Title: Combined warming and drying slow temperate-boreal tree litter decomposition, while warm-grown leaf litter foreshadows an unexpected decomposition signal

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

***Rachel A. King and Samuel P. Reed should be considered joint first author and are listed alphabetically**

Corresponding Author Email**: sam@friends-bwca.org**

Affiliations:
[1]National Center for Ecological Analysis and Synthesis, Santa Barbara, CA. USA
[2]Friends of the Boundary Waters, 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 Dept. of [8]Plant & Microbial Ecology, University of Minnesota, St. Paul, MN. USA
[9]Institute for Global Change Biology, University of Michigan, Ann Arbor, MI. USA

Conflict of Interest: There are no conflicts of interest.

Keywords: Decomposition, warming, precipitation, plant traits, temperate-boreal ecotone, carbon cycling, climate change, B4WarmED

Figures & Tables: 4 Figures (All Color), 4 Tables

Abstract

Plant litter decomposition is a primary control on terrestrial carbon fluxes and is critical to soil temperature, fauna, and nutrients, among many other biotic and abiotic factors. Individually, the key mediators of decomposition—litter traits, temperature, and moisture—are relatively well understood. However, our understanding of how combined climate drivers influence decomposition remains limited, as *in situ* experiments testing how combined warming and rainfall reduction impact decomposition are rare. Additionally, despite our knowledge that warming temperatures can alter leaf traits, few studies test how changes in leaf traits with increasing temperature can then influence decomposition. To this end, using the Boreal Forest at an Ecotone in Danger (B4warmED) experiment, we tested how warming and rainfall reduction impact the decomposition of leaf litter from eight boreal and temperate tree species. We found that combined warming and rainfall reduction increased litter half-life by 42% ± 11% in comparison to litter exposed to ambient climatic conditions. However, only rainfall reduction increased litter mean residence time by 37% ± 18% in comparison to ambient rainfall plots. We also tested how leaf litter grown in ambient and warmed growing conditions decomposed when transplanted into ambient and warmed environments. We found that warm-grown litter had a 22.4% ± 6.5% lower half life than ambient grown litter under ambient temperatures. Ambient-grown and warm-grown litter had slower, but equal decomposition rates in warmed environments. Our research indicates that climate change may slow carbon cycling in systems where moisture becomes a limiting factor. Additionally, our finding that warm-grown litter decomposition is more sensitive to temperature highlights a key limitation of many decomposition studies that only use ambient-grown litter. This result also points to a new ecological knowledge gap with ramifications for carbon modeling under global change.

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, especially in relation to how climate influences plant traits and resulting decomposition.

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 (Lu et al. 2013, Ward et al. 2015, Cornelissen et al. 2017, 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). Thus, it is particularly informative to assess if and how altered warming and moisture interact to alter litter decomposition in a northern climate, although few studies have tested both of these factors within a robust, *in situ* experimental framework (Prieto et al. 2019). Even rarer are studies that explore how global change can influence litter decomposition in boreal-temperate ecotones, where compositional change is expected to be particularly rapid with a changing climate and temperate species are expected to be favored over boreal species (Evans and Brown 2017). Whether our understanding of litter decomposition in boreal systems can be applied to decomposition in the temperate-boreal ecotone under climate change is unknown.

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 prolong leaf senescence and increase nutrient resorption, which would reduce leaf litter quality and likely slow decomposition (Yuan and Chen 2009, Estiarte and Peñuelas 2015, Prieto and Querejeta 2020, 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, very few studies test the combined influence of growth condition and decomposition environment by decomposing ambient- and warm-grown plant material under ambient and warmed environmental conditions (Prieto et al. 2019, Krna et al. 2023). By testing only how ambient litter or tea bags decompose 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 **A)** how combined warm and dry conditions influence decomposition rates and **B)** how ambient and warmed growing conditions influence plant traits and resulting decomposition under varying temperature treatments, 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). Additionally, due to this experiment's placement in the temperate-boreal ecotone, we are able to illustrate how a changing climate might influence carbon flows and soil conditions in a rapidly changing environment (Evans and Brown 2017). These changes in decomposition may then serve as an important indicator of how carbon flows and decomposition will shift as temperate species ranges shift northward (Smith and Goetz 2021). 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**; Aerts 2006). The second experiment (hereafter "Climate of Plant Growth") was designed to test interactions between plant growth conditions under different climate scenarios and whether resulting changes in plant traits altered decomposition under ambient or elevated temperatures. Specifically, we hypothesized that warm-grown litter would have reduced litter quality (e.g. higher C:N or Lignin:N ratios) resulting from either nutrient resorption from prolonger senescence (Montgomery et al. 2020) or changes in leaf construction due to warming (Suseela and Tharayil 2018), both potentially leading to slower leaf decomposition in both ambient and warmed environments (**H2**; Prieto and Querejeta 2020).

Materials & 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, mean annual precipitation is 824 mm and 715 mm, respectively, and mean annual temperature is 4.9 °C and 2.8 °C (averaged from 1980-2019 from nearby weather stations), while 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 test 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 the open canopy 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. Due to the differences in canopy conditions and experimental design between open and closed canopy plots, we did not compare decomposition responses between these plots.

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 rainfall; 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 ($1\text{-}C$) 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:

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

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 (β) and shape (α) 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 ($\mathrm{AIC_c}$; 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, our targeted 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.

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.

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).

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_{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. Litter traits themselves did not vary consistently with growth condition across species (Fig. 4, $p > 0.05$), though litter lignin:N and SLA had slight declines under warming.

