Litter biota and quality as drivers of litter decomposition in mature oak forests subject to drought or elevated CO_2

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Submitted as a *Full paper* to New Phytologist

Introduction:1,110 words, Methods: 2,525 words, Results: 1,357 words, Discussion: 1,929 words
Combined word count of sections listed of 6,921 words
Five figures (all published in colour)

Summary (Word count: 195 words)

- Increasing atmospheric CO_2 concentrations alongside more frequent and severe droughts are key global change factors impacting litter decomposition, and global carbon and nitrogen cycles. Yet, we have a poor understanding of how these perturbations impact interactions between litter chemistry and decomposer food webs.
- We tested how drought and elevated CO_2 concentrations modify litter decomposition *via* litter chemistry and the decomposer communities using two separate, long-term manipulative drought or elevated CO_2 field experiments in mature oak woodlands. Litter bags were deployed in a reciprocal transplant design whereby control and treated litter was incubated in control and treated plots. We measured litter mass loss, quality and stoichiometry, moisture content, and microbial and animal community composition.
- Elevated CO_2 and drought affected litter stoichiometry and quality which in turn affected decomposition: litter in droughted plots decomposing slower than controls, while litter from elevated CO_2 plots decomposed slower over the first three harvests. In addition, we found that litter mass loss and decomposers were related both directly and indirectly to litter C:N.
- Drought and elevated CO_2 have distinct pathways of influence on litter quality, decomposers and decomposition which challenges our ability to predict how combinations of factors influence litter decomposition.

Keywords: BIFoR FACE, Decomposition, Drought, Elevated CO_2, Mesofauna, Litter, Microbial, O_3HP

Plain Language Summary

Global change factors like drought and elevated atmospheric CO_2 concentrations can impact litter decompositions, an important ecosystem process, *via* changes to litter properties and the decomposer community. Examining links between litter properties, decomposers and decomposition is therefore critical to understand how both drought and elevated CO_2 will affect nutrient release and cycling of belowground environments.

Introduction (Word count: 1,110)

Increasing atmospheric CO_2 concentrations often modifies leaf anatomy, chemistry and physiology (Pritchard et al., 1999; Ainsworth and Long, 2005), and at larger geographic scales, significantly alters global climatic patterns, including the frequency and intensity of extreme weather events such as droughts (IPCC, 2021). For instance, in 2022, summer drought resulted in nearly half of Europe's soil moisture levels becoming critically low (Toreti et al., 2022). Both elevated atmospheric CO_2 and drought have the potential to affect critical components of terrestrial biogeochemical cycles, including through changes in root inputs and litter decomposition (Chomel et al., 2019; Deng et al., 2021; Dong et al., 2021; Norby et al., 2024; Xu et al., 2024). For decomposition, the impact of elevated atmospheric CO_2 and drought begins prior to litterfall, because the C:N ratio of leaves and shoots can increase when grown under drought and elevated atmospheric CO_2. These effects can stem from increased sugar accumulation, decreasing nitrogen (N) content, and changes to primary and secondary plant metabolites due to water stress (drought) (Chen et al., 2015; Piper et al., 2017; Orians et al., 2019). For elevated CO_2, N dilution and increased assimilation of carbon (C) can alter the C:N within leaves (Taub and Wang, 2008; Welti et al., 2020), although this effect can be dependent on soil nutrient availability (Gardner et al., 2022). As a result, decomposition is affected by drought and elevated atmospheric CO_2 *via* changes to leaf and litter quality (Cotrufo and Ineson, 1996; Kasurinen et al., 2006; Quer et al., 2022; Wilson et al., 2022). Forest ecosystems dominated by mature, established trees play a critical role in global carbon (C) cycling (Harris et al., 2021) and exhibit cellular- to ecosystem-level responses to drought and elevated atmospheric CO_2 (Blaschke et al., 2001; Cech et al., 2003; Jiang et al., 2020; Lee et al., 2021; Arain et al., 2022; Martínez-Sancho et al., 2022). As such, there is a need to better understand the mechanisms by which these environmental stressors impact litter quality and decomposition in mature forest ecosystems.

Dead organic matter, such as leaf litter, constitutes a significant portion of below-ground C (Lonsdale, 1988). Through decomposition, leaf litter is converted and released as smaller compounds, consumed by soil organisms, and taken up by plants largely in mineral forms (Krishna and Mohan, 2017). Both C are released into the atmosphere as by-products of decomposition, but also incorporated into various soil C pools (Lavallee et al., 2020), making litter decomposition a critical component of ecosystem C storage. Globally, climatic factors such as average yearly

temperature and annual precipitation, along with C:N ratio of litter (Zhang et al., 2008), are strongly correlated with decomposition rate. Decomposer communities, consisting of soil animals (e.g., mites and collembolans), bacteria, and fungi, drive decomposition through fragmentation of litter by fauna (Seastedt, 1984; Coleman et al., 2018) and microbial secretion of enzymes, such as lignin peroxidase (Janusz et al., 2017) that further breakdown detritus. As a result, litter decomposition is regulated through an interaction between biota, litter quality, and environmental factors.

Drought and elevated atmospheric CO_2 can directly (e.g., through increased susceptibility to desiccation) or indirectly (e.g., through changes to litter quality) affect microbial and animal communities. For example, fungi are generally more resistant to drought than bacteria (Yuste et al., 2011; de Vries et al., 2012, 2018; Manzoni et al., 2012, but see Santonja et al., (2017)) as drought can also be an environmental filter for soil and litter animals as moisture content strongly shapes their community structure (Kardol et al., 2011; Lindo et al., 2012; Barreto et al., 2023), and alter interaction strength between trophic levels (Aupic-Samain, et al., 2021a) that may indirectly affect litter decomposition (Lang et al., 2014). Conversely, the effect of elevated atmospheric CO_2 on litter decomposition and associated decomposer communities are more subtle and highly variable (Blankinship et al., 2011), and potentially, weaker than drought. This effect may be due to belowground systems containing greater CO_2 concentrations than the atmosphere (Enoch and Dasberg, 1971). Generally, microbial and animal communities respond to changing litter quality (Ilieva-Makulec et al., 2006; Gergócs and Hufnagel, 2016; Liu et al., 2016), often stemming from fungi favouring recalcitrant litter (relative to bacteria) and the subsequent available feeding resources for animals. Higher C:N of litter under elevated atmospheric CO_2 (Vestergård et al., 2015; Holmstrup et al., 2017) can subsequently shift associated animal and microbial communities (Cha et al., 2017; Holmstrup et al., 2017).

Changes to microbial and animal community structure and biomass under environmental stress can strongly affect litter decomposition. For example, decreasing litter moisture content can shift microbial composition, resulting in lower mass loss under warming and reduced rainfall (Prieto et al., 2019). Microbes and animals show a consistent, but highly variable ability to accelerate decomposition of ‘home’ litter relative to ‘away’ litter (i.e. the home field advantage;

HFA) (Ayres et al., 2009; Veen et al., 2015). This variation is partly driven by litter quality, where recalcitrant litter is subject to stronger HFA than labile litter (Wallenstein et al., 2013). Potentially, drought or elevated atmospheric CO_2 (along with other environmental stressors) may alter HFA, thereby affecting litter mass moss. For example, Wang et al. (2020) found generally weaker HFA effects under years of environmental stress (i.e., drier and colder climate) stemming from changes to decomposer communities. Both drought and elevated atmospheric CO_2 have potential to affect litter decomposition through changing interactions between litter quality and stoichiometry and decomposers, and ultimately C cycling within ecosystems. But it remains unknown how long-term effects of drought and elevated atmospheric CO_2 impact interactions among litter quality and stoichiometry and the biotic drivers of decomposition *in situ*, especially in mature forests. Resolving this uncertainty requires large-scale experimental infrastructure in combination with multi-variate analysis of litter properties and other factors.

