Trait functional diversity explains mixture effects on litter decomposition at the arid end of a climate gradient

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Abstract

1. Litter decomposition is controlled by climate, litter quality and decomposer communities. Because the decomposition of specific litter types is also influenced by the properties of adjacent types, mixing litter types may result in non-additive effects on overall decomposition rates. The strength of these effects seems to depend on the litter functional diversity. However, it is unclear which functional traits or combination of traits explain litter mixture effects and whether these depend on the range of trait values and the ecosystems involved. These uncertainties hamper our ability to predict decomposition in plant communities.

2. We aimed at understanding whether and how functional diversity (measured as functional dispersion, FDIs) influences litter decomposition, and how this influence varies among different climates and across decomposition stages. We calculated FDIs based on litter traits related to nutrient concentrations or to litter recalcitrance, and tested whether these diversity measures and climatic parameters (soil moisture and temperature) explained litter mixture effects on decomposition.

3. Additive mixture effects (i.e. decomposition of mixtures equalling the mean decomposition of the single litter types) were common in most of the evaluated climates. Non-additive, negative effects were mainly restricted to the driest and warmest sites, and decreased with time. Non-additive effects increased in magnitude with the mixtures’ FDIs, with positive effects being related to FDIs in nutrient traits and negative effects being related to FDIs in recalcitrance traits.

4. Synthesis. Litter mixing did not have strong effects on decomposition rates across the studied climatic gradient overall, and the direction and intensity of the mixture effects were context dependent. The effects were stronger and more negative in the dryer ecosystems. Where effects were found, functional diversity calculated from selected groups of traits (related to nutrients or litter recalcitrance) predicted mixture effects, especially where trait ranges were broad, though much of the variation remains unexplained. We propose that
1 | INTRODUCTION

Litter decomposition, that is, the breakdown of organic matter and the release of its components in mineral forms (e.g. CO₂) or as organic molecules, is a fundamental process in biogeochemical cycles and plays a central role in ecosystem functioning (Berg & McClaugherty, 2003). Litter inputs to ecosystems vary tremendously as a function of the identity and diversity of plant species, as species differ widely in their litter phenology, chemistry and morphology (Cornwell et al., 2008). This diversity is thought to influence litter decomposition (Hättenschwiler et al., 2005; Kou et al., 2020; Liu et al., 2020). Litter diversity can affect decomposition positively (faster decomposition of litter mixtures than predicted from single litter species decomposition) or negatively (slower decomposition of litter mixtures), although overall non-additive effects (decomposition of mixtures equal the mean of its parts) seem to prevail (Gartner & Cardon, 2004; Kou et al., 2020; Liu et al., 2020). These responses to litter diversity may depend on the nature of the mixtures, on environmental conditions (e.g. climate or soil properties) and on decomposition stages (Handa et al., 2014; Kou et al., 2020; Liu et al., 2020). Moreover, the multiple mechanisms that can drive positive or negative litter mixture effects remain difficult to determine (Hättenschwiler et al., 2005). Previous studies have shown that the diversity in initial litter quality (i.e. functional diversity) may drive litter mixture effects in predictable ways (Barantal et al., 2014; Handa et al., 2014), because the mechanisms behind these effects are driven by specific litter traits (Barantal et al., 2014; Handa et al., 2014; Liu et al., 2020). However, it still remains largely unclear which traits or combinations of traits are the most relevant.

While several traits have been proposed to drive litter decomposition (Canessa et al., 2021; Makkonen et al., 2012; Zhang et al., 2008), only a few of them may be particularly important in determining litter mixture effects. Nutrients such as nitrogen, potassium, calcium or magnesium can be actively transferred among different litter types within mixtures by micro-organisms (Bonanomi et al., 2014; Briones & Ineson, 1996; Handa et al., 2014; Schimmel & Hättenschwiler, 2007). Since such nutrients are frequently limiting resources for micro-organisms, transfers between litter types can help to optimize resource availability for decomposers. As a result, the relative mixing effects may be stronger for slowly than for more rapidly decomposing litter types within a mixture (Liu et al., 2020; Salamanca et al., 1998), leading to an overall positive effect, that is, faster decomposition in mixtures than predicted from their respective single-species litter (Hättenschwiler et al., 2005; Lummer et al., 2012).

