RESEARCH ARTICLE

Relative effects of climate and litter traits on decomposition change with time, climate and trait variability

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Abstract

1. Climate and litter quality drive litter decomposition, but there is currently little consensus on their relative importance, likely because studies differ in the duration, the climatic gradients and variability in litter-trait values. Understanding these drivers is important because they determine the direct and indirect (via vegetation composition) effects of climate change on decomposition and thereby on carbon and nutrient cycling.

2. We studied how microclimate (soil moisture and temperature) and litter traits interactively affect litter mass loss, by using a reciprocal litter translocation experiment along a large climatic gradient in Chile. We followed decomposition for 2 years and used 30 plant species with a wide spectrum of functional-trait values.

3. Litter traits had a strong impact on litter decomposition across the gradient, while an increase in decomposition with soil moisture was observed only in the wettest climates. Overall, soil moisture increased considerably in importance, relative to trait effects, at later decomposition stages, from *c.* 15% of the importance of traits after 3 and 6 months to *c.* 110% after 24 months. Moreover, analysing subsets of the 30 species showed that trait effects on litter decomposition gained in importance when including a greater variation in trait values.

4. *Synthesis.* The relative effects of litter traits and climate on decomposition depend on the ranges in climate and litter traits considered and change with time. Our study emphasizes the critical role of representative ranges in climate and functional trait values for understanding the drivers of litter decomposition and for improving predictions of climate-change effects on this important ecosystem process.

1 | INTRODUCTION

Unravelling the drivers of litter decomposition is crucial for understanding important ecosystem processes such as soil carbon storage and productivity, and for understanding emissions of major greenhouse gases (Berg & McClaugherty, 2003; Canadell et al., 2007; Knorr et al., 2005; Raich & Potter, 1995). Litter decomposition is responsible for the mineralization and transformation of nutrients and carbon from organic residues, providing a major flux of carbon dioxide to the atmosphere (De Deyn et al., 2008) while fostering soil functionality by releasing nutrients that are used by plants and regulating soil organic carbon formation (Scholes et al., 1997).

Environmental factors, including climate, soil conditions and decomposer activity, are important drivers of litter decomposition (Aerts, 1997; Cornwell et al., 2008; García-Palacios et al., 2013; Meentemeyer, 1978; Zhang et al., 2008). Decomposition tends to increase with temperature and precipitation because warm and moist conditions stimulate decomposer activity (Zhang et al., 2008). In addition to the external abiotic conditions, litter quality is another important control of decomposition (Cornwell et al., 2008). Leaf litter quality is determined by a suite of leaf functional traits (Dias et al., 2017; Freschet et al., 2012), that is, leaf structural and chemical properties related to the acquisition and conservation of resources (Reich et al., 1997; Wright et al., 2004). Strategies for carbon gain and nutrient economy differ widely among species and climates, ranging from high resource conservation (i.e. dense, well-defended, resistant and nutrient-poor structures) to fast resource acquisition (with opposite traits, Wright et al., 2004). Structural traits (e.g. leaf toughness and lignin content), nutrient traits (e.g. N and major cations) and defence traits (e.g. phenolic compounds) collectively control litter decomposability, modulating chemical recalcitrance and nutrient availability for decomposers (Freschet et al., 2012). For instance, litter with a high C/N ratio and a high concentration of particular phenolic compounds, such as tannin, decomposes slowly (Aerts, 1997; Makkonen et al., 2012; Zhang et al., 2008). Instead, high concentrations of nutrients such as P, K, Ca and Mg often increase decomposition rates (Makkonen et al., 2012; Zhang et al., 2008). Even though it has become clear that both litter traits and climate play a central role in controlling litter decomposition rates, the relative importance of these two main drivers is still under debate (Bradford et al., 2016; Cornwell et al., 2008).

The relationships between climate, plant traits and litter decomposition have been studied in several ecosystems (Aerts, 1997; Makkonen et al., 2012) and are the basis for model parameterizations up to the global scale (Cornwell et al., 2008; Zhang et al., 2008). Different experiments and meta-analyses show contrasting results—some refer to climate as the most relevant factor (Aerts, 1997; Dyer et al., 1990), while recent results called for more attention to litter quality-driven effects (Cornwell et al., 2008; Makkonen et al., 2012; Zhang et al., 2008). Such apparent inconsistencies may be due to differences in the decomposition stage studied (Currie et al., 2010; Zukswert & Prescott, 2017) and the width and position of the climatic gradients considered (e.g. climatic variables better predicted litter decomposition in cold ranges; Bradford et al., 2016) combined with differences in the species and the trait variation included. It is intuitive that studying a limited number of species or species with low trait variation can underestimate the effect of litter quality on decomposition (Makkonen et al., 2012). Likewise, climate gradients that fail to include sufficiently large and sensitive ranges for decomposition are unlikely to yield strong climate effects (Bradford et al., 2016). It is unclear, however, how the ranges of trait variation and climate can modify their relative importance for litter decomposition. To train models predicting direct and indirect climate-change effects on carbon cycling, experiments that simultaneously encompass wide ranges of climates and traits are therefore urgently needed.

