 hours, cleaned for dirt particles and weighed.

From the pool of litter for each species and site, a subset of the initial litter was finely ground and analyzed for total nitrogen and carbon with a Costech elemental analyzer at the University of Minnesota, USA (ECS 4010 CHNSO Analyzer Valencia, California, USA), and for carbon fractions (cell solubles, hemicelluloses plus bound protein, cellulose, and lignin plus other recalcitrants) with an ANKOM Fiber Analyzer (Ankom Technology, Macedon, New York, USA, using #F57 filter bags). Additionally, specific leaf area (SLA, $cm^2$ $g^{-1}$) was measured on green leaves from all species in 2011, 2012, and 2013. We used the mean SLA across years for each species-treatment combination as a covariate in some analyses.

## Statistical Methods

### *Decomposition model fitting and parameter estimates*

We fit four commonly used decomposition models to the proportion of litter mass remaining at each time point and estimated the parameters for each model for further comparison of the dynamics of litter decomposition. These included three decomposition models from the exponential family (single, double, and asymptotic) and the Weibull model (Cornwell *et al.* 2008; Gill *et al.* 2021). The exponential family of decomposition models is based on the single-pool decomposition model, in which the proportion of litter mass remaining, $X$, is a function of a decomposition constant, $k_s$, and time, $t$:

$$X = e^{-k_s t} \text{ (eq 1)}$$

The double-pool and asymptotic exponential models add an additional pool to the model, creating a two-pool model with litter fractions that can decompose at different rates. In the double exponential model, one fraction of litter ($1-C$) decomposes at a rate of $k_1$ and the remaining litter fraction ($C$) decomposes at a rate of $k_2$:

$$X = (1 - C)e^{-k_1 t} + (C)e^{-k_2 t} \text{ (eq 2)}$$

The asymptotic model splits the litter into two fractions, $A$ and (1-$A$), where $A$ represents a proportion of the initial litter mass with a decomposition rate of zero and the remaining litter fraction decomposes with a rate of $k_a$:

$$X = A + (1 - A)e^{-k_a t} \quad \text{(eq 3)}$$

While litter decomposition rates would never realistically be zero, over short time periods the asymptotic model's assumption of a pool with a negligible decomposition rate holds true (Berg 2014).

The last model, the Weibull model, is not based on the exponential decay model and instead represents the litter decomposition process through a continuous Weibull distribution of residence times (Weibull 1951; Cornwell and Weedon 2014). Here, litter mass remaining is a function of scale ($\beta$) and shape ($\alpha$) parameters of this distribution:

$$X = e^{-(\frac{i}{\beta})^{\alpha}}$$

The Weibull model does not have specific decomposition constants to compare across treatments, rather we estimate the time to 50% mass loss and the mean residence time (MRT) of the litter. These metrics indicate both early and late-stage litter decomposition as represented by litter half-life and MRT, respectively.

To compare the fit of the four models, we fit the models to pooled replicates for each species-treatment combination and assessed fit using Akaike's Information Criteria (AIC$_c$;(Burnham and Anderson 2004). We used a ΔAIC value of 3 between the lowest AIC value and remaining values to determine whether a model represented the data significantly better than the alternative models. The asymptotic and Weibull models performed the best based on these criteria, and there was no significant effect of our experimental treatments on the best model type (Fisher's exact test: $p = 0.96$, open canopy; $p = 0.08$, closed canopy; Table S1). For the remaining analyses, we decided to use the Weibull model for parameter estimates for two reasons: 1) using the asymptotic model sometimes poses challenges for statistical analysis when the asymptote is essentially zero, and 2) the Weibull model can capture more complex decomposition dynamics such as an initial lag phase or changes in decomposition rates over time (Cornwell and Weedon 2014). We estimated the parameters for the Weibull model on individual time-series (3 per species-treatment combination) and used these to calculate the time to 50% mass loss and the litter MRT. We screened individual time points to remove data points that were likely erroneous based on error risk after (Bjorkman *et al.* 2018).

We conducted analyses using R software v. 4.3.1 (R Core Team 2024). Any outliers for half-life and MRT greater than 2.5 standard deviations from the average half-life and MRT for open and closed canopy variables were removed. We tested how log-transformed litter half-life and MRT varied with treatment using linear mixed effects models in the *lme4* package (Bates *et al.* 2015). To test treatment effects on litter decomposition in the Climate of Decomposition experiment under an open canopy, we used warming treatment, rainfall reduction, and their interaction as fixed effects with site and species as random effects (Warming * RainfallReduction + (1|Site:Species)). Similarly, for the Climate of Plant Growth experiment under a closed canopy, we used litter source (ambient-grown or warm-grown litter), litter destination (ambient plots and warmed plots), and their interaction with site and nested species as random effects (LitterSource * LitterDestination+ (1|Site:Species)). The random effects structure was selected by comparing the performance of three different combinations of site and species random effects and choosing the structure with the lowest AIC value. These models only focus on treatment effects in order to best represent the influence of warming, rainfall reduction, and litter source on litter decomposition.

Following treatment-specific analyses, we evaluated how plant traits and abiotic factors influenced litter decomposition. To test potential mechanisms of decomposition change with treatments, separate LMMs with litter lignin:N, C:N, SLA, %N, and N per unit area, and soil moisture as covariates were created. We centered and scaled covariates prior to fitting models. Due to correlations between litter traits, we fit separate models for each litter trait and soil moisture and then selected the best model using AIC values. We then compared the performance of the models with covariates and treatments to the models with treatments alone using AIC and $R^2$ values to see if the covariates helped to explain any additional variation not encompassed by the treatment effects. All model assumptions were tested with the *DHARMa* package with Tukey adjusted post hoc analyses in the *emmeans* package (Hartig 2017; Lenth *et al.* 2022). Proportional differences between treatments are based on log-transformed means.

## Results

### *Experiment 1: Climate of Decomposition*

The climate of litter decomposition impacted both litter half-life and MRT, but the effects of temperature and rainfall reduction varied. Beneath an open canopy, 3.4 °C warming and 40% rainfall reduction individually increased litter half-life (Warming: $F_{1,\ 162.7} = 3.8$, $p = 0.052$; Rainfall Reduction: $F_{1,\ 162.4} = 22.4$, $p < 0.001$; Table 1). Specifically, rainfall reduction increased litter half-life by 28% ± 6.8% SE in comparison to plots with ambient rainfall ($t = 4.7$, $df = 162$, $p < 0.0001$), while warming alone increased litter half-life by 11% ± 5.9% SE ($t = 1.9$, $df = 163$, $p = 0.05$). Together, combined warming and rainfall reduction increased litter half-life by 42% ± 11% in comparison to plots with ambient temperatures and no rainfall reduction ($t = 4.7$, $df = 163$, $p < 0.001$; Fig. 2a), consistent with our expectations. In contrast, only rainfall reduction had a strong effect on litter MRT (Warming: $F_{1,\ 160.9} = 0.13$, $p = 0.72$; Rainfall Reduction: $F_{1,\ 161.2} =$

5.6, p = 0.02). Across all open canopy plots, rainfall reduction increased average leaf litter MRT by 37% ± 18% SE in comparison to plots with ambient rainfall (t = 2.4, df = 161, p = 0.02, Fig. 2b).

