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Is litter decomposition enhanced in species mixtures? A meta-analysis

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ABSTRACT

Litter decomposition is a key process in the carbon balance of soils. Commonly, plant litters occur in mixtures where the species differ in quality traits such as the nutrient concentration and organic carbon quality. Many studies explored if mixing litters retards or speeds up litter decomposition compared to species decomposing alone, with varying results. To identify consistent trends with an overarching quantitative synthesis, we test in a meta-analysis whether on average across studies, the mass loss of mixed litters of two plant species is faster than the average mass loss of single litters. We hypothesise that larger trait divergence of the litter quality of the species in a mixture results in a faster mass loss of the mixture than expected based on the single species. Furthermore we hypothesise that part of the variation in litter mixture mass loss can be explained by experimental design and environmental factors. Explanatory variables used were chemical litter trait dissimilarity in the C, N, P, lignin, cellulose, phenolics concentration as well as soil properties, ecosystem, climate, the duration of litter decomposition and the experimental design. Interactions were studied if supported by mechanistic hypotheses. In the majority of studies and on average, we found that the mass loss of mixed litters is equal to the weighted average of the mass loss of the constituent single litters. None of the hypothesised explanatory variables was consistently associated with litter mixture effects on the mass loss and explained variation in mass loss of significant models was invariably only a few percent of all variation. While further data exploration might elucidate further, interactive, patterns, many of these could not be explored due to lacking data. This meta-analysis therefore refutes the notion that mixing litters in general enhances rates of decomposition. We conclude that the effects of litter mixing are in many cases predictable from the decomposition rates of the individual species. According to our results, any interactive effects (positive or negative) between litter species are contextual, and cannot be generalized and predicted beyond the context in which the results were obtained.

1. Introduction

Plant litter input and its decomposition rate are the two primary controls on carbon storage in soil (Lützow et al., 2006). Thus, in order to estimate the amount of carbon returned to the soil and its potential residence time, litter decomposition rates need to be predicted (Aerts, 1997; Gessner et al., 2010). Decomposition rates are influenced by many litter quality parameters as well as the micro-climate (mainly temperature and soil moisture), soil chemistry and community of decomposer organisms (Aerts, 1997; Cornwell et al., 2008; Preston et al., 2009). The decomposition of single litters is relatively well understood. However, in nature, plants rarely grow in monocultures thus litters customarily decompose as species mixtures. Conversely, in agricultural systems, many food crops have been grown in monoculture, yet even then weeds contribute to the biomass in the field. Furthermore, crops are usually grown in a rotation of species such that litters with different quality are mixed in the soil over time. Moreover, in order to promote biodiversity and yields, intercropping, agroforestry and cover cropping are advocated, which results in mixed species litters in those systems too (Isbell et al., 2017). It is thus essential to get a better understanding of litter mixture decomposition mechanisms in order to be able to predict the consequences of plant species diversification in plant communities for carbon dynamics in soils.

As a null model, the decomposition rate of litter consisting of mixtures from different plant species can be expected to be equal to the average decomposition rate of the species in the mixture. However, when litter species with divergent qualities are mixed there could be interactions between the litters during the decomposition process,

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resulting in non-additive effects of species mixtures on decomposition (Handa et al., 2014). Litter traits of plant species vary widely both in their chemical and physical characteristics. Litter chemical quality is most often described as the N or lignin concentration, the C:N ratio or the lignin:N ratio and therefore these parameters are also frequently measured (Aerts, 1997; Campbell et al., 2016). However, multiple studies have shown that the C:N ratio alone cannot explain variation in decomposition rates (García-Palacios et al., 2016; Hättenschwiler and Jørgensen, 2010; Lin and Zeng, 2018; Wardle et al., 2003). A comprehensive study with data from 110 research sites, globally distributed, showed that the total amount of nutrients (N, P, K, Ca and Mg combined) and the C:N ratio accounted for 70.2% of the variability measured in litter decomposition (Zhang et al., 2008). Other litter chemical parameters such as cellulose, hemicellulose, sugar, starch and phenols may also influence litter decomposition rates (Delgado-Baquerizo et al., 2015; García-Palacios et al., 2013; Hättenschwiler and Jørgensen, 2010; Hoorens et al., 2003; Sariyildiz and Anderson, 2003). Polyphenols can sometimes have a larger (antagonistic) effect on decomposition rates than the more frequently measured litter quality parameters (N, P and lignin), since polyphenol-protein complexes are resistant to most decomposing organisms (Hättenschwiler et al., 2005; Hättenschwiler and Vitousek, 2000). Generally, single litters with a higher nutrient concentration and a lower concentration of complex carbon molecules are expected to decompose faster.

Non-additive effects on litter mixture mass loss have been frequently described. A review by Gartner and Cardon (2004) of all litter mixture studies available up to the year 2000 showed that by vote counting, 67% of mixtures exhibited non-additive mass loss. They found that synergistic interactions (higher mass loss in mixture than expected based on single species) were more common than antagonistic interactions (lower mass loss than expected). Since then many additional studies have been published on litter mixing. It would be valuable to integrate quantitatively how differences in litter qualities or other environmental factors can explain the variation in non-additive mass loss.

The mechanisms causing non-additive effects in litter mixture decomposition are still not fully understood (Pérez Harguindeguy et al., 2008). To explain non-additive mass loss, the nutrient transfer hypothesis is most frequently mentioned. This hypothesis states that decomposers preferentially feed on high N litters. Subsequently N is released that could then be transferred to the low N litter and thus facilitate the decomposition of the more recalcitrant litter (Hättenschwiler et al., 2005), causing non-additive mass loss in mixtures by accelerating the decomposition rate of the more recalcitrant litter (Handa et al., 2014; Hättenschwiler et al., 2005). Some studies support the hypothesis (Bonanomi et al., 2014), while others do not (Klemmedson, 1992). Hoorens et al. (2003) studied litter mixtures with a range of litter quality trait differentiation and concluded that the difference in initial single litter chemistry parameters of the components did not predict non-additive mass loss. In contrast, a recent study that looked at the environmental, decomposer and litter trait differentiation effects on litter mass loss showed that litter trait differentiation was the most important variable explaining non-additive mass loss (García-Palacios et al., 2017). Other mechanisms that could cause non-additive mass loss are improved water retention due to one of the component litters in a mixture (Wardle et al., 2003), transfer of toxic compounds and/or phenolics between litter components causing non-additive negative effect (Freschet et al., 2012), and enhanced chemical diversity fostering a richer microbial and fungal decomposer community and thus promoting litter decay rates (Hättenschwiler et al., 2005; Otsing et al., 2018). Yet, except the total litter phenolics concentration, these parameters are not often measured.

Litterbag studies generally have a standard set-up; litter of two or more species is mixed in a litterbag which is placed on or in the soil, usually in its natural decomposition environment. However, there are still methodological differences between studies. The ratio of species in the mixture is not always 50%–50% (Montané et al., 2013; Wu et al., 2014). Litterbag placement is customarily in the litter layer, yet, occasionally litterbags are buried in the soil (Li et al., 2018; Poffenbarger et al., 2015; Prieto et al., 2017). A study comparing litterbags placed at the litter-mineral soil interface to litterbags placed on top of the litter layer showed additive mass loss at the litter-soil interface whereas the same mixtures showed non-additive mass loss on top of the litter layer (Conn and Dighton, 2000). The litterbag mesh size varies greatly between studies, where mesh sizes of <100 μm only allow microfauna to reach the litter, whereas larger mesh sizes allow mesofauna (0.1–2 mm mesh) or macrofauna (>2 mm mesh) inside the litterbags (Gartner and Cardon, 2004; Kampichler and Bruckner, 2009). A diverse litter mixture in terms of the C:N:P ratio could more easily satisfy a diverse decomposer community because more food sources of different qualities are present (Lecerf et al., 2011). Interactions between litter nutrient concentrations and faunal inclusion could be expected. For example, mass loss of *Quercus petraea* litter increased with increasing litter diversity in the presence of millipedes, yet this effect was not found when earthworms were present (Hättenschwiler et al., 2005).

Next to variations in experimental set-up, litterbags are placed in a wide range of ecosystems (natural or arable), soil types and climates. Soils with a low N availability are expected to result in larger non-additive litter mixing effects since the microbial community, decomposing a N poor litter, could potentially benefit more from a high N litter present since there is not enough N in the soil that could be mined (Bonanomi et al., 2014, 2017; Knorr et al., 2005; Lummer et al., 2012). Further, a wetter climate could influence litter mixing by promoting soil moisture, thus making nutrient transfer between litters easier (Makkonen et al., 2013; Wardle et al., 2003). It would not be surprising if litter mixing in arable systems gave different results than litter mixing in natural systems, as, in contrast to natural systems, arable systems have fertiliser inputs, often mechanical disruption of soil by ploughing and (in general) a lower plant diversity. Moreover, in crop systems, the majority of the plant materials are taken away from the field at harvest.

It is essential to develop a mechanistic understanding of litter mixture decomposition in order to predict soil organic matter dynamics in natural and agricultural systems with higher plant species diversity. To date, the generality of a mechanistic understanding of litter mixing on mass loss across studies is lacking. The absence of a quantitative synthesis of previous studies constitutes an important gap in the state of knowledge on the effect of litter mixing on decomposition. The overarching aim of this paper is to find out if, on average, there are non-additive litter mixing effects and, more importantly, to quantify what parameters control the size and direction of non-additive litter mixing effects by doing a meta-analysis on all peer reviewed published litter mixture litterbag studies to date. We hypothesise that 1) greater chemical litter dissimilarity in leaf litter mixtures will cause larger non-additive mass loss in litter mixtures, and 2) larger non-additive litter mixing effects will be found in soils with a low soil N content. We further explore if other experimental design or environmental factors (such as; mesh size, exposure time, ecosystem, climate and soil quality) can explain part of the variation in litter mixture mass loss. Interactions between explanatory factors are explore in as far as these interactions can be motivated mechanistically.

2. Materials and methods

2.1. Data collection and extraction from the literature

A literature search was conducted on 29 October 2018 in the ISI-Web of Science core collection (ISI SCI) with the search terms: "Litter AND Mixture AND Decomposition NOT Stream" as well as "Decomposition AND Mixture AND Soil AND (Litter OR Residue)". This resulted in 523 and 525 publications, respectively, for each search term. After removing the duplicates we had a total of 677 publications. These publications were screened and a publication was included in our dataset if 1) It concerned a litter decomposition experiment which was conducted with the litterbag method, 2) mass loss was reported of both single species litters as well as a 2-species mixture, 3) The ratio of the two litters in the mixture was reported, 4) the time of exposure of litterbags to the environment was stated. If the litter mass loss in a publication was not reported in such a way that the data could be extracted for analysis, we reached out to the author in order to include the data in our database. After screening, 78 publications met the criteria and were used for further analysis. We chose to only include litter mixtures of 2 species because we expected larger effects of litter trait divergence when only 2 distinct litter species were included in the mixture. With more species included divergence would be smaller overall than between the extremes. An experiment was defined as a unique combination of a two-species litter mixture and incubation site, but could include multiple time points at which the litterbags were collected. If the same litter combination was used at a different site or in a different season or year, this was considered as a different experiment. Different litter combinations at the same site and time of burial also constituted different experiments. We coded each experiment within each publication in order to account for random publication and experiment effects in the data analysis. The 78 publications yielded in total 126 sites, 529 experiments and 1359 observations. The information on each publication as well as the response and explanatory variables extracted are reported in Table 1.