We investigated how drought and elevated atmospheric CO_2 independently affect litter decomposition in mature forests by conducting a reciprocal transplant across two, large-scale manipulative field experiments: the University of Birmingham Institute of Forest Research Free-Air CO_2 Enrichment (BIFoR FACE) experiment and the Oak Observatory at the Observatoire de Haute-Provence (O_3HP) drought experiment. We tested the hypotheses that elevated atmospheric CO_2 and drought (generated *via* a reduction in seasonal rainfall) would alter litter decomposition by acting *via* both litter quality and stoichiometry and the decomposer community. Although experiments are established in contrasting climates (cooler and wetter vs. warmer and drier), both drought and elevated CO_2 can shift leaf and litter properties in a similar manner *via* changes to carbon and nitrogen concentrations, and also impact the decomposer community. By using the same experimental methodology, we tested how significant correlates of decomposition (i.e., litter quality / stoichiometry and the decomposer community) are shaped by these key global change factors.

Methods (Word count: 2,525)

Overview

We collected control and experimental treated litter from the respective field experiments and transplated the two litter types into both plots to tease apart and isolate how litter quality and

stoichiometry and decomposers influence rates of litter decomposition under of long-term elevated CO_2 concentrations and drought. We harvested litterbags across four time points and measured litter decomposition (as mass loss), litter chemistry and metabolomics, and microbial (phospholipid fatty acid analysis; PLFA) and animal community structure (the abundance of mites, collembolans and other larger macrofauna). We then constructed structural equation models (SEMs) to test for significant pathways derived from well-documented relationships between abiotic (litter moisture and quality) and biotic (decomposer community) parameters with litter decomposition to determine how these relationships are directly and indirectly affected by drought and elevated atmospheric CO_2.

Experimental sites

We conducted a reciprocal transplant study at BIFoR FACE (52.801°N, 2.301°W), United Kingdom and O_3HP (43.750°N, 5.299°E) in southern France (Supplementary Figure S1). The BIFoR FACE facility is within a *Quercus robur* L. forest that was planted around 1850 (Hart et al., 2020; MacKenzie et al., 2021) containing coppice *Corylus avellana* L. and abundant self-set *Acer pseudoplatanus* L. understory. The CO_2 treatment began in April 2017 and comprises three non-infrastructure arrays (that were not used in this experiment) along with six infrastructure arrays (or plots) (elevated CO_2, n = 3, ambient CO_2, n = 3). Each array is approximately 30 m in diameter and comprises 16 peripheral towers and one central tower that extend ~ 1m above the canopy. In the elevated CO_2 plots, an additional 150 ppm of CO_2 above ambient (so, ~36 % increase over ambient) is emitted into the forest canopy, while ambient CO_2 arrays mimic the treatment arrays but only receive ambient air. The towers release CO_2 from ~April 1 to October 31 each year, coinciding with oak bud burst and last leaf fall (Supplementary Figure S2).

The O_3HP drought experiment started in 2012 on *Quercus pubescens* Willd forest, containing *Acer monspessulanum* L. (75% vs. 25% coverage, respectively) and *Cotinus coggygria* Scop understory. A rain exclusion device, measuring 15 m x 20 m excludes ~30% of precipitation, relative to the nearby control plot. In our study, the rain exclusion device was operational between the months of May to September and the total precipitation was 40% lower in rain exclusion plots over the course of the experiment (total precipitation, control: 1652 mm, drought: 997 mm;

Supplementary Information Figure S3) (see also Gauquelin et al., 2011, Santonja et al., 2017 and Aupic-Samain, et al., 2021b).

Litterbag preparation and sampling

Quercus litter was sampled from spatially separated areas of each site in BIFoR FACE and O_3HP in October 2019 and shipped in coolers to The University of Manchester, air dried and used for analysis of %C, %N, C:N and metabolomic signatures (Quer et al., 2022; see *Metabolomic signature of initial litter* in Supplementary Information for more details on methods). Litterbags comprised 1.8 mm mesh with two separate compartments (Supplementary Information Image S1), each receiving 3 g of dried litter. One compartment was used for chemical analysis of litter and assessment of microbial community composition, decomposition, and moisture content. The other compartment was used solely to characterize soil fauna communities. A total of 480 total litterbags were used (2 sites (BIFoR FACE and O_3HP) x 2 treatments (ambient and drought/elevated CO_2 x 2 litter origins (control and experimental, i.e., from either drought or elevated CO_2 plots) x 3 plots x 4-time points x 5 replicates = 480). The experiment began January 2020 and litterbags were harvested across four time points at both experimental sites. At BIFoR FACE, litterbags were harvested September 2020 (8 months; Harvest one; H1), January 2021 (12 months; Harvest two; H2), June 2021 (17 months; Harvest three, H3) and December 2021 (23 months; Harvest four, H4), corresponding to seasons 4 and 5 of the elevated CO_2 treatment. Four litter bags could not be retrieved from BIFoR FACE at H4 due to a tree limb falling and disturbing litter bags. Also, one litterbag was removed from H2 because the final dry weight of the litter was not recorded. At O_3HP, litterbags were harvested October 2020 (10 months; H1), January 2021 (13 months; H2), September 2021 (21 months; H3) and October 2022 (34 months; H4). The total time for decomposition varied between our two experiments due to differences in the carbon and nitrogen concentrations (and subsequent C:N ratio) within our initial litter (Supplementary Information Table S1). Here, the C:N ratio in our elevated CO_2 experiment was far lower than the drought experiment. We initially aimed for ~24 months of decomposition, but to ensure litter in the drought experiment had at least loss half their initial values by the end of the drought experiment, we continued incubation for an additional year. For the structural equation models (for more details, see later sections) we elected to use data from H3 where mass loss was on average 40-55% from

the drought experiment and 60-70% for the elevated CO_2 experiment (Figure 1), ensuring that decomposition was on-going within our study and had not yet plateaued.

At each sampling time, litterbags were shipped to The University of Manchester for processing. From the 'chemical analysis compartment', remaining litter was removed from the bag and leaves roughly cleaned by hand from soil residuals. The fresh weight (g) of the litter was taken before litter was frozen at -20 °C overnight and 48 hours of freeze-drying for determination of dry weight. For soil fauna litter, litter was removed from the compartment and placed on Tullgren funnels to extract individual animals for seven days into absolute ethanol. After extraction, litter was placed into ovens at 65 °C for two days before weighing to measure litter dry weight.

Litter decomposition, quality, stoichiometry, and moisture content

Litter decomposition was calculated as litter mass loss using the following equation:

$$Mass\ loss\ (\%) = \frac{Initial\ litter\ (g) - harvested\ litter\ (g)}{Initial\ litter} * 100$$

We also calculated the exponential decomposition rate coefficient (k_t) at each harvest point using the equation from (Olson, 1963):

$$k_t = \frac{-\ln\left(\frac{X_H}{X_I}\right)}{t}$$

Where X_H is the weight (in g) of harvested litter, X_I is the weight of initial litter (in g), and t is time in years since the beginning of the experiment. Litter decomposition was measured from all litterbags across all four time points. We measured the %C, %N and C:N ratio with a Elementar Vario EL element analyser (Hanau, Germany) on 5 mg of ball-milled litter (Retsch Ball Mill MM 400, Haan, Germany) to gauge litter quality in H3 and H4 time points, at both sites.