Climate and litter quality interact in their effects on litter decomposition, although this interaction is not well understood. Meentemeyer (1978) and later Currie et al. (2010) observed that, in the early stage of decomposition, the slope of the negative relationship between litter decomposition rate and initial lignin concentration decreased with decreasing actual evapotranspiration, suggesting that in drier and cooler climates, litter traits had weaker effects on decomposition rates. In order to understand climate and litter traits interactions, various studies used reciprocal translocation experiments of litter across climate zones. Most of these experimental studies were done at relatively small spatial scales (Powers et al., 2009; Zukswert & Prescott, 2017), included few litter types (Berg et al., 1993; Bradford et al., 2017; Currie et al., 2010; Trofymow et al., 2002) or focused on a particular plant functional group (Cornelissen & Thompson, 1997; Makkonen et al., 2012), thus reducing the analysed trait spectrum below that of natural communities and limiting the conclusions regarding trait effects. To disentangle climate and trait effects, however, it is essential to include sufficient variability in trait values as well as in climate (Bradford et al., 2016; Currie et al., 2010). Using a reciprocal translocation experiment of litter from 16 woody species across four climate zones ranging from subarctic to tropical forests, Makkonen et al. (2012) showed the critical importance of litter traits for decomposition, with a consistent ranking of the species decomposition rates across climate zones. Although the climate range they assessed was large, it encompassed only four points, varying mainly in temperature regimes while all sites except one (a mediterranean site) were rather moist year-round. The validity of their findings for extrapolation to other, more distinct

climate types with different vegetation than forests therefore remains uncertain. Most importantly, the potential effect of including different climate ranges or trait variability, and the changes in the relative importance of climate and traits during the decomposition process has not been assessed.

Melillo et al. (1989) and Coûteaux et al. (1995) proposed to distinguish two phases in the decomposition process. During the first phase (normally less than a year) a rapid mass loss occurs, resulting from the degradation of labile and soluble compounds, which attenuates the initial quality differences among different litter types (see also Parsons et al., 2014; Preston et al., 2009). These authors suggested that both litter traits and environmental conditions determine the rate of decomposition during the first phase, while environmental conditions dominate after that. This prediction received support from a study in North and Central America (Currie et al., 2010), where litter chemistry was observed to be a better predictor of decomposition than climate only in the early phase (first year). In contrast, Trofymow et al. (2002) showed that, in upland Canadian forests, litter quality control increased in importance over time. Thus, no consistent patterns for changes in the controls of litter decomposition with time have yet emerged and predictions may vary among ecosystems (Bradford et al., 2016; Currie et al., 2010) and litter types considered.

In this study, we assess the relative contribution of plant litter traits and climatic conditions on litter decomposition along a wide climate and vegetation gradient in the Chilean coastal range (26–38°S). The gradient is characterized by a 120-fold increase in precipitation and a decrease in temperature from north to south. This large climatic variation is ideal for disentangling the effects of climate and litter quality, evaluated through a wide range of morphological and chemical traits. Along this gradient, we used a fully reciprocal litterbag translocation experiment with 30 plant species, and followed decomposition for 2 years. We aimed to understand how climate, plant functional traits and time interact in their effects on litter decomposition, and to what extent the variation in trait values and the range of climate zones included in the experiment determine the conclusions about the relative importance of traits and climate for decomposition. We predicted that (a) plant functional traits are more important relative to climate when climate conditions are favourable for decomposition, (b) litter-trait control decreases compared to climate control along the decomposition process and that (c) the importance of litter traits for decomposition increases with increasing trait variation.

2 | MATERIALS AND METHODS

2.1 | Study sites

We conducted our study along the coastal range of Chile (26°S–38°S), along a gradient with homogenous granitoid parent material (Oeser et al., 2018). We selected six sites with contrasting macroclimatic conditions (Figure 1; Table 1): arid desert (Pampa Blanca—Pan de
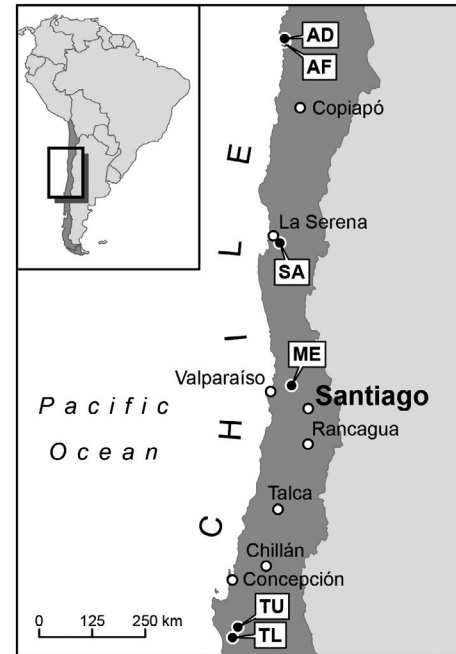

FIGURE 1 Geographic location of sites included in our litter transplant experiment in Chile. AD, Arid-Dry; AF, Arid-Fog; SA, Semi-Arid; ME, Mediterranean; TU, Temperate upland; TL, Temperate Lowland

Azúcar National Park, henceforth, 'AD' for Arid Dry), arid desert with fog influence (Las Lomitas—Pan de Azúcar National Park, "AF" for Arid Fog), semi-arid shrubland (Quebrada de Talca Private Reserve, 'SA' for Semi-Arid), mediterranean forest (La Campana National Park, 'ME' for Mediterranean), upland temperate rainforest (Nahuelbuta National Park, 'TU' for Temperate Upland) and lowland temperate rainforest (Contulmo Natural Monument, 'TL' for Temperate Lowland). The study sites are ranked along a climatic gradient with decreasing mean annual temperature from 15.5°C in AD to 7.3°C in TL, and increasing mean annual precipitation from 13 mm/year in AD to 1,642 mm/year in TU (Table 1). During the study period, the climate was drier than usual in Central Chile (Garreaud et al., 2020), which was especially notable at the ME site, so that precipitation differed little and mean soil moisture did not differ at all between the ME and SA sites. The rainfall seasonality is similar at all sites, with rainfall occurring mainly during the austral winter (from May to August). AD and AF are located in the Atacama Desert, almost without rainfall. The coastal fog, however, is a relevant source of water at AF (Lehnert et al., 2018). Some fog-water input may also occur at AD on an irregular basis, but at much lower frequency and that of overall quantity compared to AF. More detailed information about the study sites is available in Bernhard et al. (2018) and Oeser et al. (2018). At each study site, three independent 10 × 10 m plots were selected.