For both half-life and MRT, the applied climate treatments explained a small amount of variation relative to the species and site random effects. Less than 10% of the total variation explained by the models came from the fixed effects of climate treatments (Table 1), and the models for half-life explained more variation than those for MRT ($R^2_{cond} = 0.41$ vs $R^2_{cond} = 0.27$). However, all but one species showed a clear increase in both litter half-life and MRT from the ambient temperature and ambient rainfall treatments to the +3.4C and reduced rainfall treatments (Fig. S1). The half-life ranged from a minimum of 1.9 years to a maximum of 4.0 years in ambient temperature and ambient rainfall to a range of 2.8 - 5.2 years under warmed and reduced rainfall conditions. Litter MRT was substantially more variable across treatments, with a range of 4.3 years to 35.8 years in the ambient temperature and ambient rainfall treatments to 5.2 years to 30.7 years under warmed and reduced rainfall treatments.

**Table 1.** Treatment effects on litter half-life and MRT in open canopy conditions.

| | **log(weibull half life)** | | | **log(weibull mrt)** | | |
|---|---|---|---|---|---|---|
| *Predictors* | *Estimates* | *CI* | *p* | *Estimates* | *CI* | *p* |
| (Intercept) | 1.12 | 0.98 – 1.26 | **<0.001** | 2.22 | 1.97 – 2.48 | **<0.001** |
| heat | -0.05 | -0.10 – 0.00 | **0.054** | -0.02 | -0.16 – 0.11 | 0.716 |
| water | -0.12 | -0.18 – -0.07 | **<0.001** | -0.16 | -0.29 – -0.03 | **0.019** |
| heat × water | 0.02 | -0.04 – 0.07 | 0.544 | 0.09 | -0.04 – 0.22 | 0.162 |
| **Random Effects** | | | | | | |
| $\sigma^2$ | 0.13 | | | 0.78 | | |
| $\tau_{00}$ | 0.07 site:species | | | 0.20 site:species | | |
| ICC | 0.36 | | | 0.20 | | |
| N | 2 site | | | 2 site | | |
| | 8 species | | | 8 species | | |
| Observations | 181 | | | 179 | | |
| Marginal $R^2$ / Conditional $R^2$ | 0.085 / 0.415 | | | 0.033 / 0.227 | | |

Including covariates in the models improved the fit for litter half-life but not for litter MRT. For litter half-life, the best fit model with covariates improved slightly upon the inclusion of leaf $N_{area}$ in addition to the heat and water treatments (Table S2, S3). Including leaf $N_{area}$ increased the $R^2_{marg}$ from 0.08 to 0.19 for litter half-life, though the variation explained by random effects decreased from ICC of 0.36 to 0.27 (Table 2). Leaf $N_{area}$ had a positive relationship with litter half-life, so leaves with greater $N_{area}$ took longer to decompose. Including soil moisture did not improve the model fit for either litter half-life or MRT (Tables 2, S2, S4, S5, $\Delta AIC < 2$), so for litter MRT the models with treatments alone performed best.

**Table 2**. Effect of experimental treatments, soil moisture, and litter traits on litter half-life and mean residence time (MRT) in open canopy plots. Empty cells in the estimate column indicate that variable was not retained in the best model for either Half-Life or MRT.

| | **log(weibull half life)** | | | **log(weibull mrt)** | | |
|---|---|---|---|---|---|---|
| *Predictors* | *Estimates* | *CI* | *p* | *Estimates* | *CI* | *p* |
| (Intercept) | 1.14 | 1.03 – 1.26 | **<0.001** | 2.25 | 2.00 – 2.50 | **<0.001** |
| heat | -0.04 | -0.11 – 0.04 | 0.317 | 0.01 | -0.17 – 0.19 | 0.901 |
| water | -0.11 | -0.17 – -0.05 | **0.001** | -0.14 | -0.29 – 0.02 | **0.080** |
| VWC | -0.04 | -0.15 – 0.06 | 0.388 | -0.13 | -0.36 – 0.11 | 0.297 |
| N area | 0.16 | 0.04 – 0.27 | **0.009** | 0.09 | -0.16 – 0.35 | 0.474 |
| heat × water | 0.02 | -0.04 – 0.07 | 0.558 | 0.10 | -0.03 – 0.24 | 0.138 |
| **Random Effects** | | | | | | |
| $\sigma^2$ | 0.13 | | | 0.80 | | |
| $\tau_{00}$ | 0.04 site:species | | | 0.17 site:species | | |
| ICC | 0.23 | | | 0.18 | | |
| N | 2 site | | | 2 site | | |
| | 8 species | | | 8 species | | |
| Observations | 169 | | | 167 | | |
| Marginal $R^2$ / Conditional $R^2$ | 0.203 / 0.389 | | | 0.056 / 0.224 | | |

