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RESEARCH ARTICLE

Altered leaf litter quality exacerbates the negative impact of climate change on decomposition

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Abstract

1. Leaf litter decomposition is a key component of global biogeochemical cycles that influence soil carbon storage, nutrient availability and plant productivity. Ongoing climate change will lead to warmer and drier conditions in many dryland regions, potentially affecting litter decomposition and nutrient dynamics. Climate change effects can be direct and/or indirect, for example, through changes in litter quality, yet their relative importance on litter decomposition remains unclear.
2. We conducted a manipulative study in a semi-arid shrubland to assess the effects of leaf litter quality, forecasted climate change, that is, +2.5°C warming (W), 30% rainfall reduction (RR) as well as their interaction (W + RR) to elucidate their relative effects on litter decomposition.
3. Climatic effects alone reduced decomposition of a homogeneous Control leaf litter collected from *Helianthemum squamatum* shrubs growing in unmanipulated plots by 23.4%, 18.1% and 29.8% in the W, RR and W + RR treatments respectively. Leaf litter quality was lower in shrubs that had been growing in warmed plots (W and W + RR), as they had lower nutrient concentrations (P, Fe) and higher C:N and C:P ratios than leaf litter produced under ambient (Control) conditions. Lignin concentration was significantly lower in litter from W + RR plots, yet when both climate and litter quality were considered simultaneously, decomposition rates were 32.0%, 26.3% and 39.9% lower in W, RR and W + RR plots compared to Controls. In addition, we found greater microbial N immobilization in leaf litter incubated within warmed (W and W + RR) than within non-warmed plots (Control and RR). Structural equation modelling showed that higher litter moisture and microbial biomass contents stimulated decomposition. Simulated climate change (W, RR and W + RR) reduced decomposition indirectly by negatively affecting litter moisture contents and litter microbial biomass. Microbial nitrogen immobilization was stimulated by the lower quality (i.e. high C:N ratios) of the leaf litter collected in shrubs from warmed plots (W and W + RR).
4. *Synthesis*. Our findings indicate that forecasted climate change conditions slow down C and N cycling in a dryland ecosystem, an effect that is further exacerbated by climate change-induced reductions in litter quality and related reductions in bacterial and fungal biomass in litter.

KEYWORDS
climate change, drylands, Global change ecology, litter mass loss, litter traits, microbial community structure, nitrogen, warming

1 | INTRODUCTION

Leaf litter decomposition is one of the largest carbon (C) fluxes from the soil to the atmosphere and plays a crucial role in C and nutrient cycling in terrestrial ecosystems (Berg & Laskowski, 2005). Most of our knowledge on plant litter decomposition comes from mesic temperate and tropical systems, but the main drivers of litter decomposition in drylands are yet not fully understood (Parton et al., 2007; Poulter et al., 2014) even though drylands occupy around 41% of the global land area (Prăvălie, 2016; Throop & Archer, 2009). Therefore, understanding and predicting plant litter decomposition in drylands are crucial to improve our knowledge of C and nutrient stocks and fluxes in arid and semi-arid ecosystems.

Litter decomposition rates depend on multiple biotic and abiotic factors that interact to determine C and nutrient losses. Predominant among those factors are climate, including temperature and precipitation, the quality of the litter, determined mostly by litter traits (e.g. C:N ratios, lignin concentrations), and decomposer communities (Aerts, 1997; Allison et al., 2013; Bradford, Berg, Maynard, Wieder, & Wood, 2016; Cornwell et al., 2008; Freschet, Aerts, & Cornelissen, 2012a; McLaren & Turkington, 2010; Parton et al., 2007; Pietsch et al., 2014). Current climatic models predict drastic changes in the climate as a consequence of anthropogenic greenhouse gases emissions (Collins et al., 2013), with the Mediterranean region being severely affected (IPCC, 2014). Forecasted changes for this region include temperature increases of 2–5°C and reduced rainfall amounts with more frequent occurrence of extreme climatic events (Giorgi & Lionello, 2008; Guiot & Cramer, 2016; NOAA, 2015). Previous manipulative experiments have proved that alterations in the amount and distribution of rainfall and increased air temperatures have led to reductions in surface soil water availability (León-Sánchez et al., 2018; León-Sánchez, Nicolás, Nortes, Maestre, & Querejeta, 2016), potentially affecting the nutrient balance and carbon-related ecosystem processes, such as plant litter production, litter quality and decomposition dynamics (Gliksman et al., 2017; Lu et al., 2013; Poulter et al., 2014). Atmospheric sources of water other than direct precipitation, such as dew, are also important sources of moisture in drylands that can stimulate the degradation of leaf litter (Dirks, Navon, Kanas, Dumbur, & Grünzweig, 2010; Gliksman et al., 2017; Jacobson et al., 2015). However, climate change-driven increases in air temperatures and reductions in rainfall limit the number of days in which the dew point is reached (Maestre et al., 2013), thereby reducing the supply of dew-derived moisture to leaf litter, which may result in slower decomposition rates (Almagro, Maestre, Martínez-López, Valencia, & Rey, 2015; Gliksman et al., 2017).

The quality of the litter produced is also an important driver of litter decomposition (Freschet et al., 2012a; Freschet, Aerts, & Cornelissen, 2012b). Plant species that produce high-quality leaf litter (i.e. litter with high nutrient concentrations and low lignin contents and C:N ratios; Melillo, Aber, & Muratore, 1982; Cornwell et al., 2008; Lovett, Arthur, & Crowley, 2016) tend to decompose more rapidly than species that produce low-quality litter (Almagro, Martínez-López, Maestre, & Rey, 2017; Fortunel et al., 2009; García-Palacios, Prieto, Ourcival, & Hättenschwiler, 2016; Kazakou et al., 2009; Santiago, 2007). Climate change can indirectly impact decomposition processes since plant physiological adaptations to climate change modify the litter chemical composition and morphology altering its quality (Aerts, Cornelissen, Logtestijn, & Callaghan, 2007; León-Sánchez et al., 2018, 2016; Sundqvist, Giesler, & Wardle, 2011; Suseela & Tharayil, 2018). Therefore, it is important to understand how climate change-induced variations in litter quality within individual species may affect litter decomposition and, in turn, C and nutrient cycling.

Litter decomposition is also Controlled by the abundance, composition (e.g. fungi:bacteria ratio) and activity of microbial communities (Bradford et al., 2017; Glassman et al., 2018), which are also sensitive to climate change (Almagro et al., 2017; Lu et al., 2013; Yue et al., 2015). Many studies from mesic temperate systems have reported overall positive effects of warming on litter decomposition (Lu et al., 2013; Yue et al., 2015 and references therein), probably through a stimulation of microbial degradation of leaf litter with higher temperatures (Melillo et al., 2002; Wardle, 1992). However, in dry systems, warmer and drier conditions also act as environmental filters selecting for more heat- and drought-resistant microbial communities, often characterized by their lower ability to decompose leaf litter (Allison et al., 2013; Yuste et al., 2011), which may reduce decomposition rates further.

Despite recent interest in the role of climate change as a driver of litter decomposition, few studies have experimentally manipulated climate to examine the mechanisms underlying decomposition responses to environmental change in drylands (Almagro et al., 2015; Saura-Mas, Estiarte, Peñuelas, & Lloret, 2012). We manipulated abiotic conditions (precipitation and/or temperature) in a semi-arid ecosystem for 6 years from 2011 to 2017 and used a combined experimental design to evaluate the impacts of climate change, litter quality and their interaction on litter decomposition and N dynamics (Figure S1). We hypothesized that: (a) leaf litter from shrubs that had been growing under climate change conditions (increased temperature (W), reduced rainfall (RR) and their combination (W + RR)) will have a lower quality (Aerts et al., 2007; León-Sánchez et al., 2018) and thus decompose at slower rates than litter from plants growing under ambient conditions (Control); (b) increased temperature (W), reduced rainfall (RR) and their combination (W + RR) will reduce leaf litter decomposition rates and nutrient release because, on one hand,

microbial decomposition processes are highly dependent on soil and air moisture (Allison et al., 2013; Dirks et al., 2010; Gliksman et al., 2017), which are negatively affected by climate change (Almagro et al., 2015; Maestre et al., 2013), and on the other hand, the altered abiotic environment would select for more warm- and drought-resistant microbial communities (Allison et al., 2013; Yuste et al., 2011) that may be less effective in decomposing leaf litter; and (c) the combined effects of altered litter quality and the altered abiotic environment will exacerbate reductions in decomposition rates. This analysis of the individual and interactive mechanisms Controlling litter decomposition in a dryland ecosystem provides a comprehensive assessment of litter decay processes under climate change and is a stepping stone to understand how C and nutrients fluxes in drylands may be affected by climate change.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

The study was carried out near Aranjuez, in central Spain (40°02′N–3°32′W, 495 m altitude). The study area has a continental Mediterranean climate, with a mean annual temperature of 15°C and an average rainfall of 358 mm (for the period 1977–2016), concentrated mainly in the autumn and spring months (Lafuente, Berdugo, Ladrón de Guevara, Gozalo, & Maestre, 2018). Soils derive from gypsum, have pH values *c*. 7 and are classified as Gypsiric Leptosols (IUSS Working Group WRB, 2006). Soils are shallow (4–10 cm deep overlying weathered gypsum bedrock) and show a thin organic horizon (1–2 cm thick). Vegetation is a native grassland and shrubland community. Plant cover is lower than 40% and is dominated by the perennial tussock grass *Stipa tenacissima* L. and by the gypsophilous shrub *Helianthemum squamatum* (L.) Pers.

In February 2011, we established an experiment to examine the effects of two climatic factors (temperature and rainfall) according to predictions for the second half of the 21st century in the Mediterranean area (de Castro, Martín-Vide, & Alonso, 2005). Manipulated climate treatments were warming (W; 2.5°C increase in mean annual temperature), rainfall reduction (RR; exclusion of 30% of the incoming precipitation) and the combination of both factors (W + RR).

The warming treatment simulates the predictions derived from six atmosphere general circulation models for the second half of the 21st century (2040–2070) in the Western Mediterranean region (de Castro et al., 2005) and was achieved by installing open-top chambers (OTCs), which increase mean air and surface soil temperature (Figure S1). OTCs were made of transparent methacrylate. This material was selected because it has very high transmittance of both visible and ultraviolet wavelengths (information provided by the manufacturer; Decorplax S.L., Humanes, Spain). The OTCs were of hexagonal shape with six sloping slides of 40 cm × 50 cm × 32 cm (height × length × width, Figure S1), were open at the top to allow precipitation and were suspended ~3 cm above the ground by a metal frame to allow free air circulation and exchange with the surrounding environment, minimizing undesirable experimental effects (Hollister & Webber, 2000; Maestre et al., 2015). The same OTCs have been used in previous field warming (Lafuente et al., 2018; Maestre et al., 2013) and decomposition experiments (Almagro et al., 2015). Mean air temperature inside OTCs increased by 1.83 ± 1.16°C (Mean ± *SD*, winter), 2.54 ± 0.96°C (spring), 3.29 ± 1.03°C (summer) and 2.04 ± 1.21°C (autumn) for the 2011–2015 period (data from León-Sánchez et al., 2018).