2.2. Response variable

To be able to compare the decomposition rate of the litter mixtures with the expected decomposition rate based on the single species litters present in the mixture we determined the observed mass loss (Obs, in %) as reported in the publications and the expected mass loss (Exp, in %). The expected mass loss was calculated as the weighted mean mass loss of the two single species litters as follows:

$$M_{Exp} = \frac{\sum_i f_i M_i}{\sum_i f_i}$$

where M_i is the mass loss in % of a single species, and f is the mass fraction of each litter in the mixture. The response ratio of litter mixing was then calculated as follows:

$$\mathrm{Ln}(R) = \ln\left(\frac{M_{\mathrm{Obs}}}{M_{\mathrm{Exp}}}\right)$$

where M_{Obs} is the observed mass loss (in %) of the mixture and M_{Exp} is the expected mass loss (in %) of the mixture. A positive value for ln(R) indicates that the observed mass loss was greater than expected based on the mass loss of the two single species.

Table 1
Variables extracted from publications and their corresponding units.

Variable	Definition	Data type/ Unit
Title	Title of publication	Text
Authors	Authors of publication	Text
Continent	Continent where study was carried out	Text
Country	Country where study was carried out	Text
Latitude/ Longitude	Latitude and longitude of study site	Decimal degrees
Ecosystem	Ecosystem in which study was carried out	Categorical
Precipitation	Annual average precipitation of study site	mm/year
Temperature	Annual average temperature of study site	°C (average/ year)
Climate	According to Köppen classification	Categorical
SOM	The soil organic matter content at the study site	g/kg
Soil C	The total soil carbon content at the study site	%
Soil N	The total soil nitrogen content at the study site	%
Soil C:N ratio	The soil C:N at the study site	ratio
Soil pH	The soil pH at the study site	pH unit
Size litterbags	The total surface area of the litterbag	cm^2
Mesh size	The mesh size of the litterbag	mm^2
Burial location	Was the litterbag buried in or placed on top of the soil?	Categorical
Time	Exposure time of the litterbag to the decomposing environment	Days
Species	The species name of both single litters	Text
Litter type	Coniferous leaf litter, deciduous leaf litter, shrub/heath, annual plant shoot residue, annual plant root residue or peat moss	Categorical
Woody plant	Did the litter originate from a woody plant?	Categorical
Dried	Was the litter (oven) dried before placing it in a litterbag?	Categorical
Size of litter	Was the litter cut in pieces, if yes what size?	cm
Ratio litter added	The ratio of the two litters in the mixture	ratio
Litter Quality	C, N, P, Lignin, Total Phenolics, Hemicellulose, Cellulose concentration of the litters	All in %
Litter stoichiometry	The C:N, C:P, N:P and lignin:N ratio of both litters	ratio
Mass loss	The amount of mass loss reported after burial	%

2.3. Explanatory variables

Litter quality variables quantified at the start of the litter incubation were used as explanatory variables for litter mass loss: the percent dry weight in the litter of carbon, nitrogen, phosphorus, lignin, cellulose, hemicellulose and phenolics as well as the litter C:N, C:P, N:P and Lignin:N mass ratio. All chemical litter quality components were expressed as the absolute difference (in % dry weight) between the two litters used in the mixture. Furthermore we described litters based on the types of plant species in our database (e.g. coniferous tree leaf litter, deciduous tree leaf litter, shrub/heath, annual plant shoot residue, annual plant root residue or peat moss) as well as being a woody/non-woody plant (Table 1), we differentiated mixtures that had identical plant types (i.e. both coniferous tree leaves) from mixtures that had two different plant types in the mixture (e.g. coniferous + deciduous tree leaves), similarly we did this with woody/non-woody plant mixtures. We examined if the soil organic matter content (SOM), the total soil C and N content, the soil C:N ratio and the soil pH had an effect on litter mixture effects. Regarding the experimental design we examined if the litterbag exposure time or the litterbag placement (in or on the soil) had an effect on litter mixing effects. Additionally, we grouped studies according to litterbag mesh size, with the cut-off at different faunal inclusions: only micro fauna (<0.01 mm), micro- and meso fauna (between >0.01 and < 2.0 mm) and micro-, meso-, and macro fauna (>2.0 mm). In terms of the environmental conditions we tested if annual average rainfall and temperature affected the response ratio. Further we explored if litterbag placement in different continents, climates according to Geiger (1954); Köppen (1900), ecosystems, natural habitats or arable fields had an effect on the response ratio. Additionally, we checked if the size of the litter fragments or drying the litters had an effect on mass loss. ö.

2.4. Statistical analysis

In order to test if litter mixtures show non-additive litter mass loss overall, we tested if ln(R) was significantly different from zero (zero = additive mass loss, > 0 is positive non-additive mass loss, < 0 is negative non-additive mass loss) by performing a one-sample *t*-test. A one-way analysis of variance (ANOVA) was used to test if categorical variables such as continent, ecosystem, natural/arable, faunal inclusion, could explain patterns in non-additive mass loss. We used mixed models to test if initial litter quality or soil properties had a significant effect on the non-additive mass loss (Ln(R)). Random effects were included to account for the possibility of correlation between data originating from the same publication and experiment (Zuur et al., 2009). Additionally, we tested if interactions between co-variables had an effect on ln(R). These interactions were based on ecological relevance where we expected interactions between the litter nutrient concentration, the carbon compounds and/or interactions between mesh size and environmental parameters.

All statistical analyses were carried out in R, version 3.5.0 (R Development Core Team, 2018). The package nlme (Pinheiro et al., 2019) was used to fit linear mixed effects models. Model selection was conducted using the R functions AIC and ANOVA (R package stats; (R Core Team, 2018). The package function r.squaredGLMM from the MuMIn package was used to extract R^2 values of the fixed effects from the mixed effects models (Barton, 2019).

Fifty-nine mixed effects models were fitted to the data (Table A1, appendix). Observations with missing values of a variable were excluded from all analyses which required that variable. This restriction led to several non-identical subsets of the data and not all interactions between litter quality parameters could be tested.

All statistical analyses were performed on three different subsets of the data: 1) all observations extracted from literature (1359 observations), 2) observations that reported the standard error and sample size (860 observations) and 3) observations that reported significant non-additive mass loss (125 observations).

In the two subsets of data which included reported standard errors we gave weights to each observation according to the variance of ln(R). This variance was calculated as:

$$\mathrm{Var}_{\ln(R)} = \frac{SE_{obs}^2}{X_{obs}^2} + \frac{a^2 SE_{X1}^2 + (1-a)^2 SE_{X2}^2}{(a X_1 + (1-a) X_2)^2}$$

where SE is the standard error of the mass loss of litter 1, litter 2, and of the mixture, X is the mass loss of litter 1, 2 and of the mixture and a is the fraction of litter 1 in the mixture.

A funnel plot of standard error against ln(R) of each observation was made to assess publication bias.

3. Results

3.1. Publication bias

There was no publication bias in our database as the funnel plot was symmetrical (Fig. A1, Appendix). There were a few missing values in the bottom right corner which represent studies with a high standard error and a positive non-additive litter mixing effect, however, the number of data points with large SE was too small to conclude that bias exists.

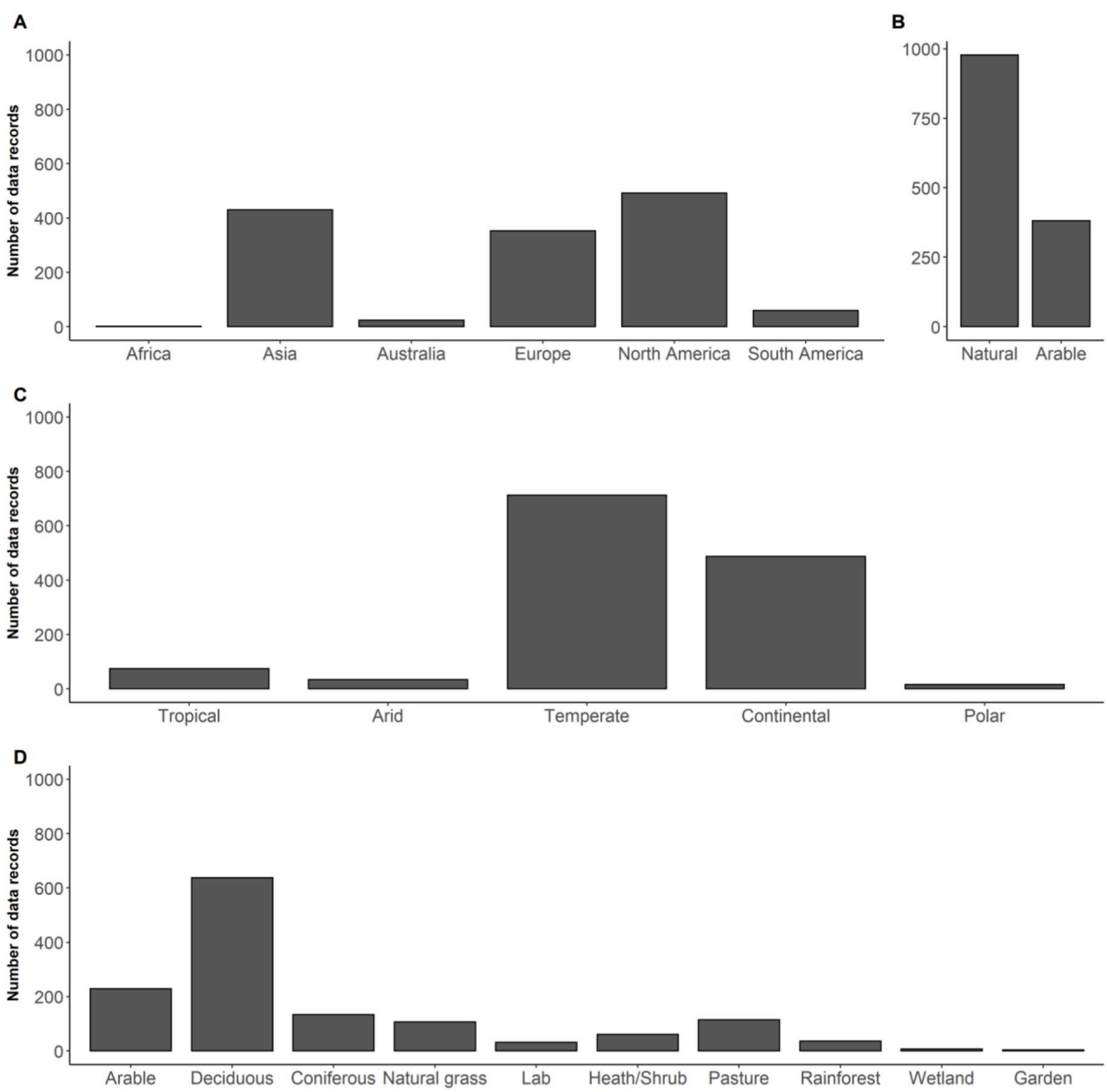

Fig. 1. Number of observations extracted from the literature separated by A) continent, B) natural and arable systems, C) climate, according to Köppen-Geiger, and D) ecosystem.