2.2 | Microclimatic data

Because conditions at the microsites in which decomposition takes place are poorly represented by macroclimatic parameters

TABLE 1 Description of study sites across the climatic gradient considered in this study, including dominant vegetation, selected species for the litter transplant experiment, latitude, meteorological and soil microclimatic data. Meteorological and microclimatic data represent the average for the experimental period (2016–2018)

Site (climate)	Dominant vegetation type and selected species	Veg. cover (%)/LAI	Latitude/ Longitude	Elevation (m)	MAT (C°)	AP (mm)	MST (C°)	MSM (m³/m³)
AD	Very open desert scrub: *Cistanthe grandiflora* (Lindl.) Schltdl., *Cristaria integerrima* Phil., *Frankenia chilensis* C. Presl ex Schult. & Schult.f., *Nolana mollis* I.M. Johnst., *Tetragonia maritima* Barnéoud	3/0.11	−25.95/−70.61	538	15.5[a]	13[d]	20.6	0.11
AF	Open coastal desert scrub: *Eulychnia breviflora* Phil., *Euphorbia lactiflua* Phil., *Nolana crassulifolia* Poepp., *Nolana paradoxa* Lindl., *Usnea* sp.	5/0.15	−26.01/−70.61	798	11.3[b]	13[d]	17.8	0.13
SA	Mediterranean scrub: *Cordia decandra* Hook. & Arn., *Flourensia thurifera* (Molina) DC., *Gutierrezia resinosa* (Hook. & Arn.) S.F. Blake, *Haplopappus decurrens* J. Rémy, *Porlieria chilensis* I.M. Johnst.	45/0.26	−30.05/−71.1	798	14.3[c]	132[c]	19.1	0.18
ME	Mediterranean sclerophyll forest: *Acacia caven* (Molina) Molina, *Aristeguietia salvia* (Colla) R.M. King & H. Rob., *Colliguaja odorifera* Molina, *Jubaea chilensis* (Molina) Baill., *Lithraea caustica* (Molina) Hook. & Arn.	91/2.90	−32.95/−71.06	719	16.1[c]	211[c]	14.1	0.18
TU	Temperate upland rainforest: *Araucaria araucana* (Molina) K. Koch, *Gaultheria mucronata* (L.f.) Hook. & Arn., *Nothofagus dombeyi* (Mirb.) Oerst., *Nothofagus obliqua* (Mirb.) Oerst., *Festuca* sp.	100/2.77	−37.81/−73.01	1,206	7.3[a]	1,642[a]	7.9	0.31
TL	Temperate lowland rainforest: *Drimys winteri* J.R. Forst. & G. Forst., *Greigia sphacelata* (Ruiz & Pav.) Regel, *Laureliopsis philippiana* (Looser) Schodde, *Lophosoria quadripinnata* (J.F. Gmel.) C. Chr., *Nothofagus obliqua* (Mirb.) Oerst.	100/5.14	−38.01/−73.18	426	11.6[c]	783[c]	10.3	0.36

Abbreviations: AD, Arid-Dry; AF, Arid-Fog; AP, annual precipitation; LAI, Leaf area index; MAT, mean air temperature; ME, Mediterranean; MSM, mean soil moisture; MST, mean soil temperature; SA, Semi-Arid; TL, Temperate Lowland; TU, Temperate Upland; Veg. cover, vegetation cover.

[a]Ehlers et al. (2019): Data represent the experimental period of June 2016–May 2018.

[b]Laboratory for Climatology and Remote Sensing, University of Marburg, Germany, personal communication, April 2019.

[c]INIA (2019): Stations Gabriela Mistral, La Cruz and La Isla were used for SA, ME and TL respectively.

[d]Thompson et al. (2003): AP for AF is assumed to be the same as for AD.

(Bradford et al., 2016, 2017), we measured local soil moisture and temperature directly next to the litterbags (see next section) in each of the three plots per site for the duration of the experiment. We measured soil temperature at a depth of 2 cm using HOBO Micro Station dataloggers (H21-002) with two sensors (S-TMB-M002) and volumetric soil moisture at a depth between 0 and 14 cm using TMS-3 dataloggers (TOMST, Czech Republic). Based on the clay and sand content of our study sites (Bernhard et al., 2018), calibrations for sandy loam (AD and AF), loamy sand (SA and ME) and loamy soils (TH and TL) were used

for the soil moisture measurements, as suggested by the provider (Wild et al., 2019). Sensors recorded data every 30 (temperature) or 15 min (moisture). We calculated mean soil temperature (MST) and soil volumetric water content (henceforth, mean soil moisture, MSM) for each decomposition period (0–3, 0–6, 0–9, 012 and 0–24 months, from June 2016 to June 2018). MST and MSM data were aggregated at the level of the plot (mean of two sensors) and site (mean of three plots, Table 1). Additionally, to characterize the radiation environment in the plots, canopy cover and leaf area index (LAI) were estimated. LAI was measured with a Licor

LAI-2200C Plant Canopy Analyzer and is given as the average of three measurements per plot (Table 1).

2.3 | Plant species and functional trait measurements

From the dominant plant species at each site, we selected five species per site (Table 1; at the AD site one lichen species was included) covering a wide spectrum of leaf traits expected to affect litter decomposition (Dias et al., 2017). For each species, we selected five individuals and measured SLA (cm^2/g) and force to punch (Fp, N/cm) on 10 randomly selected green leaves. For three to five subsamples of leaf litter per species, obtained from leaf mixtures collected from at least 10 individuals (senescent litter used in the litter translocation experiment, see next section), we determined concentrations of lignin, carbohydrates, proteins, lipids, total phenolic compounds, tannins and the elements C, N, Al, Ca, Fe, Mg, Mn, Na and P. Finally, we calculated the ratios C/N and Lignin/N. A description of specific measurements and methods of chemical analyses can be found in Appendix S1. For all analyses, traits were averaged at the species level per site.

