Title: Warming and drying slow temperate-boreal tree litter decomposition, while warm-grown litter highlights an important research frontier

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Abstract

1. Plant litter decomposition is a primary control on terrestrial carbon fluxes and is critical to soil temperature, fauna, and nutrients. Individually, key mediators of decomposition are well documented, with litter traits, temperature and moisture each known to affect decomposition.
2. However, the combined effects of these mediators on decomposition remains unclear: *in situ* experiments that test how combined warming and rainfall reduction impact decomposition are rare, and few studies have tested how litter formed under elevated temperature subsequently influences decomposition.
3. To this end, we used a unique open-air climate manipulation experiment located in the temperate-boreal ecotone of North America to test how warming and rainfall reduction affect the decomposition of leaf litter from eight boreal and temperate tree species.
4. We found that warming and rainfall reduction increased litter half-life by 11% and 28%, respectively, in comparison to litter exposed to ambient climatic conditions. However, only rainfall reduction influenced litter mean residence time, increasing it by 37% relative to ambient rainfall. We also tested how leaf litter formed in ambient versus warmed growing conditions decomposed when transplanted into ambient and warmed environments. We found that warm-grown litter had a 23% lower half life than ambient grown litter under ambient temperatures. Ambient-grown and warm-grown litter had slower, but similar decomposition rates in warmed environments.
5. Synthesis: Our findings indicate 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 points to a new ecological knowledge gap with ramifications for carbon modeling under global change and highlights the need to simultaneously consider climate change effects on litter quality and subsequent decomposition.

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, Scheu and Eisenhauer, 2011; Chang *et al.*, 2016). 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, 2006; 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 warmer temperatures will elevate litter decomposition rates as microbial decomposer activity will increase, particularly within colder regions (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, 2006) . However, there have been mixed results regarding how warming alone influences decomposition, with many studies showing either negligible or reduced decomposition rates with warming despite predictions from metabolic theory that warming should increase decomposition rates (Lu *et al.*, 2013; Ward *et al.*, 2015; Cornelissen *et al.*, 2017; Krna *et al.*, 2023; Liu *et al.*, 2024). Aerts (2006) theorized that warming effects are constrained in 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).

Current climate projects predict both warmer temperatures and more variable rainfall throughout much of the North American boreal and temperate forest (Wilson *et al.*, 2023). Thus, it is particularly informative to assess if and how altered warming and moisture interact to alter

litter decomposition in a northern climate, as 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 expected rapid changes in tree species composition favor expansion of temperate species 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 litter 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). Moreover, because of this experiment's location in the temperate-boreal ecotone, our study gives particular insight into how a changing climate might influence carbon flows and soil conditions in a region

experiencing rapid change (Evans and Brown, 2017). These changes in decomposition may indicate 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 warming would accelerate litter decomposition only under adequate moisture, whereas combined warming and rainfall reduction would lead to the slowest decomposition (**H1**; Aerts 2006). The second experiment (hereafter "Climate of Plant Growth") was designed to test interactions between the litter formed under different climate scenarios and decomposition under ambient and elevated temperatures. Specifically, we hypothesized that warm-grown litter would decompose slower in both ambient and warmed environments (**H2**; Prieto and Querejeta 2020), potentially due to reduced litter quality (e.g. higher C:N or Lignin:N ratios) due to nutrient resorption from prolonged senescence (Montgomery *et al.*, 2020) or changes in leaf construction due to warming or warming-induced moisture reductions (Suseela and Tharayil, 2018).

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 and justification 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 replicate sites within 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. Each canopy treatment was meant to represent two commonly occurring forest conditions, with open canopy conditions allowing us to evaluate rainfall reduction (Rich et al. 2015. 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. Given that Rich et al. 2015 found that most aboveground warming in B4WarmED is intercepted by the sapling canopy and does not strongly influence the soil surface, it is unlikely that this influenced decomposition. Further, any minor variability from this is accounted for in the analysis by including site as a random effect. In the open canopy plots, rainfall was also manipulated. Starting in 2012, rainout shelters were periodically deployed during rain events 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 (i.e., the ambient or warming treatment from which litter was retrieved) and then warmed plots or ambient plots as the litter destination (i.e., the ambient or warming treatment where litter was deposited). We are certain that the ambient and warm grown litter came from the planted trees for most species because the overstory was dominated by aspen with very few nearby like-species. It is possible, however, that small amounts of *P. tremuloides* 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. While it is possible that long-term litter storage influenced leaf chemistry, research has found that litter storage in dry conditions has little influence on leaf traits (Huang and Peng, 2004; Towey, Webster and Darr, 2019; Kühn *et al.*, 2024). Considering that dry storage of litter is a universal practice and we are only comparing differences in decomposition rates between dried leaves, we do not believe our storage methodology substantially influenced our results.