Apart from transferable nutrients, secondary compounds may represent another relevant group of litter traits determining litter mixture effects (e.g. polyphenols; Hättenschwiler et al., 2005). The presence of toxic or recalcitrant compounds in one litter type may inhibit microbial activity, affecting other litter types and decreasing overall decomposition (McArthur et al., 1994), consequently producing negative mixture effects (i.e. slower decomposition than predicted). This process appears to occur principally via passive transfer (e.g. leaching, water films) of inhibitory compounds (Gessner et al., 2010). Hence, any expected correlation between functional diversity and litter mixture effects may be related to relatively mobile nutrients and/or secondary compounds from specific litter types within the mixture (Gessner et al., 2010). As these trait-related mixture effects can be positive or negative, the net effect on the overall litter mixture may be zero despite the fact that specific litter types may decompose at different rates within the mixture compared to when they decompose singly. Because different mechanisms associated with distinct litter traits may be at play simultaneously within litter mixtures, it is important to characterize multiple traits to be able to disentangle their relative role in litter mixture effects (Hoorens et al., 2003). In fact, it seems that no single trait or group of traits is sufficient to reliably predict litter mixture effects (Porre et al., 2020). However, very few studies explicitly include multiple traits to study litter mixture effects, which makes it difficult to understand litter mixture effects and their drivers.

Litter mixture effects seem to differ among ecosystems. Positive effects of litter mixtures on decomposition have been reported in grasslands (Liu et al., 2020; Scherer-Lorenzen, 2008) and tree plantations (Alberti et al., 2017), where a higher functional diversity in physical and chemical traits favoured microbial activity. In natural forests, where most of litter diversity studies have been developed, null, negative or positive mixture effects have been reported (Barantal et al., 2014; Gartner & Cardon, 2004; Gripp et al., 2018; Handa et al., 2014; Leppert et al., 2017), with notable differences among climate zones. This suggests that, beyond litter quality differences, the environment (i.e. climate) and decomposer communities play an important role in litter mixture effects (Zhou et al., 2020). Overall, in temperate and subtropical forests positive effects dominate, while in boreal forests and alpine shrublands null and negative...
effects are more common (Kou et al., 2020; Liu et al., 2020). This may suggest that relatively high and mild temperatures favour positive mixture effects, whereas low temperatures with more constrained soil decomposer activity rather lead to null or negative effects (Liu et al., 2020). Perhaps, at low temperatures environmental constraints override the biotic responses that support positive mixture effects. Alternatively, where litter traits associated with more severe environmental conditions, such as secondary compounds, become more frequent, negative mixture effects may prevail. Although it is not well studied in the literature why unfavourable climate conditions could promote negative effects (Liu et al., 2020), it seems reasonable to consider that, when an active nutrient transfer does not occur, other mechanisms, such as shared effects of inhibitory compounds, can become dominant. Interestingly, however, recent meta-analyses indicate no clear relationship between litter mixture effects and temperature (Liu et al., 2020; Porre et al., 2020), and the question about how environmental constraints may modulate litter mixture effects remains poorly explored. Limitations in humidity may be even more important than temperature for the determination of litter mixture effects. Indeed, deserts and semi-arid areas are known to impose particularly strong limitations on decomposer communities via low moisture availability (Jones et al., 2018; Moskwa et al., 2020). However, very few studies address litter diversity effects on decomposition in these ecosystems (e.g. Ndagurwa et al., 2020). This lack of data across ecosystems impedes an assessment of the effects of environmental parameters and their interaction with litter traits on litter mixture effects (Porre et al., 2020).

To understand how and why litter mixture effects on decomposition differ among ecosystems, studies that concurrently investigate mixture effects across large climatic gradients including contrasting environmental conditions are urgently needed. Yet, such experimental studies are rare (but see Zhou et al., 2020) and meta-analyses are biased towards temperate ecosystems (Kou et al., 2020; Porre et al., 2020). The comparison of litter mixture effects across large environmental gradients is challenging, because of strong differences in litter decomposition rates among sites (Cornwell et al., 2008; Zhang et al., 2008), with potentially variable litter mixture effects in different decomposition stages (Santonja et al., 2019). Specifically, mixture effects seem to decrease with time (Butenschoen et al., 2014; Kou et al., 2020; Wu et al., 2013), probably due to converging litter quality during decomposition, leading to a weaker potential for mixture effects in late decomposition stages (Canessa et al., 2021; Currie et al., 2010).

Here, we present a field experiment that ran for almost 2 years to unravel the effects of two aspects of litter diversity, species richness and functional dispersion (FDIs, a measure of functional richness and divergence), on litter decomposition along a pronounced climate and vegetation gradient ranging from the Atacama Desert (26°S) to humid temperate forests (38°S) in Chile. Using different sets of functional traits to calculate FDIs, we investigated whether nutrient-related traits associated with resource transfer among litter types, or secondary compounds associated with inhibiting decomposition are important for non-additive litter mixture effects (Figure 1).