3.2. Descriptive analysis

A total of 1359 observations were extracted from the literature. Over 90% of the data originated from studies in Asia (almost solely China), North America (mostly the USA) and Europe (Fig. 1 A). The majority of studies were done in natural systems (72%, Fig. 1 B), mostly in either temperate or continental climates (Fig. 1C). The number of studies per ecosystem varied greatly. The dominant ecosystem was deciduous forest (47%) followed by arable crop fields (17%) (Fig. 1 D).

3.3. Litter mixing effects

The response ratio ln(R) varied between a minimum value of −2.17 to a maximum value of 2.42, indicating that litter mixtures at times decompose approximately 10 times faster ($e^{2.42}$) or slower ($e^{-2.17}$) than expected. Fifty percent of all the observations were close to zero with a ln(R) between −0.06 and 0.10 (Fig. A2-A, appendix). Overall, 768 observations showed positive mixing effects and 591 observations showed negative litter mixing effects on litter decomposition rate. The average response ratio of mass loss in litter mixtures was not significantly

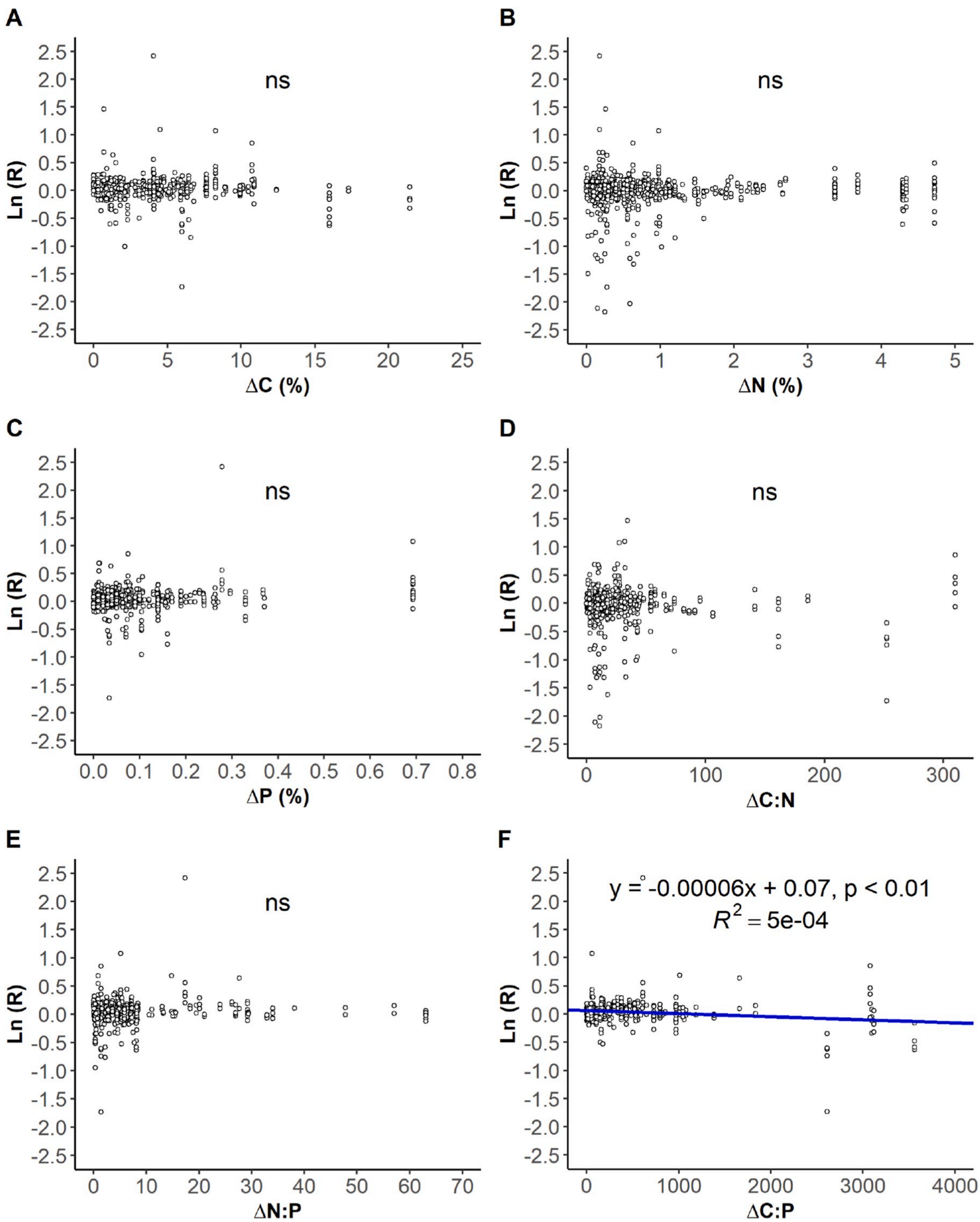

Fig. 2. Relationship between ln(R) and A) ΔCarbon, B) ΔNitrogen, C) ΔPhosphorus, D) ΔC:N, E) ΔN:P and F) ΔC:P, estimated with mixed effects models. Model 2 to 7 (Table A1, appendix), i.e. $\ln(R)_{ijk} = \beta_0 + \beta_1 * \Delta\text{Quality} + a_i + b_{ij} + \varepsilon_{ijk}$, ns = not significant ($p > 0.05$).

different from zero (−0.003 ± 0.007; $p = 0.62$), indicating that on average litter mixtures decomposed at rates similar to what was expected.

A subset of 860 observations reported the standard error and sample size. From this subset the average response ratio of mass loss in litter mixtures was slightly above zero (0.019 ± 0.008, $p = 0.02$, Fig. A2-B, appendix). Within this subset, 125 observations showed significant non-additive mass loss ($p < 0.05$), which is 15% of the litter mixtures. Fifty five percent of these observations showed significant positive non-additive mass loss and 45% showed significant negative non additive mass loss.

On average, litter mixtures did not decompose at different rates than expected, nevertheless given the variation in the response, we further explored potential litter quality effects in explaining variation in the litter decomposition response ratios.

3.4. Chemical litter trait dissimilarity

In contrast to what we hypothesised, differentiation of litter N concentration in the constituent litters in a mixture was unrelated to ln(R).

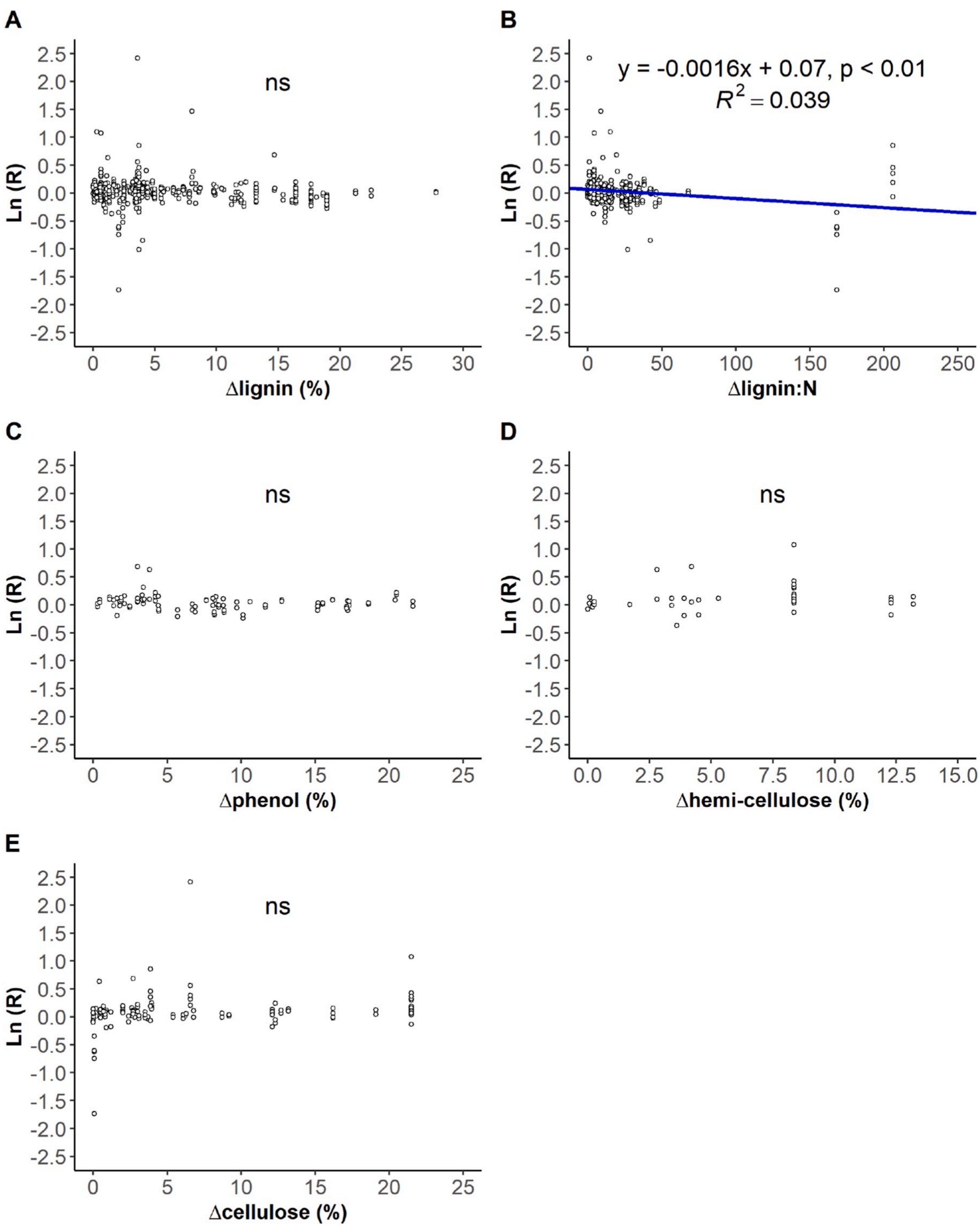

Fig. 3. Relationship between ln(R) and A) Δlignin, B) Δlignin:N, C) Δphenolics, D) Δhemicellulose and E) Δcellulose, estimated with mixed effects models. Model 8 to 12 (Table A1, appendix), i.e. $\ln(R)_{ijk} = \beta_0 + \beta_1 * \Delta\text{Quality} + a_i + b_{ij} + \varepsilon_{ijk}$, ns = not significant ($p > 0.05$).