2.4 | Litter translocation experiment

We performed a full reciprocal litterbag translocation experiment, where litter from each species and site was incubated at each site (i.e. each climate zone). We harvested fresh senescent litter from a minimum of 10 individuals per species near the study plots during the late summer of 2016, either manually or with litter traps, depending on the height and deciduousness of the species. When used, litter traps were installed only under trees that allowed to obtain leaf litter of a single species to avoid potential contamination. For succulent species, green leaves were used. Litter was not washed to avoid the loss of leachable elements, and was oven-dried at 60°C for 72 hr (or 96 hr for succulent species) until constant weight. Subsamples of this litter material were used to determine nutrient contents (Appendix S1). We prepared 10 × 10 cm bags with a polyester mesh (1 mm). Bags were filled with 2 g of oven-dry single-species litter, recording the dry weight of each sample. For a few species with small leaf sizes, we used a second layer (same mesh size) to prevent losses. Litterbags were transported in individual paper bags and the initial weights corrected for any material left in these bags during transportation. One sample per incubation period, species and site was placed in each of the three plots per site. Considering five incubation periods, 30 species and six sites (climates), this triple replication added up to a total of 2,700 litterbags.

The experiment was installed in early June 2016 (late autumn in the southern hemisphere). At each site, we carefully removed local soil litter and organic material, if present, and placed litterbags on top of the mineral soil. In study sites with a patchy vegetation cover, litterbags were placed between patches, but close (0.5–1 m) to shrubs. The experiment was protected against animals with poultry-wire mesh. In spite of this safeguard, some litterbags were damaged and could not be analysed.

Groups of litterbags were harvested at five decomposition stages: 3, 6, 9, 12 and 24 months after installation, to observe both fast short-term changes and slower middle- and long-term changes (Zukswert & Prescott, 2017). At harvesting, litterbags were placed in individual paper bags, oven-dried at 60°C for 48 hr and then litter samples were weighed. For each sample, the percentage of litter mass loss was calculated as $M_0 - M_t/M_0 \times 100$, where M_t is the final dry mass at decomposition stage t, M_0 is the initial dry mass of a sample.

2.5 | Data analysis

Mass-loss data were logit transformed given that they were proportions, whereas trait data (except for proteins, lipids, lignin and P content) were log transformed to achieve normality. As a first data exploration, we calculated the single-factor Pearson correlations of mass loss across all five harvests with the microclimatic variables (using the corresponding MST and MSM for each decomposition period). Because the autocorrelation between MST and MSM was high ($r = -0.88$, $p < 0.0001$, $n = 18$), we used the variable that best correlated to litter mass loss, MSM ($p < 0.0001$ and $r = 0.32$ for site-level data, $n = 2,556$), for subsequent statistical analyses. Likewise, we further explored our data by calculating the Pearson correlations between all traits and of all traits with litter mass loss.

We analysed how litter mass loss changed among sites (as a proxy for climate) and through time, by performing a two-way ANOVA with mass loss as a function of site and time, both as factors, followed by Tukey pairwise-comparisons as post hoc analyses.

To determine how the relative importance of climate and traits for litter mass loss and their interaction changed with decomposition stage, we used linear mixed models (LMMs) to explain mass loss for each decomposition stage separately, comparing the models to detect changes in the driving factors through time. We tested MSM, functional traits and their interaction terms as predictor variables, with study sites as a random factor, using the *lmer* function from the LME4 package (Bates et al., 2014) in R. For each decomposition stage, model selection was performed using forward selection, selecting the most parsimonious model following the Akaike information criterion (AIC). At each step, we quantified the variance inflation of the added variable, using the *check_collinearity* function (vif threshold = 10) from the PERFORMANCE package in R (Lüdecke et al., 2020) to restrict multicollinearity in the model. For each selected decomposition model (i.e. for each decomposition stage), the explained variance per predictor was approached using dominance analysis (Azen & Budescu, 2006; Luo & Azen, 2013) and calculated using the S&B R^2 metric at level 1 (Snijders & Bosker, 1994) with the DOMINANCEANALYSIS package in R (Bustos & Soares, 2020). For each decomposition model, we calculated the relative importance of traits to MSM (RI Traits) as the total variance explained by traits (traits R^2) divided by the variance explained by MSM (MSM R^2).

To evaluate the effect of trait variation (expressed as the *SD*) on the importance of traits for litter decomposition, we used randomization-based statistical procedures. For each decomposition stage, we created models with 1,000 replicates each of 6-, 8- and 10 random species selections out of our 30 species. Because this randomization uses smaller sample sizes, mixed models could not be developed (models did not converge). Therefore, we used linear models (LM) with the same predictors contained in the selected LMM for each decomposition stage. Similar to LMMs, the explained variance per predictor was approached using dominance analysis (Azen & Budescu, 2006). A comparison between these LMs and the selected LMMs shows that differences in the relative importance of their predictors are minimal (Tables S1 and S2). For each randomization, we obtained the variance explained by each trait retained in the models (trait R^2). For each retained trait at each decomposition stage, we determined the Pearson correlation between the R^2 of the trait and its *SD* in the respective randomized set of species.

As an a posteriori analysis, we explored a possible effect of photodegradation at the arid and semi-arid sites. For this, we tested for an interaction between lignin content and soil moisture in explaining litter mass loss using a LMM with site as a random factor.

All statistical analyses were implemented using the R statistical environment v.3.6.0 (R Core Team, 2019).