Litter bags (100 * 100 mm) were constructed from 1 mm nylon mesh and filled with 2 g of species-specific litter weighed to the nearest milligram. This mesh size is the standard for decomposition studies and this amount of litter approximates the average litter density resulting from annual litterfall in temperate and boreal systems (Young An *et al.*, 2017; Xie, 2020). 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 in 2018 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, Schilling and Hobbie, 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:

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

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

257 $$X = (1 - C)e^{-k_1 t} + (C)e^{-k_2 t} \text{ (eq 2)}$$

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

261 $$X = A + (1 - A)e^{-k_a t} \text{ (eq 3)}$$

262 While litter decomposition rates would never realistically be zero, over short time periods the
263 asymptotic model's assumption of a pool with a negligible decomposition rate holds true (Berg,
264 2014).

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

269 $$X = e^{-(\frac{i}{\beta})^{\alpha}}$$

270 The Weibull model does not have specific decomposition constants to compare across
271 treatments, rather we estimate the time to 50% mass loss and the mean residence time (MRT) of
272 the litter. These metrics indicate both early and late-stage litter decomposition as represented by
273 litter half-life and MRT, respectively. We note that because our decomposition experiment lasted
274 only 3 years, the values for MRT are almost all derived from extrapolation of the model beyond
275 this time period and may therefore contain more uncertainty than our estimates of time to 50%
276 mass loss.

277 To compare the fit of the four models, we fit the models to pooled replicates for each
278 species-treatment combination and assessed fit using Akaike's Information Criteria (AIC_c;
279 Burnham and Anderson, 2004). We used a ΔAIC value of 3 and 4 between the lowest AIC value
280 and remaining values to determine whether a model represented the data significantly better than
281 the alternative models. The asymptotic and Weibull models performed the best based on these
282 criteria, with similar distributions of AIC values (Fig. S1), and there was no significant effect of
283 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 present the treatment effects on the Weibull model decomposition parameters in the main text because it can capture more complex decomposition dynamics such as an initial lag phase or changes in decomposition rates over time (Cornwell and Weedon 2014). This ability was particularly important because our experiment included multiple species with non-constant decomposition trajectories indicated by a Weibull shape parameter substantially less than 1. We report results of the analyses for the asymptotic model in the supporting materials for transparency, but note that these models explained less variation in the data than the Weibull models. We estimated the parameters for the Weibull and asymptotic model on individual time-series (3 per species-treatment combination) and used these to calculate the time to 50% mass loss (half-life) and the litter MRT (Weibull) and k_a and A (asymptotic). 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) or generalized linear mixed effects models in the *glmmTMB* package if residuals suggested the need for a different distribution (Brooks *et al.*, 2017). In some cases, treatments had unequal variance, so we included a dispersion term in the model to better account for the data structure to meet model assumptions. Decay rate (k_a) for the asymptotic models were also compared with linear mixed effects models, while comparing asymptotes (A) required a two step model due to zero-inflation to first test treatment effects on the presence of an asymptote followed by a comparison of the size of the asymptote, again using the *glmmTMB* package.

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. Treatment effects for the full model use contrast coding and test significance with anova (lmerTest) or car::Anova for glmmTMB with type III sums of squares.

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). All post-hoc analyses report back-transformed treatment contrasts as models were fit on log-transformed half-life and MRT. These represent ratios of the geometric means, so ratios of 1 indicate no difference between treatments. In text, we turn the ratios into percentage change by % change = (ratio - 1) x 100%, so a ratio of 1.28 becomes an increase of 28%.

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: $F_{1, 162.7} = 3.76$, $p = 0.05$; Rainfall Reduction: $F_{1, 162.4} = 22.22$, $p < 0.001$; Table 1). Specifically, rainfall reduction increased litter half-life by 28% (95% CI: 16% - 43%) in comparison to plots with ambient rainfall ($t = 4.7$, $p < 0.0001$; Table S2), while warming alone increased litter half-life by 11% (95% CI: 0% - 23%; $t = 1.9$, $p = 0.05$). Together, the additive effects of warming and rainfall reduction result in the highest litter half-life, with a 42% (95% CI: 17% - 73%) higher half-life than ambient temperature and rainfall treatments (Fig. 2a), consistent with our