Neither did the differentiation in the carbon, phosphorus, C:N ratio, N:P ratio, lignin, phenolics or (hemi-) cellulose concentration of the two litter species in the mixture (Figs. 2 and 3). Only the C:P ratio and the lignin:N ratio showed a significant yet weak effect on non-additive mass loss ($\beta_1 = -5.6\ e^{-5}$, $p < 0.01$, $R^2 = 0.033$ and β_1 -1.6 e^{-3}, $p < 0.01$, $R^2 = 0.039$ respectively).

These analyses were repeated on the subset of the data that included standard errors and sample sizes. Here an increase in litter ΔC:N (β_1 -0.0007, $p < 0.01$) and Δ lignin:N (β_1 -0.001, $p < 0.01$) resulted in a lower ln(R) (Fig. 7A and B). While significant, these regressions explained only 0.05% and 0.07% of the variation in ln(R) respectively.

3.5. Experimental set-up, environment and ecosystem

The time of litterbag exposure did not significantly affect litter mixture effects on mass loss (Fig. 4 A). This conclusion is drawn under the limitation of the data that 84% of the studies had litter incubation times shorter than one year. The average annual rainfall an d temperature did not have a significant effect on ln(R) (Fig. 4B and C). None of the soil quality parameters significantly explained the variation in litter mixture mass loss (Fig. 5A–E). These analyses were repeated on the subset of the data that included standard errors and sample sizes. Here an increase in total soil N (β_1 -0.11, $p < 0.05$) and soil C:N ratio (β_1 -0.0006, $p < 0.05$) resulted in a lower ln(R) (Fig. 7C and D). While significant, these regressions only explained 0.03% and 0.04% respectively of the variation in ln(R).

Faunal inclusion, litterbag placement, ecosystems, continents, climates, systems (natural vs arable) and the difference between woody: woody, woody:non-woody and non-woody:non-woody species mixtures did not explain variation in litter mixture effects on decomposition (Fig. 6A–F). Non-additive effects on mass loss were not different when we differentiated mixtures that had identical plant types (i.e. both coniferous tree leaves) to mixtures that had two different plant types in the mixture (e.g. coniferous + deciduous tree leaves). Drying litters and the size to which the litters were cut before the incubation period also did not have an effect on ln(R).

3.6. Interactions

We tested interactions between the different litter quality parameters, as well as interactions between litter quality and climate, time, mesh size and soil N (models 29 to 59, Table A1, appendix). From the tested models the two-way interaction between litter ΔN * time ($p < 0.05$), litter ΔP * time ($p < 0.05$), litter ΔC:P * rainfall ($p < 0.01$), litter ΔC:P * temperature ($p < 0.05$) and the 4-way interaction between ΔN * ΔP * Δlignin * time ($p < 0.05$) were significant (Table A2, appendix). These analyses were repeated on the subset of the data that included errors and sample size. Here the interaction between and litter ΔP * time was no longer significant. Yet the two-way interaction of litter ΔC:P * rainfall ($p < 0.05$), litter ΔC:P * temperature ($p < 0.01$) and the three-way interaction between litter ΔN * ΔP * time were significant ($p < 0.05$). Additionally two-way interactions between ΔC:N * rainfall and ΔC:N * temperature as well as Δlignin:N * temperature were also significant. Yet these interactions explained only 0.06%, 0.08% and 0.08% respectively of the variation in litter mixing. Further data exploration included a repetition of above analysis executed for each ecosystem and climate separate (if the number of observations allowed). Although there were significant interactions between litter quality and experimental design and ln(R) these interactions were weak with generally a very low R^2 (Table A3 and A4 in appendix).

4. Discussion

The decomposition rate of litter mixtures composed of two species is on average not faster or slower than expected based on the decomposition rate of the single species litters and their proportions in the mixture. Many studies report non-additive mass loss in litter mixtures. In the data set assembled for this meta-analysis, 15% of the records showed a significantly higher or lower mass loss than expected, which is considerably lower than the 67% of significant non-additive mass loss reported previously in a vote-counting review by Gartner and Cardon (2004). In our analysis, none of the selected parameters explained a pattern in this data. For the majority of litter mixtures (85%) the mass

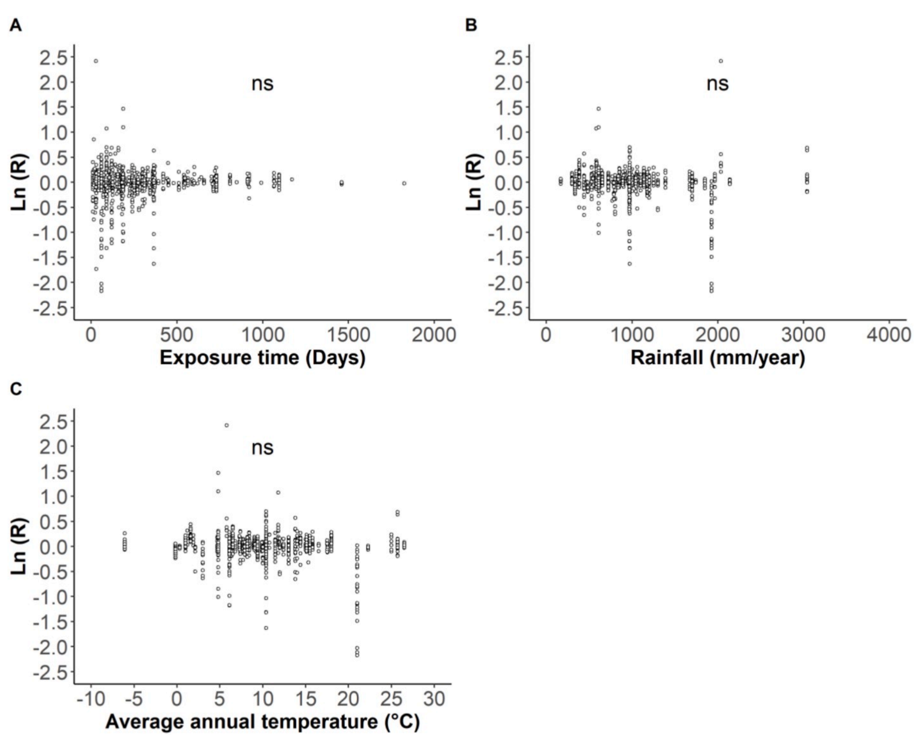

Fig. 4. Relationship between ln(R) and A) exposure time of the litterbag, B) the average rainfall per year (mm/year) and C) the average annual temperature. Estimated with model 20, 23 and 24 respectively (Table A1, appendix), i.e. $\ln(R)_{ijk} = \beta_0 + \beta_1 {*} X + a_i + b_{ij} + \varepsilon_{ijk}$, ns = not significant ($p > 0.05$).

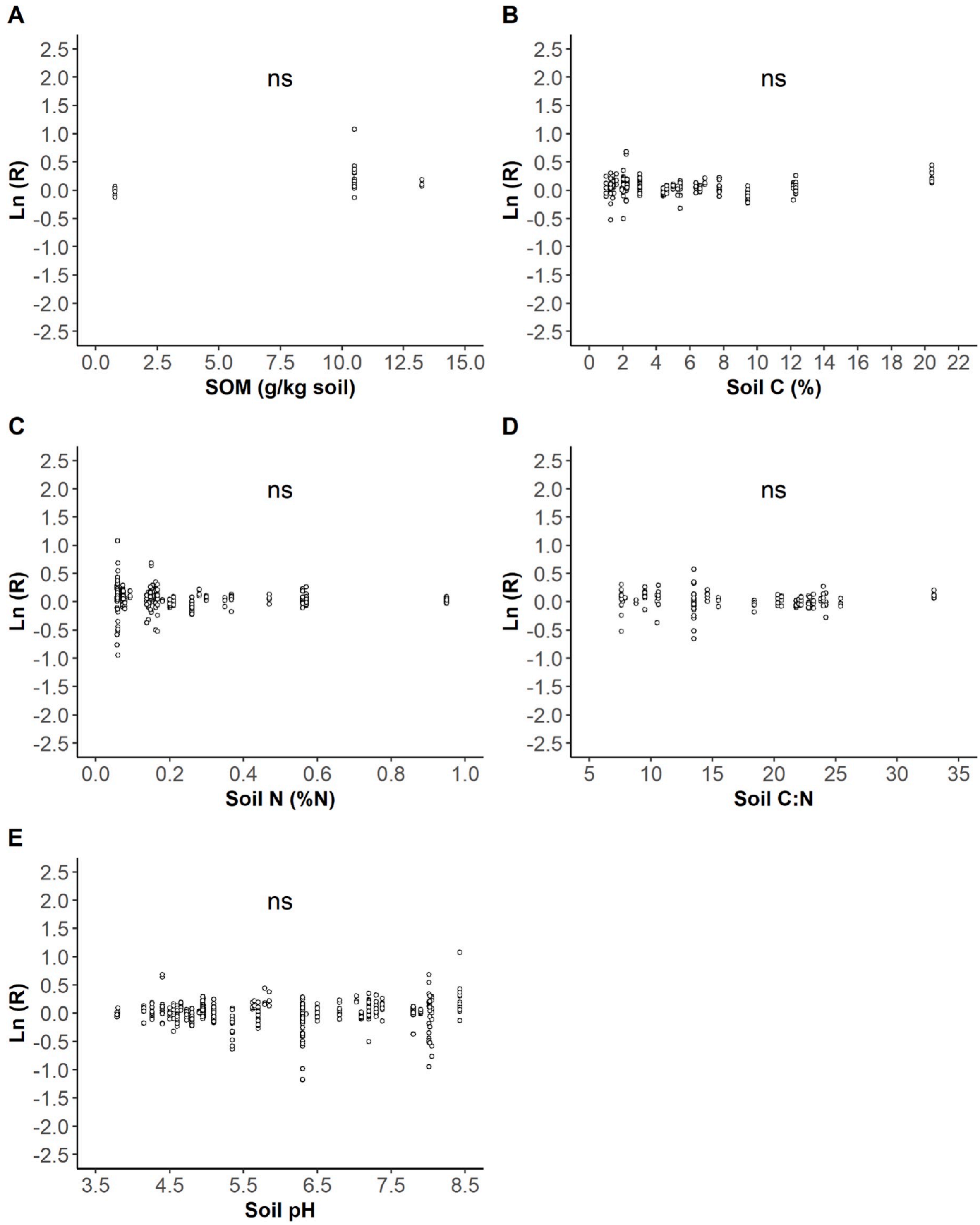

Fig. 5. Relationship between ln(R) and A) Soil organic matter, B) Soil total carbon content, C) Soil total nitrogen content, D) Soil C:N ratio, E) Soil pH, estimated with mixed effects models. Model 13 to 17 (Table A1, appendix), i.e. $\ln(R)_{ijk} = \beta_0 + \beta_1{}^*$ Soil Quality $+ a_i + b_{ij} + \varepsilon_{ijk}$, ns = not significant ($p > 0.05$).

loss can be predicted based on component single litter mass losses.