In addition, we measured litter stoichiometry on H3 and H4 litter from both sites using Fourier transform infrared (FTIR) spectroscopy, following Bell et al. (2018). Ball-milled leaves were plaved onto a Universal Attenuated Total Reflection (UATR) spectrometer and the absorbance (A cm^{-1}) measured within a 650 to 4000 A cm^{-1} range, at 4 cm^{-1} resolution and 16 scans per sample. We also ran a background correction after every ten samples measured. After

214 samples were processed, we applied a baseline correction for each spectra using the modpolyfit
215 method in the R package 'baseline'. To standardize values across our samples, we Z-transformed
216 each spectra, where values were transformed to a mean of 0 and SD of 1 (Jardine et al., 2017; Bell
217 et al., 2018). We then calculated the area of the curve for each respective functional group using
218 a shoelace formula (Wang et al., 2023). The assignment of wave number regions to leaf litter
219 functional groups was based on (Liu et al., 2016) who used FTIR to examine functional groups
220 across four deciduous litter origins, including *Quercus robur* (Supplementary Information Table
221 S2).
222
223 Finally, we also calculated leaf litter moisture content for H3 and H4 litter and both sites
224 using the fresh (or wet) weight of the harvested litter and freeze-dried litter from the chemical
225 compartment of the litterbag.
226
227 *Phospholipid fatty acid analysis (PLFA)*
228 We used PLFAs to analyse microbial community composition in H3 leaf litter (at both sites)
229 using methods adapted from (Buyer and Sasser, 2012). We quantified microbial communities with
230 ~0.4-0.5 g of ball milled, freeze-dried litter. A single litter bag (from the elevated CO_2 experiment)
231 contained 0.29 g after freeze-drying that PLFAs were measured. Four additional litterbags were
232 removed from analysis from the elevated CO_2 experiment due to either insufficient mass of litter
233 needed to measure PLFAs or no PLFAs were detected. Four ml of Bligh-Dyer extractant
234 containing C19:0 of an internal standard was added to each sample to extract lipids. Once
235 extracted, we used a gas chromatograph (Agilent 7890A Gas chromatograph, Santa Clara, CA,
236 USA) to assign and calculate peak height, where PLFA group abundances were expressed as nmol
237 g dry weight of litter^{-1}. We used 18 fatty acid markers to characterise microbial communities (Liu
238 et al., 2016; Dhaou et al., 2022; Biryol et al., 2024) with 6 and 4 markers for gram positive (i14:0,
239 i15:0, a15:0, i16:0, i17:0, a17:0) and gram negative (16:1ω7c, cy17:0, 18:1ω7, and cy19:0)
240 bacteria, respectively. In addition, we used 14:0, 15:0, 16:0 and 17:0 as general bacteria marks,
241 and 10Me16:0, 10Me17:0, and 10Me18:0 as markers for actinobacteria. The marker 18:2ω6,9 was
242 the sole fungal marker in our experiments. With these markers, we analyzed treatment and litter
243 origin effects on total PLFA concentrations (biomass), F:B ratio (by dividing 18:2ω6,9 abundance

by the summed total of bacteria markers) and PLFA community composition across both experiments.

Soil fauna community

Soil fauna community composition was quantified on H3 and H4 litter at both sites and was extracted using Tullgren funnels over seven days into absolute ethanol. Soil fauna was sorted and counted into higher taxonomic or mixed groups, comprising: Collembola (Hexapoda), Oribatida (Arachnida: Sarcoptiformes), Astigmata (Arachnida: Sarcoptiformes), Prostigmata including the mite family Nanorchestidae (hereafter, called Prostigmata, Arachnida: Trombidiformes, Sarcoptiformes), Mesostigmata (Arachnida: Parasitiformes), and 'other' fauna, which included Annelida, Isopoda, and Insecta. Soil fauna abundances were standardized by the dry weight of litter (individuals g dwt^{-1}), to account for differences in sample mass prior to analysis. We examined the effect of treatment and litter origin on total fauna and fauna group abundance and composition.

Statistical analysis

All statistical analyses were performed with the program R (version 4.3.0) (R Core Team, 2023) and figures produced with the package 'ggplot2' (Wickham, 2016). To analyze for differences in initial litter chemistry between our litter types (litter from control and experimental plots) prior to the experiment beginning, we used one-way Analysis of Variance (ANOVA) tests and Permutation Multivariate ANOVAs (PERMANOVAs) to examine for differences between C%, N% and C:N ratio (ANOVA) and leaf metabolomic profile (PERMANOVA, with Euclidean distance) between our treatments (ambient vs. drought or elevated CO_2). To do this, we used the aov function in base R and the adonis2 function in the package 'vegan' (Oksanen et al., 2022), respectively. Here, we partitioned the data by sites (BIFoR FACE and O_3HP) and ran separate models for both.

We tested the effect of treatment (ambient vs. drought or elevated CO_2) and litter origin (control vs. experimental) on our parameters, analyzing the sites (BIFoR FACE and O_3HP) and harvest time points (H1-4) separately (excluding litter decomposition, for more details see below). For univariate variables, we used linear mixed models where the fixed factors were

treatment, litter origin, and their interaction, with a random factor of experimental plot. We used linear mixed models for %C, %N, C : N ratio, total PLFA biomass (nmol g dwt^{-1}), fungi : bacteria ratio, animal total and group abundances (individuals g dwt^{-1}), which includes Collembola, Oribatida, Astigmata, Mesostigmata, Prostigmata, and 'other' fauna. Note, we did not analyze Astigmata abundances in the drought experiment as low abundances were present in samples. For litter decomposition (measured as mass loss) we included all time points together into a single model, where the fixed factors were treatment, litter origin, harvest, and their subsequent interactions with a random factor of experimental plot. To run linear mixed models, we used the lmer function in the package 'lme4' (Bates et al., 2015) where we calculated F-statistics and p-values with Satterthwaite's method using the anova function in the package 'lmerTest' (Kuznetsova et al., 2017). If model residuals were not normally distributed, we ln or arscine-transformed the dependent variable and re-ran the model. At times, we found singularity within our linear mixed models as the variance within our random factor terms was extremely low (essentially zero) and the model was overfit. When this occurred, we removed the random factor, and we re-ran the model without the random term.

For multivariate variables, including leaf litter functional groups (FTIR), microbial community composition, and animal community composition, we ran PERMANOVAs using the adonis2 function in the package 'vegan' (Oksanen et al., 2022). For leaf litter functional groups, we used Euclidean distances within our models. But for microbial and animal communities we used Bray-Curtis dissimilarity as it it better suited for compositional data (like the abundances of each PLFA peak). Each model was fitted with the same fixed factors, consisting of treatment, litter origin and their interaction. To visualize leaf litter functional groups and microbial communities we used a Principal Component Analysis (PCA) ordination plot using the rda function in the package 'vegan' (Oksanen et al., 2022). For microbial communities, we Hellinger-transformed datasets using the decostand function in the 'vegan' package prior to the PCA.

Finally, we used structural equation models (SEMs) to construct a global model to analyze the direct and indirect pathways of the effect of drought and elevated CO_2 on litter decomposition on H3 data. We constructed three *a priori* models for the drought and elevated

306 CO_2 experiment (Supplementary Information Figure S4) to detect significant pathways ($p <$
307 0.05) between parameters (Garrido et al., 2022). Here, we wanted to test whether abiotic and
308 biotic factors, abiotic factors only (litter C:N and moisture content) or biotic factors only (animal
309 and microbial communities) best explain litter mass loss in our experiments. Within our SEMs,
310 we included treatment and litter origin as binary variables where experimental litter (litter origin)
311 and elevated CO_2 and drought (treatment) where coded as 1 (with the respective controls coded
312 as 0) to reduce the number of pathways in our model. As well, we Z-transformed litter mass loss,
313 C:N ratio, litter moisture content, along with animal and microbial abundance, but not PCA axes,
314 to standardize parameters. To include parameters on microbial and animal communities in our
315 SEM that best described litter mass loss, we constructed four candidate models (linear mixed
316 models with experimental plot as random factor) that contained either total animal abundance or
317 animal community PC1 (first axis from PCA), along with total microbial abundance or microbial
318 PC1. We compared models using AIC (Akaike Information Criterion) with maximum likelihood
319 and chose the candidate model with the lowest AIC value to be included in the SEM. To
320 construct SEM models, we used the psem function in the 'piecewiseSEM' package (Lefcheck,
321 2016) where individual models within the global SEM were fitted with linear mixed models
322 (with plot as random factor) with maximum likelihood, using the lme function from the 'nlme'
323 package (Pinheiro and Bates, 2000; Pinheiro et al., 2023). To evaluate our SEM models, we used
324 AIC, $\chi 2$ goodness of fit test and Fisher's C, where p-values > 0.05 represents acceptable data fit
325 for our model.
326
327 **Results** (Word count: 1,357)
328 *Initial litter chemistry*
329 We found strong differences between the C:N ratio of the initial control and droughted
330 litter ($F_{1,8} = 13.92$, $p = 0.006$), with the C:N ratio of control litter exceeding that of the droughted
331 litter, but not between litter from ambient and elevated CO_2 treatments ($F_{1,8} = 0.001$, $p = 0.977$)
332 (Supplementary Information Table S1). Furthermore, strong differences were detected between
333 the metabolomic profiles between the initial control and droughted litter ($F_{1,8} = 3.91$, $p = 0.009$)
334 but not between litter from ambient and elevated CO_2 treatments ($F_{1,8} = 1.04$, $p = 0.336$)
335 (Supplementary Information Figure S5). Control litter from the drought experiment was mainly
336 composed of ellagitannins (from $C_{34}H_{24}O_{22}$ to $C_{56}H_{40}O_{31}$), catechin ($C_{15}H_{14}O_6$), and ellagic

hexoside ($C_{20}H_{16}O_{13}$) that were overexpressed within litter. Other metabolites such as quercetin hexosides (or rhamnoside), kaempferol hexosides, and isorhamnetin hexosides at similar quantities between control and drought treatment.