345 expectations. In contrast, only rainfall reduction had a strong effect on litter MRT (Rainfall
346 Reduction: $F_{1, 161.2} = 5.6$, $p = 0.02$; Table 1). Across all open canopy plots, rainfall reduction
347 increased average leaf litter MRT by 37% (95% CI: 5% - 78%) in comparison to plots with
348 ambient rainfall (t = 2.4, df = 161, $p = 0.02$, Fig. 2b; Table S2). When testing treatment effects
349 on the asymptotic model parameters, neither warming nor rainfall reduction influenced the
350 decomposition rate (k_a) or the asymptote (A, Tables S3).
351 For both half-life and MRT, the applied climate treatments explained a small amount of
352 variation relative to the species and site random effects. Less than 10% of the total variation
353 explained by the models came from the fixed effects of climate treatments (Table 1), and the
354 models for half-life explained more variation than those for MRT ($R^2_{cond} = 0.42$ vs $R^2_{cond} = 0.23$).
355 However, all but one species showed a clear increase in both litter half-life and MRT from the
356 ambient temperature and ambient rainfall treatments to the +3.4 ℃ and reduced rainfall
357 treatments (Fig. S2). The half-life ranged from a minimum of 1.9 years to a maximum of 4.0
358 years in ambient temperature and ambient rainfall to a range of 2.8 - 5.2 years under warmed and
359 reduced rainfall conditions. Litter MRT was substantially more variable across treatments, with a
360 range of 4.3 years to 35.8 years in the ambient temperature and ambient rainfall treatments to 5.2
361 years to 30.7 years under warmed and reduced rainfall treatments.
362 Including covariates in the models improved the fit for litter half-life but not for litter
363 MRT. For litter half-life, the best fit model with covariates improved slightly upon the inclusion
364 of leaf N_{area} in addition to the heat and water treatments (Table S4, S5). Including leaf N_{area}
365 increased the R^2_{marg} from 0.09 to 0.20 for litter half-life, though the variation explained by
366 random effects decreased from ICC of 0.36 to 0.23 (Table 2). Leaf N_{area} had a positive
367 relationship with litter half-life (Table S2), so leaves with greater N_{area} took longer to decompose
368 in contrast to our expectations. Reduced rainfall had a similar effect on litter half-life with or
369 without the covariates (Table S2), but warming became less important (Table 2). Including soil
370 moisture did not improve the model fit for either litter half-life or MRT (Tables 2, S4, S7, ΔAIC
371 < 2), so for litter MRT the models with treatments alone performed best.

372 *Experiment 2: Climate of Plant Growth*
373 Underneath a closed canopy, litter source and litter destination treatment had an
374 interactive effect on litter half-life ($\chi^2 = 4.22$, $p = 0.04$; Table 3; Fig. 3a) but not MRT ($\chi^2 = 1.9$, p

= 0.28). Warm-grown litter under warmed conditions had a 49% (95% CI: 20% - 86%) greater half-life than warm-grown litter under ambient conditions ($t = 4.65$, $p < 0.001$, Table S8), 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 23% (95% CI: 4% - 38%) shorter half-life than litter grown in ambient temperature ($t = -3.0$, $p = 0.014$). Litter from both sources had similar half-lives when decomposing under warmed conditions ($t = -0.11$, $p = 1.0$). Warming also increased litter MRT by 67% (95% CI: 30% - 115%) in comparison to ambient conditions ($\chi^2 = 15.78$, $p < 0.001$; 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). Finally, the asymptotic model decomposition rate and presence of an asymptote were relatively insensitive to treatment effects (Table S9), but the size of the asymptote appeared marginally sensitive to both warmed decomposition environment and litter source (Tables S8, S9). These effects were similar to the direction of effects for the weibull model, with warmed litter had a slightly reduced asymptote (19%, $t = -1.84$, $p = 0.07$) and warmed environment had a slightly increased asymptote (23%, $t = 1.78$, $p = 0.08$).

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 ($R^2_{marg} = 0.095$) than for litter MRT ($R^2_{marg} = 0.056$, Table 3). Species level patterns tended to show 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 (standard deviation: 0.84 yrs (ambient) vs. 1.29 yrs (warmed) (Fig. S3). Litter MRT did not show a clear trend, with some species showing increases in MRT and others decreases in each treatment (Fig. S4). Under ambient temperature with ambient-sourced litter, litter half-life ranged from 2.1 years to 5.0 years, while under warmed conditions with warmed litter the range of half-lives expanded from 1.2 years 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 substantially improve model fits for the Climate of Plant Growth experiment (ΔAICc <2). Model performance was similar for both litter half-life and MRT (Tables S10, S11) even though the variation explained by the fixed