4.1. Chemical litter trait dissimilarity

Contrary to what many studies suggest, a larger difference in litter N concentration did not result in greater non-additive litter mixture effects, even though the range of ΔN and ΔC:N included in our dataset was sufficiently large (ΔN between 0.0 and 4.72%; ΔC:N between 0.2 and 309.84) in order for nutrient transfer to have taken place. Therefore we conclude that the difference in litter N concentration does not as single factor control the size and direction of non-additive mass loss. This conclusion is consistent with two other studies. Lummer et al. (2012) found that N transfer from a N rich species to a N poor species did occur, yet mixture mass loss was still additive in these mixtures. Schimel and Hättenschwiler (2007) showed in a microcosm experiment with N-labelled litter that N transfer in litter mixtures was not determined by the difference in the N concentration between the two litters but by the mass fraction of N in the leaf litter with the higher mass fraction of N.

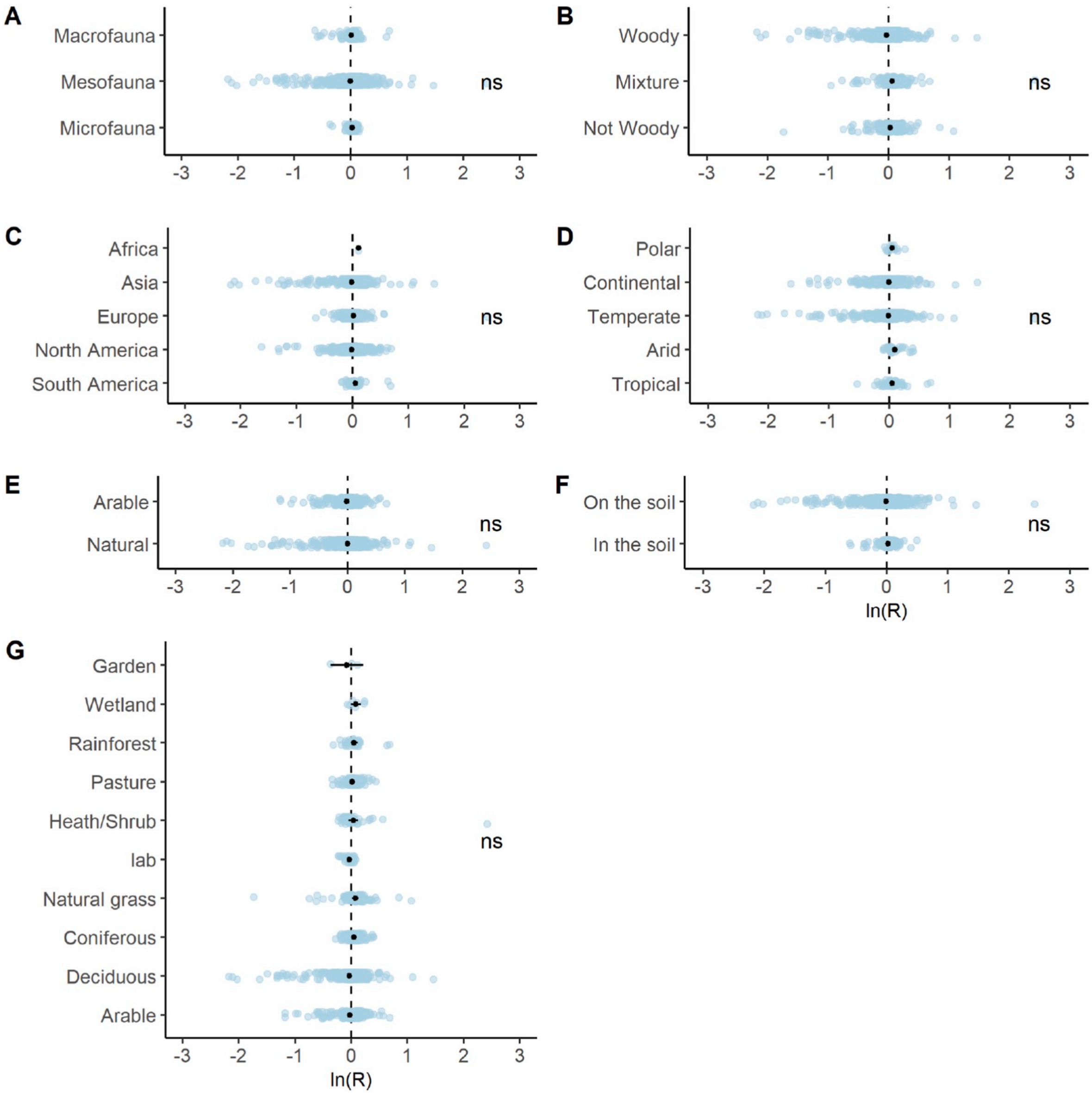

Fig. 6. Response ratio of litter mixture decomposition, ln(R), plotted against A) faunal inclusion separated into: microfauna (mesh <0.01 mm), mesofauna (mesh 0.01–2 mm) and macrofauna (mesh >2 mm), B) Litter mixtures of: only woody plants, woody and non-woody plants, and only non woody plants, C) continent, D) climate, E) natural vs. arable sites, F) location of litterbag placement and G) the ecosystem. The black dots show the average and the light blue dots show all the data on which the average is based. Error bars (hardly reach outside average) show the standard error. None of these factors significantly influenced the size of the non-additive effect ($p < 0.05$, Table A2 appendix). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Many factors apart from the difference in N concentration could affect the rate of decomposition of mixed litters. Thus, not showing an effect of different N concentration in litters on the rate of decomposition of the mixture, as we do here, does not necessarily mean that the effect does not exist, but it does mean that this effect, if it exists, is not strong enough to emerge consistently under the varying conditions represented by the data assembled for this meta-analysis. We cannot exclude that other factors, such as toxic compounds or water limitation that hamper nutrient flow, could interfere with or mask a potential effect of N transfer.

None of the other litter quality parameters could explain non-additive mass loss in mixtures. Surprisingly the presence of phenolic compounds in one of the litters did not show an antagonistic effect on litter mixture decomposition, even though the phenolics concentration ranged between 0 and 23% of dry mass (out of yields commonly reported of 1–25% of leaf dry mass (Hättenschwiler and Vitousek, 2000)). That phenolics did not cause antagonistic effects could also be explained by the fact that there is a range of phenolic compounds. The two types of phenolics, low molecular weight phenolics and condensed tannins, can either provides a substrate for microbial growth or inhibit microbial growth (Hättenschwiler et al., 2005) and thus could potentially result in opposite effects on litter mass loss (Hättenschwiler and Vitousek, 2000).

Even when we examined the subset of studies showing significant non-additive mass loss, litter chemical trait dissimilarity could not convincingly explain patterns in non-additive mass loss. This is in agreement with Tardif and Shipley (2015), who reported non-additive mass loss in a subset of 42 different litter mixtures studied yet could not generalise litter chemical diversity effects on non-additive mass loss. We further explored the data by repeating the analysis of litter quality and or the experimental set-up effects on non-additive mass loss in different ecosystems and climate zones (if enough data was available in each subset). This did not result in any clear patterns in subsets of the

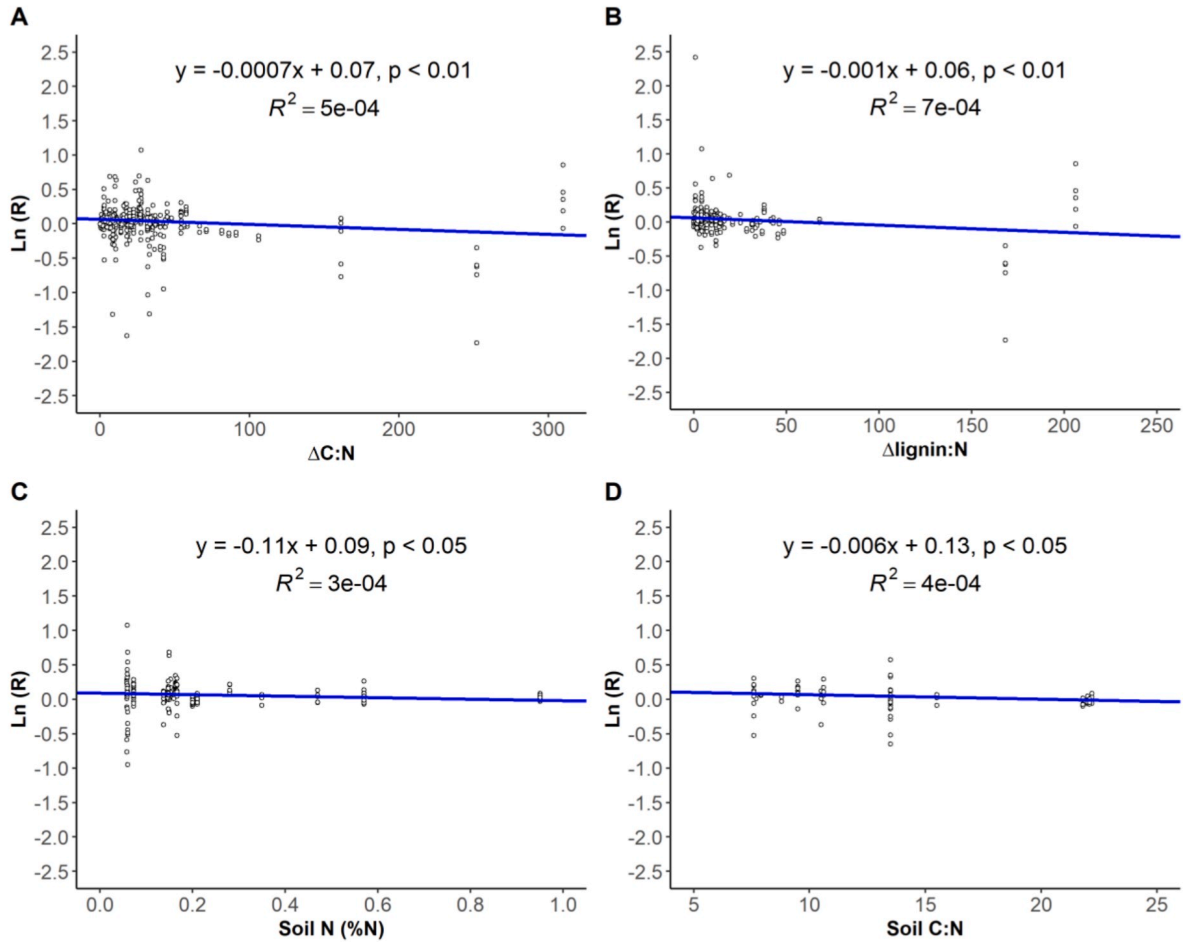

Fig. 7. The relationship between ln(R) and A) ΔC:N (unitless), B) Δlignin:N (unitless), C) Soil N (% N) and D) Soil C:N (unitless) estimated with mixed effects models on the subset of studies that reported the error term (860 observations). Model 4, 9, 15 and 16 (Table A1, appendix), i.e. $\ln(R)_{ijk} = \beta_0 + \beta_1{}^* \Delta\text{Quality} + a_i + b_{ij} + \varepsilon_{ijk}$ The data in the model were weighted according to the reported variance.

data with a specific ecosystem or climate (Table A3 and A4). It has to be noted that the majority of litterbag studies were executed in forest ecosystems; therefore additional studies in the grasslands, peatlands and arable lands are necessary in order to make a more robust analysis for these ecosystems.