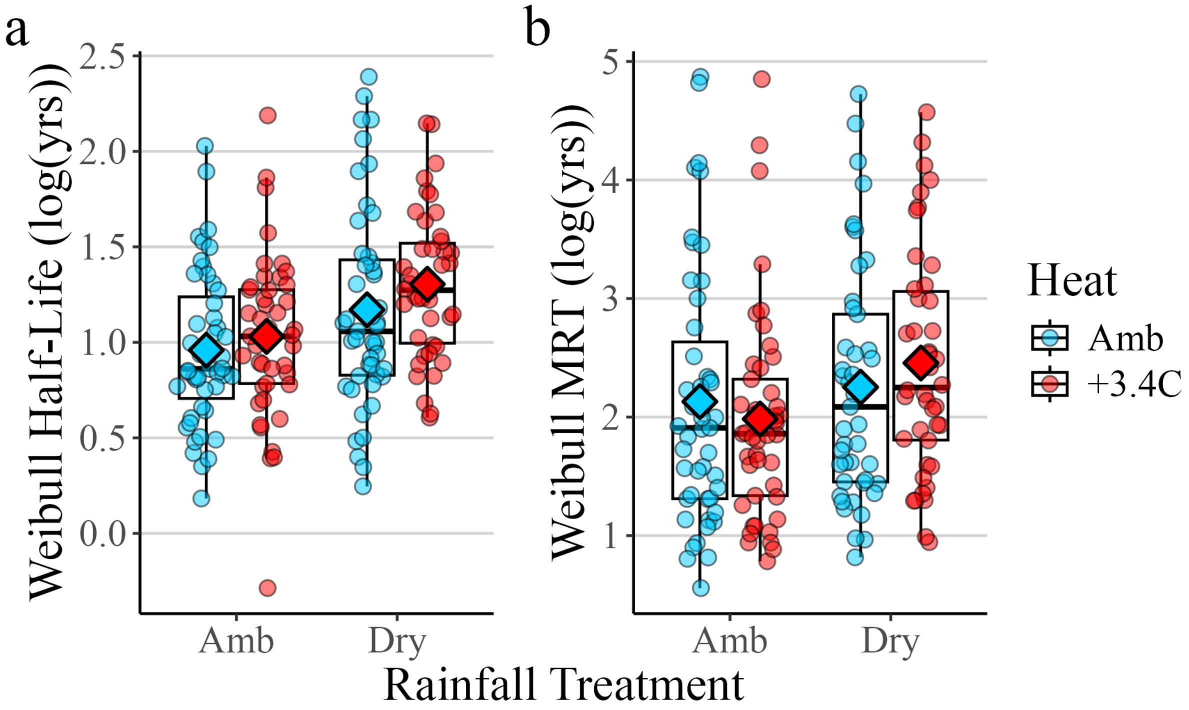

**Figure 2.** Experiment 1: Log-transformed Weibull half-life (a) or MRT (b) response to warming treatment (Amb or +3.4C) and rainfall reduction treatment (Amb or Dry) averaged across all species. Diamonds represent means while bold horizontal bars represent medians.

*Experiment 2: Climate of Plant Growth*

Underneath a closed canopy, litter source and litter destination treatment had a slight interactive effect on litter half-life ($F_{1,\,169.1}$ = 3.4, p = 0.07; Table 2; Fig. 3a). Warm-grown litter under warmed conditions had a 36% ± 11% SE greater half-life than warm-grown litter under ambient conditions (t = 3.6, df = 169, p = 0.002), while there was no difference in half-life among ambient-grown litter under ambient or warmed temperatures. Under ambient temperature conditions, litter grown in warmed plots had a 22% ± 6.5% SE shorter half-life than litter grown in ambient temperature (t = -3.0, df = 169, p = 0.015). Litter from both sources had similar half-lives when decomposing under warmed conditions (t = -0.44, df = 169, p = 0.66). Warming also increased litter MRT by 26% ± 15.4% SE in comparison to ambient conditions ($F_{1,\,162}$ = 4.4, p =

0.060; Fig. 3b). However, litter source did not influence litter MRT and there was no interaction between warming and litter source on mean residence time (Table 3).

As in the Climate of Decomposition experiment, experimental treatments explained a small amount of variation in decomposition in comparison to species and site random effects. Treatments explained slightly more variation for litter half-life ($R^2_{marg} = 0.064$) than for litter MRT ($R^2_{marg} = 0.016$, Table 3). Species level patterns showed that under ambient temperature conditions, all but one species showed a decrease in litter half-life with warm-grown litter but the trend was more variable in the warmed decomposition environment (Fig. S2). Litter MRT did not show a clear trend, with some species showing increases in MRT and others decreases in each treatment (Fig. S3). Under ambient temperature with ambient-sourced litter, litter half-life ranged from 2.1 yrs to 5.0 years, while under warmed conditions with warmed litter the range of half-lives expanded from 1.2 yrs to 6.1 years. Litter MRT followed a similar pattern: the range of MRTs increased when comparing ambient-sourced litter grown under ambient conditions (3.1 - 11.7 years) to warmed litter grown under warmed conditions (1.7 - 22.9 years).

**Table 3.** Effect of litter source and heat experimental treatments on litter half-life and mean residence time in closed canopy plots in the Climate of Plant Growth experiment.

| | **log(weibull half life)** | | | **log(weibull mrt)** | | |
|---|---|---|---|---|---|---|
| *Predictors* | *Estimates* | *CI* | *p* | *Estimates* | *CI* | *p* |
| (Intercept) | 1.08 | 0.92 – 1.24 | **<0.001** | 1.80 | 1.54 – 2.07 | **<0.001** |
| Heat | -0.10 | -0.16 – -0.04 | **0.001** | -0.12 | -0.24 – 0.00 | **0.058** |
| Litter Source | 0.07 | 0.01 – 0.13 | **0.015** | 0.02 | -0.10 – 0.14 | 0.791 |
| Heat × Litter Source | 0.05 | -0.00 – 0.11 | **0.068** | 0.03 | -0.09 – 0.15 | 0.617 |
| **Random Effects** | | | | | | |
| $\sigma^2$ | 0.17 | | | 0.67 | | |
| $\tau_{00}$ | $0.10_{\text{site:species}}$ | | | $0.23_{\text{site:species}}$ | | |
| ICC | 0.37 | | | 0.25 | | |
| N | $2_{\text{site}}$ | | | $2_{\text{site}}$ | | |
| | $8_{\text{species}}$ | | | $8_{\text{species}}$ | | |
| Observations | 188 | | | 180 | | |
| Marginal $R^2$ / Conditional $R^2$ | 0.065 / 0.410 | | | 0.017 / 0.266 | | |

Including litter traits and soil moisture as covariates did not improve model fits for the Climate of Plant Growth experiment. Model performance was similar for both litter half-life and MRT (Tables S6, S7) even though the variation explained by the fixed effects ($R^2_{\text{marg}}$) increased when covariates were included (Table 4). The litter traits that explained the most variation in the decomposition parameters varied for litter half-life and MRT: for half-life, the lignin:N ratio was the best litter trait predictor (Table S8) and for MRT it was litter %N (Table S9). However, only the lignin:N ratio had a significant impact on litter half-life, with higher lignin:N ratios resulting in longer half-lives (i.e., slower decomposition). Soil moisture did not have a substantial influence on decomposition for either half-life or MRT.