406 effects (R^2_{marg}) increased when covariates were included (Table 4). The litter traits that explained
407 the most variation in the decomposition parameters varied for litter half-life and MRT: for half-
408 life, the lignin:N ratio was the best litter trait predictor (Table S12) and for MRT it was litter %N
409 (Table S13). However, only the lignin:N ratio had a significant impact on litter half-life, with
410 higher lignin:N ratios resulting in longer half-lives (i.e., slower decomposition, Table S8). Soil
411 moisture did not have a substantial influence on decomposition for either half-life or MRT. Litter
412 traits themselves did not vary consistently with growth condition across species (Fig. 4, $p >$
413 0.05), though litter lignin:N and SLA had slight but non-significant declines under warming.
414
415 **Discussion**
416 Global climate change is leading to numerous interacting stressors and disturbances
417 within forest ecosystems, many of which can strongly influence nutrient and carbon cycling
418 (Foster *et al.*, 2016; Seidl *et al.*, 2017; Tripathy *et al.*, 2023; Sáez-Sandino *et al.*, 2025). Few
419 studies can rigorously test how key biological processes among multiple tree species respond to
420 multiple global change factors in a field-based experimental setting, posing a significant
421 knowledge gap in our understanding and predictions of climate impacts and mechanisms of
422 change. Using a globally unique experiment, our work highlights how warming and rainfall
423 reduction can slow litter decomposition, especially early-stage decomposition, of numerous
424 deciduous and coniferous tree species. We also found that warm-grown litter can have
425 unexpected responses to the decomposition environment, as warm-grown litter had the fastest
426 decomposition under ambient conditions yet similar decomposition to ambient-grown litter in a
427 warmed decomposition environment. Furthermore, soil moisture and litter trait covariates
428 resulted in little to no improvement to the models, suggesting that additional unmeasured factors,
429 such as other species-specific traits or the soil microbial community, may be important
430 mechanisms to fully understand how climate mediates decomposition.

431 Since species accounted for most of the variability in our models we can assume that
432 species and their associated traits are the predominant drivers of decomposition (Cornwell *et al.*,
433 2008). Thus, different species and their associated traits have different responses to a given
434 climate factor (Dobson and Zarnetske, 2025). This species-level variability likely contributed to
435 the lack of a single mechanistic driver for the decomposition patterns we found, as well as the
436 insignificant responses to treatment effects in the asymptotic model. Our mass loss data suggest

non-constant decomposition rates for many, but not all, species which would make detecting treatment effects across species difficult in a model that assumes a constant decomposition rate. However, that we found a climate driven trend in decomposition from the more representative Weibull model, despite our models including highly variable data from 8 different temperate and boreal species, highlights both the key role that species can play in decomposition and the generalizable nature of our findings. If we had only tested a single species response to these treatments we would likely have found stronger responses to each climate treatment and reduced model variability, but these would be far less ecologically meaningful results. Our findings represent a step forward in our understanding of decomposition processes in an era of rapid global change, with ramifications for nutrient cycling, carbon cycling, and soil processes, though there is a need for more investigations related to the specific mechanisms that underpin our research.

Rainfall reduction and warming slow decomposition

Our finding that warming and rainfall reduction can slow tree leaf litter decomposition in the temperate-boreal ecotone generally aligns with our hypotheses, ecological theory, and the limited number of studies that have experimentally manipulated both of these global change factors (Aerts, 2006; Butenschoen, Scheu and Eisenhauer, 2011; Petraglia *et al.*, 2019; Prieto *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.*, 2016), 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 did not accelerate decomposition under wetter conditions but it did lead to slower early stage decomposition (half-life) regardless of moisture. Warming did not influence later stage decomposition (MRT). Studies that have examined a combination of soil moisture and warming on litter decomposition have found that warming effects are mediated by moisture with there being strong interactive effects (Butenschoen, Scheu and Eisenhauer, 2011; Petraglia *et al.*, 2019). While moisture and warming did not interact in our study, it is likely that both exacerbated evaporative drying and slowed early stage decomposition. Warm and dry conditions have been shown to homogenize early stage decomposer communities, which were then correlated with slower decomposition (Christiansen *et al.*, 2017). Late-stage decomposition, here represented by MRT, may have been less sensitive to warming because experimental conditions suppressed decomposition of the more recalcitrant components in leaf litter enough in the absence of heat that any additional effect of warming was small (Berg, 2000). Stronger impacts early in decomposition suggests that climate change may impact C stabilization in mineral-associated organic matter and nutrient cycling more than the accumulation of particulate organic matter or steady state litter mass (Schlesinger *et al.*, 2016; Sokol *et al.*, 2022). 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, 2005). Our results add needed context to our understanding of litter decomposition by showing how both warming and moisture can slow decomposition, however more research is needed on the exact mechanisms of decompositional change in cold biomes (Baldrian, López-Mondéjar and Kohout, 2023).

Considering that our work takes place in the temperate-boreal ecotone and that we found a response to our climate variables 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 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). 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 an interactive effect between growth condition and warming, where warm-grown litter in ambient decomposition environments decomposed the fastest. In contrast, we found no difference in the half-life of warm-grown and ambient-grown litter in warm decompositional conditions. 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 litter traits.

Considering that 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), these contrasting findings highlight the differential ways in which warming can influence eventual decomposition. The sensitivity of warm-grown litter to ambient conditions would suggest that litter quality changed in some way that was not captured by our selected traits. Considering the high amount of variability introduced by the number of species in our experiment, it is possible that there were different species-specific responses to growth environments as well (Baruah *et al.*, 2017; Dobson and Zarnetske, 2025).

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). Similar to litter half-life responses to global change treatments, there was no conclusive trait-based explanation for this finding as well.