2 | MATERIALS AND METHODS

2.1 | Study sites

We conducted our study along the coastal cordillera of Chile, from 26°S to 38°S, including six sites with contrasting climates (Figure 2, Table S1) but homogeneous granitoid parent material (Oeser et al., 2018): dry-arid desert (Pampa Blanca—Pan de Azúcar National Park), coastal arid desert with fog influence (Las Lomitas—Pan de Azúcar National Park), semi-arid shrubland (Quebrada de Talca Private Reserve), Mediterranean forest (La Campana National Park), highland temperate rainforest (Nahuelbuta National Park) and lowland temperate rainforest (Contulmo Natural Monument). The study sites are situated along a climatic gradient that decreases in mean annual temperature from 14.4°C at the dry-arid site to 6.7°C in the highland-temperate site, and increases in annual precipitation from...
13 to 2167 mm year$^{-1}$ (Table S1). The monthly rainfall distribution pattern is similar at all sites, where most of the rainfall occurs during the austral winter months, from May to August. The two arid sites are located in the Atacama Desert with almost no rainfall but, at the site with fog influence, the coastal fog is a relevant source of water (Lehnert et al., 2018). At the dry-arid site, some fog-water input may also occur, but with a much lower frequency and magnitude. Further information on the study sites can be found in Bernhard et al. (2018) and Oeser et al. (2018).

2.2 Plant species and functional traits

At each study site, we characterized plant communities in three independent 10×10 m plots on representative mid-slopes and estimated the percentage cover per species at each plot. Data were then averaged at the site level and plant species were selected for the experiment based on their relative abundance (cover >5%, except for the arid sites where the threshold was 3%) and litter availability, with the aim to cover a large range of functional traits while including the most abundant species at each site. This led to a selection of between 7 and 10 species per site, with a total of 50 species (Table S2). Among these, two species occurred at two different study sites (Nolana crassulifolia at the two arid sites, and Nothofagus obliqua at the two temperate sites), but were considered as two different litter types and used only in their site of origin. For each selected species, we measured a range of litter traits known to commonly correlate with litter decomposition (Canessa et al., 2021; Makkonen et al., 2012; Zhang et al., 2008) and to potentially influence litter mixture effects (Hättenschwiler et al., 2005). As traits related to the nutritional quality of litter (Cornelissen et al., 2003; García-Palacios et al., 2016), which could be important in nutrient-transfer-related mechanisms of litter mixture effects (Hättenschwiler et al., 2005), we determined the C-to-N ratio (C:N) and concentrations of Ca, Mg and Na. As traits related to plant defence (Pérez-Harguindeguy et al., 2013; Wright & Cannon, 2001) and to litter recalcitrance, we determined the force to punch (Fp, the physical strength of leaves), and concentrations of lignin, tannins and total phenolics. We included litter C:N rather than N concentration, because it was shown that potential N transfer not only depends on N concentration, but also on the C available to decomposer organisms (Handa et al., 2014; Manzoni et al., 2008). Traits were measured in five individuals per species and 10 leaves per individual. For 30 species, the mentioned functional traits were retrieved from Canessa et al. (2021). For other species not present in that study, data of Fp, C:N, tannins and total phenolics were measured, following the same methodology used in Canessa et al. (2021). All traits were averaged at the species level.

2.3 Decomposition experiment

We performed a litterbag decomposition experiment, where single litter from each species, as well as species mixtures, were incubated at their home site. For each site, we prepared between 7 and 10 different mixtures containing two species (depending on the species richness of each site), two mixtures with four species and one mixture with six species, adding to a total of 68 litter mixtures (Table S3). Using a large set of litter species and mixtures at each site, we covered a wide spectrum of functional diversity values per site (see Section 2.5), allowing us to test diversity and climate effects.

To prepare the litterbags, we harvested senescent litter directly from the plants during the late summer period of 2017, either manually, with litter traps, or by shaking trees. For five succulent species, green leaves were used, since fresh (without signs of decomposition) senescent litter was not found on the plants. Litter was oven-dried at 60°C for 72 h (or 96 h for succulent species). Subsamples of this litter material were used to measure the chemical traits mentioned above.