To simulate projected reductions in precipitation (de Castro et al., 2005), we used passive rainout shelters that intercept and exclude ~30% of the incoming rainfall from the plots. The permanent (non-moveable) rain exclusion shelters are made of transparent methacrylate troughs (same material as for the OTCs) covering ~30% of the area of the experimental plots. Rainfall reduction is achieved by suspending the methacrylate troughs over an aluminium frame above the experimental plots (height 130 cm, width 100 × 100 cm, Figure S1). The methacrylate troughs had an inclination of 20° so that intercepted rainwater is diverted through collection pipes, stored in tanks placed next to the experimental plots and removed after each rainfall event. The RR treatment reduced mean annual topsoil (0–5 cm) water content by 2%–3% on absolute terms compared to Control plots, and did not affect air or soil temperatures (León-Sánchez et al., 2018; Maestre et al., 2013). Finally, the combined W + RR treatment is achieved by installing both OTCs and rainfall exclusion shelters over the same experimental plot (Figure S1).

The experiment includes 10 replicate plots per each climate manipulation treatment plus 10 Control plots, making a total of 40 experimental ~1 m^2 plots distributed across a 100 × 50 m area (León-Sánchez et al., 2018). These plots were randomly assigned to the different climate treatments and were at least 2 m distant from each other. The target shrub *H. squamatum* is the dominant (often the only) plant species present in the experimental plots (Figure S1).

2.2 | Leaf litter sampling and analyses

In late Spring 2015 (mid-June), we collected standing senescent leaf litter from *H. squamatum* shrubs growing inside the different treatment plots ($Control_{litt}$, W_{litt}, RR_{litt} and $W + RR_{litt}$). Ten subsamples from each of the treatments were air-dried in paper bags for 10 days until constant weight and used for litter decomposition determination in the field (see section 2.3 'Litter decomposition experiments'). Additionally, we determined the initial litter morphology and chemistry on six subsamples per treatment (*N* = 24). Four air-dried senesced leaves from each of the six subsamples were submerged in deionized water for 24 hr, drained, weighed to obtain their drained saturated weight (SW, g) and oven-dried at 60°C for 48 hr to determine their dry weight (DW, g). Litter dry matter content (litter DMC, mg/g) was then calculated as the ratio between their drained saturated weight and their dry weight [Litter DMC = (SW × 1,000)/DW] following Pérez-Harguindeguy et al. (2013). The water holding capacity, an index of the water uptake capacity of each leaf litter type, was determined by subtracting the oven-dried mass from the drained wet mass, dividing by the oven-dried mass and multiplying by 100. The

remaining litter material from the five subsamples per treatment was then oven-dried at 60°C for 72 hr to establish the air-dried to oven-dried mass relationships for estimating initial oven-dried litter mass in the litterbags and later used to determine initial leaf litter chemistry. After weighing, these samples were finely ground with a ball-mill, weighed and placed into tin capsules for chemical and isotopic analyses. The C and N concentrations and $\delta^{15}N$ isotopic composition of leaf litter were measured by elemental analyser/continuous flow isotope ratio mass spectrometry (ANCA/SL elemental analyser coupled with a Finnigan MAT Delta PlusXL IRMS). Delta values are expressed relative to atmospheric N_2 (‰) and long-term external precision of analyses was 0.15‰. Leaf P, K, Ca, Mg, Fe and Mn concentrations were measured by inductively coupled plasma optical emission spectrometry (ICP-OES, Thermo Elemental Iris Intrepid II XDL, Franklin, MA, USA) after a microwave-assisted digestion with HNO_3:H_2O_2 (4:1, v:v) at the Ionomics laboratory at CEBAS-CSIC (Spain). The lignin concentration of these subsamples was determined according to the American National Standards Institute and American Society for Testing and Materials (1977). Briefly, dry litter was digested with a 72% H_2SO_4 solution and the remaining acid-insoluble lignin is filtered off, dried and weighed.

In addition to morphological and chemical analyses, three additional subsamples per treatment were kept frozen at −20°C for the determination of the biomass and structure of the litter microbial community through phospholipid fatty acid analysis (PLFAs). Lipids were extracted from 200 mg of litter with a mixture containing chloroform:methanol:citrate buffer (1:2:0.8 v/v/v) (Dyer & Bligh, 1959). Lipids were then fractionated (Frostegard, Baath, & Tunlid, 1993) and phospholipids were transformed into fatty acid methyl esters (FAMES) by alkaline methanolysis (Guckert, Antworth, Nichols, & White, 1985). The samples were analysed with a Trace Ultra Thermo Scientific gas chromatograph fitted with a 60-m capillary column (ThermoTR-FAME 60 m × 0.25 mm ID × 0.25 μm film), using helium as the carrier gas. The following fatty acids are characteristic bacterial fatty acids and were chosen as bacterial biomarkers: i15:0, a15:0, 15:0, i16:0, i17:0, cy17:0, cy19:0, 16:1ω7c, 16:1ω7t, 18:1ω9c and 18:1ω9t (Dungait et al., 2011; Frostegard et al., 1993). The fatty acid 18:2ω6 was used as an indicator of fungal biomass (Brant & Chen, 2015; Rinnan & Bååth, 2009). Fatty acids used to represent Gram-positive bacteria were i15:0, a15:0, i16:0 and i17:0. Fatty acids used to represent Gram-negative bacteria were cy17:0, cy19:0, 16:1ω7c, 16:1ω7t, 18:1ω9c and 18:1ω9t (Dungait et al., 2011; Frostegard et al., 1993). The 10Me-branched FAMES (10Me16:0 and 10Me18:0) were taken as specific actinobacterial biomarkers within the Gram-positive bacteria (Dungait et al., 2011).

2.3 | Litter decomposition experiments

After climate change treatments had been in place for 5 years (since 2011), we set up three concurrent experiments to isolate the effects of leaf litter quality, climate change and their combination on litter decomposition (Figure S2). 'Litter quality' (Exp. 1) represents the chemical and morphological traits of *H. squamatum* senesced leaves after 5 years of exposure to three climate change scenarios (from 2011 to 2015 when leaf litter was collected) incubated under ambient conditions. 'Climate change' (Exp. 2) represents the effect of abiotic conditions under the three climate manipulation treatments on homogeneous *H. squamatum* leaf litter. The combined effects of litter quality and climate change ('Litter quality × climate change', Exp. 3) represent the combination of litter traits after 5 years of exposure to the climatic treatments (i.e. litter quality) and the direct effect of altered abiotic conditions. In the first assay (Exp. 1), we isolated the effects of leaf litter quality. To do this, litter collected from *H. squamatum* individuals that had been growing for 5 years within each of the climate change treatments (W, RR and W + RR), and in Controls (C), unmanipulated plots outside treatments were enclosed in litterbags (n = 76), and these litterbags were incubated in unmanipulated Control plots, that is, under homogeneous soil and environmental conditions (subscript litt hereafter, C_{litt}, W_{litt}, RR_{litt}, $W + RR_{litt}$, Figure S2). In a second assay (Exp. 2), we tested the effects of climate change. To do this, homogenous litter collected from *H. squamatum* individuals growing in unmanipulated plots outside treatments (i.e. Control litter, C) was enclosed in litterbags and these were incubated inside the climate change treatments (C_W, C_{RR} and C_{W+RR}) and in the Controls outside the treatments (n = 80, Figure S2). In a third assay (Exp. 3), we incubated litterbags (n = 76) containing litter collected from *H. squamatum* individuals that had been growing within the climate change treatments inside their own climate manipulation plots (W_w, RR_{RR}, $W + RR_{W+RR}$) and in the Controls outside the treatments. Control litter (C) incubated in the Controls outside the treatments was the same for the three experiments (Exps. 1, 2 and 3, Figure S2). Each experiment consisted of 20 replicates per treatment (10 replicates × 2 collection dates), except for W + RR where n = 16 (8 replicates × 2 collection dates).

For each litterbag, 1 g of air-dried senesced leaves was weighed and enclosed in a polyamide tissue litterbag that partially excluded UV light to reduce photodegradation (Diatex, Villeurbanne, France, 4 × 10 cm, 48.67 ± 0.28% UV-radiation transmittance). Litterbags had a mesh size of 50 μm, were sewn on three sides leaving one side open to enclose leaves and were then closed on the remaining side with staples. Litterbags inside and outside treatment plots were deployed on bare spaces between *H. squamatum* shrubs, and the ground beneath the litterbag was levelled and manually cleared of vegetation. Periodic vegetation clipping was carried out to prevent litterbag shading. All litterbags were placed in the field plots on the same day at the end of the winter period (20 January 2016) so that the initial decomposition period (first 6 months) comprised the spring period (wet and warm) when microbial activity and decomposition are most active at our site (Almagro et al., 2017). A single litterbag was randomly selected from each plot and experiment and removed on the same day in the early morning hours (between 8 and 10 a.m.) at 6 and 18 months after deployment. These dates correspond to the end of the first spring season (early July 2016) and the end of the second spring season (early July 2017). In this study, we identified how different biotic and abiotic factors influenced decomposition from initial stages to an advanced decay

stage of up to 45% of initial mass lost, which is similar to mass losses observed in other studies in Mediterranean ecosystems (Almagro et al., 2017; Dirks et al., 2010; Saura-Mas et al., 2012).

Retrieved litterbags were placed on sealed plastic bags and kept cold in a cooler for transportation to the laboratory on the same day they were collected. The material inside the litterbags was extracted and carefully brushed to eliminate any adhered mineral soil particles. Samples were then fresh-weighed and a subsample (~300 mg) was kept frozen at −20°C for microbial biomass determination. The remaining material was oven-dried at 60°C for 72 hr and reweighed. The litter moisture content (%) was calculated as the relative difference between the litter fresh and dry weights. The fresh to dry weight was calculated and used to recalculate the total oven-dried weight of the whole sample using the total fresh weight. The litter was ground using a ball mill and subsamples for each litterbag were analysed for litter C, N and $\delta^{15}N$ using the method described above for the initial litter material. The uptake or release of N from the litterbags was estimated as the relative difference between the litter N content at each sampling period and that of the initial litter. The difference between the initial litter $\delta^{15}N$ and the litter $\delta^{15}N$ at each decomposition stage (6 and 18 months) was also calculated ($\Delta^{15}N$). The ash content of each litterbag was determined by combusting a subsample (~100 mg) in a muffle furnace at 550°C for 5–7 hr. The initial (M_0) and remaining (M_f) litter dry mass in the litterbags were expressed on an ash-free basis to exclude any mineral soil material remaining attached to the litter. Ash-free dry litter mass loss (ML; %) for each litterbag was calculated as the proportional difference between the initial and successive litter masses in the two collection dates. The decomposition constant decay rate (k, yr^{-1}) was determined for each litterbag using a single exponential decay model (Olson, 1963):

$$M_t = M_0 e^{-kt}$$

where M_t and M_0 are the ash-free mass in the litterbag at time t and at time 0.