Regardless of an inconclusive 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 and Tharayil, 2018). 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.*, 2025), our results indicate that we are likely missing important causal mechanisms in our understanding of how global change influences plant traits and resulting decomposition, particularly at early stages. 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 substantial fluctuations between warmer and cooler temperatures over the course of a growing season could lead to faster litter decomposition in cool conditions among 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.

Limitations, Opportunities, 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. Considering we did not find that litter C:N or lignin:N explained this trend, future decomposition studies manipulating warming, drought, and litter growing conditions should measure a wider array of plant traits and soil biotic and abiotic factors that might potentially influence decomposition (Cornwell *et al.* 2008). Additionally, as trends in the Climate of Decomposition

561 experiment showed an unexpected positive trend with leaf N_{area} and litter half-life, it is possible
562 that this trait was correlated with others like leaf toughness that have stronger negative
563 relationships with decomposition and could be investigated in future studies (Wang *et al.*, 2025).
564 Researchers should also measure the influence of soil microfauna on decomposition in relation to
565 climate, as they have a strong influence on decomposition at local and regional scales and have
566 been shown to change in response to warming and rainfall reduction, which likely influenced our
567 decomposition outcomes (García-Palacios *et al.*, 2013; Bradford *et al.*, 2016; Christiansen *et al.*,
568 2017; Nave *et al.*, 2024). Our study also primarily evaluated leaf litter from saplings with
569 ectomycorrhizal associations, meaning that future research should evaluate climate impacts on
570 decomposition trends from litter from fully grown trees, trees with arbuscular mycorrhizal
571 associations, herbaceous species, and shrubs (Cornelissen *et al.*, 2007; Keller and Phillips, 2019).
572 Lastly, our work occurred in the drier, warmer end of the boreal forest. Therefore, in a colder and
573 wetter boreal environment, we might see faster decomposition, particularly if the positive effects
574 of increased temperature on microbial activity offset any potential negative effects caused by
575 reduced litter moisture (Aerts 2006).
576 Taken together, our results highlight that combined global change factors can directly
577 (through effects on litter microclimate) slow decomposition, and indirectly (through warming
578 effects on growing leaves) influence litter decomposition rates in both cold climates and in
579 vulnerable temperate-boreal ecotones. However, the exact mechanisms driving these indirect
580 decomposition responses are complex, revealing a major research frontier. Changes in
581 decomposition rates with warming and rainfall reduction may have a number of broader
582 ecological implications. Most directly, our results point to slower C cycling with reduced
583 decomposition from warming and drought. However, whether soil organic matter would be
584 converted to more stable forms of C and increase the amount of C stored in soils remains unclear
585 (Prescott, 2010; Rocci *et al.*, 2024). An increase in dry litter could also increase the likelihood of
586 understory fires, meaning that there may be more litter but this C is more vulnerable to
587 disturbance (Cornelissen *et al.* 2017). Alternatively, if warm-grown litter is more susceptible to
588 faster decomposition in cooler years, then we may see swings in decomposition rates with more
589 variable temperatures. Each of these potential ecological ramifications highlight the importance
590 of litter decomposition for forest ecosystems and the need for further study of how
591 decomposition is changing with global change factors at local, regional, and global scales.

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838 **Table 1.** Treatment effects on litter half-life and mean residence time (MRT).

	Half-life		MRT	
	F (df)	**p**	**F (df)**	**p**
Fixed effects				
Warming	3.76 (1, 162.7)	*0.05*	0.13 (1, 160.9)	0.72
Reduced Rainfall	22.22 (1, 162.4)	***<0.001***	5.65 (1, 161.3)	***0.02***
Warming x Reduced Rainfall	0.37 (1, 162.3)	0.54	1.97 (1, 160.3)	0.16
Random effects				
τ_{00} (random intercept)	0.071		0.197	
σ^2 (residual)	0.126		0.782	
ICC	0.360		0.201	
Model fit				
Marginal R^2	0.085		0.033	
Conditional R^2	0.415		0.227	
N (site:species)	16		16	
Observations	181		179	

839 Notes: ICC = intraclass correlation coefficient; test-stats derived with Kenward-Roger
840 approximation for degrees of freedom.
841

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.

	Half-life		**MRT**	
	F (df)	**p**	**F (df)**	**p**
Fixed effects				
Warming	0.97 (1, 140.0)	0.33	0.02 (1, 134.1)	0.90
Reduced Rainfall	12.37 (1, 162.1)	***<0.001***	3.05 (1, 158.6)	*0.08*
VWC	0.69 (1, 65.0)	0.41	1.01 (1, 50.7)	0.32
N_{area}	6.91 (1, 12.5)	***0.02***	0.51 (1, 12.4)	0.49
Warming x Reduced Rainfall	0.34 (1, 150.5)	0.56	2.23 (1, 148.7)	0.14
Random effects				
τ_{00} (random intercept)	0.040		0.172	
σ^2 (residual)	0.132		0.796	
ICC	0.233		0.178	
Model fit				
Marginal R^2	0.203		0.056	
Conditional R^2	0.389		0.224	
N (site:species)	15		15	
Observations	169		167	

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.