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. 2025). Few studies can rigorously test how key biological processes among multiple tree species respond to multiple global change factors 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, especially early-stage decomposition, of numerous deciduous and coniferous tree species. We also found that warm-grown litter can have unexpected responses to the decomposition environment, as warm-grown litter had the fastest decomposition under ambient conditions yet similar decomposition to ambient-grown litter in a warmed decomposition environment. Furthermore, soil moisture and litter trait covariates resulted in little to no improvement to the models, suggesting that additional unmeasured factors, such as the soil microbial community, 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.

Combined rainfall and warming slow decomposition

Our finding that combined warming and rainfall reduction can slow tree leaf litter decomposition in the temperate-boreal ecotone generally aligns with our hypothesis, ecological theory, and the limited number of studies that have experimentally manipulated both of these global change factors (Aerts 2006, Butenschoen et al. 2011, Prieto et al. 2019, 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 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 leads to reductions in microbial biomass (García-Palacios et al. 2016b), as well as decreases the abundance of soil fauna involved in decomposition (Biryol et al. 2024). As such, future studies investigating how soil organisms are changing in response to reduced rainfall will advance our understanding of how decomposition is influenced by changing climatic conditions.

Our hypotheses regarding warming treatments were only partially supported, as warming alone resulted in slower 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 decomposer communities 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).

Considering that our work takes place in the temperate-boreal ecotone and found consistent responses from numerous species from both biomes, our results indicate that both northern-temperate and southern-boreal forests may experience slowing decomposition with warming and decreased precipitation. The most obvious impact of slowing decomposition is that leaf litter may accumulate to a greater degree with warming and rainfall reduction in each forest biome. 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, which is particularly important for soil fauna in the temperate forest (Sayer 2006). Each of these potential ecological outcomes are possible in boreal and temperate forests but highlight the substantial uncertainty of global climate change's localized ecological effects.

Warm-grown litter is more sensitive to temperature

In contrast to our second hypothesis, where we predicted that warm-grown litter would lead to slower decomposition regardless of temperature treatment, we found that warm-grown litter in ambient decomposition environments had the lowest half-life. This may lead us to expect that warm-grown litter in warmed decomposition environments would also have a lower half-life. However, in warmed environments we found no difference in the half-life of warm-grown and ambient-grown litter. This finding partially contrasts Prieto et al (2019)–to our knowledge, the only similar experimental study. Prieto et al. (2019) decomposed ambient- and warm-grown litter from a dryland shrub in each litter type's home conditions and found that combined warm growing conditions and warming decomposition environments led to a 32% decrease in decomposition activity compared to ambient litter decomposition (Prieto et al. 2019). This contrast could potentially be explained by warming significantly reducing litter quality in Prieto et al. (2019) in comparison to our study, which saw little to no effect of warming on our measured litter traits. Additionally, current ecological theory predicts that temperature sensitivity of decomposition increases as litter carbon quality decreases (Fierer et al. 2005, Conant et al. 2008, Suseela et al. 2013, Schwieger et al. 2025). Our measure of litter quality (% lignin measured on ANKOM) is relatively coarse, but the higher sensitivity of warm-grown litter would suggest that litter quality changed in some way. These theoretical and experimental contrasts could have important ramifications for carbon modeling under global change, especially if models incorporate climate-driven changes in litter quality into their projections.

Warm grown litter decomposing faster in ambient environments is potentially 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, Sáez-Sandino et al. 2025). Although we hypothesized that leaf litter C:N would increase in warm grown litter, responses were inconsistent across species, with increases in C:N for some species and decreases in others. This aligns with a global meta-analysis by Schwieger et al. (2024) where C:N did not correlate with warming. Other studies emphasize the importance of micronutrients (e.g., Na, Mg, Ca, K) and protein content, which we did not examine (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 growing environment impacts decomposition rates. Additionally, why there were no differences in warm- and ambient-grown litter in warmed decomposition environments is similarly unclear. It is possible that the effects of warming overwhelmed the effects of leaf traits and resulting litter quality. Or, alternatively, homogenized or altered decomposer communities at warmer temperatures led to slower decomposition rates regardless of litter quality (Treseder et al. 2016). Indeed, recent work in the same experimental platform has shown warming affects the composition of decomposer communities, which might help to explain why the difference in decomposition rates between ambient-grown and warm-grown litter was not consistent in ambient and warmed plots (Cantoran et al. 2025, Sáez-Sandino et al. 2025).

Regardless of a missing trait-based explanation, few studies, if any, have tested whether plant growth from multiple tree species under simulated climatic conditions can then influence litter decomposition rates under ambient and warmed environments (Suseela & Tharayil 2017). Our finding that warm-grown litter was particularly sensitive to changing temperatures and decomposed faster under ambient temperatures highlights an important contribution to how we experimentally test the effects of global change factors on litter decomposition. Considering that most decomposition experiments can only use ambient-grown litter or use tea bags (Schwieger et al. 2024), our results indicate that we are likely missing important causal mechanisms in our understanding of how global change influences plant traits and resulting decomposition. Similarly, our finding that warm-grown litter decomposed at the same rate as ambient-grown litter under warm conditions indicates that future changes in leaf traits with warming may not have an appreciable effect on decomposition, particularly if growing seasons are consistently hot. Conversely, it is possible that a more variable climate with fluctuations between warmer and cooler temperatures could lead to faster litter decomposition in cool years, especially among recently dropped leaves with traits that developed in warmer conditions. These findings highlight both a new ecological knowledge gap and a major opportunity to refine our understanding of plant traits, planetary warming, and decomposition.

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, our finding that warm-grown litter decomposes differently than ambient-grown litter highlights a need for further exploration of the linkages between plant traits and decomposition. Future decomposition studies manipulating warming, drought, and litter growing condition 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 plant traits) influence litter decomposition rates in both cold climates and in vulnerable temperate-boreal ecotones. 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.