We prepared 10×10 cm bags with a 1-mm mesh size. Bags were labelled and filled with 2 g (±0.2 g) of oven-dry litter, either with one single species or with treatment-specific mixtures with each species contributing an equal amount. Leaf sizes within species varied to some degree to ensure equal weights of all species in each litterbag, especially for the species with large and heavy leaves (i.e. Drimys...
winteri and Laureliopsis philippiana). For the largest leaves from Jubaea chilensis and Greigia spachelata, all leaves needed to be cut into smaller pieces to make them fit into the litterbags. For species with very small leaves, we lined a second layer of mesh (same size) to prevent losses while maintaining a uniform size of decomposers that can access the litter, thus not altering decomposition (van den Brink et al., 2021). Litterbags were placed into individual paper bags and the initial weight was corrected for any material left in these bags after transportation. To follow the temporal dynamics in decomposition, we prepared nine litter bags per litter treatment, with three bags placed in each of the three independent plots (three per plot) to be harvested after three decomposition periods. With a total of 52 single-species litterbags, 68 mixtures, three decomposition periods and three replicates, this added up to a total of 1080 litterbags.

The installation of the experiment took place in early June 2017 (late autumn in the southern hemisphere). At each site, the local litter layer and organic material, if present, were carefully removed, and litterbags were placed on top of the soil. The experiment was protected against damage from small herbivores with poultry-wire.

Groups of litterbags were harvested 6, 12 and 20 months after installation. At each harvest, litterbags were placed in individual paper bags, oven-dried at 60°C for 48 h and then litter samples were weighed. For each litterbag, the percentage of litter mass loss was calculated as \((M_f - M_i)/M_i \times 100\), where \(M_f\) is the final dry mass after decomposition and \(M_i\) is the initial dry mass. Unfortunately, some litterbags recovered after 20 months of decomposition were accidentally lost, including all bags for one plot at the arid-dry and temperate-upland sites, and for two plots at the temperate-lowland site. Therefore, the temperate-lowland site was not included in the analyses of the latest decomposition stage.

At each plot and at each site, we installed a TMS-3 datalogger (TOMST, Czech Republic) directly next to the litterbags. This allowed us to obtain in situ measures of volumetric soil moisture and soil temperature for the duration of the experiment. We calculated mean soil moisture and mean soil temperature for each decomposition period, that is, 0–6, 0–12 and 0–20 months. Calibrations for soil moisture were done using the clay and sand content of soils (obtained from Bernhard et al., 2018) as suggested by the provider (Wild et al., 2019).

### 2.4 Mixture effects

Litter mass loss of each species decomposing alone was calculated at the plot level (hereafter, single-species mass loss). For each mixture at each plot, we averaged the single-species mass loss of all the species that constituted a mixture to calculate the predicted mass loss \((M_p)\) of a mixture. The litter mixture effect (\(\%\)), that is, the percent difference in the observed mass loss of a mixture \((M_f)\) relative to \(M_p\), was calculated as \((M_f - M_p)/M_p \times 100\) for each mixture and plot individually. Non-additive mixture effects occurred when the observed mixture mass loss was significantly different from the predicted mixture mass loss. These non-additive effects were positive or negative when the observed mixture mass loss was higher or lower than the predicted mass loss, respectively.

### 2.5 Functional diversity

We expressed functional diversity as the functional dispersion index (FDIs, sensu Laliberté & Legendre, 2010). For each litter mixture, FDIs was calculated using the \textit{fdisp} function in the \textit{fd} package in \textit{R} (Laliberté et al., 2014) on a species-by-species distance matrix (Gower dissimilarity matrix) computed from the measured functional traits. We calculated and tested the effect of two different FDIs values, based on different groups of traits. The included traits were selected to represent, on the one hand, well-documented traits that correlate with litter decomposition generally (Canessa et al., 2021; Makkonen et al., 2012; Zhang et al., 2008), and on the other hand, a direct link to the proposed mechanisms behind litter mixture effects (Bonanomi et al., 2014; Hättenschwiler et al., 2005; Lummer et al., 2012; McArthur et al., 1994). Thus, we calculated (1) the index ‘nutrients FDIs’ based on a distance matrix using traits that are potentially related to nutrient transfer among litter and thus, may mostly cause positive mixture effects (C:N, Mg, K and Ca) and (2) the index ‘recalcitrance FDIs’ based on a distance matrix using traits that generally inhibit decomposition, and thus, are expected to produce negative mixture effects (tannins, total phenolics, lignin and Fp; Hättenschwiler et al., 2005). If trait data were missing for some or all of the species in a mixture, FDIs was based on the available data, that is, sometimes the number of traits to calculate the FDIs was lower. A Pearson correlation analysis indicated that nutrients FDIs and recalcitrance FDIs were not correlated \((r[66] = 0.17, p = 0.17)\).