4.2. Experimental design

We did not find a difference between the different faunal inclusions on the size of non-additive mass loss in litter mixtures. Previously, Barantal et al. (2014) showed that soil fauna played a key role as a driver of litter mixture effects. As expected they found that synergistic non-additive mass loss increased with larger trait dissimilarity when meso- and macrofauna were included. Yet, in our meta-analysis, there was no significant interaction between ΔN and faunal inclusion.

Another major factor which did not explain the size of non-additive mass loss was the exposure time of the litterbags to the environment. A longer exposure time has been shown to create larger non-additive effects (Srivastava et al., 2009). These authors hypothesised that the mechanisms of litter decomposition and thereby potential non-additive effects in litter mixtures change over time from rapid nutrient leaching to an increasing reliance on the soil fauna to breakdown more complex molecules. Perhaps we did not see this trend because the large majority of the studies (84%) had an exposure time of less than 1 year.

Additionally we also expected factors like the litterbag placement (in or on soil) to have an effect (Conn and Dighton, 2000). Litterbags buried in the soil are in close contact with soil microbes and mineral surfaces whereas litterbags placed on top of the soil are in contact with other litters, thus surrounding leaves may interact with the litter species in the litterbags, creating more diverse mixtures. However when we distinguished between studies in which the litters were buried in the soil (no contact with other litters) and studies with litterbags placed on the soil (contact with other litters) we did not find significant differences. The issue with this is that some studies are performed in sites with single litter species (litter bed), and others in a site with a wide variety of litters present (natural forest). It can therefore be argued that studies examining litter mixture decomposition when placing litter on a litter layer might not always be valid due to other interactions present with external litters.

4.3. Environment

We expected that poor soils in terms of the mineral N content would show larger non-additive mass loss effects. We did not find a significant effect of the soil N content on the size of non-additive mass loss. However this is perhaps not surprising since the soil nutrient status was not often reported, and when soil N was reported it was as the total N content. A large part of this total N content could be unavailable to the decomposer community, depending on the soil type, and this could thus influence the mass loss. Moreover, Vivanco and Austin (2011) found that additive litter mixture effects in soil without N addition turned into synergistic effects when N was added to the system. They suggested that it might be possible that once N limitation was removed, other limitations constrained mass loss, and synergistic effects were observed again indicating that the N availability in itself is not a good predictor of litter mixture effects. Contrary to what we expected we did not find a significant difference in litter mixture effects between natural and arable systems.

4.4. Lacking explanatory variables

Surprisingly, the large majority of litter mixtures had close to additive mass loss (Fig. A2, appendix). And only 15% of the data showed significant non-additive mass loss in mixtures. Moreover, no litter or soil quality parameter showed a (strong) significant relationship with the direction/size of the non-additive effect. Even so, non-additive effects are found with mass loss being sometimes ten times as fast or slow as expected. Thus litter mixing can sometimes have a substantial effect on the C balance, hence it is important to predict these occasionally strong litter mixing effects.

The majority of litterbag studies (78%) report litter N concentration, yet few publications report a more extensive range of litter quality parameters (such as; C, N, P, lignin, phenol) (Barantal et al., 2014; Makkonen et al., 2013). Additionally, other litter characteristics, such as litter physical traits (leaf thickness/elongation), are hardly ever measured and could be important in interaction with litter chemical trait dissimilarity. A mixture of small and large litter fragments could ameliorate the microclimate for decomposition, which has been proposed as a mechanism to explain non-additive effects of litter mixture decomposition (Hättenschwiler et al., 2005). Makkonen et al. (2013) showed indeed that micro-climatic conditions and litter physical traits can determine if non-additive effects were synergistic or antagonistic. Thus, they proved that litter physical and chemical trait dissimilarity alone cannot predict the direction of litter mixture interaction. In a study by Anderson and Hetherington (1999) the chemical composition of the two litters was very similar and still non-additive mass loss was found. They speculated that decomposition was enhanced by the synergistic interaction of different fungal species associated with the two litter types. Therefore it is an issue that most studies to date have focussed on either extensive litter chemical quality measurements or only on soil decomposer communities or on climate. Only few studies have included all relevant parameters, even though this could be necessary to predict non-additive litter mixture mass loss.

Overall, there are a myriad of factors that can influence the litter mixing effects on mass loss such as the initial litter quality, the experimental design and environmental conditions. Besides the parameters mentioned in this study, which were often measured, many other factors such as leaf thickness, decomposer community, the presence or absence of a certain decomposer and the soil structure could also play a (minor) role. This could make it nearly impossible to predict if mass loss will be non-additive and what the direction and size this non-additive mass loss in mixtures will have. Even minute differences in the starting situation could create a wide range of different outcomes in terms of litter mixture mass loss. Perhaps any small change in the litter quality, micro-climate, soil quality and decomposer community at the start of the experiment could overrule the effects of more commonly reported (and also in this study included) litter quality parameters. There are many interactions possible between many parameters that not a single study has reported on all variables. As an example, if we compare a litter mixture of a moss + deciduous leaf to a litter mixture of a coniferous + deciduous leaf, not only the litter nutrient concentration or C structure is important. Many other factors such as the litter thickness, hydrophobicity, wax layer, water holding capacity, size, etc. are likely to covary and play a role.

5. Conclusion

This meta-analysis shows that the majority of reported results of studies on litter mixture mass loss can be predicted based on single litter mass loss since 85% of all 2-species litter mixtures show additive mass loss. Even so, non-additive effects are found with litter mixture mass loss being sometimes ten times greater or smaller than expected. The number of cases with less than additive mass loss (49) was only somewhat lower than the number of cases with more than additive mass loss (76). We found no overriding dominant trends in litter traits driving additive, less than additive, or more than additive mass loss in litter mixtures. However, evidence exists that such effects do emerge under specific circumstances. None of the parameters that were tested stand out alone as a dominant driver that can explain a significant portion of the variability present among the studies included in our meta-analysis. Besides the most often observed chemical litter quality traits, other parameters such as other nutrients than N and P, leaf size, structure, soil quality, climate, soil fauna and their interactions could play a role. This raises the question if we need more studies that integrate all possible parameters that could influence litter mixing effects or if it is simply impossible to predict non-additive mass loss since minute differences in the starting situation could alter the size and direction of non-additive mass loss.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix

Table A1

Specification of the models fitted to the data, where the effect of explanatory variables on the response ratio are modelled. Where β_0 and β_1 report the intercept and the slope, a_i is a random publication effect and b_{ij} is a random experiment effect nested within the *i*th publication. ε_{ijk} is a residual random error assumed normally distributed with constant variance. ε_{ijk} is constant in models without weights and variable in models with weights (on the subset of data with standard errors reported). The variance terms a_i, b_{ij} and ε_{ijk} were all assumed independent. The final columns indicate the number of publications, experiments and observations that could be included in each model (without weights).