**Table 4.** Effect of experimental treatments, soil moisture, and litter traits on litter half-life and mean residence time (MRT) in closed canopy plots. Empty cells in the estimate column indicate that variable was not retained in the best model for either Half-Life or MRT.

| | **log(weibull half life)** | | | **log(weibull mrt)** | | |
|---|---|---|---|---|---|---|
| *Predictors* | *Estimates* | *CI* | *p* | *Estimates* | *CI* | *p* |
| (Intercept) | 0.64 | 0.23 – 1.05 | **0.002** | 1.80 | 1.50 – 2.09 | **<0.001** |
| Heat | -0.11 | -0.18 – -0.04 | **0.003** | -0.15 | -0.29 – -0.00 | **0.047** |
| Litter Source | 0.11 | 0.04 – 0.17 | **0.003** | 0.06 | -0.08 – 0.20 | 0.364 |
| VWC | -0.00 | -0.10 – 0.09 | 0.965 | -0.09 | -0.28 – 0.10 | 0.358 |
| Lignin:N | 0.02 | 0.00 – 0.04 | **0.034** | | | |
| Heat × Litter Source | 0.03 | -0.04 – 0.10 | 0.362 | 0.00 | -0.13 – 0.14 | 0.954 |
| % N | | | | -0.18 | -0.42 – 0.06 | 0.133 |
| **Random Effects** | | | | | | |
| $\sigma^2$ | 0.17 | | | 0.66 | | |
| $\tau_{00}$ | 0.09 $_{\text{site:species}}$ | | | 0.22 $_{\text{site:species}}$ | | |
| ICC | 0.35 | | | 0.25 | | |
| N | 2 $_{\text{site}}$<br>7 $_{\text{species}}$ | | | 2 $_{\text{site}}$<br>7 $_{\text{species}}$ | | |
| Observations | 147 | | | 138 | | |

| | | |
|---|---|---|
| Marginal $R^2$ / Conditional $R^2$ | 0.149 / 0.443 | 0.078 / 0.308 |

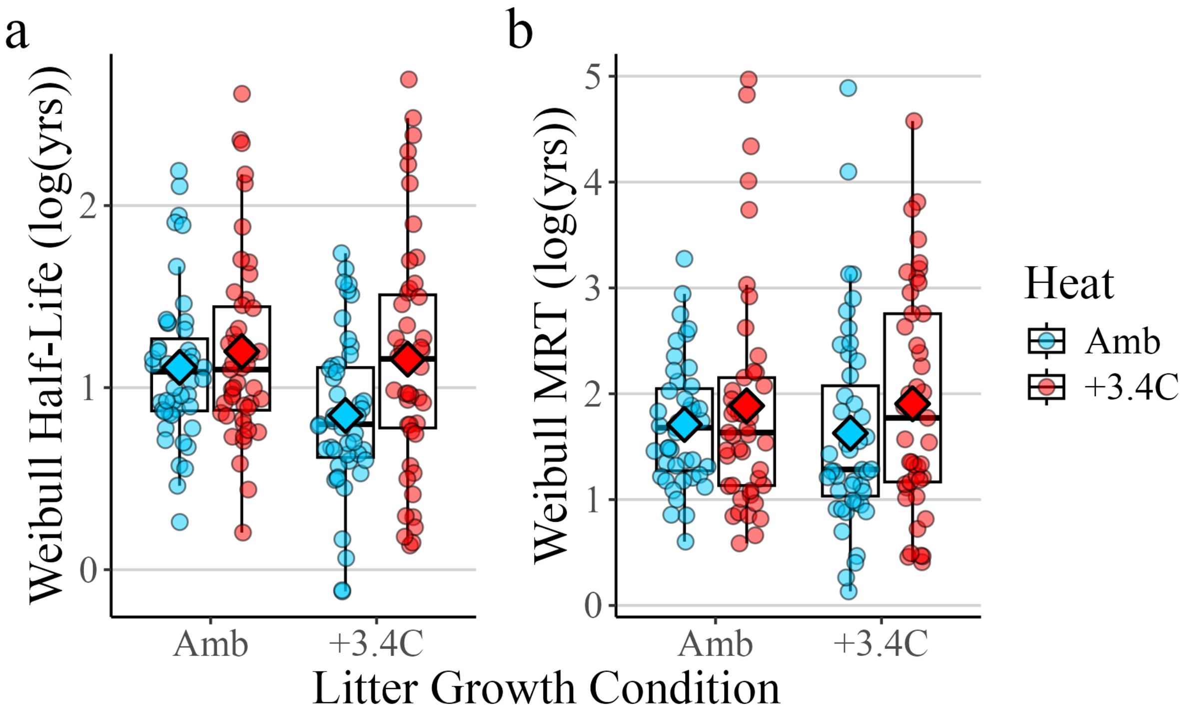

**Figure 3.** Experiment 2: Log-transformed Weibull half-life (a) and MRT (b) response to destination heating treatment (AMB or +3.4C) and litter source treatment (AMB or Warmed) averaged across species.

## Discussion

Global climate change is leading to numerous interacting stressors and disturbances within forest ecosystems, many of which can strongly influence nutrient and carbon cycling (Foster *et al.* 2016; Seidl *et al.* 2017; Tripathy *et al.* 2023; Sáez-Sandino *et al.* 2024). Few studies can rigorously test how multiple global change factors impacting multiple tree species influence key biological processes in a field-based experimental setting, posing a significant knowledge gap in our understanding and predictions of climate impacts and mechanisms of change. Using a globally unique experiment, our work highlights how combined warming and rainfall reduction can slow litter decomposition of numerous deciduous and coniferous tree species. We also found that the direct effects of warming on decomposition can overwhelm indirect warming-induced leaf trait changes (and hence litter properties), as increased temperatures slowed decomposition regardless of whether litter was grown in warmed or ambient conditions. Furthermore, soil moisture and litter trait covariates resulted in little to no improvement to the models, suggesting that additional unmeasured factors, such as soil microbes, may be important mechanisms to fully understand how climate mediates decomposition. Each of these results represents a significant step forward in our understanding of decomposition processes in an era of rapid global change, with particularly important ramifications for nutrient cycling and soil processes, though there is still room to investigate the specific mechanisms that underpin our research.

### *Experiment 1: Climate of Decomposition*

Our finding that combined warming and rainfall reduction can slow tree leaf litter decomposition in cold biomes generally aligns with our hypothesis, ecological theory and the limited number of studies that have manipulated both of these global change factors (Aerts 2006; Butenschoen *et al.* 2011; Petraglia *et al.* 2019). Since rainfall reduction led to slower early and late-stage decomposition, regardless of warming treatment, our experiment points to moisture as a key limiting factor that mediates throughout the litter decomposition process. Soil moisture is fundamental to microbial decomposition, as water is a needed resource for microbes and facilitates the transport and consumption of organic resources from the litter (Schimel 2018). When soil conditions become too dry, microbial communities can also go dormant, leading to slower decomposition (Jones and Lennon 2010).