3 | RESULTS

3.1 | Climate and functional traits effects through time

After 12 months, the site-average litter mass loss ranged from 27% at the semi-arid (SA) to 63% at the temperate lowland site (TL). At all sites, the variation among species was very high (*SD* between 26% and 27%, Table S3). The smallest mass loss was 3% (the lichen *Usnea* sp. when decomposing at the SA), the largest 97% (the succulent *Frankenia chilensis* when decomposing at the TL). After 24 months of decomposition, the site-average litter mass loss ranged from 41% (*SD* = 26%) at the dry arid site (AD) to 85% (*SD* = 27%) at TL (Table S3). The smallest mass loss was 6% (the tree fern *Lophosoria quadripinnata*) at the mediterranean site (ME). At TL, some species (e.g. the soft-leaved species *Cristaria integerrima*, *Nolana crassulifolia*, *Euphorbia lactiflua*) were completely decomposed.

Across all species and decomposition stages, litter mass loss was strongly positively related to soil moisture (MSM, $r = 0.30$, $p < 0.0001$) and negatively to soil temperature (MST, $r = -0.21$, $p < 0.0001$). Litter mass loss differed significantly among climates at all decomposition stages (3 months: $F_{5,494} = 15.9$, $p < 0.0001$; 6 months: $F_{5,507} = 16.7$, $p < 0.0001$; 9 months: $F_{5,507} = 36.1$, $p < 0.0001$; 12 months: $F_{5,504} = 35.6$, $p < 0.0001$; 24 months: $F_{5,514} = 55.5$, $p < 0.0001$, Figure 2). In general, differences were small among the four driest sites (AD, AF, SA and ME) and high between these and the two wettest sites (TU and TL), as well as between the two wet sites in later decomposition stages. After 3 months
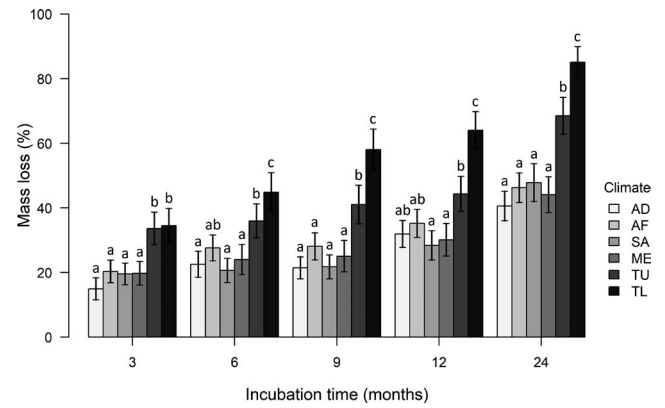

FIGURE 2 Mean litter mass loss (%) after 3, 6, 9, 12 and 24 months of decomposition under different climates. Error bars represent ± 1 *SE*. Different letters indicate significant differences ($p < 0.05$) among climates for each incubation period after post hoc analyses, where mass loss was logit transformed. Refer to Table 1 for climate names
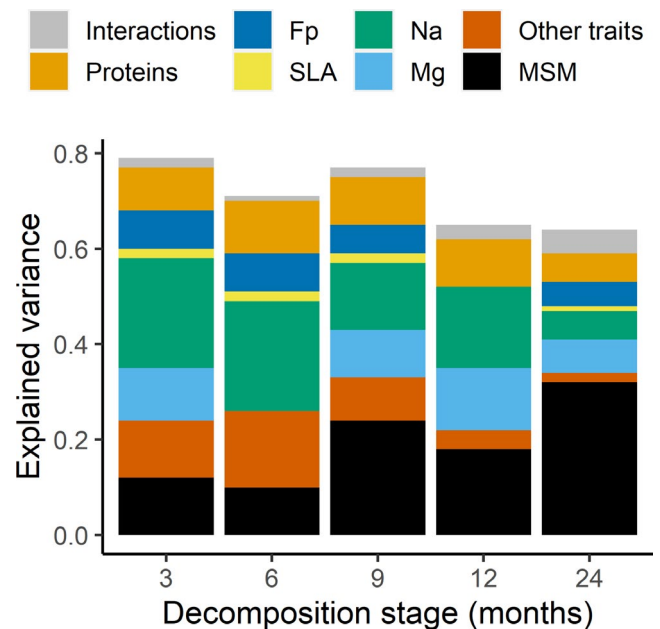

FIGURE 3 Explained variance of mean soil moisture (MSM), functional traits and their interaction in models of litter mass loss across different decomposition stages, for 30 plant species used in a reciprocal litter transplant experiment along the coastal cordillera of Chile. Explained variance of the predictors was approached as the S&B R^2 contribution at level 1 (Snijders & Bosker, 1994) using dominance analysis (Azen & Bodescu, 2006)

of decomposition, the four driest sites already had significantly lower mass loss than the two wettest sites (Figure 2). In the following stages, differences increased between the two wet sites, with the lowland temperate site (TL) having the highest mass losses (TL, Figure 2). The four driest sites did not differ in mass loss at any stage.