References:

Aerts, R. 1997. Climate, Leaf Litter Chemistry and Leaf Litter Decomposition in Terrestrial Ecosystems: A Triangular Relationship. - Oikos 79: 439–449.

Aerts, R. 2006. The freezer defrosting: global warming and litter decomposition rates in cold biomes. - J. Ecol. 94: 713–724.

Baldrian, P., López-Mondéjar, R. and Kohout, P. 2023. Forest microbiome and global change. - Nat. Rev. Microbiol. 21: 487–501.

Bates, D., Mächler, M., Bolker, B. and Walker, S. 2015. Fitting Linear Mixed-Effects Models Using lme4. - J. Stat. Softw. 67: 1–48.

Biryol, C., Aupic-Samain, A., Lecareux, C., Gauquelin, T., Baldy, V. and Santonja, M. 2024. Interactive effects of soil moisture, air temperature and litter nutrient diversity on soil microbial communities and Folsomia candida population. - Oikos 2024: e10345.

Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Weiher, E., et al. 2018. Plant functional trait change across a warming tundra biome. - Nature 562: 57–62.

Bradford, M. A., Berg, B., Maynard, D. S., Wieder, W. R. and Wood, S. A. 2016. Understanding the dominant controls on litter decomposition (W Cornwell, Ed.). - J. Ecol. 104: 229–238.

Briones, M. J. I. 2018. The Serendipitous Value of Soil Fauna in Ecosystem Functioning: The Unexplained Explained. - Front. Environ. Sci. in press.

Burnham, K. P. and Anderson, D. R. 2004. Multimodel Inference: Understanding AIC and BIC in Model Selection. - Sociol. Methods Res. 33: 261–304.

Butenschoen, O., Scheu, S. and Eisenhauer, N. 2011. Interactive effects of warming, soil humidity and plant diversity on litter decomposition and microbial activity. - Soil Biol. Biochem. 43: 1902–1907.

Canessa, R., van den Brink, L., Saldaña, A., Rios, R. S., Hättenschwiler, S., Mueller, C. W., Prater, I., Tielbörger, K. and Bader, M. Y. 2021. Relative effects of climate and litter traits on decomposition change with time, climate and trait variability. - J. Ecol. 109: 447–458.

Cantoran, A., Maillard, F., Bermudez, R., Stefanski, A., Reich, P. B. and Kennedy, P. G. 2025. Warming and Reduced Rainfall Alter Fungal Necromass Decomposition Rates and Associated Microbial Community Composition and Functioning at a Temperate–Boreal Forest Ecotone. - Glob. Change Biol. 31: e70536.

Chang, Y., Sokol, N. W., van Groenigen, K. J., Bradford, M. A., Ji, D., Crowther, T. W., Liang, C., Luo, Y., Kuzyakov, Y., Wang, J. and Ding, F. 2024. A stoichiometric approach to estimate sources of mineral-associated soil organic matter. - Glob. Change Biol. 30: e17092.

Chapin, F. S. 2003. Effects of Plant Traits on Ecosystem and Regional Processes: a Conceptual Framework for Predicting the Consequences of Global Change. - Ann. Bot. 91: 455–463.

Christiansen, C. T., Haugwitz, M. S., Priemé, A., Nielsen, C. S., Elberling, B., Michelsen, A., Grogan, P. and Blok, D. 2017. Enhanced summer warming reduces fungal decomposer diversity and litter mass loss more strongly in dry than in wet tundra. - Glob. Change Biol. 23: 406–420.

Chuckran, P. F., Reibold, R., Throop, H. L. and Reed, S. C. 2020. Multiple mechanisms determine the effect of warming on plant litter decomposition in a dryland. - Soil Biol. Biochem. 145: 107799.

Conant, R. T., Drijber, R. A., Haddix, M. L., Parton, W. J., Paul, E. A., Plante, A. F., Six, J. and Steinweg, J. M. 2008. Sensitivity of organic matter decomposition to warming varies with its quality. - Glob. Change Biol. 14: 868–877.

Cornelissen, J. H. C., Van Bodegom, P. M., Aerts, R., Callaghan, T. V., Van Logtestijn, R. S. P., Alatalo, J., Stuart Chapin, F., Gerdol, R., Gudmundsson, J., Gwynn-Jones, D., Hartley, A. E., Hik, D. S., Hofgaard, A., Jónsdóttir, I. S., Karlsson, S., Klein, J. A., Laundre, J., Magnusson, B., Michelsen, A., Molau, U., Onipchenko, V. G., Quested, H. M., Sandvik, S. M., Schmidt, I. K., Shaver, G. R., Solheim, B., Soudzilovskaia, N. A., Stenström, A., Tolvanen, A., Totland, Ø., Wada, N., Welker, J. M., Zhao, X. and Team, M. O. L. 2007. Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. - Ecol. Lett. 10: 619–627.

Cornelissen, J. H. C., Grootemaat, S., Verheijen, L. M., Cornwell, W. K., van Bodegom, P. M., van der Wal, R. and Aerts, R. 2017. Are litter decomposition and fire linked through plant species traits? - New Phytol. 216: 653–669.

Cornwell, W. K. and Weedon, J. T. 2014. Decomposition trajectories of diverse litter types: a model selection analysis. - Methods Ecol. Evol. 5: 173–182.

Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., Hobbie, S. E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H. M., Santiago, L. S., Wardle, D. A., Wright, I. J., Aerts, R., Allison, S. D., Van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T. V., Díaz, S., Garnier, E., Gurvich, D. E., Kazakou, E., Klein, J. A., Read, J., Reich, P. B., Soudzilovskaia, N. A., Vaieretti, M. V. and Westoby, M. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. - Ecol. Lett. 11: 1065–1071.