2.4 | Statistical analyses

Firstly, we assessed differences in initial litter morphology, chemistry and microbial biomass (PLFAs content) using general linear models (LMs) with litter type (C_{litt}, W_{litt}, RR_{litt} and $W + RR_{litt}$) as a factor. When models were statistically significant ($p < 0.05$), these were followed by Tukey post hoc tests to determine differences among litter types. We performed a principal component analysis (PCA) with 13 litter traits (C, N, P, K, C:N, C:P, N:P, lignin, Ca, Mg, Fe, Mn, litter DMC) to obtain a multidimensional overview of the quality of the initial litter. We then extracted the loadings of the first PCA axis (Axis $1_{quality}$) and carried out general linear models with litter type (C_{litt}, W_{litt}, RR_{litt} and $W + RR_{litt}$) as a factor followed by Tukey post hoc tests to assess differences among litter types.

Principal component analysis (PCA) with the relative abundance of microbial groups (fungal, Gram-positive bacteria, Gram-negative bacteria and actinobacterial phospholipid fatty acids) was carried out to obtain a multidimensional overview of the structure of the microbial community after 6 and 18 months of decomposition. Three different PCAs were carried out, one for each of the assays, and the loadings of the first PCA axis of each individual plot were then extracted (Axis 1_{PLFAs}).

Changes in litter mass loss, litter moisture, litter N content, $\Delta^{15}N$, C:N ratios and differences in the overall structure of the microbial community (Axis 1_{PLFAs}) during decomposition were analysed using a general linear mixed model (LMMs) with either litter type (C_{litt}, W_{litt}, RR_{litt} and $W + RR_{litt}$) or climate (C, W, RR and W + RR) and 'collection date' as fixed factors and 'plot' as a random effect. In this case, the random variability (i.e. autocorrelation of successive individual observations) stems from repeatedly collecting the litterbags in the same plot over time. When significant, these analyses were carried out for each date separately using general linear models (LMs) followed by Tukey post hoc analyses to test for differences between litter quality (Exp. 1, C_{litt}, W_{litt}, RR_{litt} and $W + RR_{litt}$), climate (Exp. 2, C_{cont}, C_W, C_{RR} and C_{W+RR}) or both (Exp. 3, C_C, W_W, RR_{RR} and $W + RR_{W+RR}$). Differences in litter constant decay rates (k, $year^{-1}$) were analysed separately for each experiment using LMs with the same structure and followed by Tukey post hoc tests to assess differences between litter quality (Exp. 1), climate (Exp. 2) or both (Exp. 3). Additionally, differences in litter decay rates (k) between Exp. 2 (climate effects) and Exp. 3 (climate × litter quality) were evaluated for each treatment separately (W, RR and W + RR) using LMs with 'experiment' as a fixed factor. For all LMMs and LMs, residuals were assessed for normality (Shapiro–Wilk's test at $p > 0.05$) and data log-transformed when necessary and analyses were performed for each of the experiments separately.

T tests against a constant value (zero) were used to test whether differences between initial litter $\delta^{15}N$ and the litter $\delta^{15}N$ at each decomposition stage (6 and 18 months; $\Delta^{15}N$) were significantly different from zero.

General linear regression analyses were used to evaluate relationships between mass loss and litter moisture or microbial community structure (first axis of the PCAs) and between litter moisture and microbial community structure after 18 months, with samples from the three assays together and for each of the assays separately.

All the analyses described above adequately assess the effects of litter type, climate change and their interaction over time and their relationships with litter moisture and microbial structure. However, the relative effects of the underlying biotic and abiotic drivers of litter decomposition and N dynamics need to be examined together. To investigate the relative effect of the different factors on mass loss or microbial N immobilization in litter, we used comparisons based on structural equation modelling (SEM). Changes in temperature and rainfall alter soil microbial communities (Bastida et al., 2017; Castro, Classen, Austin, Norby, & Schadt, 2010), litter quality (García-Palacios et al., 2016; León-Sánchez et al., 2018) and influence the litter moisture content (Almagro et al., 2015), and these variables have an interactive effect on litter decomposition and N dynamics (Gliksman et al., 2017). Based on this previous knowledge, we proposed an a priori model of hypothesized relationships within a path diagram (Figure S3), allowing

a causal interpretation of the model outputs (Grace, 2006). Climate change treatments were introduced as two experimental factors represented as binary variables coding for warming (W, which includes the treatments with OTCs, i.e. W and W + RR, vs. non-warmed plots, that include Control and RR) or rainfall reduction (RR, which includes treatments with rainfall exclusion troughs, i.e. RR and W + RR, vs. plots with ambient rainfall, that include Control and W). This approach allows evaluating the separate effects of warming, rainfall reduction and their interaction (full factorial design, as in León-Sánchez et al., 2018 and Grossiord et al., 2017) and reduces the number of pathways introduced in the model. Direct paths between climate change treatments and mass loss or N immobilization are introduced to account for litter quality and potential additional drivers other than litter moisture or microbial communities (e.g. abiotic thermal degradation, Austin & Vivanco, 2006; Baker & Allison, 2015). In the SEM, to reduce the dimensionality of the different microbial groups, microbial community structure was the result of the ordination of PLFA contents along a single axis of variation in the PCA (Axis 1_{PLFAs}). We assessed the goodness of fit of the SEM models using the traditional χ^2 goodness-of-fit test, but because of its sensitivity to sample size, the Root Mean Square Error of Approximation (RMSEA), the Bentler comparative fit index (CFI) and the incremental fit index (IFI) were also considered (Grace, 2006). For SEM analyses, contrary to other statistical analyses, *p*-values higher than 0.05 in the χ^2 and RMSEA indices, respectively (Schermelleh-Engel, Moosbrugger, & Müller, 2003), and values close to 1 (>0.90) for CFI and IFI indices are required to guarantee an acceptable fit (Hu & Bentler, 1999). Since we were interested in assessing the relative effects of biotic (i.e. litter quality) and abiotic (i.e. climatic) variables on litter decomposition and N dynamics, separate SEM models were conducted for each of the experiments (Exps. 1, 2 and 3) with pooled data from the two stages of decomposition (6 and 18 months).

All calculations and statistical analyses were performed with the R software (v 2.15.3, R Core Team, 2016) using the packages ade4 (Chessel, Dufour, & Thioulouse, 2004), effects (Fox et al., 2014), Hmisc (Harell Jr, 2015), lme4 (Bates et al., 2015) and nlme (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2014). SEM was carried out with the AMOS extension in SPSS (Arbuckle, 2014). Data shown throughout the text are mean ± standard error (SE).

3 | RESULTS

3.1 | Initial litter quality and microbial PLFA contents

We found strong differences in the quality of the standing leaf litter collected within the different climate manipulation treatments after 5 years of exposure (Table 1). The first two axes of the litter quality PCA explained 75.1% of the variation in litter quality (Table S1). The

TABLE 1 Initial chemical and physical characteristics of *Helianthemum squamatum* standing litter collected in the different climatic treatments in July 2015

Initial chemistry	Control	W	RR	W + RR
C (%)	34.42 ± 0.11a	35.7 ± 0.1c	34.75 ± 0.06ab	35.22 ± 0.2bc
N (%)	0.52 ± 0.02a	0.48 ± 0.02a	0.59 ± 0.02b	0.46 ± 0.01a
P (%)	0.013 ± 0.001b	0.011 ± 0.001a	0.017 ± 0.000c	0.012 ± 0.000ab
K (%)	0.32 ± 0.01a	0.37 ± 0.01b	0.29 ± 0.01a	0.43 ± 0.01c
C:N	66.66 ± 1.77a	75.42 ± 2.97b	59.03 ± 1.94a	76.21 ± 1.69b
C:P	2,666 ± 94b	3,414 ± 237c	2,046 ± 32a	3,024 ± 65bc
N:P	40.02 ± 1.13ab	45.42 ± 3.11b	34.79 ± 0.85a	39.84 ± 1.55ab
Lignin (%)	35.34 ± 0.51b	35.92 ± 0.22b	36.77 ± 0.31b	32.56 ± 0.61a
Lignin:N ratio	68.43 ± 1.52ab	75.99 ± 2.67b	62.59 ± 2.45a	70.48 ± 1.98ab
Ca (%)	4.16 ± 0.1ab	3.85 ± 0.1a	4.16 ± 0.15ab	4.50 ± 0.22b
Mg (%)	0.33 ± 0.01a	0.35 ± 0.01a	0.34 ± 0.01a	0.43 ± 0.01b
Fe (mg/kg)	132.25 ± 3.92b	86.22 ± 3.32a	131.86 ± 5.09b	92.27 ± 5.29a
Mn (mg/kg)	34.08 ± 0.53a	42.84 ± 1.02b	33.82 ± 1.05a	44.27 ± 1.31b
$\delta^{15}N$ (‰)	−1.30 ± 0.24b	−1.74 ± 0.30ab	−1.67 ± 0.34ab	−2.54 ± 0.32a
Litter DMC (mg/g)	319.63 ± 0.66bc	324.68 ± 6.24c	298.68 ± 5.65ab	294.38 ± 5.15a
Litter dry weight (mg/leaf)	11.92 ± 0.56c	8.88 ± 0.52b	6.92 ± 0.44a	7.64 ± 0.28ab
Water holding capacity (%)	212.86 ± 0.65ab	208.57 ± 6.04a	229.72 ± 3.89bc	240.22 ± 5.94c
Litter quality (Axis 1)	0.508 ± 0.121b	−0.810 ± 0.144a	1.296 ± 0.103c	−0.994 ± 0.067a

Note. Litter trait abbreviations are as follows: C, N, P, K: litter carbon, N, P and K concentrations, C:N, C:P and N:P: litter C to N, C to P and N to P ratios; Lignin: litter lignin concentrations; Lignin:N ratio: litter lignin to N ratios; Ca, Mg, Fe and Mn: litter Ca, Mg, Fe and Mn concentrations; $\delta^{15}N$: litter isotopic N composition; Litter DMC: litter dry matter content; Litter quality (Axis 1): loadings on the first axis of variation in the litter quality principal component analysis (see Materials and Methods). Treatments are: Control, W = Warming, RR = Rainfall reduction and W + RR=warming and rainfall reduction.