Elevated CO_2 experiment

During the first eighteen months of the decomposition experiment, litter from elevated CO_2 plots (i.e., experimental litter) decomposed slower than litter from control plots (litter origin: $F_{1,215.09} = 5.932$, $p = 0.016$) through H1-3 (time: $F_{3,215.46} = 155.97$, $p < 0.001$) until H4. Whereafter, mass loss varied little between the two treatments and litter origins (Figure 1, Supplementary Information Table S3 contains exponential decomposition rate coefficient, k_t, values). Similarly, the C:N ($F_{1,56} = 6.03$, $p = 0.02$) of litter was higher in experimental litter (i.e., initial litter that was harvested from elevated CO_2 plots) at H3, but not at H4 (Supplementary Information Table S4 and S5), suggesting that litter characteristics converged over time. This finding is also supported by FTIR spectroscopy analysis, which showed significant, but limited differences in litter functional groups at H3 between litter origins ($F_{1,56} = 4.33$, $p = 0.03$). Litter functional group composition between control and experimental litter was no longer significant at H4 ($F_{1,52} = 0.26$, $p = 0.81$) (Figure 2A-B). Neither treatment or litter origin affected litter moisture content at either H3 or H4 (Supplementary Information Table S4 and S5).

Treatment and litter origin did not influence PLFA abundance, the fungi : bacteria (F:B) ratio, or microbial community composition at H3 (Supplementary Information Table S4, Supplementary Information Figure S4). Likewise, no individual or total animal group abundances, along with entire community structure, were affected by treatment or litter origin in H3. In H4, however, the abundance of Mesostigmata ($F_{1,52} = 5.04$, $p = 0.03$) and Prostigmata ($F_{1,52} = 7.30$, $p = 0.009$) was significantly greater in control litter relative to experimental litter, but animal abundance composition did not shift with litter origin ($F_{1,48} = 1.24$, $p = 0.28$) (Supplementary Information Table S5).

The SEM revealed several significant pathways between parameters in response to elevated CO_2 (Figure 5) with strong goodness-of-fit where model 1 (containing both abiotic and biotic factors) best explained mass loss. Litter moisture content was negatively correlated with microbial

community structure. On PC1, microbial composition was driven by fungal abundance (PLFA marker C18:2ω6,9) (Supplementary Information Figure S6); the negative association between moisture and microbial community composition suggests that drier litter supported greater fungal abundance. In addition, microbial community structure was correlated with mass loss, meaning lower litter moisture content indirectly shaped mass loss through changes to microbial community composition. Litter origin indirectly affected mass loss *via* litter C:N, as experimental litter (litter derived from elevated CO_2 plots) led to higher C:N in litter, which corresponded with slower decomposition. In addition, higher C:N ratio was negatively associated with animal abundance within litter bags, with greater animal abundance being associated with faster decomposition. Treatment had no significant direct or indirect effect in the SEM, further supporting that elevated CO_2 did not directly affect litter decomposition or associated microbial or animal communities in our study.

Drought experiment

By contrast to elevated CO_2, there were stronger effects of both treatment and litter origin on measured parameters in response to drought. First, litter decomposition was slower in droughted plots (relative to ambient moisture plots) (treatment: $F_{1,4} = 147.91$, $p < 0.001$) as remaining litter mass decreased over time ($F_{1,220} = 494.76$, $p < 0.001$) and at varying rates (treatment x time: $F_{1,220} = 4.56$, $p = 0.004$) (Figure 1; Supplementary Information Table S3). Litter had lower C:N ratios in ambient plots (H3: $F_{1,4} = 21.92$, $p = 0.009$; H4: $F_{1,56} = 37.85$, $p < 0.001$) compared to drought plots. In addition, experimental litter (i.e., litter derived from drought plots) had lower C:N ratio, relative to the control litter (H3: $F_{1,52} = 32.53$, $p < 0.001$; H4: $F_{1,56} = 9.54$, $p = 0.003$) suggesting both treatment and litter origin affected litter quality during the experiment (C:N but also %C and %N; Figure 3; Supplementary Information Table S6 and S7).

Similarly, we observed a strong effect of treatment on leaf litter functional compounds (Figure 2C-D). FTIR spectroscopy revealed that drought (H3: $F_{1,56} = 6.73$, $p = 0.006$; H4: $F_{1,56} = 15.32$, $p = 0.002$) shifted litter C-biochemistry; hydroxyl groups (B1) and amides (I and II, B4 and B6) were grouped together along PC1 in drought litter at both H3 and H4 time points. Conversely, carboxylates (B5), sulfones and esters (B10), along with aromatics (B15) were correlated with

ambient litter and both H3 and H4. The functional groups B11 (phenols) and B14 (carbohydrates) were correlated in both H3 and H4 litter.

We found divergent effects of the drought treatment with litter moisture content in the drought experiment. At H3, litter moisture content significantly decreased (by around 35%) in drought plots ($F_{1,4} = 85.96$, $p < 0.001$; Supplementary Information Table S6). However, at H4, when litter moisture content in ambient conditions was already low, there was no significant difference between the ambient moisture or drought plots ($F_{1,56} = 1.086$, $p = 0.30$; Supplementary Information Table S7).

After 21 months of decomposition (H3), experimental litter (i.e., litter from the droughted plots) had greater concentrations of PLFAs ($F_{1,52} = 9.06$, $p < 0.004$, Figure 4A), but the drought treatment reduced total PLFA concentrations ($F_{1,4} = 15.69$, $p = 0.02$) in litter regardless of its origin. The F:B ratio was also greater in the experimental litter ($F_{1,52} = 8.43$, $p = 0.005$, Figure 4B). Both litter origin ($F_{1,56} = 6.64$, $p < 0.004$) and treatment ($F_{1,56} = 23.59$, $p < 0.001$; Figure 4C) shifted PLFA composition. Microbial composition in response to treatments was largely explained by PC1 whereas microbial composition in response to litter origin was explained more by PC2. These axes reflected distinct PLFAs, with the fungal-related PLFA C18:2ω6,9 driving separation in both PC1 and PC2 (Fig. 4C). In addition, animal communities responded more to the drought treatment than litter origin (Supplementary Information Table S6 and S7). At both H3 and H4, animal communities shifted under drought (H3: $F_{1,56} = 8.07$, $p < 0.001$; H4: $F_{1,56} = 6.70$, $p < 0.001$): mesostigmatid (H3: $F_{1,56} = 31.18$, $p < 0.001$) and prostigmatid mite (H4: $F_{1,56} = 7.65$, $p = 0.007$) abundances significantly decreased, and there was a trend for drought to reduce total animal abundances at H4 ($F_{1,4} = 6.04$, $p = 0.07$). Notably, there was a significant interaction of treatment and litter origin on 'other' fauna abundances at H3 (treatment x litter origin: $F_{1,52} = 6.51$, $p = 0.01$) where abundances were greatest in the drought treatment with control litter.

The SEM for the drought experiment yielded several significant pathways and had acceptable goodness-of-fit where model 2 (abiotic factors only) best explained mass loss (Figure 5). First, litter origin affected litter mass loss directly, but also indirectly through litter C:N, with higher C:N ratio of litter corresponding to slower mass loss (which also matched the result from

the SEM describing pathways under elevated CO_2). Greater litter moisture also led to lower C:N ratio but moisture content did not directly affect litter mass loss. Similar to mass loss, microbial community structure was also negatively associated with litter C:N. Here, PC1 represented a gradient from fungal dominated to bacterial dominated communities (Figure 4C), where higher C:N ratio corresponded with fungal dominated litter communities. The SEM provides robust evidence that litter mass loss was shaped strongly by litter C:N rather than a shift in the composition of microbial and animal communities in the drought experiment.