Cotrufo, M. F., Soong, J. L., Horton, A. J., Campbell, E. E., Haddix, M. L., Wall, D. H. and Parton, W. J. 2015. Formation of soil organic matter via biochemical and physical pathways of litter mass loss. - Nat. Geosci. 8: 776–779.

De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B. R., Zellweger, F., Aalto, J., Ashcroft, M. B., Christiansen, D. M., Decocq, G., De Pauw, K., Govaert, S., Greiser, C., Gril, E., Hampe, A., Jucker, T., Klinges, D. H., Koelemeijer, I. A., Lembrechts, J. J., Marrec, R., Meeussen, C., Ogée, J., Tyystjärvi, V., Vangansbeke, P. and Hylander, K. 2021. Forest microclimates and climate change: Importance, drivers and future research agenda. - Glob. Change Biol. 27: 2279–2297.

Elser, J. J., Fagan, W. F., Kerkhoff, A. J., Swenson, N. G. and Enquist, B. J. 2010. Biological stoichiometry of plant production: metabolism, scaling and ecological response to global change. - New Phytol. 186: 593–608.

Estiarte, M. and Peñuelas, J. 2015. Alteration of the phenology of leaf senescence and fall in winter deciduous species by climate change: effects on nutrient proficiency. - Glob. Change Biol. 21: 1005–1017.

Evans, P. and Brown, C. D. 2017. The boreal–temperate forest ecotone response to climate change. - Environ. Rev. 25: 423–431.

Fierer, N., Craine, J. M., McLauchlan, K. and Schimel, J. P. 2005. Litter quality and the temperature sensitivity of litter decomposition. - Ecology 86: 320–326.

Foster, C. N., Sato, C. F., Lindenmayer, D. B. and Barton, P. S. 2016. Integrating theory into disturbance interaction experiments to better inform ecosystem management. - Glob. Change Biol. 22: 1325–1335.

García-Palacios, P., Maestre, F. T., Kattge, J. and Wall, D. H. 2013. Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. - Ecol. Lett. 16: 1045–1053.

García-Palacios, P., McKie, B. G., Handa, I. T., Frainer, A. and Hättenschwiler, S. 2016a. The importance of litter traits and decomposers for litter decomposition: a comparison of aquatic and terrestrial ecosystems within and across biomes. - Funct. Ecol. 30: 819–829.

García-Palacios, P., Prieto, I., Ourcival, J.-M. and Hättenschwiler, S. 2016b. Disentangling the Litter Quality and Soil Microbial Contribution to Leaf and Fine Root Litter Decomposition Responses to Reduced Rainfall. - Ecosystems 19: 490–503.

Gill, A. L., Schilling, J. and Hobbie, S. E. 2021. Experimental nitrogen fertilisation globally accelerates, then slows decomposition of leaf litter. - Ecol. Lett. 24: 802–811.

Grootemaat, S., Wright, I. J., van Bodegom, P. M., Cornelissen, J. H. C. and Cornwell, W. K. 2015. Burn or rot: leaf traits explain why flammability and decomposability are decoupled across species. - Funct. Ecol. 29: 1486–1497.

Hartig, F. 2017. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models.

Jones, S. E. and Lennon, J. T. 2010. Dormancy contributes to the maintenance of microbial diversity. - Proc. Natl. Acad. Sci. 107: 5881–5886.

Keller, A. B. and Phillips, R. P. 2019. Leaf litter decay rates differ between mycorrhizal groups in temperate, but not tropical, forests. - New Phytol. 222: 556–564.

Kirschbaum, M. U. F. 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. - Soil Biol. Biochem. 27: 753–760.

Klotzbücher, T., Kaiser, K., Guggenberger, G., Gatzek, C. and Kalbitz, K. 2011. A new conceptual model for the fate of lignin in decomposing plant litter. - Ecology 92: 1052–1062.

Krna, M. A., Tate, K. R., Saggar, S., Buckley, H. L. and Rapson, G. L. 2023. Temperature dependency of litter decomposition is not demonstrated under reciprocal transplantation of tussock leaves along an altitudinal gradient. - Funct. Ecol. 37: 1158–1169.

Lavelle, P., Blanchart, E., Martin, A., Martin, S. and Spain, A. 1993. A Hierarchical Model for Decomposition in Terrestrial Ecosystems: Application to Soils of the Humid Tropics. - Biotropica 25: 130–150.

Lenth, R. V., Buerkner, P., Herve, M., Love, J., Miguez, F., Riebl, H. and Singmann, H. 2022. emmeans: Estimated Marginal Means, aka Least-Squares Means.

Liu, Y., Zhang, A., Li, X., Kuang, W. and Islam, W. 2024. Litter decomposition rate response to multiple global change factors: A meta-analysis. - Soil Biol. Biochem. 195: 109474.

Lu, M., Zhou, X., Yang, Q., Li, H., Luo, Y., Fang, C., Chen, J., Yang, X. and Li, B. 2013. Responses of ecosystem carbon cycle to experimental warming: a meta-analysis. - Ecology 94: 726–738.

McLauchlan, K. K., Craine, J. M., Oswald, W. W., Leavitt, P. R. and Likens, G. E. 2007. Changes in nitrogen cycling during the past century in a northern hardwood forest. - Proc. Natl. Acad. Sci. 104: 7466–7470.

Molofsky, J. and Augspurger, C. K. 1992. The Effect of Leaf Litter on Early Seedling Establishment in a Tropical Forest. - Ecology 73: 68–77.

Montgomery, R. A., Rice, K. E., Stefanski, A., Rich, R. L. and Reich, P. B. 2020. Phenological responses of temperate and boreal trees to warming depend on ambient spring temperatures, leaf habit, and geographic range. - Proc. Natl. Acad. Sci. 117: 10397–10405.