However, rainfall reduction may result in additional changes to the decomposition environment that are not captured just by water availability. When we tested soil moisture as a covariate along with rainfall reduction, the rainfall reduction treatment remained significant in the models. This suggests that soil moisture contributes to decomposition but that additional changes from reduced rainfall could be occurring in our experimental plots and mediate the observed changes in decomposition. Other studies have found that persistent rainfall reduction results in reductions in microbial biomass and changes to their physiology (García-Palacios *et al.* 2016b), as well as decreases in soil fauna involved in decomposition (Biryol *et al.* 2024). As such, future studies at our study sites investigating how soil organisms are changing in response to reduced rainfall will further understanding of how decomposition is altered by changing environmental conditions.

Our hypotheses regarding warming treatments were only partially supported, as warming alone resulted in slowed decomposition. However, it is likely that the combined warming and rainfall reduction treatments exacerbated evaporative drying and further slowed early-stage decomposition, considering that litter half-life was slowest in dry and warm conditions in accordance with our hypothesis. The few studies that have examined a combination of soil moisture and warming on litter decomposition have also found that warming effects are mediated by moisture (Butenschoen *et al.* 2011; Petraglia *et al.* 2019). This may be due to early-stage decomposers becoming homogenized with dry conditions; for example, Christiansen *et al.* 2017 demonstrated that warming-induced decomposer homogenization can be correlated with lower decomposition rates. Homogenized decomposer communities may reduce the number of functional groups and potential facilitative interactions, which can be important for decomposition (Christiansen *et al.* 2017). However, there are likely numerous controls on litter decomposition that are positively correlated with warming and moisture, highlighting the complexity and peril of selecting a single mechanistic explanation (Prescott 2005a). Our results add needed context to our understanding of litter decomposition by showing how the effects of warming can be mediated by moisture, however more research is needed on the exact mechanisms of decompositional change in cold biomes (Baldrian *et al.* 2023).

Assuming our results hold across similar cold-biome conditions, slowing decomposition with warming and decreased precipitation poses several ecological consequences. The most obvious implication of slowing litter decomposition is that leaf litter may accumulate to a greater degree with warming and rainfall reduction in cold biomes. This litter accumulation could then slow soil nutrient cycling, which would add further stress to trees in an already N-limited ecosystem (Reich *et al.* 1997; McLauchlan *et al.* 2007). Additionally, this dry and slow-decomposing litter may be less likely to be transformed into mineral-associated organic matter, potentially altering the ratios of carbon stored in mineral-associated versus particulate organic matter within forests and the overall stability of carbon in the soil (Cotrufo *et al.* 2015; Prescott and Vesterdal 2021). More dry, slow-decomposing litter may also be vulnerable to fire and resulting carbon release (Grootemaat *et al.* 2015; Cornelissen *et al.* 2017). Alternatively, an accumulation in litter could moderate a drying environment and further support species that are dependent on the “brown” food web (Sayer 2006). Each of these potential ecological outcomes are possible but highlight the substantial uncertainty of global climate change’s localized ecological effects.

*Experiment 2: Climate of Plant Growth*

In contrast to our second hypothesis, where we predicted that warm-grown litter would lead to slower decomposition, we found that warm-grown litter’s half life was lower in ambient treatments in comparison to warm-grown litter in warmed plots. This result is likely due to warming-induced changes to plant traits that made these leaves more palatable to early-stage decomposers in the ambient plots (Prescott 2005b; Moorhead and Sinsabaugh 2006). In addition, ambient- and warm-grown litter had the same half-life when decomposed in warmed treatments, with both having slower decomposition rates than in ambient plots.

Although our results point to changes in leaf litter as the underlying mechanism altering decomposition rates of warm- vs. ambient-grown litter, the specific traits causing this effect remain uncertain. The reduction in litter half-life for warmed litter decomposing under ambient conditions was consistent across species, yet changes in measured litter traits did not follow any particular pattern. Although we hypothesized that leaf litter C:N would increase with warming, responses were inconsistent across species with increases in C:N for some species and decreases in others. Regardless of why the traits did not change consistently, given that decomposition changed directionally across species, our study may have missed the traits most influenced by warming that led to the observed changes in decomposition. For example, some studies emphasize the importance of micronutrients (e.g., Na, Mg, Ca, K) and protein content, which we did not examine in this study, rather than just N content as mediators of litter decomposition (García-Palacios *et al.* 2016a; Canessa *et al.* 2021; Wang *et al.* 2021). The composition of the leaf endophytes in litter has also been proposed as a mediator of decomposition (Wolfe and Ballhorn 2020), and could be another way the litter source impacts decomposition rates. However, support for the importance of endophytes in decomposition remains relatively undeveloped. With the specific drivers of the effects of litter source on decomposition in our study uncertain, additional work is needed to explain how litter source results in varied decomposition.

Few studies, if any, have tested whether plant growth under ambient and warmed conditions influences litter decomposition rates. Our finding that warm-grown litter decomposed faster in ambient temperature than in warmed conditions highlights an important contribution to how we experimentally test the influence of global change factors on litter decomposition. It is likely that most studies exploring these relationships between warming and decomposition use ambient-grown litter (Krna et al. 2023). If ambient-grown litter shows no response to warming treatments, then we are likely missing important causal mechanisms in our understanding of how global change influences plant traits and resulting decomposition. While we were not able to determine the exact mechanism for why warm-grown litter showed such strong responses to the temperature destination treatments, our study highlights a major opportunity to refine our understanding of plant traits, planetary warming, and decomposition. Further, from an ecological perspective, it is possible that a year with cooler temperatures could lead to faster litter decomposition, especially among recently dropped leaves that grew in warmer conditions.

In Experiment 2, warming also increased litter MRT, or long-term decomposition, while litter source had no effect on this variable. Warming-induced increases in MRT were likely due to increased evapotranspiration with higher temperatures that caused soil moisture limitation, similar to the findings in Experiment 1. This increase in evapotranspiration with warming may be particularly influential under a closed canopy, where the forest floor is cooler and wetter (Muscolo *et al.* 2014; De Frenne *et al.* 2021). This result serves as an indirect source of evidence that moisture is a key factor in biotic, late-stage decomposition of litter (Klotzbücher *et al.* 2011).