Mean and *SEs* are shown (n = 6). Different letters denote significant differences between treatments (Tukey HSD, $p < 0.05$).

first axis alone accounted for 51.6% of the total variation, with litter C, K and Mn concentrations and C:N, C:P ratios contributing negatively to this axis, whereas litter N, P, Fe and lignin concentrations contributed positively to this axis. The second axis of the PCA was negatively related to N:P ratios and positively to Mg and Ca concentrations and the third axis was related to litter DMC. The W and W + RR treatments had significantly lower litter quality (i.e. negative scores in the first PCA axis) than Control or RR litter (Table 1, $p < 0.05$). Overall, standing leaf litter collected in warmed plots (W_{litt} and W + RR_{litt}) had higher C, C:N and C:P ratios than litter collected in plots with ambient temperature conditions ($Control_{litt}$ and RR_{litt}). Litter in warmed plots also had lower P and Fe concentrations and higher K and Mn concentrations than in non-warmed plots. In addition to these differences, litter from W + RR_{litt} plots had lower lignin concentrations than litter from the rest of the treatments (Table 1). Litter dry weight was reduced by all three climatic treatments (W, RR and W + RR). Leaf litter from rainfall reduction plots (RR_{litt} and W + RR_{litt}) had lower litter DMC than litter from warmed only plots (W_{litt}) and litter water holding capacity was lower in W_{litt} than in RR_{litt} or W + RR_{litt} (Table 1).

The PLFA content of the different microbial groups, indicative of their microbial biomass, was most affected by the combination of warming and rainfall reduction (W + RR_{litt}) with standing leaf litter from W + RR_{litt} plots having significantly greater microbial biomass than the rest of the treatments in most groups (i.e. fungi, bacteria, Gram positive, Gram negative and Actinobacteria, Table S2). Microbial biomass ratios did not differ between litter types except for a higher Gram-positive/Gram-negative PLFA ratio in litter collected from rainfall reduction plots (RR_{litt}) compared to the rest of the treatments.

3.2 | Litter decomposition

When examining the effects of litter quality on decomposition (Exp. 1), we found that litter mass loss differed between litter types (Figure 1a, Table S3), although litter quality effects were only apparent at the first stages of decomposition (6 months) when mass loss in the litter from warmed plots (W_{litt}) was lower than in the litter from W + RR_{litt} and Control plots. However, litter quality did not have a significant effect on decay rates over the whole study period (18 months) (*k*, Table 2 and Table S4).

When analysing the effects of climate change alone (Exp. 2), we found that the mass loss of the standard litter (litter collected from Control plots) differed between climatic treatments (Figure 1b, Table S3). When analysed separately for each collection date, litter mass loss was lower in litterbags incubated in warmed (C_W and C_{W+RR}) than in non-warmed plots (C_{Cont} and C_{RR}) after 6 months of decomposition. After 18 months, litter mass loss was also lower in litterbags in warmed plots (C_W and C_{W+RR}) with respect to Controls but neither these or the Controls differed from the reduced rainfall treatment (C_{RR}). As a result of this dynamics, litter decay rates (*k*) were reduced by 23.4%, 18.1% and 29.8% in the C_W, C_{RR} and C_{W+RR} treatments, respectively, compared to litter incubated under ambient conditions (Table 2 and Table S4). Under the most realistic conditions (Exp. 3), the combination of altered litter quality and climate change affected litter mass loss with a similar pattern to that of climate change alone, yet the magnitude of the effects was greater when litter quality and climate change were acting together (Figure 1c, Table S3). After 6 months of decomposition, litter mass loss was significantly lower in warmed (W_W and W + RR_{W+RR}) and rainfall reduction plots (RR_{RR}) than in Control plots (Figure 1c). After 18 months of decomposition, mass loss was substantially lower in all three climatic treatments (W_W, RR_{RR} and W + RR_{W+RR}) compared to the Controls (Figure 1c). As a result, litter decay rates (*k*) were, on average, 32.0%, 26.3% and 39.9% lower in W_W, RR_{RR} and W + RR_{W+RR}, respectively, compared to Control litter incubated under ambient conditions (Table 2 and Table S4). The addition of litter quality effects (Exp. 3) thus resulted in additional decreases of 8.6%, 8.2% and 10.1% in litter decay rates in W, RR and W + RR plots, respectively, compared to climatic effects alone (Exp. 2; *t* test, $p < 0.05$).

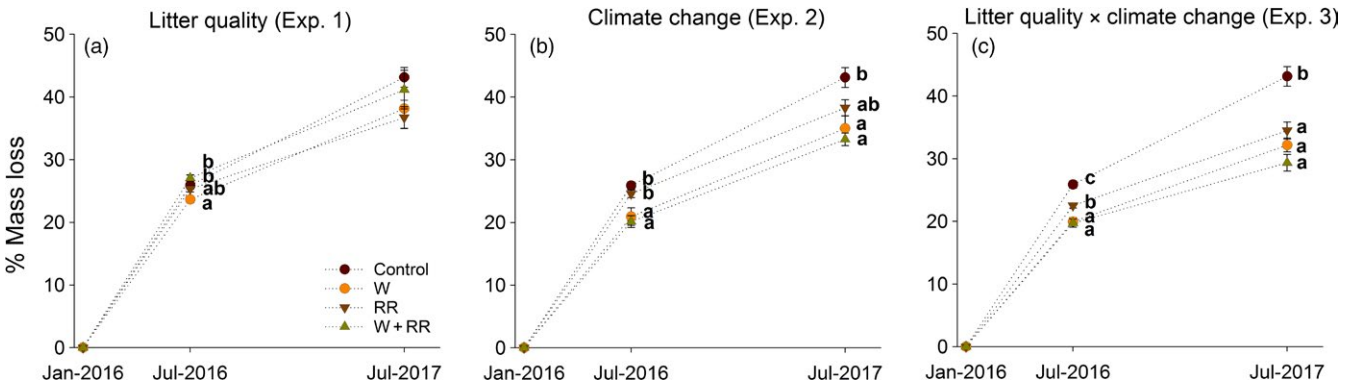

FIGURE 1 Average percentage mass loss (%) with time in the three assays testing for the effects of (a) litter quality (Exp. 1; *Helianthemum squamatum* leaf litter collected from the climate treatments and incubated in Control plots under common environmental conditions), (b) climate change (Exp. 2; *H. squamatum* leaf litter collected in the Controls and incubated in Control, W, RR and W + RR plots) and (c) litter quality and climate change effects (Exp. 3; *H. squamatum* leaf litter collected from the climate treatments and incubated in their own treatment plots). Values are mean ± *SE* (*n* = 8–10). See Table S1 for statistical analyses. For each sampling time, significant differences in remaining mass among litter types (a) or climate change treatments (b, c) are denoted by different lowercase letters (Tukey post hoc tests, $p < 0.05$). W: warming, RR: rainfall reduction, W + RR: warming and rainfall reduction

TABLE 2 Average decomposition rates (k, year^{-1}) after 18 months in the three assays testing for the effects of (a) litter quality (Exp. 1; *Helianthemum squamatum* leaf litter collected from the climate treatments and incubated in Control plots under common ambient environmental conditions), (b) climate change (Exp. 2; *H. squamatum* leaf litter collected in the Controls and incubated in Control, W, RR and W + RR plots) and (c) combined litter quality and climate change effects (Exp. 3; *H. squamatum* leaf litter collected from the climate treatments and incubated in their own treatment plots)

	Control	W	RR	W + RR
(a) Litter quality (Exp. 1)	0.157 ± 0.009a	0.133 ± 0.009a	0.125 ± 0.006a	0.148 ± 0.017a
(b) Climate change (Exp. 2)	0.157 ± 0.009b	0.121 ± 0.009a	0.129 ± 0.007a	0.111 ± 0.005a
(c) Litter quality × climate change (Exp. 3)	0.157 ± 0.009b	0.107 ± 0.005a	0.116 ± 0.006a	0.094 ± 0.006a

Values are mean ± *SE* (n = 8–10). See Table S2 for statistical analyses. Significant differences in k among litter types (a) or climate change treatments (b, c) are denoted by different lowercase letters (Tukey post hoc tests, $p < 0.05$). Control: Control, W: warming, RR: rainfall reduction, W + RR: warming and rainfall reduction.

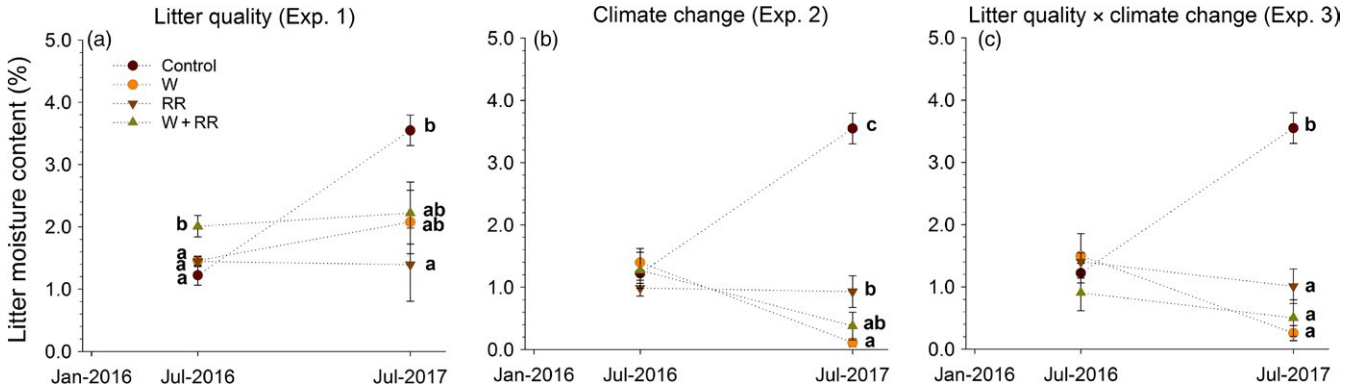

FIGURE 2 Average litter moisture content with time in the three assays testing for the effects of (a) litter quality (Exp. 1; *Helianthemum squamatum* leaf litter collected from the climate treatments and incubated in Control plots under common environmental conditions), (b) climate change (Exp. 2; *H. squamatum* leaf litter collected in the Controls and incubated in Control, W, RR and W + RR plots) and (c) litter quality and climate change effects (Exp. 3; *H. squamatum* leaf litter collected from the climate treatments and incubated in their own treatment plots). Values are mean ± *SE* (n = 8–10). See Table S2 for statistical analyses. For each sampling time, significant differences in remaining mass among litter types (a) or climate change treatments (b, c) are denoted by different lowercase letters (Tukey post hoc tests, $p < 0.05$). W: warming, RR: rainfall reduction, W + RR: warming and rainfall reduction

Within Exp. 1, we detected a negative relationship between the initial lignin concentration in leaf litter and litter mass loss both after 6 and 18 months of decomposition under ambient conditions ($p < 0.05$, Figure S4), and a positive correlation between Ca and Mg concentrations and litter mass loss at 6 months ($r = 0.49$, $p < 0.05$ and $r = 0.42$, $p < 0.05$ respectively). No other significant relationships between leaf litter traits, chemical or morphological and mass loss were detected ($p > 0.10$).