Moorhead, D. L. and Sinsabaugh, R. L. 2006. A Theoretical Model of Litter Decay and Microbial Interaction. - Ecol. Monogr. 76: 151–174.

Muscolo, A., Bagnato, S., Sidari, M. and Mercurio, R. 2014. A review of the roles of forest canopy gaps. - J. For. Res. 25: 725–736.

Nave, L. E., Gough, C. M., Clay, C., Santos, F., Atkins, J. W., Benjamins-Carey, S. E., Bohrer, G., Castillo, B. T., Fahey, R. T., Hardiman, B. S., Hofmeister, K. L., Ivanov, V. Y., Kalejs, J., Matheny, A. M., Menna, A. C., Nadelhoffer, K. J., Propson, B. E., Schubel, A. T. and Tallant, J. M. 2024. Carbon cycling across ecosystem succession in a north temperate forest: Controls and management implications. - Ecol. Appl. in press.

Petraglia, A., Cacciatori, C., Chelli, S., Fenu, G., Calderisi, G., Gargano, D., Abeli, T., Orsenigo, S. and Carbognani, M. 2019. Litter decomposition: effects of temperature driven by soil moisture and vegetation type. - Plant Soil 435: 187–200.

Prescott, C. E. 2005a. Do rates of litter decomposition tell us anything we really need to know? - For. Ecol. Manag. 220: 66–74.

Prescott, C. E. 2005b. Decomposition and Mineralization of Nutrients from Litter and Humus. - In: Nutrient Acquisition by Plants: an ecological perspective. pp. 15–41.

Prescott, C. E. 2010. Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? - Biogeochemistry 101: 133–149.

Prescott, C. E. and Vesterdal, L. 2021. Decomposition and transformations along the continuum from litter to soil organic matter in forest soils. - For. Ecol. Manag. 498: 119522.

Prieto, I. and Querejeta, J. I. 2020. Simulated climate change decreases nutrient resorption from senescing leaves. - Glob. Change Biol. 26: 1795–1807.

Prieto, I., Almagro, M., Bastida, F. and Querejeta, J. I. 2019. Altered leaf litter quality exacerbates the negative impact of climate change on decomposition. - J. Ecol. 107: 2364–2382.

Reich, P. B., Grigal, D. F., Aber, J. D. and Gower, S. T. 1997. Nitrogen Mineralization and Productivity in 50 Hardwood and Conifer Stands on Diverse Soils. - Ecology 78: 335–347.

Reich, P. B., Sendall, K. M., Stefanski, A., Rich, R. L., Hobbie, S. E. and Montgomery, R. A. 2018. Effects of climate warming on photosynthesis in boreal tree species depend on soil moisture. - Nature 562: 263–267.

Rich, R. L., Stefanski, A., Montgomery, R. A., Hobbie, S. E., Kimball, B. A. and Reich, P. B. 2015. Design and performance of combined infrared canopy and belowground warming in the B4WarmED (Boreal Forest Warming at an Ecotone in Danger) experiment. - Glob. Change Biol. 21: 2334–2348.

Rocci, K. S., Cotrufo, M. F., Ernakovich, J., Foster, E., Frey, S., Georgiou, K., Grandy, A. S., Malhotra, A., Reich, P. B., Schlerman, E. P. and Wieder, W. R. 2024. Bridging 20 Years of Soil Organic Matter Frameworks: Empirical Support, Model Representation, and Next Steps. - J. Geophys. Res. Biogeosciences 129: e2023JG007964.

Sáez-Sandino, T., Reich, P. B., Maestre, F. T., Cano-Díaz, C., Stefanski, A., Bermudez, R., Wang, J., Dhar, A., Singh, B. K., Gallardo, A., Delgado-Baquerizo, M. and Trivedi, P. 2025. A Large Fraction of Soil Microbial Taxa Is Sensitive to Experimental Warming. - Glob. Change Biol. 31: e70231.

Sayer, E. J. 2006. Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. - Biol. Rev. 81: 1–31.

Schimel, J. P. 2018. Life in Dry Soils: Effects of Drought on Soil Microbial Communities and Processes. - Annu. Rev. Ecol. Evol. Syst. 49: 409–432.

Schwieger, S., Dorrepaal, E., Petit Bon, M., Vandvik, V., le Roux, E., Strack, M., Yang, Y., Venn, S., van den Hoogen, J., Valiño, F., Thomas, H. J. D., te Beest, M., Suzuki, S., Petraglia, A., Myers-Smith, I. H., Munir, T. M., Michelsen, A., Løkken, J. O., Li, Q., Koike, T., Klanderud, K., Karr, E. H., Jónsdóttir, I. S., Hollister, R. D., Hofgaard, A., Hassan, I. A., Genxu, W., Filippova, N., Crowther, T. W., Clark, K., Christiansen, C. T., Casanova-Katny, A., Carbognani, M., Bokhorst, S., Björnsdóttir, K., Asplund, J., Althuizen, I., Alonso, R., Alatalo, J., Agathokleous, E., Aerts, R. and Sarneel, J. M. 2025. Environmental Conditions Modulate Warming Effects on Plant Litter Decomposition Globally. - Ecol. Lett. 28: e70026.

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M. J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T. A. and Reyer, C. P. O. 2017. Forest disturbances under climate change. - Nat. Clim. Change 7: 395–402.

Smith, A. J. and Goetz, E. M. 2021. Climate change drives increased directional movement of landscape ecotones. - Landsc. Ecol. 36: 3105–3116.

Stefanski, A., Bermudez, R., Sendall, K. M., Montgomery, R. A. and Reich, P. B. 2020. Surprising lack of sensitivity of biochemical limitation of photosynthesis of nine tree species to open-air experimental warming and reduced rainfall in a southern boreal forest. - Glob. Change Biol. 26: 746–759.