	Half-life		MRT[1]	
	Chi-sq (df)	**p**	**Chi-sq (df)**	**p**
Fixed effects				
Warming	20.40 (1)	***<0.001***	15.78 (1)	***<0.001***
Litter Source	4.80 (1)	***0.03***	0.11 (1)	0.73
Warming x Litter Source	4.22 (1)	***0.04***	1.90 (1)	0.28
Random effects				
τ_{00} (random intercept)	0.104		0.432	
σ^2 (residual)	0.159		0.531	
ICC	0.396		0.448	
Model fit				
Marginal R^2	0.095		0.056	
Conditional R^2	0.453		0.479	
N (site:species)	16		16	
Observations	188		180	

[1]Note that the MRT model shows estimates for fixed effects from the model with a dispersion term, but model fit is assessed on the model without the term.

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.

	Half-life		MRT	
	F (df)	**p**	**F (df)**	**p**
Fixed effects				
Warming	9.33 (1, 133.8)	***0.003***	3.70 (1, 125.9)	*0.06*
Litter Source	9.32 (1, 135.2)	***0.003***	0.82 (1, 123.2)	0.37
VWC	0.00 (1, 135.1)	0.97	0.97 (1, 117.9)	0.33
Lignin:N	4.46 (1, 16.2)	***0.05***		
Warming x Litter Source	0.84 (1, 129.9)	0.36	0.00 (1, 120.9)	0.95
%N			1.69 (1, 23.8)	0.2
Random effects				
τ_{00} (random intercept)	0.089		0.275	
σ^2 (residual)	0.169		0.685	
ICC	0.345		0.287	
Model fit				
Marginal R^2	0.149		0.071	
Conditional R^2	0.443		0.337	
N (site:species)	13		13	
Observations	147		138	

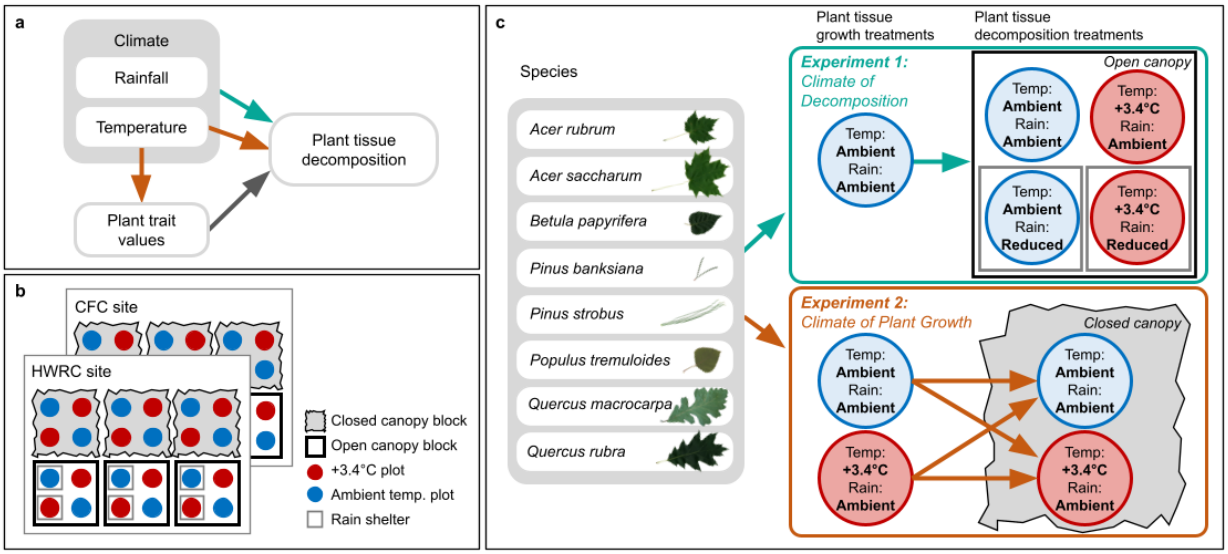

Figure 1 Conceptual framework and design of the two experiments that examine the effects of climate (temperature and rainfall) on plant leaf litter decomposition. **(a)** We hypothesized that climatic conditions directly affect decomposition as well as indirectly affect decomposition via effects on substrate chemistry. Arrow colors relate to each variable (rainfall, temperature, and plant trait values). **(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. Given that there was a full canopy overhead that likely led to different microclimates, ambient conditions are not directly comparable between both experiments.