### *Next Steps and Conclusions*

Our experiments pose a number of important considerations for future research. First and foremost, we were not able to conclusively link the changes in the decomposition rates of warm-grown leaf litter in Experiment 2 to any of the litter traits measured. Future decomposition studies manipulating warming, drought, and litter source should measure a wider array of plant traits and soil biotic and abiotic factors that might potentially influence decomposition (Cornwell *et al.* 2008). Researchers should also measure soil microfauna, as they have a strong influence on decomposition at local and regional scales and have been shown to change in response to warming and rainfall reduction, which likely influenced our decomposition outcomes (García-Palacios *et al.* 2013; Bradford *et al.* 2016; Christiansen *et al.* 2017; Nave *et al.* 2024). Our study also primarily evaluated leaf litter from saplings with ectomycorrhizal associations, which may have different traits and resulting decomposition trends than litter from fully grown trees, trees with arbuscular mycorrhizal associations, herbaceous species, and shrubs (Cornelissen *et al.* 2007; Keller and Phillips 2019). This work also occurred in the drier, warmer end of the boreal forest. Therefore, in a colder and wetter boreal environment, warming might lead to faster decomposition, particularly if the positive effects of increased temperature on microbial activity offset any potential negative effects caused by reduced litter moisture (Aerts 2006).

Taken together, our results provide compelling evidence that combined global change factors will both directly (through effects on litter microclimate) and indirectly (through effects on litter chemistry) influence litter decomposition rates in cold climates. Changes in decomposition rates with warming and rainfall reduction may have a number of broader ecological implications. Most obviously, our results point to slower C cycling with reduced decomposition from warming and drought. However, whether soil organic matter would be converted to more stable forms of C and increase the amount of C stored in soils remains unclear

(Prescott 2010; Rocci *et al.* 2024) An increase in dry litter could also increase the likelihood of understory fires, meaning that there may be more litter but this C is more vulnerable to disturbance (Cornelissen *et al.* 2017). Alternatively, if warm-grown litter is more susceptible to faster decomposition in cooler years, then we may see swings in decomposition rates with more variable temperatures. Each of these potential ecological ramifications highlight the importance of litter decomposition for forest ecosystems and the need for further study of how decomposition is changing with global change factors at local, regional, and global scales.

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# Supplement

**Table S1.** Percentage of treatment combinations best represented by each model. A model was considered a “best fit” if it had the lowest AIC value or if the ΔAIC was <= 3 or 4.

| Model | ΔAIC <= 3 | ΔAIC<= 4 |
|---|---|---|
| Single Exponential | 53.3% | 58.5% |
| Double Exponential | 24.2% | 67.2% |
| Asymptotic | 97.7% | 97.7% |
| Weibull | 71.1% | 98.4% |

**Table S2.** Comparison of treatment only and treatment plus covariate models for litter half-life in open canopy plots.

| Model | AIC | AICc | R2_cond | R2_marginal | ICC | RMSE | Sigma |
|---|---|---|---|---|---|---|---|
| Treatment | 555.4 | 555.9 | 0.401 | 0.088 | 0.342 | 0.343 | 0.361 |
| Treatment + Covariates | 553.1 | 554.0 | 0.389 | 0.203 | 0.233 | 0.346 | 0.363 |

**Table S3.** Comparison of covariate models for litter half-life in open canopy plots. All models had the same structure except for the litter trait listed in the first column: half-life = heat * water + VWC + [litter trait] + (1|site:species).

| Litter Trait | AIC | AICc | R2_conditional | R2_marginal | ICC | RMSE | Sigma |
|---|---|---|---|---|---|---|---|
| %N | 856.7 | 857.8 | 0.308 | 0.078 | 0.250 | 0.784 | 0.815 |
| C:N | 856.5 | 857.7 | 0.312 | 0.082 | 0.251 | 0.784 | 0.814 |
| Lignin:N | 857.9 | 859.0 | 0.343 | 0.052 | 0.307 | 0.778 | 0.810 |
| $N_{area}$ | 858.2 | 859.3 | 0.332 | 0.051 | 0.296 | 0.780 | 0.812 |
| SLA | 858.6 | 859.7 | 0.340 | 0.044 | 0.309 | 0.779 | 0.811 |

**Table S4.** Comparison of covariate models for litter MRT in open canopy plots. All models had the same structure except for the litter trait listed in the first column: MRT = heat * water + VWC + [litter trait] + (1|site:species).

| Litter Trait | AIC | AICc | R2_conditional | R2_marginal | ICC | RMSE | Sigma |
|---|---|---|---|---|---|---|---|
| %N | 856.7 | 857.8 | 0.308 | 0.078 | 0.250 | 0.784 | 0.815 |
| C:N | 856.5 | 857.7 | 0.312 | 0.082 | 0.251 | 0.784 | 0.814 |
| Lignin:N | 857.9 | 859.0 | 0.343 | 0.052 | 0.307 | 0.778 | 0.810 |
| $N_{area}$ | 858.2 | 859.3 | 0.332 | 0.051 | 0.296 | 0.780 | 0.812 |
| SLA | 858.6 | 859.7 | 0.340 | 0.044 | 0.309 | 0.779 | 0.811 |

**Table S5.** Comparison of treatment only and treatment plus covariate models for litter MRT in open canopy plots.

| Model | AIC | AICc | R2_conditional | R2_marginal | ICC | RMSE | Sigma |
|---|---|---|---|---|---|---|---|
| Treatment | 1,208.7 | 1,209.2 | 0.231 | 0.040 | 0.199 | 0.848 | 0.887 |
| Treatment + Covariate | 1,211.2 | 1,212.1 | 0.224 | 0.056 | 0.178 | 0.852 | 0.892 |

**Table S6.** Comparison of treatment only and treatment plus covariate models for litter half-life in closed canopy plots.

| Model | AIC | AICc | R2_conditional | R2_marginal | ICC | RMSE | Sigma |
|---|---|---|---|---|---|---|---|
| Treatment | 488.3 | 488.9 | 0.445 | 0.087 | 0.392 | 0.390 | 0.411 |
| Treatment + Covariates | 487.6 | 488.7 | 0.443 | 0.149 | 0.345 | 0.389 | 0.411 |

**Table S7.** Comparison of treatment only and treatment plus covariate models for litter MRT in closed canopy plots.

| Model | AIC | AICc | R2_conditional | R2_marginal | ICC | RMSE | Sigma |
|---|---|---|---|---|---|---|---|
| Treatment | 855.5 | 856.2 | 0.312 | 0.034 | 0.287 | 0.787 | 0.829 |
| Treatment + Covariates | 856.8 | 857.9 | 0.337 | 0.071 | 0.287 | 0.782 | 0.828 |

**Table S8.** Comparison of covariate models for litter half-life in closed canopy plots. All models had the same structure except for the litter trait listed in the first column: half-life = heat * litter source + VWC + [litter trait] + (1|site:species).