Sun, Y., Wang, C., Chen, H. Y. H., Luo, X., Qiu, N. and Ruan, H. 2021. Asymmetric responses of terrestrial C:N:P stoichiometry to precipitation change. - Glob. Ecol. Biogeogr. 30: 1724–1735.

Suseela, V. and Tharayil, N. 2018. Decoupling the direct and indirect effects of climate on plant litter decomposition: Accounting for stress-induced modifications in plant chemistry. - Glob. Change Biol. 24: 1428–1451.

Suseela, V., Tharayil, N., Xing, B. and Dukes, J. S. 2013. Labile compounds in plant litter reduce the sensitivity of decomposition to warming and altered precipitation. - New Phytol. 200: 122–133.

Treseder, K. K., Marusenko, Y., Romero-Olivares, A. L. and Maltz, M. R. 2016. Experimental warming alters potential function of the fungal community in boreal forest. - Glob. Change Biol. 22: 3395–3404.

Tripathy, K. P., Mukherjee, S., Mishra, A. K., Mann, M. E. and Williams, A. P. 2023. Climate change will accelerate the high-end risk of compound drought and heatwave events. - Proc. Natl. Acad. Sci. 120: e2219825120.

Waksman, S. A. and Gerretsen, F. C. 1931. Influence of Temperature and Moisture Upon the Nature and Extent of Decomposition of Plant Residues by Microorganisms. - Ecology 12: 33–60.

Wan, L., Liu, G., Cheng, H., Yang, S., Shen, Y. and Su, X. 2023. Global warming changes biomass and C:N:P stoichiometry of different components in terrestrial ecosystems. - Glob. Change Biol. 29: 7102–7116.

Wang, L., Chen, Y., Zhou, Y., Zheng, H., Xu, Z., Tan, B., You, C., Zhang, L., Li, H., Guo, L., Wang, L., Huang, Y., Zhang, J. and Liu, Y. 2021. Litter chemical traits strongly drove the carbon fractions loss during decomposition across an alpine treeline ecotone. - Sci. Total Environ. 753: 142287.

Ward, S. E., Orwin, K. H., Ostle, N. J., Briones, M. J. I., Thomson, B. C., Griffiths, R. I., Oakley, S., Quirk, H. and Bardgett, R. D. 2015. Vegetation exerts a greater control on litter decomposition than climate warming in peatlands. - Ecology 96: 113–123.

Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setälä, H., Van Der Putten, W. H. and Wall, D. H. 2004. Ecological Linkages Between Aboveground and Belowground Biota. - Science 304: 1629–1633.

Wolfe, E. R. and Ballhorn, D. J. 2020. Do Foliar Endophytes Matter in Litter Decomposition? - Microorganisms 8: 446.

Young An, J., Park, B. B., Chun, J. H. and Osawa, A. 2017. Litterfall production and fine root dynamics in cool-temperate forests. - PLOS ONE 12: e0180126.

Yuan, Z. Y. and Chen, H. Y. H. 2009. Global-scale patterns of nutrient resorption associated with latitude, temperature and precipitation. - Glob. Ecol. Biogeogr. 18: 11–18.

Zani, D., Crowther, T. W., Mo, L., Renner, S. S. and Zohner, C. M. 2020. Increased growing-season productivity drives earlier autumn leaf senescence in temperate trees. - Science 370: 1066–1071.

Zhang, D., Hui, D., Luo, Y. and Zhou, G. 2008. Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. - J. Plant Ecol. 1: 85–93.

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**
Warming	-0.05	-0.10 – 0.00	**0.054**	-0.02	-0.16 – 0.11	0.716
Reduced Rainfall	-0.12	-0.18 – -0.07	**<0.001**	-0.16	-0.29 – -0.03	**0.019**
Warming × Reduced Rainfall	0.02	-0.04 – 0.07	0.544	0.09	-0.04 – 0.22	0.162
Random Effects						
σ^2	0.13			0.78		
τ_{00}	$0.07_{\text{site:species}}$			$0.20_{\text{site:species}}$		
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		

Notes: ICC = intraclass correlation coefficient

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**
Warming	-0.04	-0.11 – 0.04	0.317	0.01	-0.17 – 0.19	0.901
Reduced Rainfall	-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
Warming × Reduced Rainfall	0.02	-0.04 – 0.07	0.558	0.10	-0.03 – 0.24	0.138
Random Effects						
σ^2	0.13			0.80		
τ_{00}	$0.04_{\text{site:species}}$			$0.17_{\text{site:species}}$		
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		

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**
Warming	-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
Warming × Litter Source	0.05	-0.00 – 0.11	**0.068**	0.03	-0.09 – 0.15	0.617
Random Effects						
σ^2	0.17			0.67		
τ_{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		

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**
Warming	-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**			
Warming × 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						
σ^2	0.17			0.66		
τ_{00}	0.09 $_{\text{site:species}}$			0.22 $_{\text{site:species}}$		
ICC	0.35			0.25		
N	2 $_{\text{site}}$			2 $_{\text{site}}$		
	7 $_{\text{species}}$			7 $_{\text{species}}$		
Observations	147			138		
Marginal R^2 / Conditional R^2	0.149 / 0.443			0.078 / 0.308		