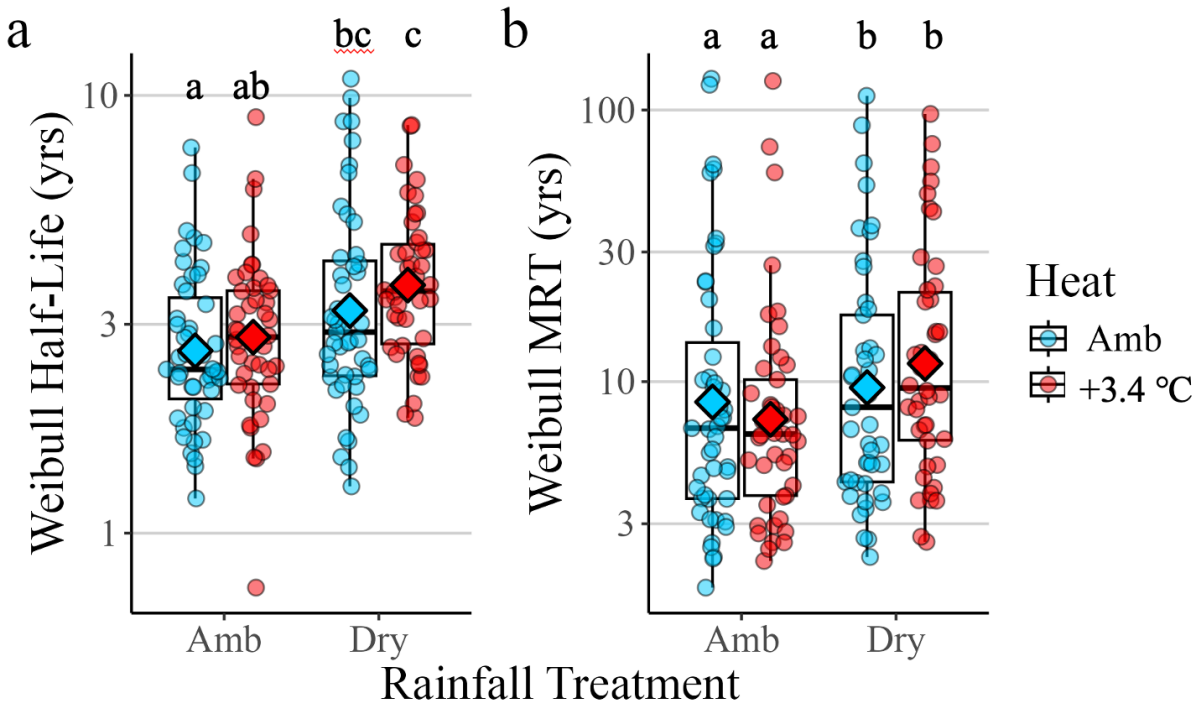

Figure 2. Experiment 1: Weibull half-life (a) or MRT (b) response to warming treatment (Amb or +3.4 °C) and rainfall reduction treatment (Amb or Dry) averaged across all species. Diamonds represent means while bold horizontal bars represent medians. Lowercase letters indicate significant differences between treatments from post-hoc tests, and the y-axis is $\log_{10}$ scaled.