Discussion (Word count: 1,929)

Our results reveal that long-term *in situ* manipulations of drought and increased atmospheric CO_2 concentrations to mature oak forests have contrasting impacts on rates of litter decomposition. We found that after experimental summer drought, representing an average 40% reduction in rainfall, litter had greater C:N ratio and reduced mass loss compared to controls. The SEM revealed that the main drivers of litter mass loss were the origin of litter, i.e., whether it was derived from plants subjected to drought or not. Litter origin had clear effects on both the C:N ratio of the litter and on the composition of secondary metabolites, and both of the these factors likely led to litter origin having both direct and indirect effects on mass loss. The reduction of seasonal rainfall influenced mass loss mainly by reducing the water content of the litter which also affected the C:N of litter. By contrast, elevated CO_2 mainly affected the C:N of the litter, which was associated with a shift in the abundance of soil fauna, while the environment itself was not a significant factor driving decomposition.

Our findings generally support those from previous studies conducted with other plant litter species and often more artificial experimental set-ups (Cotrufo and Ineson, 1996; Norby et al., 2001; Santonja et al., 2015; Vestergård et al., 2015; Holmstrup et al., 2017; Prieto et al., 2019; Quer et al., 2022) that drought and elevated CO_2 concentrations will impact litter decomposition. In general, both drought and eCO_2 treatments had substantial impacts on the 'quality' of litter entering and residing in the decomposer subsystem. We found that the C:N ratio, a general indicator of litter quality, is critical at determining decomposition rate. Higher C:N ratios generally corresponded with slower mass loss (Zhang et al., 2008), and our results highlight the robustness of this relationship in the mature forests. Of note is the observation that our initial litter from

control plots (at O_3HP) had a higher C:N than the litter from the droughted plot, which carried over into subsequent harvests, and which stemmed from the litter from droughted plots having relatively high nitrogen concentration, at least compared to past work at this site (Aupic-Samain et al., 2021b). Nitrogen concentration within leaves can be affected by both nutrient availability in soil, climatic factors like precipitation, and their interaction (Cheaib et al., 2025), but we do not know why nitrogen concentrations differed in our experiment compared to past work. Our SEM revealed decomposition in response to drought was driven indirectly via litter C:N and also through other, albeit unknown, direct pathways.

The SEM from BIFoR FACE showed that both animal abundances and microbial community structure were correlated with mass loss, along with litter C:N, providing further evidence that animals and microbes are important contributors to litter decomposition (Hättenschwiler et al., 2005; Rouifed et al., 2010; Handa et al., 2014; Tan et al., 2021; Njoroge et al., 2022). By contrast, litter quality (litter C:N, directly) and moisture content (indirectly) best explained mass loss in the drought experiment. Notable climate differences exist between the two sites; BIFoR FACE is in a cool, wet temperate climate (MacKenzie et al., 2021), while O_3HP is in a seasonally hot-dry Mediterranean climate (Gauquelin et al., 2011) (Figures S2 and S3). Joly et al. (2023) re-affirmed the role of climate in regulating decomposition, and strong climate x decomposer community interactions underlie mass loss (Glassman et al., 2018; Yin et al., 2019). For instance,Wall et al. (2008) found that soil fauna enhanced decomposition in temperate and wetter climates, but had limited effects on decomposition when constrained by relatively cooler temperatures and/or lower precipitation inputs. When not as constrained by climate, like at BIFoR FACE, animal and microbial communities were strongly associated with decomposition rates. Furthermore, we found that the decomposer community was strongly correlated to mass loss at later stages of decomposition when around half of the original litter mass remained. Understanding the interactions between biota and litter quality on decomposition is crucial to predict how environmental stressors will impact decomposition and biogeochemical cycling. Our findings demonstrate that the influence of drought and elevated CO_2 on decomposition was strongly dictated by indirect effects acting via litter chemistry (notably C:N), while direct influences on decomposer abundance and community composition were apparent only when not constrained by temperature or moisture.

Past studies have demonstrated drought can lead to fungal-dominated communities due to their ability to persist under water stress (Yuste et al., 2011; Biryol et al., 2024) as the SEM model showed fundamental linkages between moisture content, litter C:N, and microbial communities. Here changes to litter moisture content was critical as it indirectly affected microbes *via* litter C:N. Specifically, drought impacted carbon and nitrogen concentrations in litter by limiting moisture, inducing water stress conditions that shifted the decomposer community and was indirectly correlated with fungal-rich communities. By contrast, the SEM from the elevated CO_2 experiment found a significant relationship between litter C:N and animal abundances, with a higher C:N ratio corresponding with fewer animals. This result was found alongside the preferential feeding of defoliator insects on elevated CO_2 leaves in 2019 prior to litter collection (Norby et al., 2024), further highlighting how elevated CO_2 will affect multiple dimensions of the ecosystem. Holmstrup et al. (2017) found two years of elevated CO_2 to a heathland changed litter C:N that affected animal diversity, while microbes (denoted by fungi : bacteria) were unaffected. In our study, microbial and animal communities differed significantly between the two experiments; foodwebs in the drought experiment were dominated by fungi with few animals, while in the elevated CO_2 experiment foodwebs were dominated by bacteria with many animals. The contrasting relationships among animal and microbial communities with litter quality between our experiments may partly be attributed to litter C:N being far higher in the drought experiment compared to the elevated CO_2 experiment. Although the mechanisms underpinning these contrasting relationships is unknown, we posit that climate and environmental stressors, or differences in litter quality, may modify linkages between litter and their decomposers.

Home-field advantage (HFA) stipulates that decomposer communities are more adept to decomposing litter from their own environment ('home') relative to litter from other locations ('away') (Ayres et al., 2009; Veen et al., 2015). We did not find strong evidence for home-field effects, as decomposition of home and away litter were similar as no significant interaction between treatment and litter type was observed. Higher litter quality dissimilarity leads to stronger HFA effects (Veen et al., 2015). We found weak or no differences in litter C:N between control and experimental litter in the elevated CO_2 experiment (both in the initial litter and across two harvests), but strong treatment and litter origin effects in the drought experiment. Notably, the

metabolic profiles of initial leaf litter differed strongly from control and droughted litter, while litter leaf functional groups (measured by Fourier transform infrared spectroscopy) also differed between litter incubated in droughted plots and removed at H3 and H4. However, our data suggests that differences in litter properties between the experimental treatments were potentially not large enough to observe a HFA effect which has often been found in situations where litter properties vary considerably, such as between coniferous and deciduous litter (Chomel et al., 2015), or more generally, recalcitrant versus labile litter (Wallenstein et al., 2013). Individual and group microbial and animal abundances shifted strongly under drought, but HFA may have been negligible as litter quality, rather than direct feeding and processing of litter by decomposer communities, was the main correlate of decomposition rates within the O_3HP experiment. Potentially, if environmental stressors or climate weaken linkages between decomposers and litter mass loss, HFA may lessen within a given system, thereby affecting the efficiency of biotic communities on litter decomposition and nutrient release.

We found few significant effects of elevated CO_2 experimental litter on microbial communities and most animal groups, but elevated CO_2 experimental litter was associated with fewer mesostigmatid and prostigmatid mites at H4. Most mesostigmatid mites, and some prostigmatid mite species, are predators, feeding on arthropods and nematodes (Lindquist et al., 2009; Walter et al., 2009). Lower abundances within experimental litter but also the drought treatment suggest that changes to prey composition (but likely not group abundances in our experiments) hindered predators in our litterbags. Changing mesofauna and macrofauna predator composition can indirectly influence litter decomposition (Lang et al., 2014; Koltz et al., 2018) and may have impacted decomposition in our study as well. For example, predators can reduce competion amongst lower trophic levels resulting in higher litter decomposition (Melguizo-Ruiz et al., 2020), highlighting the complexity of these trophic interactions on litter decomposition. Although not statistically significant, oribatid mite abundance was, on average, less under drought than control conditions, which aligns with past studies (Aupic-Samainet al., 2021b; Santonja et al., 2017). But overall, experimental manipulation had greater effects on predator abundances compared to other animal groups.