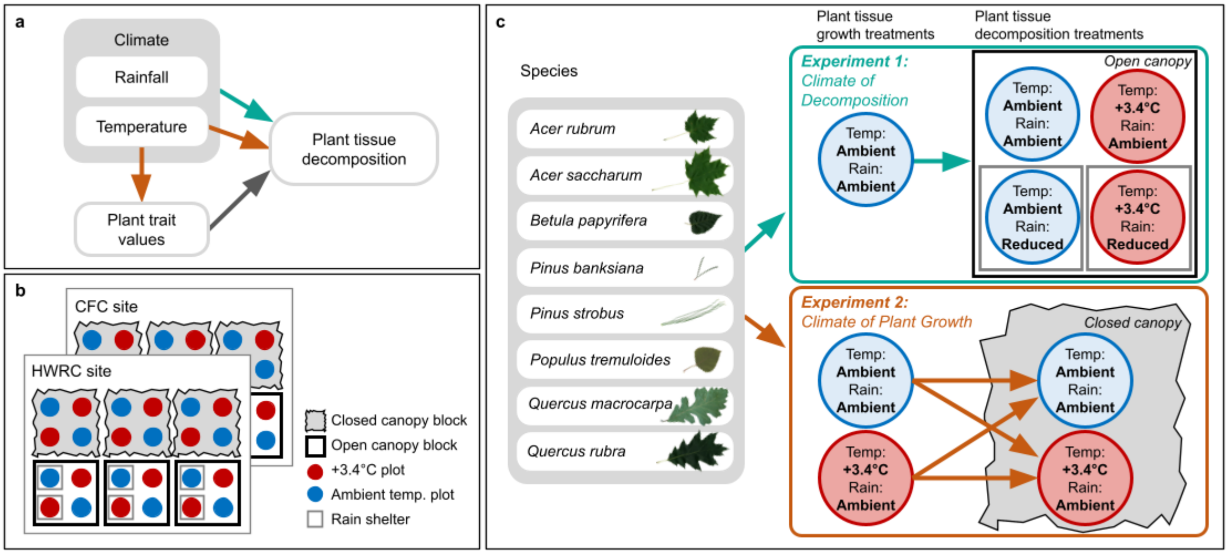

Figure 1 Conceptual framework and design of the two experiments that examine the effects of climate (temperature and rainfall) on plant leaf litter decomposition. (a) We hypothesized that climatic conditions directly affect decomposition as well as affect decomposition via effects on substrate chemistry. (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.

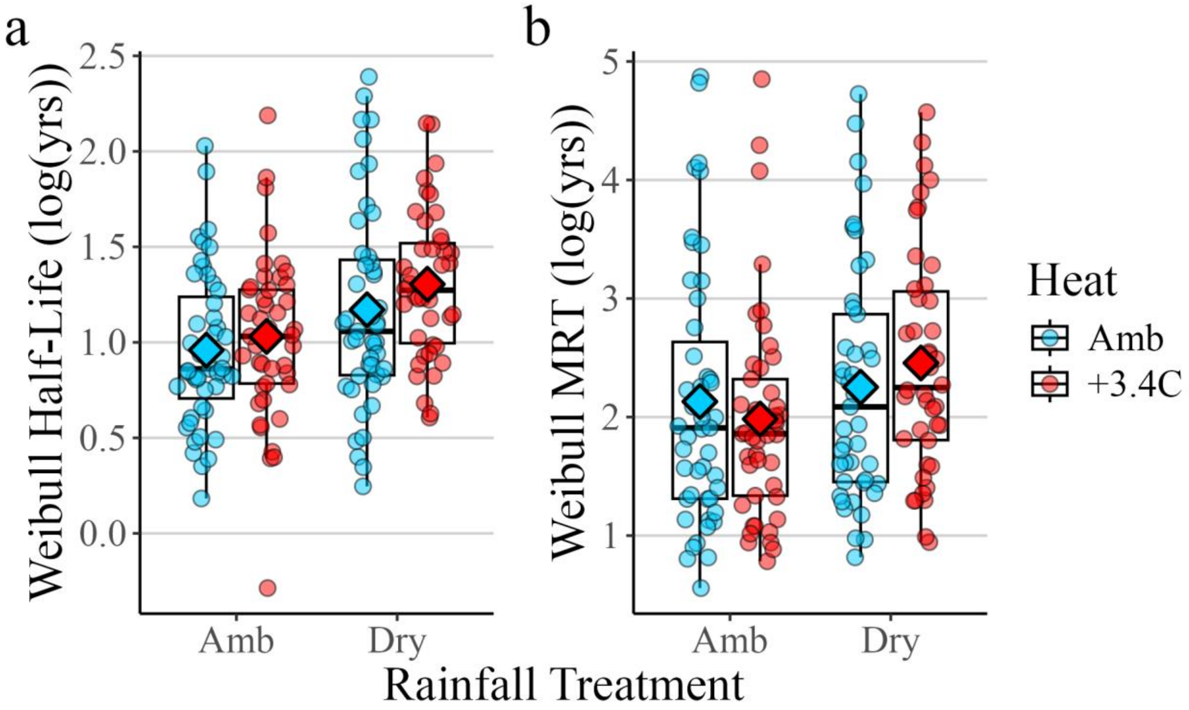

Figure 2. Experiment 1: Log-transformed Weibull half-life (a) or MRT (b) response to warming treatment (Amb or +3.4C) and rainfall reduction treatment (Amb or Dry) averaged across all species. Diamonds represent means while bold horizontal bars represent medians.