In almost all decomposition stages, soil moisture, proteins, sodium (Na) and magnesium (Mg) content and SLA correlated positively with decomposition, while force to punch (Fp) correlated negatively
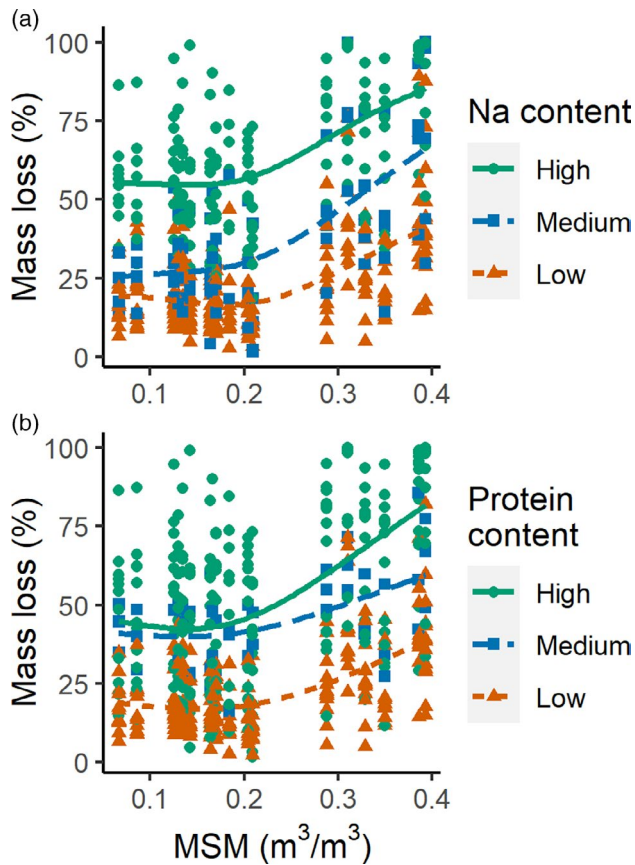
FIGURE 4 Mass loss (%) after 12 months of leaf litter decomposition for 30 species translocated along the coastal cordillera in Chile showing the significant interactive effects of soil moisture (MSM, *x*-axis) with two plant functional traits: (a) sodium (Na) and (b) protein content). The interaction is visualized using three categories for each trait (green, high; blue, medium; orange, low; with cuts at median ± 0.25 × *SD*). Lines shown are smoothed fits through the data, for illustration only, and do not represent the final models. Each point represents observed data for one species decomposing in one plot. Similar results were observed for other decomposition stages; therefore, those results are not shown

(Figure 3; Tables S1 and S4). Among traits, Na was consistently the strongest predictor, followed by the protein and Mg content (Figure 3). Small but significant interactions between MSM and Na, and between MSM and protein content were included in the models at several decomposition stages (Figure 4; Table S1), suggesting that the effect of these litter traits on decomposition changed along the climatic gradient and that the effect of climate differed in dependence of the trait values. In the driest range of the gradient (<0.25 m^3/m^3), litter mass loss differed between species with medium and high Na content and between medium and low protein content, but did not change with soil moisture (Figure 4). In contrast, in the wettest range, the mean and the variation in litter mass loss increased and were driven by both traits and climate (Figure 4). Interactions of MSM with some other traits were also significant, but less frequent across decomposition stages (Table S1). An interaction between climate and lignin was hypothesized because of the contrasting roles of lignin for photodegradation versus biological decomposition (Figure 5a; see Section 3), but this interaction was not observed (Tables S1 and S5; Figure 5b). In all species, independently of their lignin content, decomposition decreased with decreasing moisture in the wetter sites and remained stable in the drier site (Figure 5b). Some traits usually correlating well with decomposition speed, such as C/N, were not included in the models because they were strongly correlated to other factors included (e.g. C/N to protein content) and were thus removed by the variance inflation criterion (vif). This does not imply of course, that they are not related to decomposition (see Table S4), but for example, protein content (which is rarely measured in decomposition studies as this is more elaborate than C/N) was a better predictor.

The importance of traits for litter mass loss (traits R^2) decreased and the importance of MSM increased with time (Figure 3; Table S1). Thus, during the first year of decomposition, traits exhibited higher relative importance than MSM (with traits about 6× more important than MSM after 3 and 6 months and 2.5× after 9 and 12 months), while MSM became more important than traits (with traits 0.8× the importance of MSM) after 24 months of decomposition.
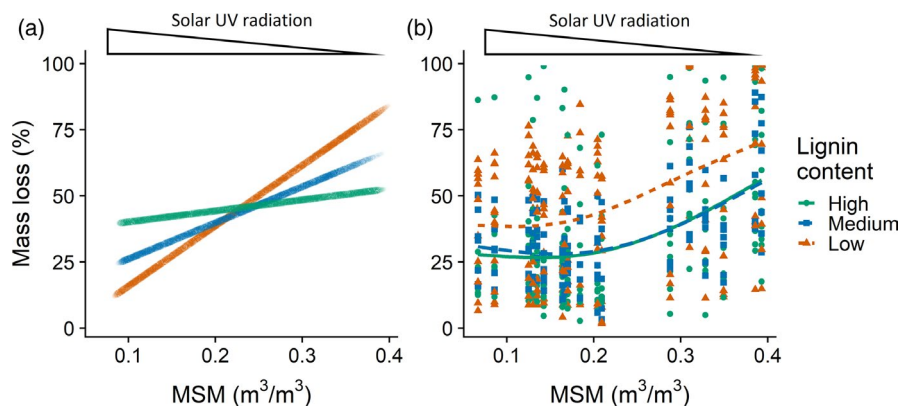

FIGURE 5 (a) Hypothesized and (b) observed response of litter mass loss (%) to mean soil moisture (MSM) and solar UV radiation (increasing from right to left) gradients after 12 months of decomposition for species with different lignin content (green, high; blue, medium; orange, low). Lignin-content groups were divided at the median ± 0.25 × *SD*. Lines shown are smoothed fits through the data, for illustration only, not related to the linear model, which showed no interaction between the effects of lignin content and MSM

TABLE 2 Pearson correlation coefficients of the importance of different traits with the range of trait-values considered in the selected linear models of litter mass loss at different decomposition stages. The importance of each trait was approached as the R^2 using dominance analysis (Azen & Bodescu, 2006). The range of a trait was expressed as its *SD*. Data represent 1,000 randomizations of a 10-species selection out of the 30 species studied, for each model of litter mass loss. Randomizations with six and eight species yielded similar results and thus results are not shown. Bold values represent correlations with $p < 0.05$