Evaluating environmental stressors across time is critical to understand their impact on C cycling and the release of other mineral nutrients during decomposition because the relative effects of climate and litter traits on decomposition changes temporally. Initial decomposition (e.g., 1-2 years) is correlated relatively more with litter traits, but climate regulates mass loss at later stages (Currie et al., 2010; Canessa et al., 2021). Similarly, the biotic contributions to decomposition also diminishes with time (García-Palacios et al., 2016). Because we conducted separate experiments (within contrasting climates and varying litter quality), we cannot fully tease apart the temporal and climatic effects that drove experimental results. However, by conceptually merging the SEM models, our results indicate litter mass loss was slower in the warmer Mediterranean climate where litter C:N was higher, as litter quality consistently drives mass loss rates (within the first 2-3 years at least). While in the cooler, wetter temperate climate of BIFoR FACE, the decomposer community was correlated with mass loss when half the litter remained. Future research at both these on-going experimental sites (of BIFoR FACE and O_3HP) and elsewhere, should incorporate multiple stressors (Rillig et al., 2019) and recognize that climate x temporal interactions may be critical to disentangling the contributions of litter quality and and local enviromental conditions on biota and subsequently litter decomposition.

Conclusions

Our findings reveal how elevated CO_2 and drought can impact decomposition through their effects on litter properties, decomposer communities, and the environment. Drought and elevated CO_2 independently impacted litter mass loss by shifting litter C:N, which was a significant determinant of decomposition in both SEMs. Moreover, litter quality influenced animal abundances in the elevated CO_2 experiment and microbial communities in the drought experiment. The decomposer community was only correlated with mass loss in the elevated CO_2 experiment, which might be because the climate being cooler and wetter than in southern France where the drought experiment was located. Our findings help interpret the broader impacts of drought and elevated CO_2 on ecosystem dynamics. Future climate scenarios of increased atmospheric CO_2 concentractions will alter litter decomposition primarily with alterations to litter quality, specifically, through higher C:N ratio. Reduced seasonal rainfall will both strongly shape litter properties and associated decomposer communities. Non-additive responses between treatment and litter type were largely absent within the drought experiment, as prior exposure of leaves to

reduced rainfall did not distinctly alter litter decomposition. Here, drought will have a continuous, pervasive effect on litter decomposition, specifically, changing litter quality, decomposer communities, and dampening litter mass loss rates and nutrient release. Overall, these findings provides us with a more complete understanding of how elevated CO_2 and drought will impact C inputs to forests, but highlights a need to disentangle the individual and interactive effects of these perturbations on litter inputs, properties and decomposition.

Acknowledgments

This study was carried out as part of UK Natural Environment Research Council (NERC) grant NE/S002189/1. ARMK gratefully acknowledges additional support from NERC through grant NE/S015833/1 (QUINTUS). TC acknowledges support by Research Ireland (20/FFP-P/8584). The BIFoR-FACE facility acknowledges generous underpinning support from the JABBS Foundation, Norbury Park Estate, The John Horseman Trust, Ecological Continuity Trust, and the University of Birmingham. We thank Dr Kris Hart and the operations team at BIFoR FACE, Dr. Ully Kritzler, Deborah Ashworth, Dr. Thomas Bishop and Dr. Benjamin Bell for technical support. We thank Dr. Stéphane Greff (Aix-Marseille Université) for analyzing leaf litter and Jean-Phillipe Orts (Aix-Marseille Université) for collecting litter from the O_3HP experimental site.

Conflict of Interest Statements

The authors have no conflict of interest to declare.

Data availability statement

Data will be submitted to the Natural Environment Research Council (NERC) data repository (Environmental Information Data Center) upon acceptance of the manuscript.

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MC, ARB, VB, RDB, and DJ conceptualized the study and attained funding. MLM, MC, ZV and KJF collected data. MLM and MC curated data, and MLM performed the data analysis with support from TC. MLM wrote the first version of the manuscript and MC, KJF, TC, ARB, VB, RDB, and DJ provided feedback and contributed to finalizing the manuscript.

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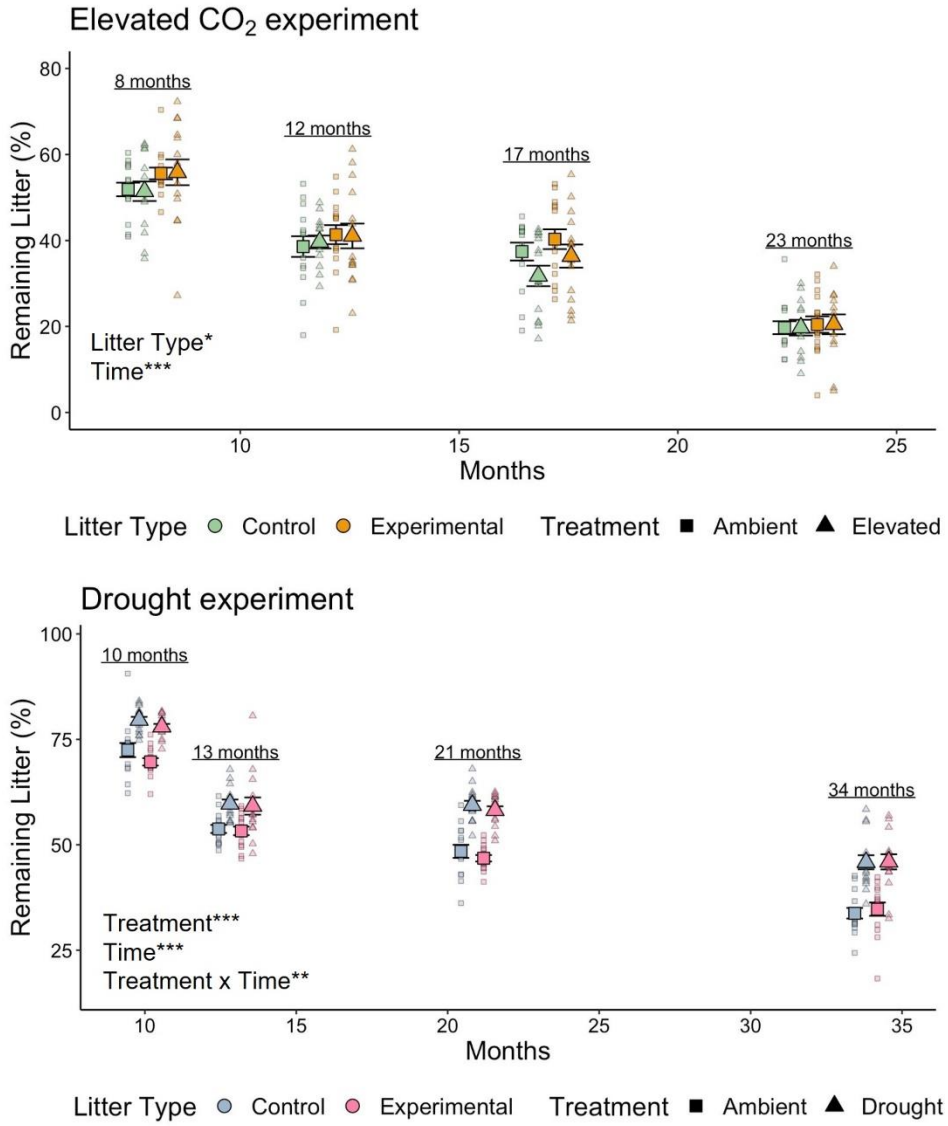

Figure 1. Litter decomposition (shown as % remaining litter) for the elevated CO_2 experiment (top) and drought experiment (bottom). The x-axis indicates the number of months since initiation of the experiment and differs for upper and lower panels. Larger points represent mean (± SE) while smaller points are the raw data values. * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$. We have only provided factor p-values that were statistically significant. Litter bags in the elevated CO_2 experiment were harvested after 8 (H1), 12 (H2), 17 (H3) and 23 (H4) months, while litter bags in the drought experiment were harvested after 10 (H1), 13 (H2), 21 (H3), and 34 (H4) months. To improve plot interpretation, points were positioned with greater spacing on the x-axis. Note the differences in y axis-es between the two experiments if comparing results with one another.