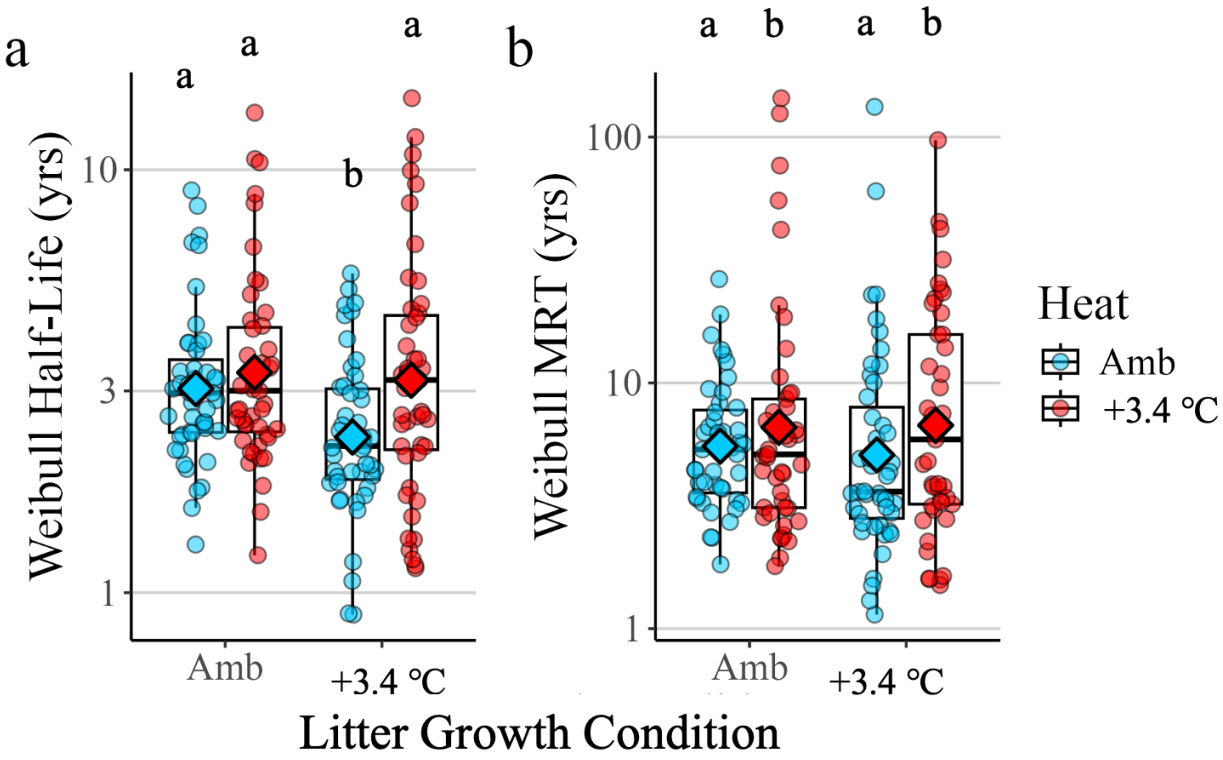

Figure 3. Experiment 2: Weibull half-life (a) and MRT (b) response to destination heating treatment (Amb or +3.4 °C) and litter source treatment (Amb or Warmed) averaged across species. Lowercase letters indicate significant differences between treatments and the y-axis is $\log_{10}$ scaled, but note that we show each treatment for MRT though only the destination heating treatment main effect was significant.

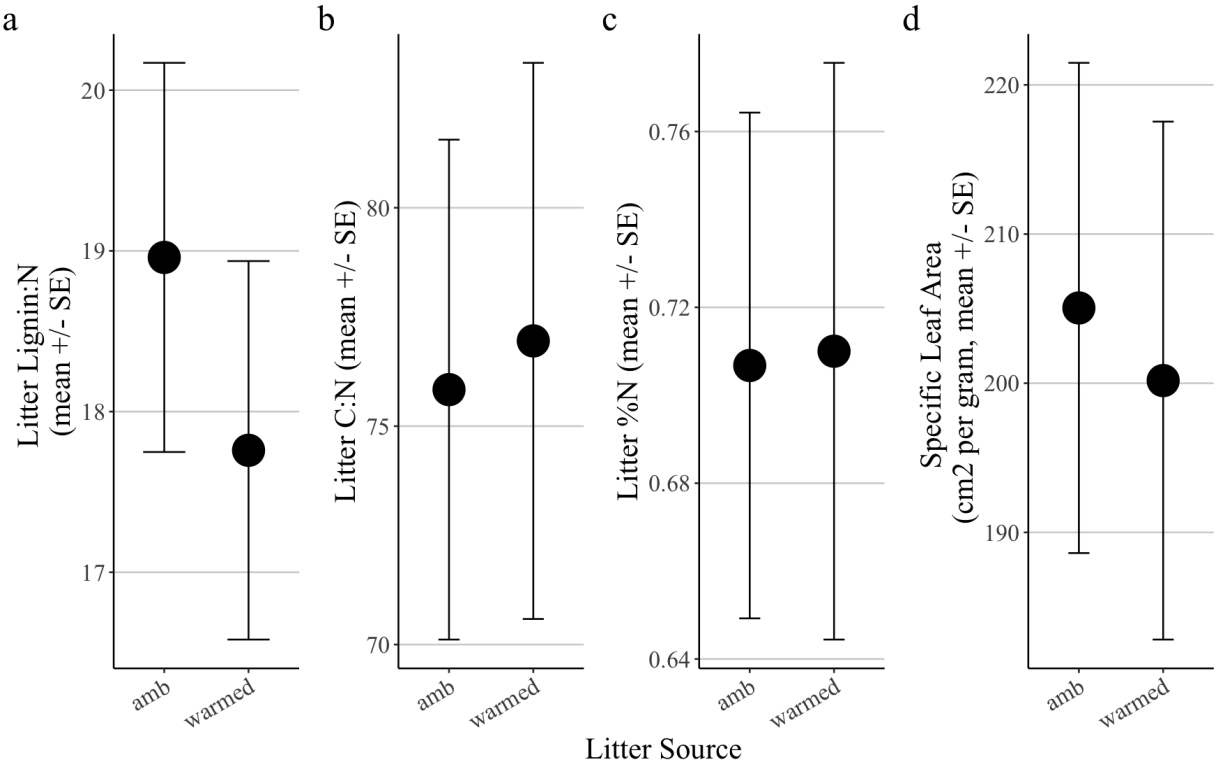

Figure 4. Select traits of leaf litter grown under ambient (amb) or +3.4 °C (warmed) conditions. Leaf lignin:N (a), C:N (b), Percent N (c), and Specific Leaf Area (SLA, d). Traits did not vary consistently between warmed and ambient conditions ($p > 0.05$ for all, linear mixed model with litter source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