### 2.6 Statistical analyses

To test for differences between observed and predicted mass loss for each mixture and decomposition stage, we used \textit{t}-tests. To test for the influence of diversity measures (species richness, nutrients FDIs and recalcitrance FDIs) and climate (i.e. mean soil moisture and mean soil temperature) on litter mixture effects, we used linear mixed models, for each decomposition period, using site as a random factor and including diversity–climate interactions. Interactions were particularly interesting based on our hypotheses, stating that the magnitude and sign of mixture effects vary as a function of climatic conditions (Handa et al., 2014; Liu et al., 2020; Porre et al., 2020). A model selection procedure was performed by comparing model fits using the corrected Akaik information criterion (AICc) to select the best model predictors (\(\Delta \text{AICc} < 2\)). This procedure was performed using the \textit{dredge} function in the \textit{MuMin} \textit{k} package (Barton, 2018). As several models were selected, model averaging was performed based on AICc weights, using the \textit{model.avg} function in the same package. Model residuals were checked for normality. All predictors were standardized prior to analyses. This allowed us to calculate the relative importance of each predictor using the ratio between its...
model parameter estimate and the sum of all parameter estimates, expressed in %. Marginal and conditional $R^2$ values ($R^2_m$ and $R^2_c$, respectively) were calculated using the Nakagawa and Schielzeth’s method, where $mR^2$ corresponds to the variance explained by the fixed factors, and $cR^2$ corresponds to the variance explained by the fixed and random factors together (Nakagawa & Schielzeth, 2013).

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

3 | RESULTS

Decomposition of single-species litter differed considerably among study sites (Figure S1) and species (Table S2, Figure S2). Litter mass loss of individual species varied from 4% (Echinopsis deserticola) to 59% (Nolana paradoxa) at the arid-fog site and from 35% (Cristaria integerrima) to 80% (Frankenia chilensis) at the arid-dry site during the first 6 months (Table S2). Litter mass loss at the semi-arid and the Mediterranean sites varied less among species, that is, from 11% (Porlieria chilensis) to 34% (Senna cumingii) and from 10% (Jubaea chilensis) to 58% (Geranium robertianum), respectively, for the same period. At the temperate-upland site, mass loss varied from 11% (Araucaria araucana) to 83% (Viola maculata) and at the temperate-lowland site, from 6% (Lophosoria quadripinnata) to 59% (Laureliopsis philippiana) (Table S2). Differences in litter mass loss among species were similarly large after 12 and 20 months, although with overall higher mass loss compared to that observed after 6 months (Table S2, Figure S2).

Litter mixture effects varied among litter mixtures (Figure 3a) and among sites (Figure 3b). The majority of the different litter mixtures (88% across sites and time, Figure 4) showed additive effects, that is, the decomposition of litter mixtures did not significantly differ from that predicted based on the decomposition of the individual species (Table S3). Overall, 12% of all litter mixtures showed non-additive effects on decomposition, but this varied among decomposition stages (with fewer litter mixtures showing additive effects after 20 months) and among sites (Figure 4). Overall, non-additive effects were more frequent towards the arid end of the gradient, irrespective of the decomposition stage (Figure 4). After 12 months, when the highest number of non-additive litter mixture effects occurred, 40% of the mixtures showed significant negative mixture effects at the most arid site (Figure 4). On average, these negative effects consisted of a 17.8% lower mass loss than predicted (Figure 3b). At the semi-arid and the lowland-temperate sites, the mixture effects

![Figure 3](image-url)

**Figure 3** Observed mass loss of 68 litter mixtures (%; n = 3) against predicted mass loss (a) and litter mixture effects (b) at six different sites across a climatic gradient in Chile (colours) after 6, 12 and 20 months of decomposition (columns). Predicted mass loss of a mixture is the averaged single-species mass loss of all the species that constitute this mixture. Values above and below the dashed lines indicate positive and negative effects, respectively, and in (a) they represent a 1:1 relationship. AD, arid-dry; AF, arid-fog; ME, Mediterranean; SA, semi-arid; TL, temperate lowland; TU, temperate upland.
were also negative on average, but these were both weaker, with on average 3.9% (semi-arid) and 8.3% (lowland-temperate) lower mass loss than predicted (Figure 3b). At the remaining three sites (arid with fog influence, Mediterranean and upland-temperate), the mixture effects were overall positive after 12 months, but still not particularly frequent (18%, 15% and 8% of all mixtures showed non-additive effects, respectively (Figures 3b and 4). These positive non-additive effects led to an average higher mass loss of 3.4% (arid site with fog influence), 2.8% (Mediterranean) and 3.2% (upland-temperate) than predicted.