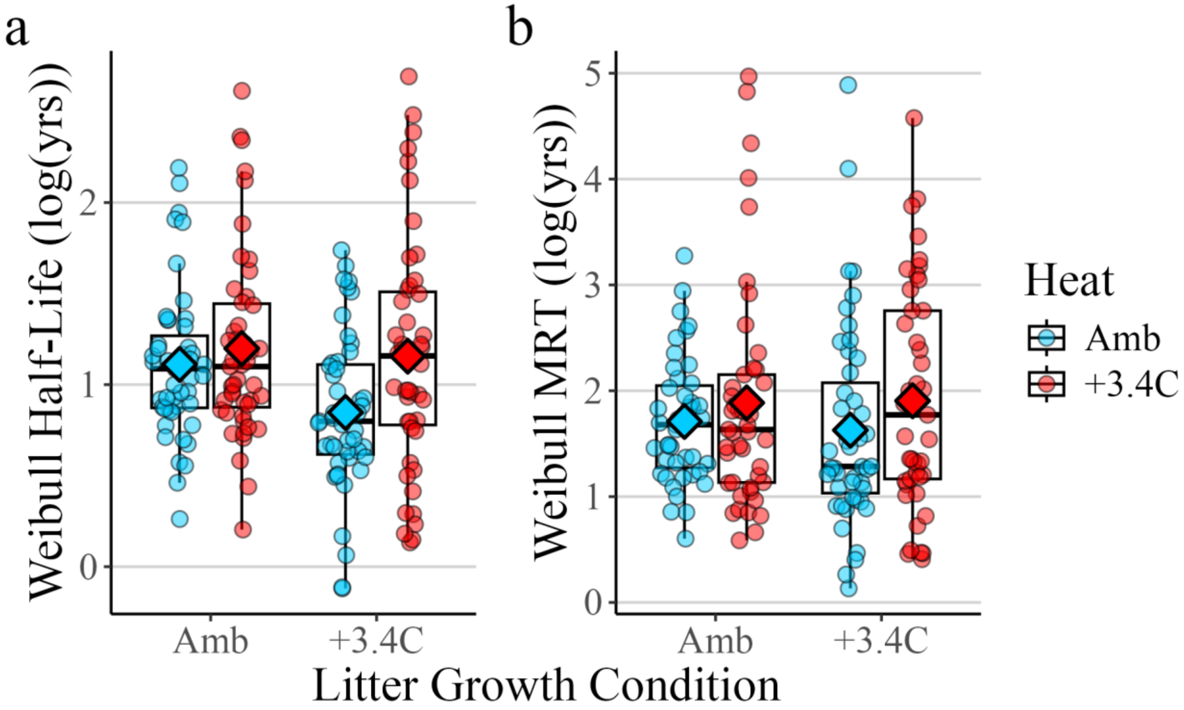

Figure 3. Experiment 2: Log-transformed Weibull half-life (a) and MRT (b) response to destination heating treatment (AMB or +3.4C) and litter source treatment (AMB or Warmed) averaged across species.

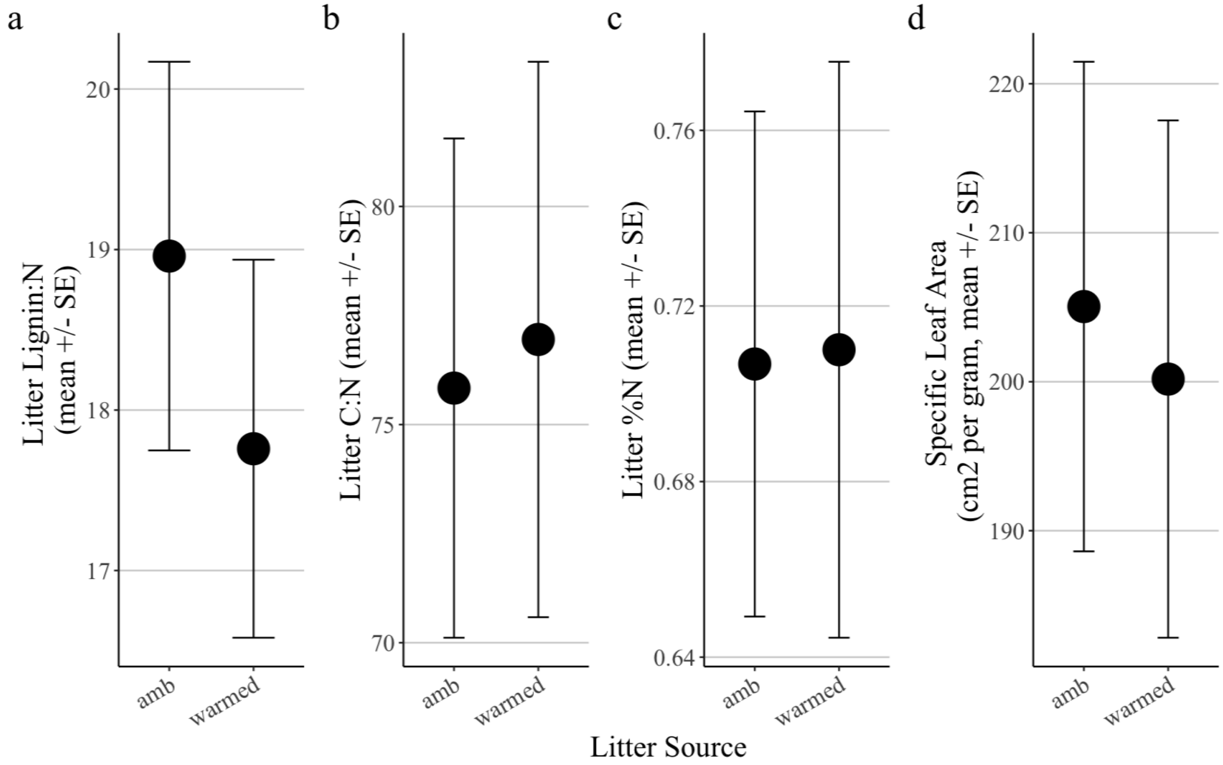

Figure 4. Select traits of leaf litter grown under ambient (amb) or +3.4C (warmed) conditions. Leaf lignin:N (a), C:N (b), Percent N (c), and Specific Leaf Area (SLA, d). Traits did not vary consistently between warmed and ambient conditions ($p > 0.05$ for all).