Trait	Decomposition stages (months)				
	3	6	9	12	24
Na	**0.14**	**0.19**	**0.14**	**0.17**	**0.15**
Mg	**0.24**		**0.33**	**0.14**	**0.16**
K	**0.19**	**0.31**	**0.18**		
Fp	**0.25**	0.03	**0.22**		**0.13**
SLA	0.03	0.02	**0.14**		**0.13**
Protein	**0.26**	**0.27**	**0.36**	**0.28**	**0.22**
Lignin/N	**0.10**	**0.07**	0.03		
Tannins	**0.08**		0.02		
Carbohydrates		**0.26**		**0.27**	
Lignin		**0.26**			
Lipids				**0.10**	
Fe	**0.19**				0.07
Mn	0.01		0.08		

3.2 | Effects of trait variation on the importance of traits for decomposition

Litter varied strongly in Fp, tannins, Ca, Na and P content (>100-fold variation), considerably in SLA, C/N, Lignin/N, protein, lignin, Al, Mg content (≥10-fold variation) and to a less degree in carbohydrate and Fe content (<10-fold variation, Table S6). For most traits, an increase in trait variation (higher *SD*), for the same number of species (6 or 8 or 10), led to an increase in the average importance of traits (trait R^2) in explaining differences in decomposition (Table 2). Correlations between trait *SD* and trait explanatory power (R^2) were generally weak, even when significant, with a maximum R^2 of 0.36, but consistently positive. Of all traits retained in the models, the variation of proteins and carbohydrates presented the strongest correlation with the R^2 of these traits (Table 2).

4 | DISCUSSION

Our results show that both climate (represented by mean soil moisture, MSM) and litter traits are key factors for litter decomposition, with traits being most important in early and climate in later decomposition stages. Moreover, the importance of traits relative to climate increased with the range of trait values included and the importance of climate was dependent on the particular section of the climate gradient considered. Therefore, it is clear that the relative importance of litter traits and climate in controlling litter decomposition depends not only on the decomposition stage, but also on the variability in both factors.

4.1 | Effects of climate and plant functional traits

We observed higher mass loss in climate zones with higher precipitation and soil moisture, in line with global patterns (Bradford et al., 2017). While a lower mass loss in climates with higher soil temperature appears to contradict the prevalent positive relationship with decomposition (Cornwell et al., 2008; Zhang et al., 2008), this was likely due to the negative correlation of temperature and moisture within our gradient. Differences in decomposition between the two wet sites (upland and lowland temperate sites) show that higher temperatures indeed result in higher decomposition when moisture is not limiting decomposer activity.

Litter mass loss varied among climates in all decomposition stages, but not among the four driest sites. This is remarkable, given the considerable difference in rainfall among these climate zones, at least between the two arid sites and the semi-arid and mediterranean sites—these last two differed less in precipitation than usual due to a very dry period in Central Chile (rainfall deficits between 20% and 40%, Garreaud et al., 2020). We had expected lower decomposition rates at the arid end of the gradient than at the semi-arid and particularly the Mediterranean areas, because of low humidity and very shallow soils, which together with the patchy plant distribution create unfavourable conditions for decomposers (Bernhard et al., 2018; Coûteaux et al., 1995). On the other hand, litter decomposition studies from arid and semi-arid areas have shown that solar radiation can cause photodegradation of plant material and thereby increase litter decomposition (Austin & Vivanco, 2006; Gallo et al., 2006) irrespective of biotic drivers. This process could provide an additional factor for decomposition at our three driest sites (AD, AF and SA), where radiation loads are high and litter was not shaded under vegetation. Although we did not explicitly assess the effects of solar radiation in our study, we evaluated its potential impact by comparing litter mass loss of species with low and high lignin content along the latitudinal gradient. Lignin is difficult to break down by microorganisms but is a preferential target of photodegradation (Austin & Ballaré, 2010). We therefore predicted that if photodegradation would be compensating for the lack of biological decomposition in the arid areas, the litter mass loss of species with high lignin contents should decrease less towards the driest, sun-exposed sites compared to species with low lignin contents. If photodegradations (in arid areas) were stronger than biological decomposition (in wetter areas) in these high-lignin species, they could even show a reversed response, with the highest decomposition at the driest end of the gradient. However, we found no interaction in the effects of lignin content and soil moisture on litter mass loss, and no difference in the shape of the response between species with

low or high lignin contents along the gradient. High-lignin species showed lower decomposition than low-lignin species in all climate zones, as expected if biological decomposition dominated everywhere. Based on this result, it seems unlikely that photodegradation explains the lack of a climate effect among the driest four sites. This does not mean that photodegradation does not occur, but it probably could not compensate for a decrease in biological decomposition completely.

Apart from photodegradation, regular input of fog water to the soil surface at one of the arid sites (AF; Lehnert et al., 2018) could also stimulate decomposition of surface litter without any measurable effects on soil humidity. This process might explain why decomposition was not much lower at this arid site compared to semi-arid and mediterranean sites, in spite of the higher rainfall in the latter two, though it does not explain why in the low-fog site decomposition was also only slightly and non-significantly slower than in the semi-arid and mediterranean sites. Perhaps the most important explanation for the small effect of climate among the four dry sites may lie in the fact that the climate during the experimental period was drier than usual in Central Chile (with rainfall deficits between 20% and 40%; Garreaud et al., 2020), reducing the expected differences among them. The low rainfall frequency observed could particularly have slowed down decomposition, by leading to temporary litter dryness and by severely limiting substrate diffusion and the enzymatic activity of decomposers (Vanlauwe et al., 1995).