After 20 months of decomposition, litter mixture effects continued to occur, particularly at the dry-arid site (with similar results as after 12 months), but in all other sites, less than 10% of litter mixtures exhibited significant non-additive effects (Table S3, Figure 4).

With linear mixed models, we could explain between 13% and 24% of the variance ($R^2_c$) in litter mixture effects observed (Figure 5, Table S4). Regardless of the decomposition stage, most of the explained variance was related to climatic variables either directly or in interaction with other factors, but those still did not explain more than 16% of total variance. Moreover, the $R^2_c$ of the selected models was twice as large as their $R^2_m$ (Table S4), indicating a strong effect of the random factor (i.e. sites or climate zones). After 6 months of decomposition, the interaction between mean soil moisture and functional diversity (in particular, recalcitrance FDIs) contributed significantly to the observed litter mixture effects (Figure 5, Table S4). This interaction showed that, at the dry end of the gradient, a higher recalcitrance FDIs (functional dispersion index based on traits related to decomposition inhibition) promoted more negative mixture effects (Figure 6a, Figure S3). After 12 months of decomposition, this interaction was no longer significant, but functional diversity in nutrient traits, soil moisture and the interaction between species richness and soil temperature, instead, were significant predictors of mixture effects (Figure 5, Table S4).
nutrients FDIs of mixtures correlated with more positive litter mixture effects (Figure 5, Figure S3). The interaction between richness and soil temperature showed that higher negative effects (i.e. slower decomposition of mixtures than predicted) were observed towards the warmer end of the climatic gradient (i.e. the arid sites), and that richness effects were stronger, with more negative effects at higher richness values (Figure 6b). After 20 months, none of the evaluated parameters explained litter mixture effects significantly, which is likely due to the fewer non-additive mixture effects observed for the final harvest.

4 | DISCUSSION

Our findings from a decomposition experiment along a pronounced precipitation gradient revealed that only a relatively small number of litter mixtures (overall 12%) showed significant non-additive effects on decomposition (both positive and negative). These were on average four times more frequent and three times larger in the most arid than in the more humid range of the gradient, opposite to what we predicted in our first hypothesis. Litter mixture effects were related to soil moisture and temperature, although most of the variation remained unexplained. Functional dispersion (FDIs) of litter mixtures affected mixture effects (both after 6 and 12 months), thus supporting our second hypothesis. Specifically, FDIs based on litter traits related to nutrient concentrations correlated with positive mixture effects on decomposition, whereas traits related to inhibiting secondary compounds correlated with negative mixture effects. This indicates that different mechanisms drive mixture effects and that their relative importance depends on trait expression of site-specific plant communities. Finally, in line with our third hypothesis, litter mixture effects decreased in frequency and magnitude with time in most of the study sites. Collectively, our study indicates that mixture effects on decomposition are comparatively rare across a wide climatic gradient, but when they occur, they are partially predictable from litter-trait diversity.

4.1 | Litter mixture effects across sites and time

Our experiment used a large number of litter mixtures comprising a large variety of species combinations from widely different environmental conditions and of variable litter quality. Still, only a relatively small number of mixtures showed significant non-additive effects, that is, for most litter mixtures the decomposition was similar to the average decomposition of the individual species in the mixture. The range of the means of these litter mixture effects was similar to that reported in a recent meta-analysis (ca. 3%–5%; Liu et al., 2020), with the exception of the most arid site, where, after the first year, the decomposition of mixtures was on average 18% lower than predicted.

After a year, litter mixture effects decreased considerably in magnitude and frequency at most of the study sites, except at the arid-dry site where the effects seemed to remain the same during the second year of decomposition. Previous studies also found that litter diversity effects decrease with time (Butenschoen et al., 2014; Gartner & Cardon, 2004; Lecerf et al., 2011; Wu et al., 2013; but see Santonja et al. (2019) for an opposite result). As decomposition proceeds, different litter types may converge to a similar poor quality, as soluble compounds leach and recalcitrant structural and secondary litter compounds remain (Coûteaux et al., 1995). Thus, if an active translocation and leaching of nutrients between functionally different litters are the mechanisms causing non-additive effects in the early decomposition stages, it is consistent to think that these effects could decrease in later stages. Because litter decomposition
could be more advanced after a certain time in the humid temperate sites than in the arid desert sites (Canessa et al., 2021), one could hypothesize that, after a specific period of time, mixtures from the temperate sites should exhibit less-pronounced mixture effects compared to mixtures of the dry sites. However, contrary to expectations, litter mass loss at the temperate sites was not higher than at the arid sites. Most sites actually presented overall similar decomposition rates, with the arid-dry site showing the highest average rates (Figure S2), indicating that differences in the magnitude and frequency of litter mixture effects across sites are not an effect of differences in the progression of litter mass loss. The average higher litter quality found in arid sites compared to the litter found in the other sites may explain this counterintuitive result in litter mass decay along the climatic gradient (van den Brink et al., 2021).