3.3 | Litter moisture content

The effects of litter quality and climate change on litter moisture contents, either alone or in combination, were time dependent (Figure 2a–c and Table S3). Within Exp. 1 (litter quality), litter moisture content was slightly higher in W + RR_{litt} than in the other treatments after 6 months, whereas after 18 months of decomposition, $Control_{litt}$ had significantly higher moisture than the rest of the litter types (Figure 2a). Climate treatments alone (Exp. 2) resulted in a significantly higher moisture content in litter incubated under ambient conditions (C_{cont}), followed by litter incubated in plots with decreased rainfall (C_{RR} and C_{W+RR}) and was lowest in litter incubated in warmed plots (C_W), after 18 months (Figure 2b). Similar to climate effects alone, the combined effect of litter quality and climate change (Exp. 3) resulted in a higher moisture content in Control litter incubated under ambient conditions (C_{cont}, Figure 2c) compared to other litter types and climate treatments (W_W, RR_{RR} and W + RR_{W+RR}). Across the three experiments, litter mass loss rates increased with increasing litter moisture content after 18 months, irrespective of the type of litter or climate conditions (Figure S5). When the relationship was examined within each of the experiments separately, we did not detect a significant relationship ($p > 0.20$) within Exp. 1 (litter quality). However, we found positive relationships between litter mass loss and litter moisture content when litter was incubated within the experimental climate treatments irrespective of the type of litter, that is, significant positive relationships within both Exps. 2 and 3 ($p < 0.001$ in both cases, Figure S5).

3.4 | Litter N immobilization

During decomposition, litter N accumulated with time with contrasting accumulation patterns among litter types (Table S3). In Exp. 1 (litter quality), warming (W_{litt} and W + RR_{litt}) tended to enhance

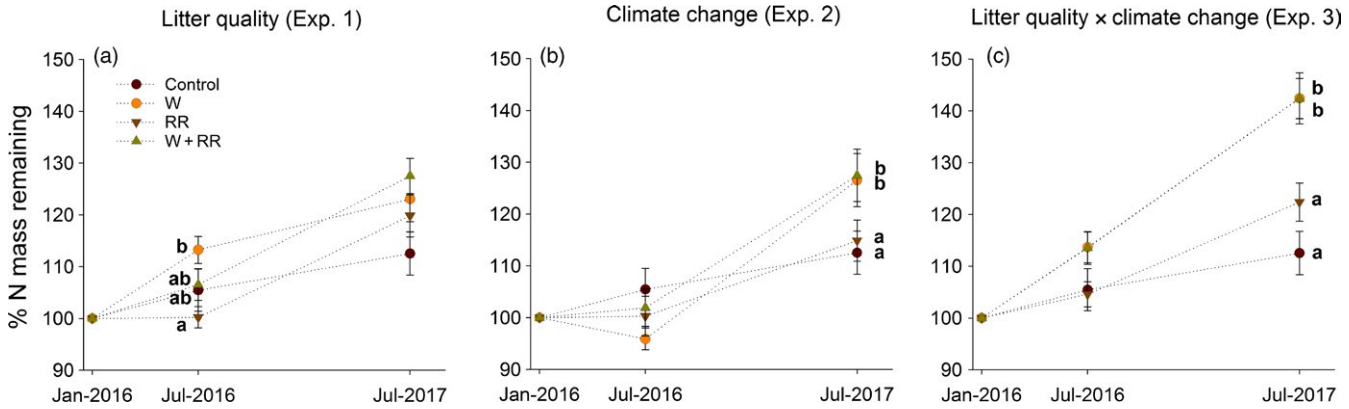

FIGURE 3 Average N immobilization (% N mass remaining) with time in the three assays testing for the effects of (a) litter quality (Exp. 1; *Helianthemum squamatum* leaf litter collected from the climate treatments and incubated in Control plots under common environmental conditions), (b) climate change (Exp. 2; *H. squamatum* leaf litter collected in the Controls and incubated in Control, W, RR and W + RR plots) and (c) litter quality and climate change effects (Exp. 3; *H. squamatum* leaf litter collected from the climate treatments and incubated in their own treatment plots). Values are mean ± *SE* (n = 8–10). See Table S2 for statistical analyses. For each sampling time, significant differences in remaining mass among litter types (a) or climate change treatments (b, c) are denoted by different lowercase letters (Tukey post hoc tests, $p < 0.05$). W: warming, RR: rainfall reduction, W + RR: warming and rainfall reduction

N immobilization in litter after 6 months but not after 18 months, and this was stronger for the W(arming) only treatment (Figure 3a). When climate treatments acted alone (Exp. 2), there was substantial N immobilization in litter during decomposition but differences only appeared after 18 months, when N immobilization was significantly greater in litter incubated within warmed plots (C_W and C_{W+RR}, Figure 3b) than within non-warmed plots (C_{cont} and C_{RR}). In Exp. 3 (litter quality and climate), litter incubated in warmed plots (W_W and W + RR_{W+RR}) immobilized twice as much N than litter incubated in non-warmed plots after 6 months of decomposition ($p = 0.08$), a difference that increased to 2.5 times higher N immobilization in warmed than in non-warmed plots after 18 months ($p < 0.05$, Figure 3c).

Leaf litter generally became less enriched in ^{15}N as decomposition progressed (i.e. lower $\delta^{15}N$) resulting in negative $\Delta^{15}N$ values (i.e. a negative difference between $\delta^{15}N$ of initial and incubated leaf litter; t test against zero, $p < 0.05$; Figure 4a–c). The only exceptions were W + RR_{litt} incubated in Control plots (Exp. 1) and W_W and W + RR_{W+RR} litter incubated within their own climate treatments in Exp. 3 where $\Delta^{15}N$ values did not differ from zero (t test, $p > 0.20$; Figure 4a,c). Furthermore, litter from the W + RR treatment, whether incubated under ambient conditions (Exp. 1, W + RR_{litt}) or under climate change conditions (Exp. 3, W + RR_{W+RR}), had significantly higher $\Delta^{15}N$ values than the rest of the treatments (Figure 4a,c). Litter C:N ratios decreased during decomposition (date, $p < 0.001$, Table S5) and differed between litter types and between climate change treatments (Table S5). Litter C:N ratios were generally lower in litter from Control and RR plots incubated under ambient environmental conditions (Exp. 1, Figure 4d). When only climate effects were evaluated (Exp. 2), litter C:N ratios were higher in warmed plots (C_W) than in the rest of the treatments (C_{cont}, C_{RR} and C_{W+RR}) after 6 months, and were higher in all climate treatment plots (C_W, C_{RR} and C_{W+RR}) than in Control plots (C_{cont}) after 18 months (Figure 4e). When both litter quality and climate change effects were combined (Exp. 3), litter C:N ratios were higher in warmed (W_W and W + RR_{W+RR}) than in non-warmed plots (C_{cont} and RR_{RR}) both after 6 and 18 months of decomposition (Figure 4f).

3.5 | Litter PLFAs contents

PLFA contents increased in the litter with time during decomposition (*date*, $p < 0.001$, Figure 5a–c) and a significant *climate change × date* interaction was found in all the experiments ($p < 0.01$). The microbial community structure of leaf litter in litterbags from Exp. 1 (litter quality) differed among treatments after 6 months of decomposition for all four microbial groups (Fungi, Gram-positive bacteria, Gram-negative bacteria and Actinobacteria), although the differences between litter types were strongly time dependent (Figure 5a, Table S6). We observed greater PLFA contents of all four microbial groups on litter collected in plots with decreased rainfall (RR_{litt}) than in the rest of the treatments (C_{litt}, W_{litt} and W + RR_{litt}) after 6 months of decomposition (Tukey, $p < 0.05$). After 18 months, however, microbial community structure converged between litter types and no differences were found among them (Figure 5a, see Table 3 for separate analyses for each microbial group). Separate ANOVAs for climate effects alone (Exp. 2) showed that, after 6 months, microbial PLFA contents were higher when litter was incubated in W + RR plots (C_{W+RR}, Tukey, $p < 0.001$). After 18 months, the litter incubated under ambient conditions (Control) had higher litter PLFA contents than litter incubated under all climate change conditions (Tukey, $p < 0.01$, see Table 3 for separate analyses for each microbial group). When examining the combined effects of climate and litter quality (Exp. 3), separate ANOVAs showed that, at earlier stages (6 months), only litter in warmed plots (W_W) had higher PLFA contents with respect to Controls. The opposite pattern was found at later decomposition stages (18 months), with lower PLFA contents in warmed plots (W_W and W + RR_{W+RR}, Figure 5c, see Table 3 for separate analyses for each microbial group) than in non-warmed plots (RR_{RR} and W + RR_{W+RR}).