| Model | AIC | AICc | R2_conditional | R2_marginal | ICC | RMSE | Sigma |
|---|---|---|---|---|---|---|---|
| %N | 490.6 | 491.6 | 0.401 | 0.131 | 0.311 | 0.393 | 0.409 |
| C:N | 491.8 | 492.8 | 0.420 | 0.105 | 0.352 | 0.392 | 0.408 |
| Lignin:N | 487.5 | 488.6 | 0.419 | 0.159 | 0.310 | 0.389 | 0.405 |
| $N_{area}$ | 492.3 | 493.3 | 0.432 | 0.091 | 0.375 | 0.391 | 0.407 |
| SLA | 489.2 | 490.2 | 0.424 | 0.144 | 0.326 | 0.390 | 0.406 |

**Table S9.** Comparison of covariate models for litter MRT in closed canopy plots. All models had the same structure except for the litter trait listed in the first column: MRT = heat * litter source + VWC + [litter trait] + (1|site:species).

| Model | AIC | AICc | R2_conditional | R2_marginal | ICC | RMSE | Sigma |
|---|---|---|---|---|---|---|---|
| %N | 856.7 | 857.8 | 0.308 | 0.078 | 0.250 | 0.784 | 0.815 |
| C:N | 856.5 | 857.7 | 0.312 | 0.082 | 0.251 | 0.784 | 0.814 |
| Lignin:N | 857.9 | 859.0 | 0.343 | 0.052 | 0.307 | 0.778 | 0.810 |
| $N_{area}$ | 858.2 | 859.3 | 0.332 | 0.051 | 0.296 | 0.780 | 0.812 |
| SLA | 858.6 | 859.7 | 0.340 | 0.044 | 0.309 | 0.779 | 0.811 |

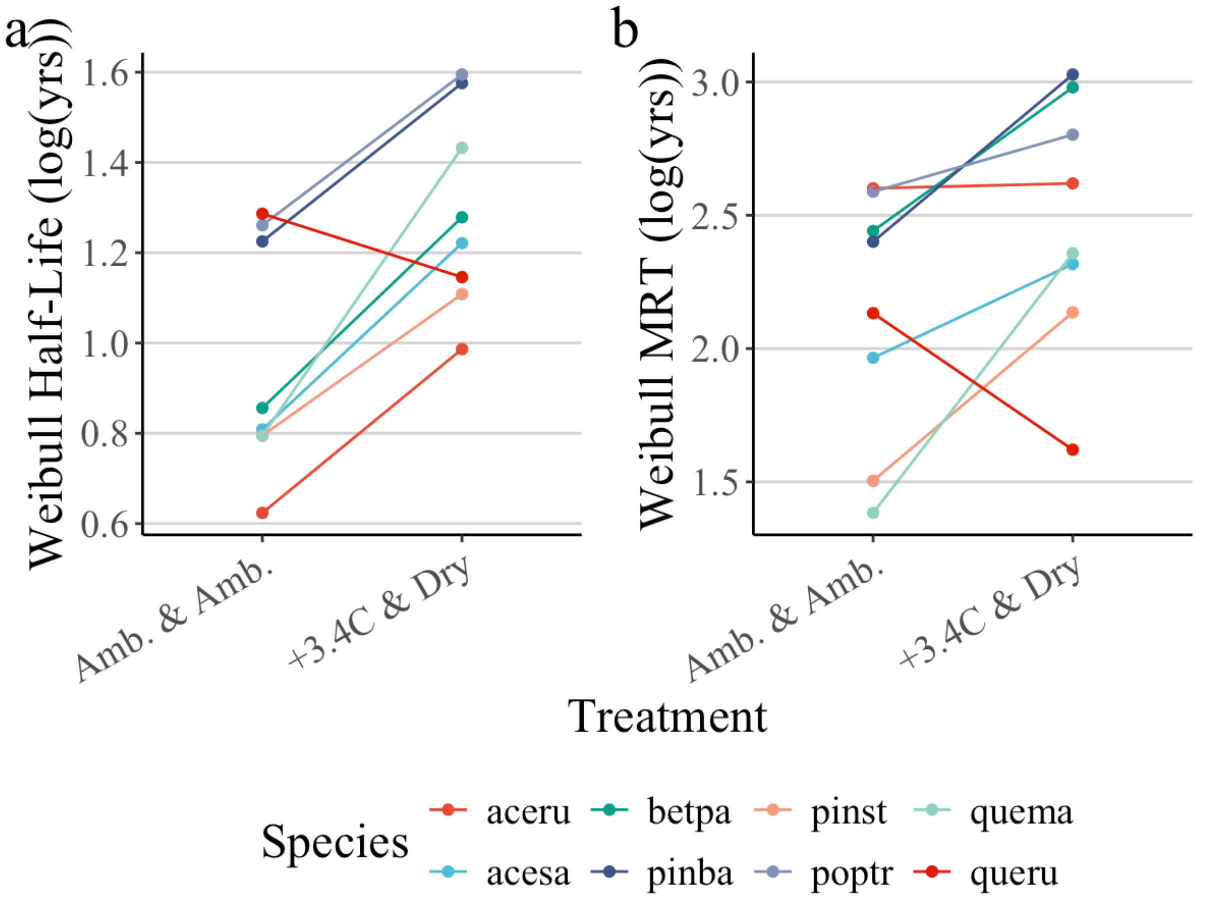

**Figure S1.** Species level means of (a) weibull half-life and (b) MRT for ambient temperature and precipitation compared to warmed and reduced precipitation treatments in the Climate of Decomposition experiment.