Overall, more species combinations showed significant and larger litter mixture effects in the most arid climates compared to Mediterranean and temperate humid climates. This indicates that litter mixture effects vary across climate zones, a hypothesis that has rarely been tested along wide climatic gradients (but see Zhou et al., 2020). While most case studies in temperate and tropical areas showed small positive effects of litter mixtures on decomposition (Gartner & Cardon, 2004; Liu et al., 2020), we observed mainly additive (i.e. null) effects in our semi-arid, Mediterranean and temperate sites. Additionally, our results suggest that arid environments can exhibit both positive and negative mixture effects, similar to studies in other harsh environments such as alpine shrublands and boreal grasslands (Duan et al., 2013; Liu et al., 2020).

4.2 Climate and functional diversity as drivers of mixture effects

Although litter mixture effects varied across the gradient, our models showed that climatic parameters such as mean soil moisture and temperature explained little variance during the first decomposition year, and no variance at all during the second year. In any case, it is interesting to notice that the inclusion of site (representing the different climate zones) as a random effect significantly increased the model fits, indicating that other site or climatic parameters, not represented by soil temperature and moisture, likely determine litter mixture effects. Similar to our results, a recent meta-analysis by Porre et al. (2020) showed that litter mixture effects seem to differ among climates, but no climatic parameter (e.g. rainfall or annual temperature) could strongly predict them.

Some alternative environmental variables, such as soil nutrient availability (i.e. soil C:N and N content), could be related to mixture effects: in low-nutrient areas, the presence of a high-quality litter could imply an important input of nutrients for decomposers and thus accelerate the decomposition of adjacent low-quality litter types, producing positive litter mixture effects. This could particularly be the case of the most arid sites of our climatic gradient, which show a strong nutrient limitation (Bernhard et al., 2018). Interestingly, at these sites, both positive (at the arid site with fog influence) and negative (at the arid-dry site) effects were found. The differences may rely on the different microclimatic conditions of these sites: the fog input, which increases superficial moisture (Jung et al., 2020; Lehnert et al., 2018), may facilitate nutrient movements within the litter mixtures, favouring more positive mixture effects with higher trait dispersion at this site. In contrast, at the dry-arid site, the lack of moisture likely limited nutrient transfer as well as microbial activity, likely impeding positive mixture effects, but still allowing alternative mechanisms underlying mixture effects, such as decomposition inhibition by secondary compounds. At the opposite end of the gradient, the lack of mixture effects could be related to the high rainfall, associated with increasing leaching rates: this process implies a quick loss of nutrients, potentially limiting an active nutrient transfer among litter types by micro-organisms (Powers et al., 2009; Schreeg et al., 2013). In fact, Kou et al. (2020) found a significant (although weak) negative correlation between litter mixture effects and precipitation in forests, with smaller mixture effects at sites with higher rainfall. Thus, climatic parameters such as soil moisture or rainfall might have an effect, but are unlikely the dominant factors in determining the strength of mixture effects.

Functional diversity expressed as the dispersion of litter traits (FDIs) had significant, though weak, effects on the decomposition of litter mixtures, especially towards the arid sites during the first year. The lack of an effect of FDIs towards the wet end of the gradient is probably related to the lack of significant litter mixture effects with increasing precipitation. Thus, it may just be less likely to identify potential mechanisms when there are fewer mixture effects and this study cannot correctly conclude about the drivers of potential litter mixture effects in the humid-temperate study sites.

Interestingly, our study showed that higher functional diversity of litter mixtures produced stronger litter mixture effects: litter mixtures with high diversity in inhibitory traits (recalcitrance FDIs) showed more negative mixture effects, whereas litter mixtures with higher diversity in nutrient traits showed more positive effects. That is, there may be a relationship between the variability of nutrient or recalcitrance traits involved and the strength of the effect of this variability on litter decomposition. In other words, a broader trait dispersion range may improve the signal-to-noise ratio when assessing the relationship between litter functional diversity and litter mixture effects on decomposition.