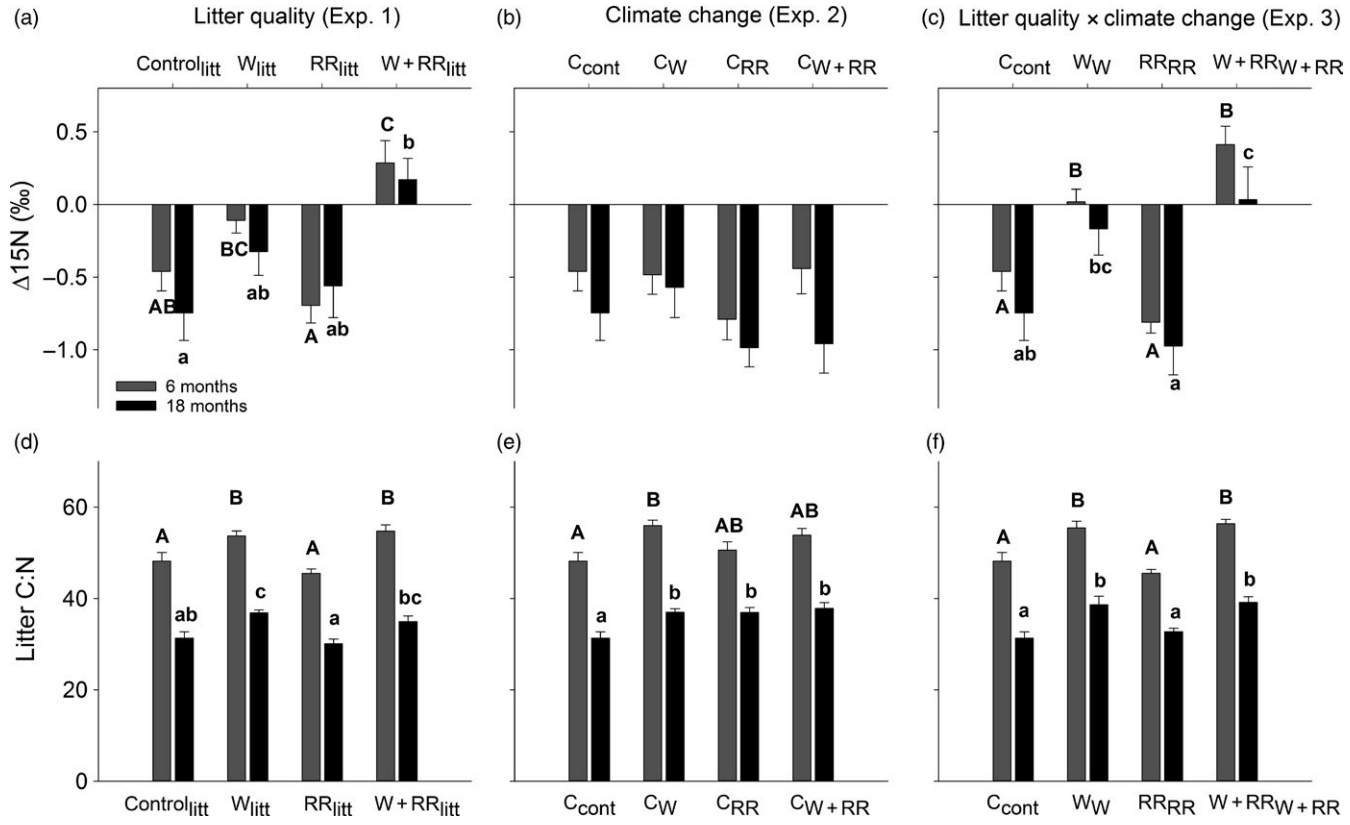

FIGURE 4 Average differences in $\delta^{15}N$ between initial litter and litter after 6 and 18 months of decomposition ($\Delta^{15}N$) and litter C:N ratios in the three assays testing for the effects of (a, d) litter quality (Exp. 1; *Helianthemum squamatum* leaf litter collected from the climate treatments and incubated in Control plots under common environmental conditions), (b, e) climate change (Exp. 2; *H. squamatum* leaf litter collected in the Controls and incubated in Control, W, RR and W + RR plots) and (c, f) litter quality and climate change effects (Exp. 3; *H. squamatum* leaf litter collected from the climate treatments and incubated in their own treatment plots). Values are mean ± *SE* (*n* = 8–10). See Table S5 for statistical analyses. For each sampling time, significant differences in $\Delta^{15}N$ or litter C:N among litter types (a, d), climate change treatments (b, e) or litter quality and climate change effects (c, f) are denoted by different uppercase (6 months) and lowercase (18 months) letters (Tukey post hoc tests, $p < 0.05$). C: Control, W: warming, RR: rainfall reduction, W + RR: warming and rainfall reduction

Across the three experiments, no significant relationships between litter mass loss and microbial community structure were found in the early stages of decomposition (6 months, $p > 0.20$), but after 18 months, we found that overall, litter decomposition increased with increasing PLFA contents (positive scores in the Axis 1_{PLFAs}, Figure S6). Similar to relationships with litter moisture, the relationship between mass loss and microbial PLFA contents (Axis 1_{PLFAs}) did not hold when only litter quality effects were tested (Exp. 1), but strong positive relationships were found within experiments looking at climate treatment effects alone or in combination with litter quality (Exps. 2 and 3; $p < 0.001$ in both cases, Figure S6). The microbial PLFA contents (Axis 1_{PLFAs}) were also positively correlated with litter moisture within Exps. 2 ($R^2 = 0.62$, $p < 0.001$) and 3 ($R^2 = 0.30$, $p < 0.05$) but not within Exp. 1.

3.6 | Drivers of litter decomposition and N dynamics

The use of SEM analyses revealed that when evaluating litter quality effects alone (i.e. litter from plants that had been growing under climate change conditions incubated under similar soil and environmental conditions in Control plots, Exp. 1, Figure 6a), the only supported pathway by which warming (i.e. litter from warmed plots) negatively influenced litter mass loss was an indirect pathway via a negative effect of altered litter quality on bacterial, fungal and actinobacterial PLFA contents (Microbial structure, Axis 1_{PLFAs}, $\beta = -1.41$, $p = 0.011$), which resulted in a net negative effect (6.4%) of warming (i.e. altered litter produced under warmed conditions) on mass loss (Figure S7a). In this model, litter produced under rainfall reduction conditions did not have an effect on any of the variables in the model ($p > 0.05$). The hypothesized direct pathways of litter quality effects (either litter produced under warming or rainfall reduction conditions) on litter mass loss or the indirect pathway through effects on litter moisture were not supported by the model ($p > 0.05$). We could not evaluate climate effects alone on litter mass loss (Exp. 2) since the resulting model did not have an acceptable goodness of fit (χ^2 and RMSEA, $p < 0.05$, CFI < 0.90 and IFI < 0.90). Interestingly, when both litter quality and climate change acted interactively (Exp. 3, Figure 6c), the model was different from that in Exp. 1 and pointed to an indirect inhibition of decomposition by both warming and rainfall reduction (Figure S7b). In this model, higher litter moisture contents resulted in greater litter

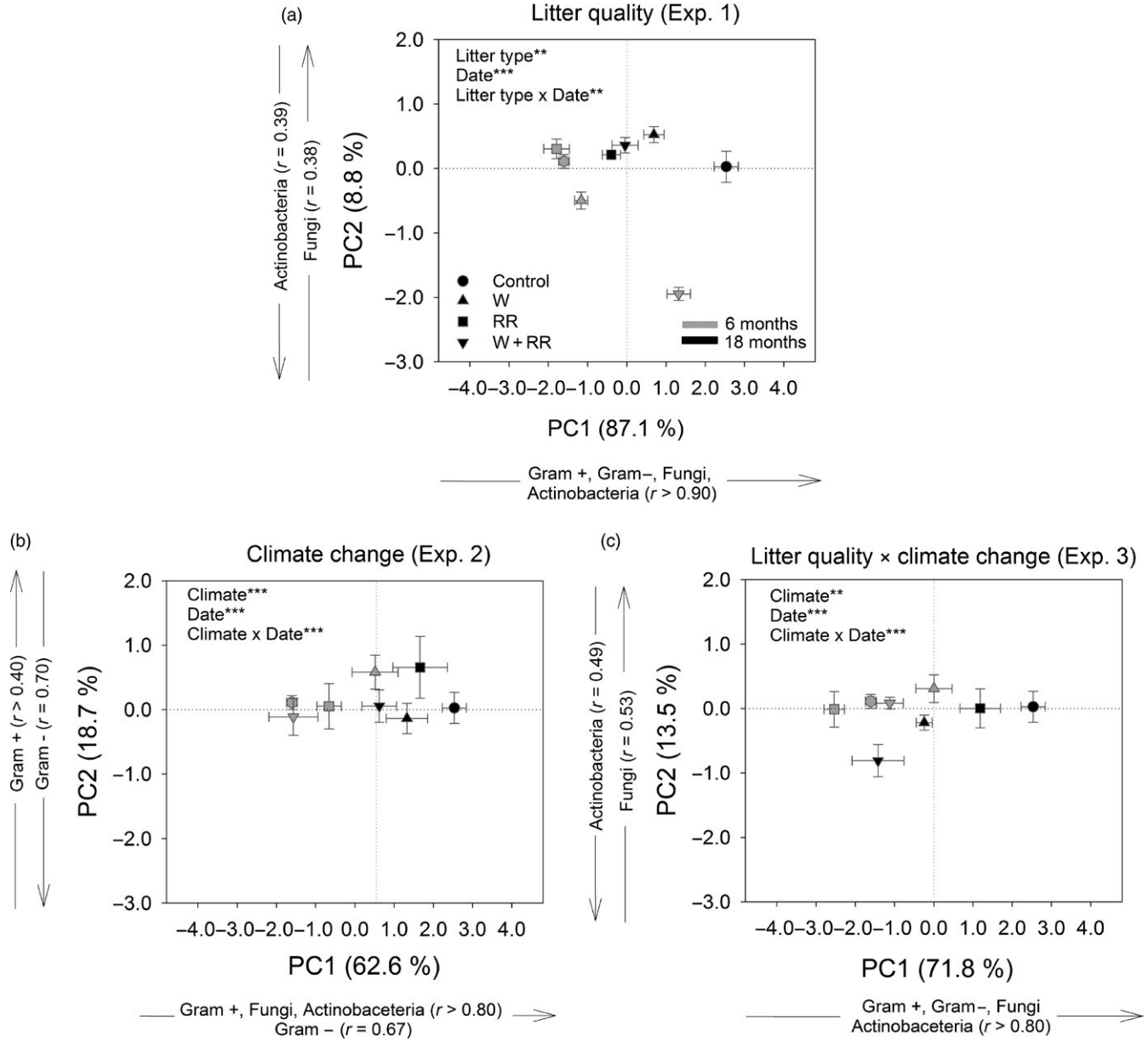

FIGURE 5 Effects of litter quality (a, Exp. 1), climate change (b, Exp. 2) and their combination (c, Exp. 3) on litter microbial community structure. Asterisks indicate significant effects (*p < 0.05, **p < 0.01; ***p < 0.001), see Tables S4 and S5 for statistical analyses. Significant Pearson correlations between the principal component analysis axes and the individual microbial groups are shown parallel to axes, with the arrow representing the sign of the correlation. Pearson correlation coefficients and p-values are shown in brackets next to the individual microbial groups. Values represent mean ± SE (n = 4–5). Control: Control, W: warming, RR: rainfall reduction, W + RR: warming and rainfall reduction

microbial PLFA contents (β = 0.58, p = 0.03) that, in turn, resulted in faster decomposition rates (β = 0.03, p = 0.001; Figure 6c and Figure S7b). Although the effect of litter microbial PLFA contents was direct (49%), leaf litter moisture content enhanced mass loss indirectly (13.6%, Figure S7b). Since both warming and rainfall reduction negatively affected litter moisture content (β = −0.85, p = 0.005 for W and β = −0.65, p = 0.031 for RR), they both had a strong indirect negative impact on microbial community structure and biomass and on litter mass loss (Figure 6c and Figure S7a). The lack of support for the direct hypothesized pathways between W and RR and litter mass loss (p > 0.05) and the comparison with results from the model evaluating exclusively litter quality effects (showing that litter quality did not affect litter moisture; Figure 6a) point to climatic, rather than litter quality, effects on litter moisture and, in turn, on litter decomposition.