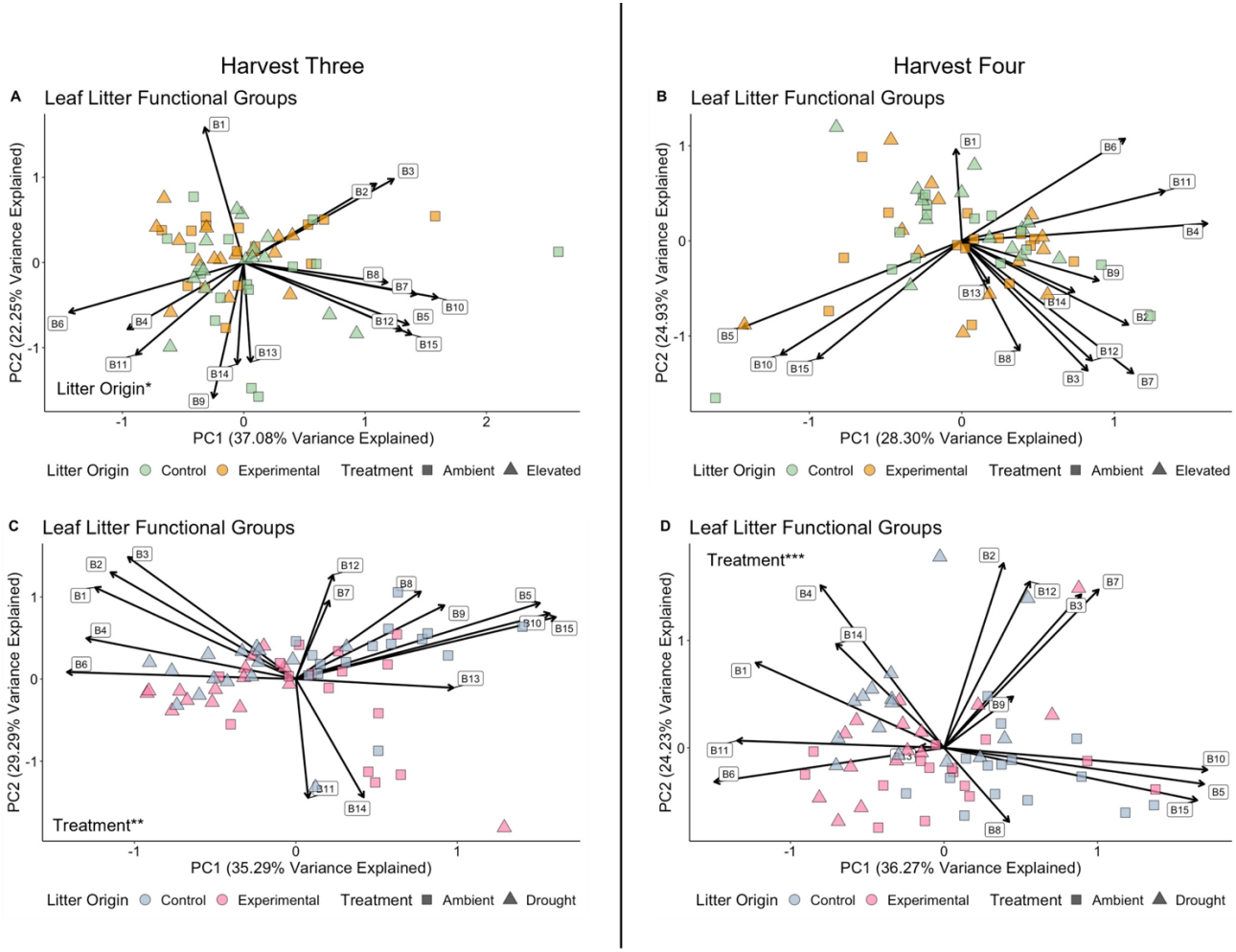

Figure 2. Principal component analysis (PCA) ordinations of leaf litter functional groups measured by Fourier transform infrared (FTIR) spectroscopy for the elevated CO_2 experiment (top) and drought experiment (bottom) at harvest three (A and C, left) and four (B and D, right). Corresponding functional groups for band numbers (B1, B2, B3, etc.) can be found in Supplementary Information Table S2. * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$. We have only provided factor p-values that were statistically significant.

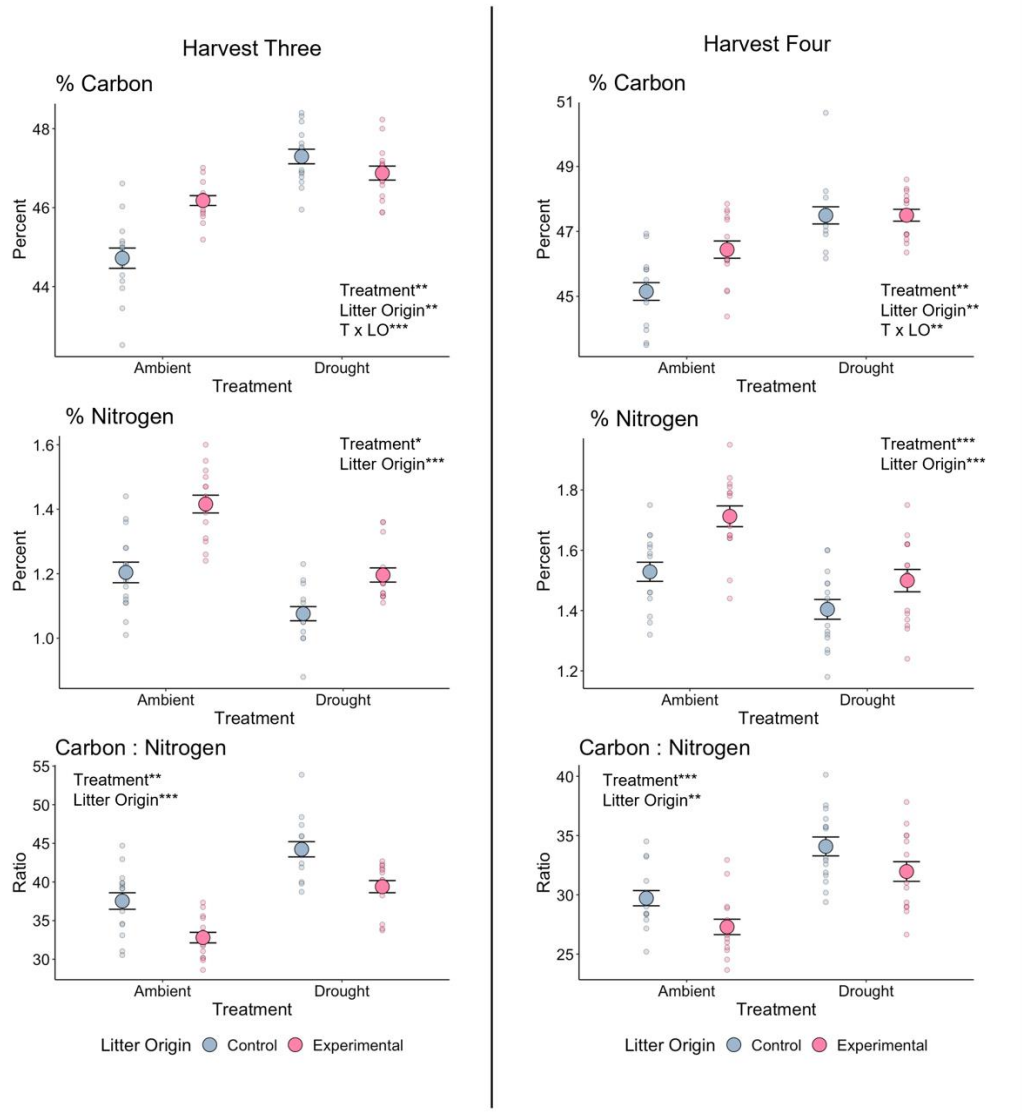

Figure 3. Litter quality indices of %carbon (%C; top), %nitrogen (%N; middle) and C:N (bottom) of drought experiment litter at harvest three (left) and four (right). Larger points represent mean (± SE) while smaller points are the raw data values. * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$. We have only provided factor p-values that were statistically significant. T = treatment and LT = litter origin. Note the differences in y axis-es between the two harvests if comparing results between each other.