The influences of some litter traits on litter decomposition varied along the latitudinal gradient. As indicated by the interactions between some traits (e.g. Na and Proteins) and MSM, and by the differences between the sites through time, litter decomposition was mainly associated to litter traits at the less favourable end of the range (i.e. driest sites). At the most favourable end (wet temperate sites), litter decomposition was related to both trait and soil moisture values. Consequently, our results do not support our first hypothesis that traits should have a stronger relative effect in favourable climates (Bradford et al., 2016). It is likely that in the drier climates, where moisture should strongly limit decomposition, a combination of the above-mentioned reasons (i.e. some additional decomposition due to photodegradation, additional water input from fog and the relatively small differences in soil moisture due to the exceptionally dry year) partially decoupled decomposition rates from gradients in soil moisture and temperature or reduced the strength of these gradients, giving more relative weight to litter-trait effects.

4.2 | Drivers of litter decomposition through time

Traits were clearly important determinants of decomposition rates and together explained between 26% and 66% of the total variation in litter mass loss, with decreasing explanatory power along the decomposition stages. Both nutrient-related traits (Na, proteins and Mg), and morphological traits (Fp, SLA) were found to be good predictors of litter decomposition rates at several stages of decomposition. One of the main controllers of mass loss was Na, an element abundantly available near coastlines due to deposition of oceanic aerosols and critical for consumers but not plants. Previous studies have demonstrated that the addition of Na can promote detritivore activity and decomposition (Kaspari et al., 2014). Clay et al. (2015) reported higher decomposition rates in coastal compared to inland tropical forests, while the addition of Na alleviated these differences. In our study sites, plants with high sodium content were mostly found in the coastal arid and semi-arid sites. In line with previous findings (Clay et al., 2015), our study suggests that Na may stimulate litter decomposition in these coastal ecosystems. However, further experiments (e.g. coastal vs. inland experiments) are needed to confirm this geographic pattern.

By following the decomposition process for over 2 years, we revealed a shift in the relative importance of plant traits and climate for litter decomposition. In the first year, trait effects exceeded climate effects. In the second year, however, climate gained in importance relative to traits, but traits remained influential. Due to the loss of soluble and labile compounds in early decomposition stages, litter materials tend to attain a more similar chemical quality over time (Preston et al., 2009; Parsons et al., 2014; but see Wickings et al., 2012), after which abiotic conditions become the main drivers of decomposition. García-Palacios et al. (2016) found that biotic factors, in particular the decomposer community, are the most important drivers during early-stage decomposition, and that abiotic factors, mostly soil moisture, were increasingly important in the late stages of decomposition. Still, they also observed a marked legacy effect of litter traits in late-stage decomposition, which is also supported by our results. Currie et al. (2010), in a 10-year litter decomposition experiment that included six litter types, found that climate provided superior predictors on both long and short time-scales, while, similar to our findings, litter quality declined in its predictive power with time. Currie et al. (2010) also reported that climate-trait interactions occurred during the first-year decomposition, but not afterwards. However, our results suggest that climate and litter-trait interactions must be interpreted with caution because different interaction terms were retained in different decomposition stage models and overall their relative importance was small.

4.3 | Importance of the ranges of climate and plant functional traits studied

Our results support our hypothesis that the relative importance of plant functional traits for litter decomposition increases with the variation of the trait values covered by the species included in the evaluation. This is an important finding, given that the conclusion of whether it is climate or traits that are more important in controlling decomposition dynamics may be determined simply by the range of traits considered. In other words, when inter- and intraspecific variation in litter traits of a specific plant community are not well

represented, it is difficult to determine the drivers of decomposition correctly, which in the past may have contributed to the prevailing climate-control paradigm (Zhang et al., 2008). Our study included litter from 30 species, with high variation in litter traits among species (e.g. 12-fold in lignin/N, and 13-fold in C/N, which is higher than the variation reported in any previous study, including Harmon et al. (2009), based on nine litter types and 10-fold variation in lignin/N, or Zhang et al. (2008), who used litter types with 2.5-fold variation in C/N). Trait variation resulted in important differences in litter decomposition among species, with the litter of some species almost completely decomposed after 1 year of incubation, while others remained mostly intact, even after 2 years. By reciprocally translocating litter from species of very different ecosystem types, we may have inflated the range of trait values compared to local plant communities. High variation in litter traits, however, was also present within each community (e.g. an average of fivefold variation in C/N and Lignin/N, or 17-fold in Na per community). Moreover, the ranges in trait values reported here are comparable to species-rich plant communities such as tropical rainforests (Hättenschwiler et al., 2008). Our study also shows that the range in climatic conditions and the types of climate zones included in decomposition studies affect the relative importance of trait versus climate in driving decomposition.

5 | CONCLUSIONS

Our study is unique in its very wide range of litter trait values, climatic conditions and the relatively long litter incubation time, including harvests at several decomposition stages. This combination made it possible to identify the major factors that determine the relative importance of climate and litter traits for decomposition dynamics. Soil moisture and plant functional traits both played a key role in driving litter decomposition. Importantly though, their relative contribution and interactions varied through time and with the range of climates and trait variation considered, larger variation leading to larger effect size and relative importance. Experiments in other broad climate ranges, including a similarly large variation in trait values as in our experiment and several litter harvests along the decomposition process, are recommended to further elucidate under what conditions climate dominates as the driver of litter decomposition and when traits become more important. Quantifying these drivers is essential to correctly model decomposition rates and their role in carbon cycling on a global scale. As climate change will additionally induce shifts in the trait distributions of the vegetation, the outcome of carbon-model scenarios depends strongly on a profound and balanced understanding of both vegetation processes and plant- and climate-based controls on litter decomposition.

AUTHORS' CONTRIBUTIONS

M.Y.B. conceived the ideas and designed methodology, in coordination with K.T., A.S. and R.S.R.; R.C. and L.v.d.B. developed the experiment and collected the data; R.C., C.W.M., I.P. and S.H. provided laboratory results; R.C. analysed the data and led the writing of the manuscript, supervized by M.Y.B. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.ttdz08kwb (Canessa et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.