In the case of N immobilization in leaf litter, when evaluating litter quality effects alone (Exp. 1, Figure 6b), the supported pathways were only those by which the lower quality of the litter in warmed plants reduced N immobilization through an indirect negative effect on leaf litter microbial structure and biomass (β = −1.41, p = 0.011)

TABLE 3 Microbial phospholipid fatty acids (PLFAs) measured in *Helianthemum squamatum* leaf litter collected after 18 months of decomposition (July 2017) for (a) Exp. 1; *Helianthemum squamatum* litter collected from individuals growing within climate change treatment plots and incubated in Control plots (litter quality) (b) Exp. 2; *H. squamatum* litter collected from individuals growing outside treatments (Control) and incubated within climate change treatment plots (climate change effects) and (c) Exp. 3; *H. squamatum* litter collected from individuals growing within climate change treatment plots and incubated inside their own plots (combined litter quality and climate change effects)

(a) Litter quality (Exp. 1)	**Control**	**W**	**RR**	**W + RR**
Fungi	100.66 ± 6.68a	93.32 ± 5.76a	87.64 ± 10.11a	94.57 ± 6.91a
Bacteria	77.76 ± 6.89a	68.53 ± 6.97a	57.91 ± 5.76a	65.34 ± 6.82a
Gram positive	33.22 ± 4.5a	30.51 ± 3.08a	22.69 ± 1.77a	27.3 ± 3.5a
Gram negative	44.54 ± 2.77a	38.02 ± 4.08a	35.22 ± 4.17a	38.04 ± 3.5a
Actinobacteria	0.73 ± 0.14a	0.56 ± 0.11a	0.47 ± 0.02a	0.55 ± 0.11a
Gram positive:Gram negative	0.74 ± 0.07a	0.81 ± 0.05a	0.66 ± 0.05a	0.71 ± 0.05a
Fungi:Bacteria	1.33 ± 0.14a	1.39 ± 0.09a	1.51 ± 0.08a	1.47 ± 0.08a
(b) Climate change (Exp. 2)	**Control**	**W**	**RR**	**W + RR**
Fungi	100.66 ± 6.68b	80.29 ± 6.4ab	67.12 ± 4.61a	66.66 ± 10.11a
Bacteria	77.76 ± 6.89b	47.83 ± 3.62a	33.95 ± 3.8a	38.96 ± 3.62a
Gram positive	33.22 ± 4.5b	19.21 ± 2.03a	9.28 ± 1.34a	12.03 ± 1.96a
Gram negative	44.54 ± 2.77b	28.63 ± 2.17a	22.15 ± 0.8a	26.93 ± 1.86a
Actinobacteria	0.73 ± 0.14b	0.44 ± 0.06ab	0.36 ± 0.02a	0.45 ± 0.04ab
Gram positive:Gram negative	0.74 ± 0.07b	0.68 ± 0.07b	0.37 ± 0.03a	0.44 ± 0.05a
Fungi:Bacteria	1.33 ± 0.14a	1.68 ± 0.09ab	2.02 ± 0.13b	1.68 ± 0.16a
(c) Litter quality × climate change (Exp. 3)	**Control**	**W**	**RR**	**W + RR**
Fungi	100.66 ± 6.68b	120.62 ± 24.29b	56.83 ± 4.34a	19.29 ± 8.05a
Bacteria	77.76 ± 6.89b	70.82 ± 12.59b	43.42 ± 3.92ab	29.42 ± 10.85a
Gram positive	33.22 ± 4.5b	24.79 ± 3.3ab	18.64 ± 2.55ab	9.74 ± 4.81a
Gram negative	44.54 ± 2.77b	38 ± 7.29ab	24.77 ± 1.95ab	19.68 ± 6.31a
Actinobacteria	0.73 ± 0.14b	0.47 ± 0.07a	0.32 ± 0.02a	0.30 ± 0.10a
Gram positive:Gram negative	0.74 ± 0.07a	0.59 ± 0.07a	0.75 ± 0.08a	0.43 ± 0.17a
Fungi:Bacteria	1.33 ± 0.14ab	1.55 ± 0.04b	1.32 ± 0.05ab	0.82 ± 0.29a

Units for variables are in nmol/g_{soil}. Significant differences between litter types are denoted by lowercase letters (Tukey post hoc tests, $p < 0.05$). Values are mean ± *SE* (n = 4–5). Abbreviations are as follows: Gram positive/Gram negative: Gram positive to Gram negative ratio; Fungi/Bacteria: Fungal to bacterial biomass ratio. Abbreviations for treatments are as follows: Control, W = warming, RR = rainfall reduction and W + RR=warming and rainfall reduction.

and a direct effect of the lower quality of leaf litter in warmed plots directly increasing N immobilization ($\beta = 0.05$, $p < 0.001$, Figure S7a). These interactive effects resulted in a net increase in N immobilization on litter from warmed plots (36.4%, Figure S7a). The hypothesized pathways of a direct or indirect effect of the litter quality of plants that had been growing under rainfall reduction conditions affecting N immobilization were not supported by the model ($p > 0.05$) nor were any pathways involving effects on litter moisture (Figure 6b). We could not evaluate climate effects alone on nutrient immobilization (Exp. 2) since the resulting model did not have an acceptable goodness of fit (χ^2 and RMSEA, $p < 0.05$, CFI < 0.90 and IFI < 0.90). When both litter quality and climate change acted interactively (Exp. 3, Figure 6d), the indirect pathways mediated by litter moisture or the microbial community structure were not supported by the model ($p > 0.05$, Figure 6d). Instead, and similar to litter quality effects alone, the only supported pathway in the model was that of warming directly enhancing N immobilization ($\beta = 0.06$, $p < 0.001$, Figure 6d), which accounted for most of the total effects in the model (52%, Figure S7b). The similarities between models evaluating litter quality effects (Exp. 1) and both litter quality and climate effects on N immobilization (Exp. 3, Figure 6a) point to litter quality, rather than climate, being largely responsible for the effects on N immobilization.

4 | DISCUSSION

Climatically induced reductions in litter moisture content and microbial community biomass were the main drivers of slowed litter decay under simulated climate change in our dryland ecosystem but reductions in litter quality with warming further decreased litter decomposition rates (Figure 6a). Climate change-induced reductions in both litter quality and litter moisture content increased litter N

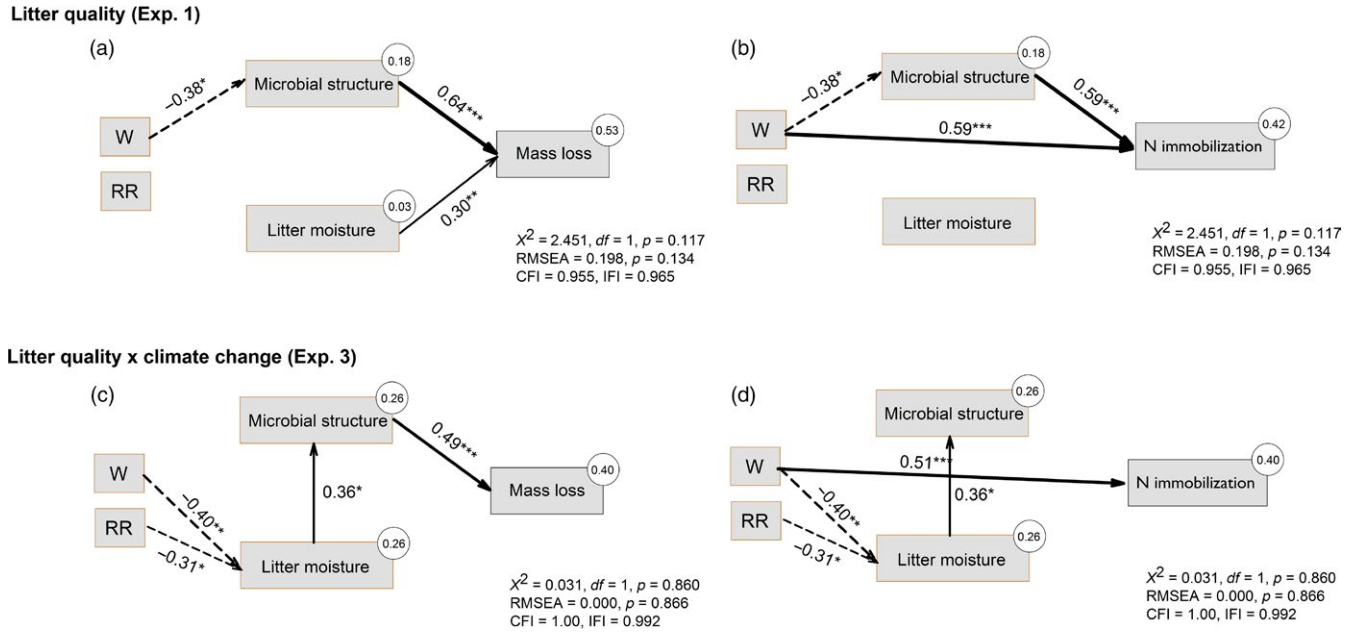

FIGURE 6 Effects of warming (W), rainfall reduction (RR), microbial community structure (component 1 from the different principal component analysis, see Figure 5) and litter moisture content on litter mass loss (left panels) and on microbial N immobilization (right panels) in experiments testing for the effects of (a, b) litter quality (Exp. 1; *Helianthemum squamatum* leaf litter collected from the climate treatments and incubated in Control plots under common environmental conditions, $n = 38$), and (c, d) litter quality and climate change effects acting simultaneously (Exp. 3; *H. squamatum* leaf litter collected from the climate treatments and incubated in their own treatment plots, $n = 37$). Continuous and dashed black arrows indicate positive and negative relationships respectively. Numbers adjacent to lines indicate the effect size and significance (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$) of the path and arrow thickness is proportional to the effect size. Numbers within circles indicate squared multiple correlations for the variables. Overall goodness-of-fit tests (χ^2, RMSEA, CFI and IFI) are shown at the bottom of each model. Models for the experiment evaluating abiotic environmental effects of climate change (Exp. 2, *H. squamatum* leaf litter collected in the Controls and incubated in Control, W, RR and W + RR plots, $n = 40$) are not shown since they did not have an acceptable fit (χ^2 and RMSEA, $p < 0.05$ and CFI and IFI values lower than 0.90 for both litter mass loss and N immobilization)

immobilization (Figure 6b,d). Interestingly, litter decomposition rates showed the largest reductions when climate-induced decreases in litter quality interacted with climate change conditions in the climate manipulation treatments.

4.1 | Effects of climate change-induced alterations in litter quality

Our first hypothesis that climate change-induced alteration of leaf chemistry and morphology would affect litter decomposition and nutrient release was supported for N dynamics and partially supported for litter decay. Climate change treatments lowered the quality of leaf litter (mainly through increased C:N and C:P ratios), with litter morphology not being strongly affected. Nonetheless, changes in litter chemistry under (W)arming resulted in slower decomposition rates, at least during early decomposition stages (6 months). Lignin concentrations were lower in the W + RR treatment and explained part of the variation in litter mass loss among litter types under ambient conditions (Exp. 1), which is consistent with previous studies (Cornwell et al., 2008; Freschet et al., 2012a; Prieto, Stokes, & Roumet, 2016). However, the potential positive effect of a lower lignin content was overwhelmed by climate-induced reductions in litter decomposition in the W + RR treatment.