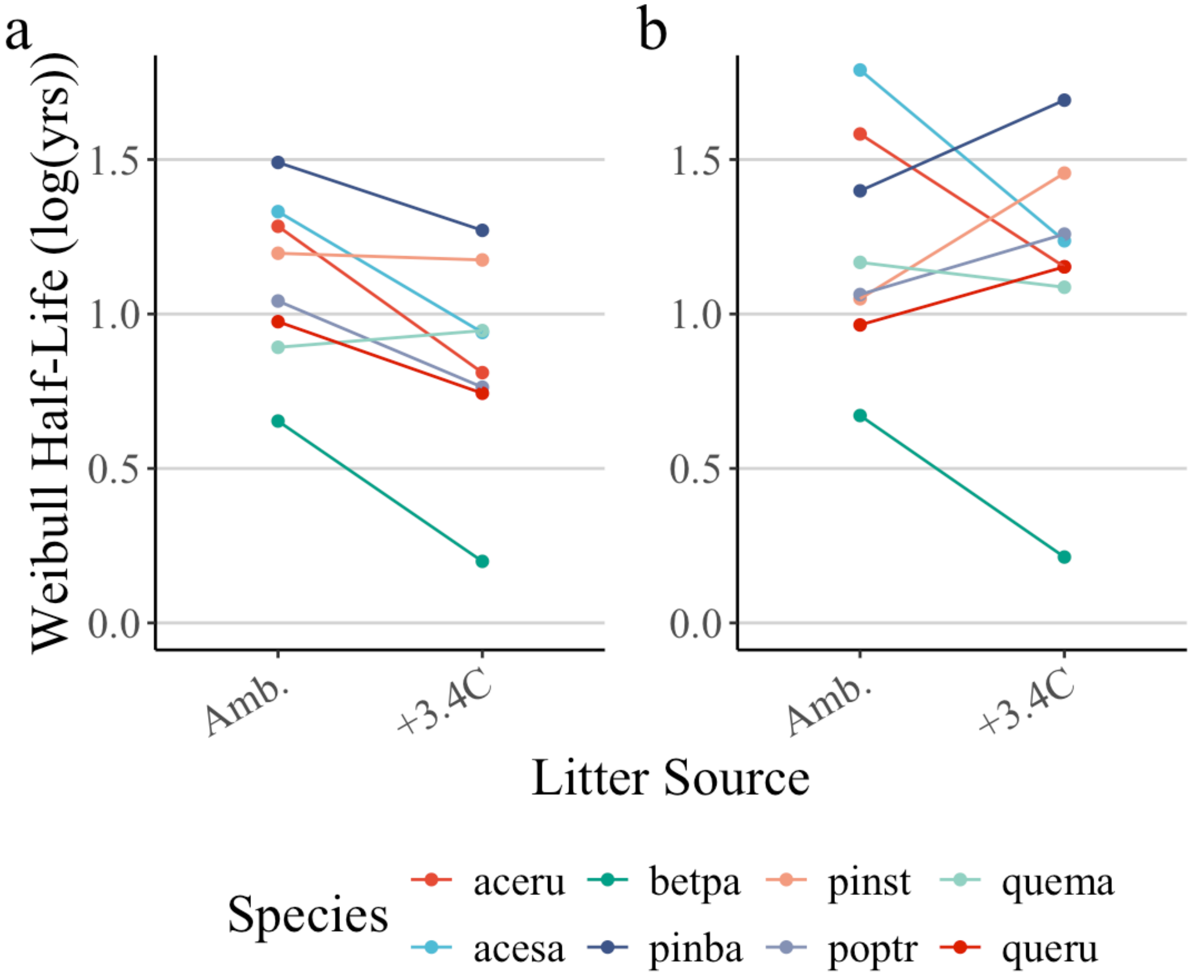

**Figure S2.** Comparison of litter source by species in the climate of decomposition experiment for litter half-life for (a) an ambient decomposition environment and (b) a warmed decomposition environment.

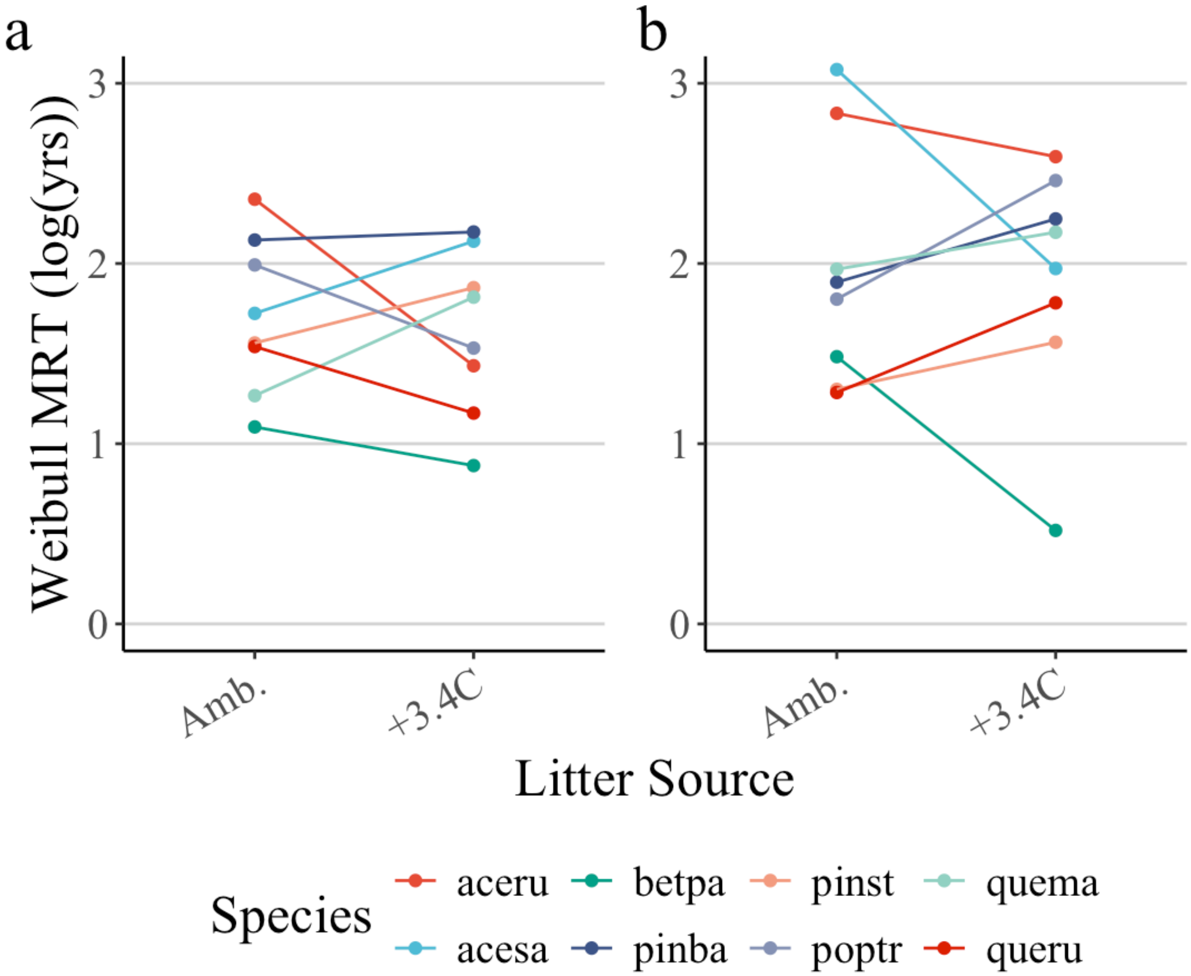

**Figure S3.** Comparison of litter source impact on litter MRT in the climate of decomposition experiment for (a) ambient and (b) a warmed decomposition environment.