At the arid site with fog influence, a large variance in nutrient traits among species (particularly in C:N and Mg) permitted to have mixtures with very similar (e.g. Nolana divaricata + N. paradoxa) and very different (e.g. Echinopsis deserticola + N. divaricata) litter quality and decomposition rates. Here, for instance, a nutrient transfer from N. divaricata (of high-quality litter) to E. deserticola (low-quality litter) may have benefited the overall litter decomposition of the mixture (Hättenschwiler et al., 2005). In contrast, at the dry-arid site, a variance in recalcitrance traits (mainly total phenolics) permitted mixtures with similar (e.g. Cristaria inegerrima + N. crassulifolia) and very different (C. inegerrima + Frankenia chilensis) quality. Here, for example, the presence of inhibitory compounds in F. chilensis (rich in phenolics and lignin) could have reduced the decomposition of C.
intergestrilla (with high litter quality) and thus, of the whole mixture (Schimel et al., 1998). Therefore, a larger diversity in one of these sets of litter traits could explain that one of the two possible mechanisms involved (nutrient transfer or decomposition inhibition) dominated, leading to contrasting results between these two arid sites. Plants from arid and semi-arid areas are known to have high phenolic content as chemical defences to herbivory and environmental stress (Bár Lamas et al., 2016; Hättenschwiler & Vitousek, 2000). However, in arid areas with some fog or dew input, succulent species with high litter quality are also common (Griffiths & Males, 2017), as is the case of our study sites (e.g. Nolana species). This wide range in key litter traits likely provided enough variation to observe a range of diversity effects (i.e. negative, null and positive) on mixtures decomposition. In contrast, in sites such as the Mediterranean, where most of the species are sclerophyllous and rich in secondary compounds (e.g. Lithraea caustica, Crytocaria alba, Colliguaja odorifera), FDis values were lower, potentially limiting strong litter mixture effects. Secondary compounds are not systematically measured in studies on litter decomposition and, if they are, protocols are often different, making it difficult to fully appreciate the variable effects different groups of secondary compounds may have during decomposition (Coq et al., 2010; Schimel et al., 1998). Thus, to understand the role of these two sets of traits, we recommend using a functionally variable set of litter mixtures across different climate zones.

Our study suggests that both climatic parameters and diversity estimates can partially predict where and when litter mixture effects occur. In addition, when they occur, both nutrients and secondary compounds could be involved in the mechanisms behind mixture effects, and the functional dispersion in these related traits could help to disentangle both mechanisms. However, the present study did not directly measure the occurrence of these mechanisms. Further studies that measure chemical changes in the decomposing litter combined with stable isotope tracing, the effect of isolated specific secondary compounds, or decomposer community composition and activity, in the presence of litter with variable litter quality, could likely close these research gaps.

That said, it is important to highlight that a high proportion of variance in litter mixture effects remained unexplained. Apart from relating to local-scale environmental variation, this unexplained variation may suggest that alternative mechanistic explanations of litter mixture effects rely on species-specific and litter-decomposer interactions that were not studied here.

## 5 CONCLUSIONS

Our study of litter diversity effects on decomposition including a wide range of litter mixtures of many different plant species across a large climate gradient shows that additive effects dominate along this gradient, although both positive and negative non-additive mixture effects also occurred. These non-additive effects were most common in the arid climates, contrary to our prediction, and decrease with time, as expected. Our results suggest that different mechanisms such as nutrient transfer among litter types or inhibition by secondary compounds could be at play, and that their relative importance depends on the diversity of litter functional traits (i.e. litter quality) within mixtures, but also on climate (e.g. moisture, soil nutrient content). It seems particularly important to account for trait-based functional diversity including different litter traits associated to distinct processes (e.g. C/N, K vs. lignin, phenolics) for understanding the driving mechanisms of litter mixture effects that may vary in different climates. Overall, with the very large range of climatic conditions, species and mixture types covered here, our results suggest that litter diversity effects are small relative to other sources of variation in litter decomposition rates, and they may have only little impact on decomposition processes at a large spatial scale.

## AUTHORS’ CONTRIBUTIONS

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

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## CONFLICT OF INTEREST

All authors declare that there is no conflict of interest.

## PEER REVIEW

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## DATA AVAILABILITY STATEMENT

All data supporting the results are available at the Dryad Digital Repository 10.5061/dryad.qrfj6q5jr (Canessa et al., 2022). Other data sources are correspondingly mentioned in the methods and cited in the reference list.
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