The observed differences in litter quality among climate treatments proved to be more important for N dynamics as shown by the direct pathways between warming and litter N immobilization in the SEMs where litter quality was included (Exps. 1 and 3), thus highlighting the importance of microbial N demand and immobilization during decomposition (Parton et al., 2007). Across treatments, the leaf litter of *H. squamatum* generally became less enriched in ^{15}N as decomposition progressed, as previously observed in other experiments (Gautam, Lee, Song, Lee, & Bong, 2016; Melillo et al., 1989). However, the higher $\Delta^{15}N$ values in litter from warmed treatments in Exps. 1 and 3 at the end of the study are a clear indication of greater import of external N from the underlying soil during microbial decomposition, as soil N usually has higher $\delta^{15}N$ values than plant N (Craine et al., 2015; Ruiz-Navarro, Barberá, Albaladejo, & Querejeta, 2016). This is in agreement with recent findings reporting that, as the C:N ratio of plants increased, microbes transitioned from C to N limitation leading to N immobilization in litter (Averill & Waring, 2018), which explains the direct positive correlations between warming and litter N immobilization in the SEM models (Figure 6b,d). When leaf litter is poor in nitrogen (high C:N ratios), microbial communities need to mine external sources of N (i.e. soil organic matter) in order to be able to degrade this low-quality material (Averill & Waring, 2018; Craine et al., 2015; Fanin et al., 2012; Fanin, Fromin, Buatois,

& Hättenschwiler, 2013). The 'Nutrient Mining Hypothesis' suggests that N-limited microorganisms (such as those inhabiting high C:N litter) can mineralize soil organic matter to access the N contained within it (Fontaine et al., 2011; Moorhead & Sinsabaugh, 2006), this trait being often attributable to fungi (Boberg, Finlay, Stenlid, & Lindahl, 2010; Rousk, Michelsen, & Rousk, 2016). Therefore, it appears that microbial communities degrading the low-quality litter from warmed plots may have mined and imported greater amounts of N from external sources (e.g. the surrounding soil) to compensate for the high litter C:N ratios in order to be able to decompose other labile C compounds (Craine et al., 2015; Fanin et al., 2012, 2013).

4.2 | Effects of the altered abiotic environment

Our second hypothesis that climate change treatments (warming, drought and their interaction) would reduce litter decomposition rates and nutrient release was supported by our findings. Simulated increases in temperature and decreases in rainfall slowed litter decomposition (both mass loss and decomposition rates) and increased N immobilization in leaf litter. In agreement with previous studies conducted in semi-arid ecosystems (Almagro et al., 2015, 2017; Gliksman et al., 2017), we found that the effects of climate change treatments alone strongly reduced litter decomposition rates (Exp. 2).

In line with our results, most studies dealing with litter decay, including some meta-analyses, have reported significant reductions in litter decomposition with rainfall reduction, but contrary to our results, they found mostly positive effects of warming on this process (Lu et al., 2013; Yue et al., 2015). The negative effect of warming and rainfall reduction in our study may be explained by the desiccating effects of warming on leaf litter moisture and the decreased water inputs under rainfall reduction conditions (Almagro et al., 2015; León-Sánchez et al., 2018; Maestre et al., 2013; Saura-Mas et al., 2012). In drylands, warming increases air temperature and vapour pressure deficit, and thus reduces the frequency of favourable periods for dew formation and deposition, thereby reducing leaf litter moisture (Almagro et al., 2015; Maestre et al., 2013). Although leaf litter moisture content at time of litterbag sampling (summer) was rather low across climate treatments in our study (<5%), observed litter moisture decreases in response to climate manipulation in our study mirrored similar decreases in upper soil moisture content with climate manipulation in previous studies (León-Sánchez et al., 2018; Maestre et al., 2013). Moreover, the effects of decreased litter moisture content on litter decomposition in our study followed the same general pattern previously observed in other semi-arid ecosystems (Almagro et al., 2015; Gliksman et al., 2017). To further support the key role of water availability in decomposition processes in drylands (Almagro et al., 2017; Dirks et al., 2010; Gliksman et al., 2017), and consistent with our finding that interactive effects of litter quality and climate change occurred mainly via decreases in litter moisture content (Figure 6c), litter moisture content was positively correlated with litter mass loss when litter was incubated under climate change treatments, regardless of litter type (Exps. 2 and 3). This is in line with previous findings in other semi-arid Mediterranean ecosystems that reported a positive effect of litter moisture on microbial activity (Almagro et al., 2015; Dirks et al., 2010; Gliksman et al., 2017; Jacobson et al., 2015), and is further supported by the positive relationships between litter moisture and microbial community structure and biomass (PLFAs) within Exps. 2 and 3 ($p < 0.05$). Several studies have observed negative impacts of drought on both the biomass and activity of soil microbial communities, including enzymes involved in C cycling, changes that were linked to an altered microbial community composition (Baldrian et al., 2013; Barnard, Osborne, & Firestone, 2013; Felsmann et al., 2015). Thus, the negative effects of warming and rainfall reduction on litter decomposition in our study were likely indirectly mediated through decreases in litter moisture and/or shifts in the structure and biomass of microbial communities growing on litter, as previously observed (Glassman et al., 2018; Maynard et al., 2018).

4.3 | Interactive effects of altered litter quality and altered abiotic environment

In addition, in support of our third hypothesis, we also found that reductions in litter mass loss within climate change treatments were substantially greater (8%–10%) when litter quality and/or initial microbial communities interacted with climate change. The larger reductions in decomposition when litter quality interacted with climate change conditions, compared to effects of climate change treatments alone, could be related to differences in the initial microbial communities present in each leaf litter type. Indeed, warming and rainfall reduction decreased microbial biomass and increased the fungal-to-bacterial PLFA ratio (only in RR), likely due to the greater resistance of fungi than bacteria against drought due to their hyphal habit and resistant cell walls (de Vries et al., 2012). Although warming normally enhances the activity of microbes when moisture is not limiting (Bergner, Johnstone, & Treseder, 2004; Sardans, Peñuelas, & Estiarte, 2008), the temperature sensitivity of microbes may decline at high temperatures and/or microbial communities may become acclimatized (Melillo et al., 2002; Zogg et al., 1997). Microbial growth and activity can be inhibited when subjected to large temperature changes (>3°C, Lu et al., 2013) and Maestre et al. (2015) found that warming (~2°C) increased soil microbial physiological stress in a gypsum semi-arid ecosystem. Thus, increased abiotic stress may have further contributed to the negative response of microbial communities to warming observed in this study with the subsequent associated negative effect on litter mass loss. Indeed, it has been proposed that persistent climate shifts may force variation towards a soil microbial community that is better adapted to the new conditions (Bell et al., 2014; Sistla & Schimel, 2012).

Decreased precipitation under rainfall reduction, and the subsequent reduction in soil and litter moisture, can result in inhibition of microbial processes (Sardans et al., 2008) and exerts a negative impact on the biomass and activity of the microbial community (Baldrian et al., 2013; Bastida et al., 2017; Sheik et al., 2011). This may explain the indirect negative effect of rainfall reduction on litter

decomposition in our study. Interestingly, in the W + RR treatment (the most realistic scenario), the influence of low lignin concentration in litter (expected to lead to faster decomposition) was clearly outweighed by the comparatively stronger negative effects of this climate change treatment on litter moisture and microbial biomass contents, which led to the slowest decomposition rates. This highlights the importance of considering interactions between litter quality and climate when designing climate change experiments, since studying the effects of climate alone using standard litter types may underestimate the impacts on C loss and N immobilization during decomposition.

Soil organic matter stabilization is a complex process (Six, Conant, Paul, & Paustian, 2002) and depends on multiple abiotic (e.g. soil) and biotic (e.g. microbial communities) factors whose relative influence on C storage is currently under debate (Cotrufo et al., 2015; Cotrufo, Wallenstein, Boot, Denef, & Paul, 2013). A slower leaf litter decomposition and increased N-immobilization under climate change conditions could contribute to slower rates of C and N loss and thus lead to greater C storage and a slower N cycling in the ecosystem (Mueller et al., 2015). However, soil C and nutrient storage are also strongly dependent on the amount of organic matter inputs to soil (Carrera, Bertiller, & Larreguy, 2008; Zhang et al., 2013). In a previous study at the same site (León-Sánchez et al., 2018), we observed a strong decrease in leaf biomass production coupled with lower leaf N contents in *H. squamatum* shrubs that had been growing under climate change treatments (W, RR and W + RR), which will likely overwhelm any potential positive effect of the observed lower decomposition rates on C sequestration. Indeed, we found in a concurrent study that C and N incorporation into the labile organic matter fraction in the topsoil (0–5 cm depth) was lower under warming conditions (W and W + RR) in this ecosystem (I. Prieto and J.I. Querejeta, pers. obs.) pointing to an overall decreased potential for ecosystem C and nutrient storage under climate change conditions.

5 | CONCLUDING REMARKS

Our experimental approach examining the separate and combined effects of litter quality and climate manipulation on decomposition allowed disentangling the drivers of litter decomposition and N dynamics under forecasted climate change in a dryland ecosystem and how climate treatment-induced shifts in microbial communities on litter are associated with shifts in decomposition processes. Climate change-induced reductions in both litter moisture content and microbial biomass lead to large reductions in decomposition rates and support recent findings of the strong microbial Control of litter decomposition at multiple scales (Bradford et al., 2017; Glassman et al., 2018). It is noteworthy that litter N dynamics (e.g. N-immobilization) were more Controlled by changes in litter quality and less by reductions in microbial biomass in response to warming, thus highlighting the different Controls on litter decomposition and N immobilization in this dryland ecosystem. Moreover, this study demonstrates that the interactive effects of an altered climate and changes in litter quality could amplify the adverse impacts of climate change on the biogeochemical functioning of dryland ecosystems, which represent a significant advance in our current understanding of the Controls over litter decay under climate change in drylands (Almagro et al., 2015; Baker & Allison, 2015; Gliksman et al., 2017). Along with the incorporation of direct climatic effects, litter decomposition models should also consider indirect effects related to climate stress-induced alterations in litter quality and microbial communities when studying biogeochemical C and N cycling processes under climate change scenarios.

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AUTHORS' CONTRIBUTIONS

I.P. and J.I.Q. designed and conceived the experiment and M.A. assisted with the designing of the experiment. I.P. performed the field experiment and analysed the data. F.B. carried out microbial analyses and helped with interpretation of results. I.P. wrote the first draft of the manuscript and all authors contributed substantially to revisions.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.cf540df (Prieto, Almagro, Bastida, & Querejeta, 2019).

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