Model	Equation	Publication	Experiment	Observation
1	$\ln(R)_{ijk} = \beta_0 + a_i + b_{ij} + \varepsilon_{ijk}$	78	529	1359
2	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta C + a_i + b_{ij} + \varepsilon_{ijk}$	47	299	768
3	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta N + a_i + b_{ij} + \varepsilon_{ijk}$	63	406	1056
4	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta C/N + a_i + b_{ij} + \varepsilon_{ijk}$	49	327	779
5	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta P + a_i + b_{ij} + \varepsilon_{ijk}$	36	189	535
6	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta N/P + a_i + b_{ij} + \varepsilon_{ijk}$	36	189	535
7	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta C/P + a_i + b_{ij} + \varepsilon_{ijk}$	29	155	437
8	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta \text{Lignin} + a_i + b_{ij} + \varepsilon_{ijk}$	28	173	432
9	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta \text{Lignin}/N + a_i + b_{ij} + \varepsilon_{ijk}$	27	169	416
10	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta \text{Phenol} + a_i + b_{ij} + \varepsilon_{ijk}$	6	80	97
11	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta \text{HemiCell} + a_i + b_{ij} + \varepsilon_{ijk}$	5	29	46
12	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta \text{Cellulose} + a_i + b_{ij} + \varepsilon_{ijk}$	11	82	137
13	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{SOM} + a_i + b_{ij} + \varepsilon_{ijk}$	3	8	26
14	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{SoilC} + a_i + b_{ij} + \varepsilon_{ijk}$	24	100	303
15	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{SoilN} + a_i + b_{ij} + \varepsilon_{ijk}$	27	108	341
16	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{SoilCN} + a_i + b_{ij} + \varepsilon_{ijk}$	10	56	161
17	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{SoilpH} + a_i + b_{ij} + \varepsilon_{ijk}$	36	155	503
18	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Mesh} + a_i + b_{ij} + \varepsilon_{ijk}$	77	525	1347
19	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Burial location} + a_i + b_{ij} + \varepsilon_{ijk}$	76	527	1350
20	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Time} + a_i + b_{ij} + \varepsilon_{ijk}$	78	529	1359
21	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Ecosystem} + a_i + b_{ij} + \varepsilon_{ijk}$	77	526	1356
22	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Climate} + a_i + b_{ij} + \varepsilon_{ijk}$			
23	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Rainfall} + a_i + b_{ij} + \varepsilon_{ijk}$	64	473	1121
24	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Temperature} + a_i + b_{ij} + \varepsilon_{ijk}$	64	473	1121
25	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{LitterType} + a_i + b_{ij} + \varepsilon_{ijk}$	78	529	1359
26	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Woody} + a_i + b_{ij} + \varepsilon_{ijk}$	78	529	1359
27	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Dried} + a_i + b_{ij} + \varepsilon_{ijk}$	59	341	878
28	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Size litter} + a_i + b_{ij} + \varepsilon_{ijk}$	8	42	182
29	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta C + \beta_2\ \Delta N + \beta_3\ \Delta C{*}\Delta N + a_i + b_{ij} + \varepsilon_{ijk}$	47	299	768
30	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta C + \beta_2\ \Delta P + \beta_3\ \Delta C{*}\Delta P + a_i + b_{ij} + \varepsilon_{ijk}$	29	155	437
31	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta N + \beta_2\ \Delta P + \beta_3\ \Delta N{*}\Delta P + a_i + b_{ij} + \varepsilon_{ijk}$	36	189	535
32	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta N + \beta_2\ \Delta \text{Phenol} + \beta_3\ \Delta N{*}\Delta \text{Phenol} + a_i + b_{ij} + \varepsilon_{ijk}$	6	80	97
33	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta C + \beta_2\ \Delta N + \beta_3\ \Delta P + \beta_4\ \Delta C{*}\Delta N{*}\Delta P + a_i + b_{ij} + \varepsilon_{ijk}$	29	155	437
34	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta N + \beta_2\ \Delta P + \beta_3\ \Delta \text{Lignin} + \beta_4\ \Delta N{*}\Delta P{*}\Delta \text{Lignin} + a_i + b_{ij} + \varepsilon_{ijk}$	14	82	212
35	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta N + \beta_2\ \Delta \text{Lignin} + \beta_3\ \Delta N{*}\Delta \text{Lignin} + a_i + b_{ij} + \varepsilon_{ijk}$	27	169	416
36	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta N + \beta_2\ \Delta \text{Lignin} + \beta_3\ \Delta \text{Phenol} + \beta_4\ \Delta N{*}\Delta \text{Lignin} * \Delta \text{Phenol} + a_i + b_{ij} + \varepsilon_{ijk}$	5	78	89
37	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta N + \beta_2\ \text{Time} + \beta_3\ \Delta N * \text{Time} + a_i + b_{ij} + \varepsilon_{ijk}$	63	406	1056
38	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta P + \beta_2\ \text{Time} + \beta_3\ \Delta P * \text{Time} + a_i + b_{ij} + \varepsilon_{ijk}$	36	189	535
39	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta \text{Lignin} + \beta_2\ \text{Time} + \beta_3\ \Delta \text{Lignin} * \text{Time} + a_i + b_{ij} + \varepsilon_{ijk}$	28	173	432
40	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta N + \beta_2\ \Delta P + \beta_3\ \text{Time} + \beta_4\ \Delta N * \Delta P * \text{Time} + a_i + b_{ij} + \varepsilon_{ijk}$	36	189	535
41	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta N + \beta_2\ \Delta P + \beta_3\ \Delta \text{Lignin} + \beta_4\ \text{Time} + \beta_5\ \Delta N * \Delta P * \Delta \text{Lignin} * \text{Time} + a_i + b_{ij} + \varepsilon_{ijk}$	14	82	212
42	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Mesh} + \beta_2\ \text{Time} + \beta_3\ \text{Mesh} * \text{Time} + a_i + b_{ij} + \varepsilon_{ijk}$	77	525	1347
43	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Mesh} + \beta_2\ \Delta N + \beta_3\ \text{Mesh} * \Delta N + a_i + b_{ij} + \varepsilon_{ijk}$	62	402	1044
44	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Temperature} + \beta_2\ \Delta C + \beta_3\ \text{Temperature} * \Delta C + a_i + b_{ij} + \varepsilon_{ijk}$	38	256	580
45	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Rainfall} + \beta_2\ \Delta C + \beta_3\ \text{Rainfall} * \Delta C + a_i + b_{ij} + \varepsilon_{ijk}\ \varepsilon_{ijk}$	38	256	580
46	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Temperature} + \beta_2\ \Delta N + \beta_3\ \text{Temperature} * \Delta N + a_i + b_{ij} + \varepsilon_{ijk}$	51	355	837
47	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Rainfall} + \beta_2\ \Delta N + \beta_3\ \text{Rainfall} * \Delta N + a_i + b_{ij} + \varepsilon_{ijk}$	51	355	837
48	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Temperature} + \beta_2\ \Delta P + \beta_3\ \text{Temperature} * \Delta P + a_i + b_{ij} + \varepsilon_{ijk}$	28	170	454
49	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Rainfall} + \beta_2\ \Delta P + \beta_3\ \text{Rainfall} * \Delta P + a_i + b_{ij} + \varepsilon_{ijk}$	28	170	454
50	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Temperature} + \beta_2\ \Delta C/N + \beta_3\ \text{Temperature} * \Delta C/N + a_i + b_{ij} + \varepsilon_{ijk}$	39	302	690
51	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Rainfall} + \beta_2\ \Delta C/N + \beta_3\ \text{Rainfall} * \Delta C/N + a_i + b_{ij} + \varepsilon_{ijk}$	39	302	690
52	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Temperature} + \beta_2\ \Delta C/P + \beta_3\ \text{Temperature} * \Delta C/P + a_i + b_{ij} + \varepsilon_{ijk}$	24	144	387
53	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Rainfall} + \beta_2\ \Delta C/P + \beta_3\ \text{Rainfall} * \Delta C/P + a_i + b_{ij} + \varepsilon_{ijk}$	24	144	387
54	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Temperature} + \beta_2\ \Delta N/P + \beta_3\ \text{Temperature} * \Delta N/P + a_i + b_{ij} + \varepsilon_{ijk}$	28	170	454
55	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Rainfall} + \beta_2\ \Delta N/P + \beta_3\ \text{Rainfall} * \Delta N/P + a_i + b_{ij} + \varepsilon_{ijk}$	28	170	454
56	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Temperature} + \beta_2\ \Delta \text{Lignin}/N + \beta_3\ \text{Temperature} * \Delta \text{Lignin}/N + a_i + b_{ij} + \varepsilon_{ijk}$	22	155	364
57	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \text{Rainfall} + \beta_2\ \Delta \text{Lignin}/N + \beta_3\ \text{Rainfall} * \Delta \text{Lignin}/N + a_i + b_{ij} + \varepsilon_{ijk}$	22	155	364
58	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta N + \beta_2\ \text{Ecosystem} + \beta_3\ \Delta N * \text{Ecosystem} + a_i + b_{ij} + \varepsilon_{ijk}$	63	406	1056
59	$\ln(R)_{ijk} = \beta_0 + \beta_1\ \Delta N + \beta_2\ \text{Soil N} + \beta_3\ \Delta N * \text{Soil N} + a_i + b_{ij} + \varepsilon_{ijk}$	25	100	313

Table A2
Model results of single variables, two- and three-way interactions on ln(R). The p-values are given for each model (Table 1) as well as the R^2 value in case of a significant linear model result for the complete dataset, the dataset that reported standard errors and the dataset that reported significant non-additive mass loss. The number of observations in each model is between brackets. NA = not enough observations for model testing

Variable	Analysis without weights, all data	Analysis with weights, subset for data having SEs	Analysis with weights, for observations with significant non-additive mass loss
ΔC	0.0811 (768)	0.2237 (480)	0.6665 (75)
ΔN	0.4500 (1056)	0.2847 (660)	0.4907 (101)
ΔC:N	0.1113 (779)	**0.0028, R^2=5e^{-4} (384)**	**0.0316, R^2=5e^{-4} (74)**
ΔP	0.1438 (535)	0.9695 (324)	0.5243 (56)
ΔN:P	0.4739 (535)	0.1115 (324)	0.2877 (56)
ΔC:P	**0.0064, R^2=0.03 (437)**	0.0883 (237)	**0.0369, R^2=9e^{-4} (49)**
ΔLignin	0.3900 (432)	0.7070 (220)	0.2846 (50)
ΔLignin:N	**0.0051, R^2=0.04 (416)**	**0.0074, R^2=7e^{-4} (220)**	0.0990 (50)
ΔPhenol	0.4386 (97)	0.7849 (86)	0.7243 (20)
ΔHemicellulose	0.4437 (46)	0.7912 (40)	0.1784 (11)
ΔCellulose	0.1736 (137)	0.7270 (104)	0.5354 (25)
SOM	0.2997 (26)	NA (15)	NA (8)
Soil C	0.2851 (303)	0.7275 (205)	0.7994 (31)
Soil N	0.4475 (341)	**0.0415, R^2=3e^{-4} (235)**	**0.0001, R^2=1e^{-4} (39)**
Soil C:N	0.3250 (161)	**0.0126, R^2=4e^{-4} (89)**	0.2443 (20)
Soil pH	0.5927 (503)	0.8127 (308)	0.0761 (49)
Mesh size	0.9143 (1347)	0.5966 (848)	0.5981 (125)
Burial location	0.9213 (1350)	0.7474 (860)	0.7085 (125)
Time	0.0992 (1359)	0.5519 (860)	0.7874 (125)
Ecosystem	0.7783 (1356)	0.8397 (857)	**0.0001, R^2=4e^{-4} (124)**
Climate	0.9223 (1324)	0.4918 (842)	0.2650 (123)
Rainfall	0.4312 (1121)	**0.0489, R^2=2e^{-4} (676)**	0.0549 (105)
Temperature	0.1562 (1121)	0.4317 (676)	0.3202 (105)
Natural/arable system	0.6473 (1356)	0.1671 (857)	**0.0377, R^2=8e^{-4} (124)**
Litter type	0.4107 (1359)	0.9689 (860)	0.7292 (125)
Woody	0.5531 (1359)	0.4636 (860)	0.9948 (125)
Litter drying	0.5262 (878)	0.0811 (671)	0.2965 (111)
Litter size	0.5757 (182)	0.5713 (162)	NA (16)
ΔC * ΔN	0.8647 (768)	0.9818 (480)	0.9421 (75)
ΔC * ΔP	0.0898 (437)	0.4358 (237)	0.4181 (49)
ΔN * ΔP	0.8580 (535)	0.7966 (324)	0.1520 (56)
ΔN * ΔPhenol	0.2527 (97)	0.5641 (86)	0.8685 (20)
ΔC * ΔN * ΔP	0.1289 (437)	0.4080 (237)	**0.0211, R^2=2e^{-3} (49)**
ΔN * ΔP * ΔLignin	0.8751 (212)	0.3375 (136)	NA (26)
ΔN * ΔLignin	0.5970 (416)	0.5258 (220)	0.9446 (50)
ΔN * ΔLignin * ΔPhenol	0.2960 (89)	0.1645 (86)	0.5867 (20)
ΔN * Time	**0.0256, R^2=0.04 (1056)**	**0.0005, R^2=8e^{-4} (660)**	0.7223 (101)
ΔP * Time	**0.0311, R^2=0.02 (535)**	0.1501 (324)	0.7175 (56)
ΔLignin * Time	0.9911 (432)	0.7083 (220)	0.6174 (50)
ΔN * ΔP * Time	0.9507 (535)	**0.0280, R^2=2e^{-4} (324)**	0.5344 (56)
ΔN * ΔP * ΔLignin * Time	**0.0131, R^2=0.10 (212)**	**0.0167, R^2=4e^{-3} (136)**	NA (26)
Mesh size * Time	0.5734 (1347)	0.6108 (848)	0.9690 (125)
Mesh * ΔN	0.4305 (1044)	0.7558 (648)	0.8148 (101)
ΔN * Ecosystem	0.8721 (1056)	0.2396 (660)	**0.0006, R^2=5e^{-4} (101)**
ΔN * Soil N	0.4864 (313)	0.2677 (223)	0.1232 (37)
ΔC * Rainfall	0.7110 (580)	0.8411 (324)	0.8321 (56)
ΔC * Temperature	0.9909 (580)	0.9165 (324)	0.1972 (56)
ΔN * Rainfall	0.5060 (837)	0.8939 (479)	0.9142 (81)
ΔN * Temperature	0.9255 (837)	0.3000 (479)	0.0633 (81)
ΔP * Rainfall	0.6044 (454)	0.5683 (278)	0.9621 (47)
ΔP * Temperature	0.7115 (454)	0.6203 (278)	**0.0185, R^2 = R^2=1e^{-3} (47)**
ΔC/N * Rainfall	0.0516 (690)	**0.0001, R^2=6e^{-4} (323)**	**0.0010, R^2=1e^{-3} (63)**
ΔC/N * Temperature	0.1182 (690)	**0.0001, R^2=8e^{-4} (323)**	**0.0087, R^2=1e^{-3} (63)**
ΔC/P * Rainfall	**0.0041, R^2=0.07 (387)**	**0.0281, R^2=1e^{-3} (216)**	**0.0397, R^2=7e^{-3} (41)**
ΔC/P * Temperature	**0.0137, R^2=0.05 (387)**	**0.0080, R^2=1e^{-3} (216)**	**0.0018, R^2=6e^{-3} (41)**
ΔN/P * Rainfall	0.8665 (454)	0.9192 (278)	0.6460 (47)
ΔN/P * Temperature	0.6811 (454)	0.9607 (278)	0.4298 (47)
ΔLignin/N * Rainfall	0.7651 (364)	0.2129 (205)	0.2860 (44)
ΔLignin/N * Temperature	0.2800 (364)	**0.0304, R^2=8e^{-4} (205)**	NA (44)