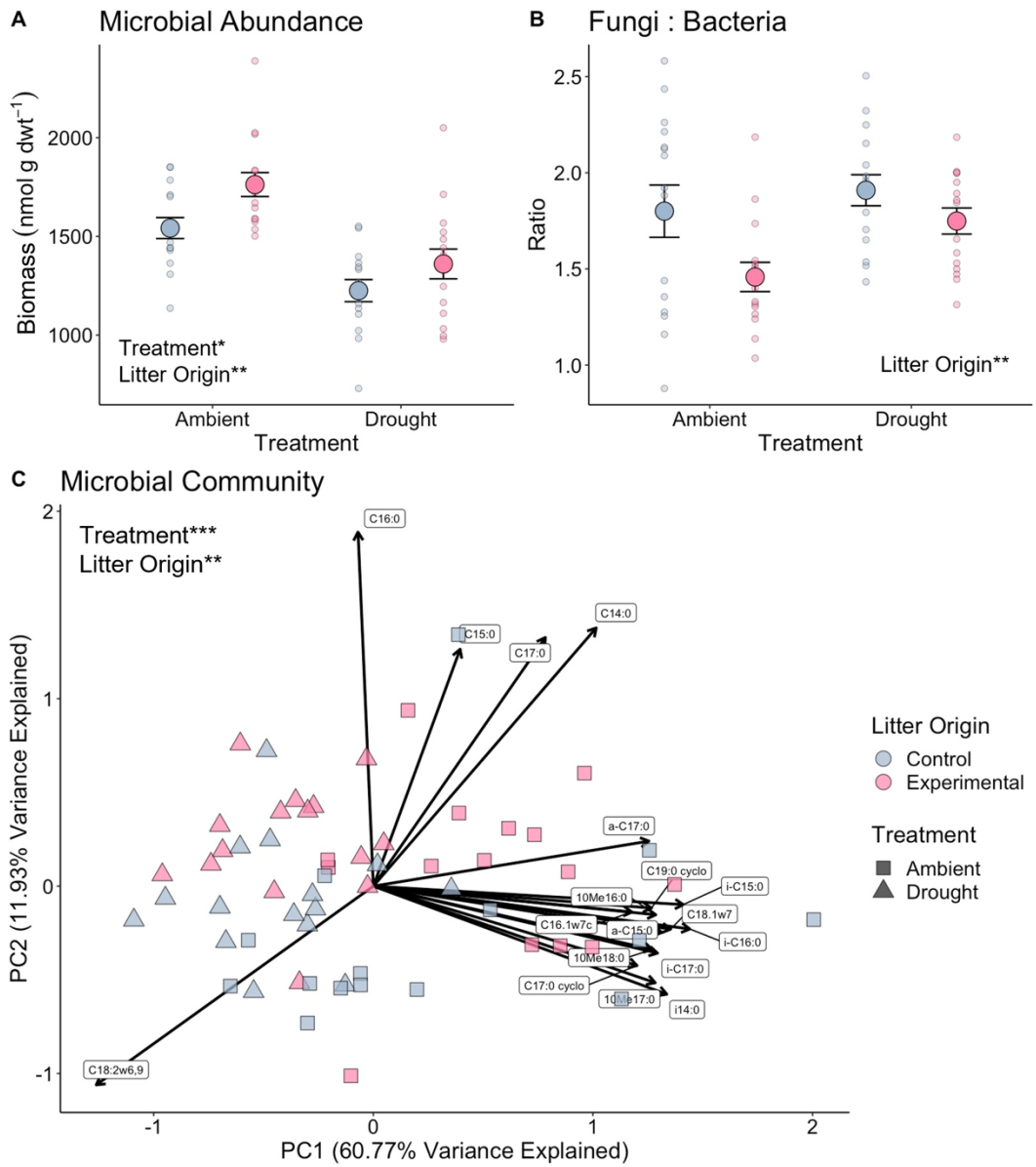

Figure 4. Microbial community indices as measured by phospholipid fatty acid analysis (PLFA) in litter for the drought experiment after 21 months (harvest 3). For A) (total PLFA) and B) (fungi : bacteria) larger points represent mean (± SE) while smaller points are the raw data values. C) Principal component analysis (PCA) ordination of microbial community structure. * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$. We have only provided factor p-values that were statistically significant.

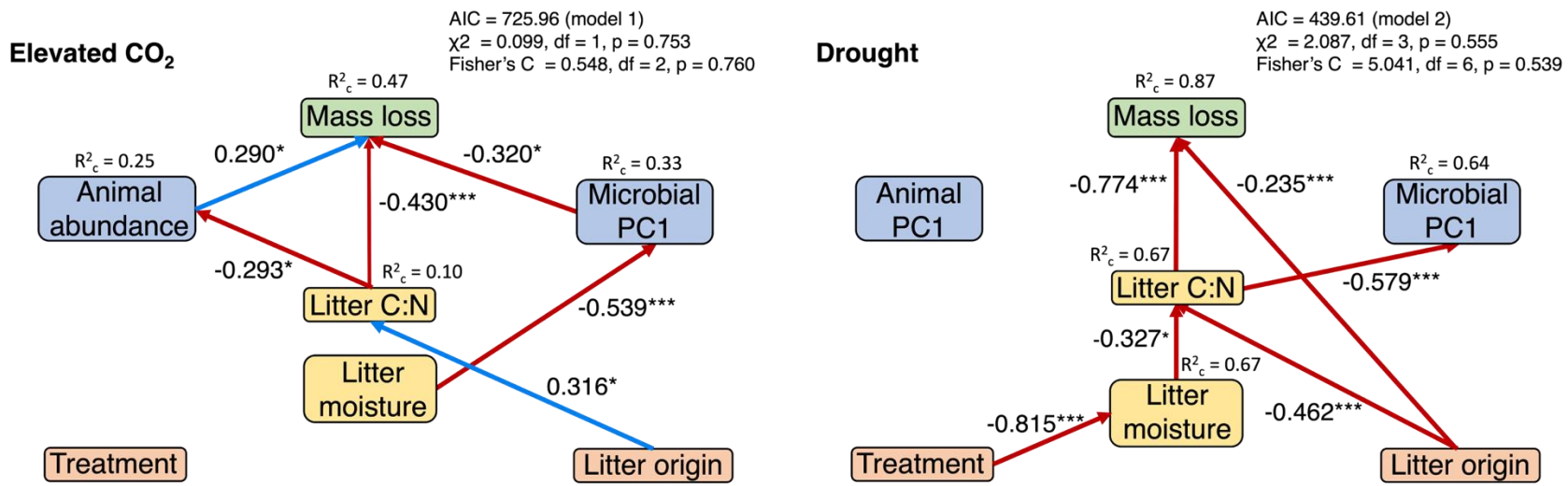

Figure 5. Structural equation models (SEMs) showing significant pathways between parameters from the elevated CO_2 experiment (n = 56, left) and drought experiment (n = 60, right). Data to parameterize models were derived solely from thethird harvest in both experiments. Four litterbags were removed from analysis from the elevated CO_2 model as microbial community structure was not measured. Blue arrows indicate positive, significant pathways, while red pathways indicate negative, significant pathways where the standardized path estimates are provided. Parameters are coloured by categories: experiment manipulations (treatment and litter origin, red), litter chemistry and environmental factors (litter moisture and C:N, yellow), biota (animals and microbes, blue) and mass loss (green). Asterisks indicate significance of path, * = $p < 0.05$, and *** = $p < 0.001$. We have only provided parameter p-values that were statistically significant. Numbers above individual parameters indicate conditional R-square (R^2_c) of models. In the top-right corner of each figure, goodness-of-fit tests are provided ($\chi 2$ and Fisher's C). Please see Supplementary Information Table S8 for AIC values and goodness-of-fit metrics for all models tested.