Table A3
Model results of single variables and their effect on ln(R) for each of the climates provided if enough data was available. The p-values are given for each model (Table 1) as well as the R^2 value in case of a significant linear model.

Variable	Tropical	Temperate	Continental
ΔC	0.0537 (66)	0.7787 (477)	0.0015**, R^2 = 0.06 (231)
ΔN	0.0990 (75)	0.7528 (628)	0.0880 (353)
ΔC:N	0.9737 (65)	0.1324 (385)	**0.0285, R^2=0.02 (311)**
ΔP	0.9860 (49)	0.2096 (271)	0.6546 (213)
ΔN:P	0.7109 (49)	0.2574 (271)	0.5848 (213)
ΔC:P	0.0566 (43)	0.1716 (241)	**0.0001***, R^2=0.27 (151)**
ΔLignin	0.1043 (52)	0.2284 (251)	0.7196 (151)
ΔLignin:N	**0.0385*, R^2=0.12 (36)**	0.0575 (235)	**0.0041**, R^2=0.07 (135)**
ΔPhenol	0.4065 (12)	0.4874 (15)	0.6909 (70)
ΔHemicellulose	0.6827 (12)	0.3678 (34)	NA (0)
ΔCellulose	0.7213 (18)	0.1821 (79)	0.5697 (40)
SOM	NA (8)	NA (15)	NA (3)
Soil C	**0.0180*, R^2=0.12 (81)**	0.1233 (163)	0.1307 (95)
Soil N	0.6821 (82)	0.3284 (208)	0.7216 (85)
Soil C:N	NA (12)	0.0966 (73)	0.7524 (70)
Soil pH	0.9478 (92)	0.4375 (279)	0.4777 (174)
Mesh size	0.1369 (97)	0.9571 (736)	0.4051 (510)
Burial location	0.6875 (108)	0.9930 (747)	NA (513)
Time	0.4143 (109)	**0.0058**, R^2=0.01 (748)**	0.8473 (522)
Ecosystem	0.1226 (109)	0.7669 (748)	**0.0067**, R^2=0.08 (522)**
Natural/arable system	0.1219 (109)	0.4788 (748)	0.5335 (522)
Litter type	**0.0246*, R^2=0.07 (109)**	0.2498 (748)	0.1029 (522)
Woody	0.7976 (109)	0.9716 (748)	**0.0286*, R^2=0.04 (522)**
Litter drying	NA (105)	0.5269 (739)	NA (522)
Litter size	NA (35)	0.5404 (164)	NA (41)

Table A4
Model results of single variables and their effect on ln(R) for each of the ecosystems provided if enough data was available. The p-values are given for each model (Table 1) as well as the R^2 value in case of a significant linear model.

Variable	Arable	Deciduous forest	Coniferous forest	Natural grass	Pasture
ΔC	0.6128 (136)	0.0045**, R^2 = 0.03 (406)	0.3645 (84)	0.2856 (53)	0.5240 (48)
ΔN	0.9669 (160)	0.5101 (539)	0.4811 (94)	0.6706 (104)	0.9784 (66)
ΔC:N	0.1933 (30)	0.9570 (420)	0.5698 (108)	0.3041 (71)	**0.0139*, R^2=0.08 (90)**
ΔP	0.0790 (34)	0.2235 (284)	0.0517 (68)	0.2339 (89)	**0.0274*, R^2=0.42 (19)**
ΔN:P	0.3134 (34)	0.5917 (284)	0.1161 (68)	0.5771 (89)	0.4390 (19)
ΔC:P	NA (10)	**0.0001***, R^2=0.17 (279)**	0.1383 (68)	0.2986 (53)	NA (1)
ΔLignin	NA (10)	0.0549 (264)	0.2981 (36)	0.8490 (45)	0.5943 (6)
ΔLignin:N	NA (10)	**0.0086**, R^2=0.04 (264)**	0.9632 (36)	0.3536 (45)	0.5943 (6)
ΔPhenol	NA (0)	0.5724 (55)	NA (8)	NA (0)	NA (0)
ΔCellulose	NA (0)	0.6811 (55)	0.3009 (18)	0.2693 (30)	0.5943 (6)
Soil C	**0.0419*, R^2=0.36 (16)**	0.6130 (140)	NA (24)	NA (44)	0.0716 (31)
Soil N	0.5912 (40)	0.7188 (151)	0.6402 (28)	0.4306 (59)	NA (12)
Soil C:N	0.5957 (26)	0.1654 (92)	0.1485 (40)	NA (0)	NA (0)
Soil pH	0.9552 (83)	0.5726 (233)	0.1810 (28)	0.3459 (77)	0.5968 (31)
Mesh size	0.9540 (229)	0.9902 (637)	NA (134)	NA (107)	NA (114)
Burial location	0.0818 (229)	NA (637)	NA (134)	NA (99)	0.6441 (113)
Time	**0.0304*, R^2=0.03 (229)**	**0.0312*, R^2=0.007 (637)**	0.7435 (134)	0.7510 (107)	0.1291 (114)
Litter type	0.4759 (229)	0.1797 (637)	**0.0128*, R2=0.11 (134)**	**0.0188*, R^2=0.12 (107)**	**0.0002**, R^2=0.40 (114)**
Woody	0.1120 (229)	0.7357 (637)	0.2676 (134)	0.5887 (107)	**0.0005**, R2=0.41 (114)**
Litter drying	NA (171)	NA (633)	0.1064 (110)	NA (107)	NA (114)
Litter size	NA (120)	NA (0)	NA (0)	0.7151 (18)	NA (13)

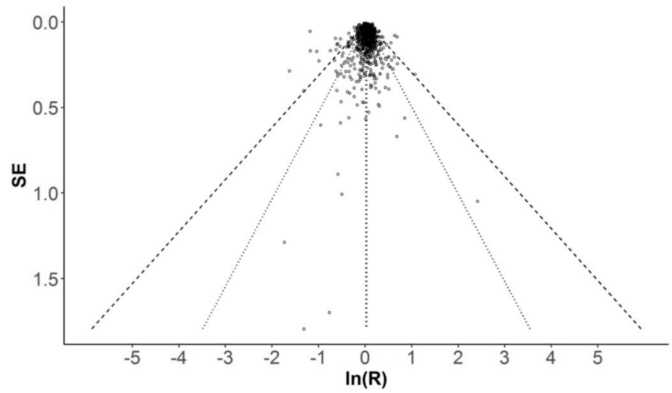

Fig. A1. Funnel plot of standard error against the log of the response ratio (ln(R)). The vertical line represents the estimated mean of ln(R) via mixed effect model 1: $\ln(R)_{ijk} = \beta_0 + a_i + b_{ij} + \varepsilon_{ijk}$. The dotted line indicates the 95% CI and the dashed line the 99% CI.

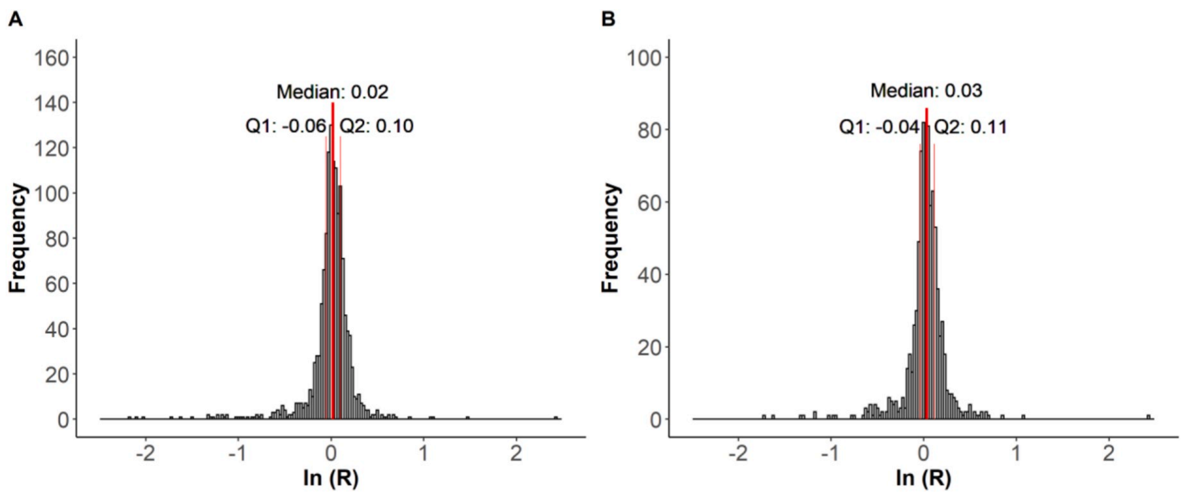

Fig. A2. A histogram of the natural logarithm of the response rate. Where R is the expected mass loss divided by the observed mass loss. Thus a value of ln(R) of zero indicates additive mass loss, any value above zero indicates positive non-additive mass loss and below zero indicates negative non-additive mass loss. A) the complete data set and B) the subset of data that reported errors and samples sizes. Vertical lines in the panels of the frequency distribution indicate the first quartile (Q1), median and the third (Q2) quartile of ln(R).

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