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Title

Flow intermittence alters carbon processing in rivers through chemical diversification of leaf litter

Running Head

Flow intermittence alters carbon processing

List of authors

Rubén del Campo*†[1,2,3], Roland Corti†[1,4], Gabriel Singer[1,3]

1.- Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany

2.- Department of Ecology and Hydrology, University of Murcia, Murcia, Spain

3.- Department of Ecology, University of Innsbruck, Innsbruck, Austria

4.- UR RiverLY, IRSTEA, Villeurbanne Cedex, France

†RdC and RC contributed equally to the development of the manuscript.

* Corresponding author at: Department of Ecology, University of Innsbruck Technikerstrasse 25, A-6020 Innsbruck (Austria). ruben.del-campo@uibk.ac.at, telephone: +43(0)512507-51737

Author contribution statement

GS and RC conceived the study and designed the experiment; RC conducted the field and laboratory experiments and collected the data; RC and RdC performed laboratory analyses. RdC led data analysis with inputs of RC and GS; RdC led the writing of the manuscript; GS and RC revised the manuscript critically and gave their final approval for publication. The authors declare no conflict of interest.

Data accessibility statement

Whether the manuscript is accepted, all the data supporting our results will be uploaded to Figshare.

Abstract

The dry phase of intermittent rivers promotes the emergence of diverse terrestrial and aquatic habitats where large amounts of leaf litter can accumulate. This environmental heterogeneity can cause diverse chemical alterations in leaf litter by the co-occurrence of multiple physical and biological degradation processes across these different habitats. After flow resumption, these chemically diversified leaves are mixed and continue decomposition downstream in fully aquatic conditions. We hypothesized that environmental heterogeneity during the dry phase can translate into a chemical diversification of leaf litter, that may affect leaf litter decomposition in re-established lotic conditions. Our laboratory treatments mimicking dry-phase habitats caused a strong chemical diversification of leaf litter, which – upon combination in mixed litter bags – accelerated its decomposition in a perennial river reach. Intermittent river reaches may act as hotspots of organic matter diversification, with potential implications on C processing at river-network scale.

Keywords:

Intermittent rivers, dry phase, chemical diversity, decomposition, river networks, biodiversity

Scientific Significance Statement

Intermittent rivers are among the most dynamic ecosystems worldwide. Their functioning is regulated by the alternation of wet and dry phases. During drying, the cessation of surface flow results in the emergence of a mosaic of diverse terrestrial and aquatic habitats (e.g. isolated pools), where large amounts of riparian leaf litter can accumulate under contrasting environmental conditions. After flow resumption, variously conditioned organic matter is mixed and transported downstream; however, the implications for its final decomposition are unknown. Here we demonstrate that spatial environmental heterogeneity during the dry phase of intermittent rivers can result in a chemical diversification of the accumulated organic matter, which in turn, can accelerate its decomposition further downstream, potentially affecting C fluxes at river-network scale.

Introduction

The fundamental role of hydrology in regulating C cycling in freshwater ecosystems (Raymond et al. 2016) becomes particularly evident in intermittent rivers (Datry et al. 2018). There, the alternation of dry and wet phases is thought to drive a pulsed processing of organic matter in cycles of accumulation, transport, and decomposition (Larned et al. 2010; Datry et al. 2018). Briefly, accumulation of organic matter – mainly riparian leaf litter - on riverbeds during the dry phase (Sanpera-Calbet et al. 2016; Datry et al. 2018) is opposed to active processing during the wet phase (Corti et al. 2011; Abril et al. 2016). In-between, the resumption of surface flow mobilizes and transports material downstream (Corti & Datry 2012). This simplistic model has been challenged, mainly because the exposure of leaf litter to various environmental conditions during the dry phase (in this context also called "preconditioning") can trigger chemical changes, which ultimately affect leaf decomposition after flow resumption (Dieter et al. 2013; del Campo et al. 2019: Mora-Gómez et al. 2019). For instance, the exposure of leaf litter to solar radiation on dry riverbeds can increase its biodegradability due to photodegradation-induced loss of lignin (Austin et al. 2016). In contrast, leaf litter accumulated in stagnant isolated pools can decrease in biodegradability due to leaching of labile compounds and accumulation of phenols (Dieter et al. 2013). These are two examples from a great variety of terrestrial and aquatic habitats that emerge during the fragmentation of water flow (e.g. wet and shaded remnant sediments, pools connected to hyporheos, etc.) (Stanley et al. 1997; Datry et al. 2014). As accumulation and preconditioning of leaf litter happen across this mosaic of aquatic-terrestrial habitats, chemical diversification of leaf litter can occur (see Wickings et al. 2012, Fig. 1). The re-establishment of water flow then triggers mixing of variously preconditioned leaf litter during downstream transport (see here an example during a rewetting event in the Albarine river, France). Finally, upon retention, decomposition proceeds in reassembled, chemically diversified litter packs in fully lotic conditions.

Under aquatic conditions, decomposition is mainly controlled by leaf litter traits (Zhang et al. 2019). The mixing of various species can have non-additive effects on decomposition (Gessner et al. 2010), meaning that the decomposition rate of mixtures is either below or above those expected from individual species` rates (Gartner & Cardon 2004). Negative effects of litter diversity are associated to inhibition of decomposer activity by secondary metabolites like polyphenols (Chomel et al. 2016). Positive effects are attributed to fungi-driven nutrient transfer (Tonin et al. 2017) or nutritional complementarity among leaves with contrasting chemical qualities (López-Rojo et al. 2020). Owing to the increased chance of obtaining essential compounds, the functional diversity of leaf mixtures *per se* may accelerate decomposition (Lecerf et al. 2011; Stoler et al. 2016).

Our understanding of chemical (bio)diversity effects on decomposition is still incomplete, for instance with regard to natural mechanisms that could promote chemical diversity in particulate organic matter beyond the diversity of leaf species. Indeed, the hydrological dynamics of intermittent tributaries could create a powerful mechanism of chemical diversification of leaf litter with unknown consequences for decomposition dynamics at river-network scale. Intermittent rivers represent over half of the length of global river networks, and this fraction will likely increase due to climate and global change (IPCC 2013); therefore, accounting for dry-phase-associated diversity effects could be critical to achieve mechanistic understanding and realistic modelling capacity for C fluxes at regional and global scale (Marcé el al. 2019).

Here we test the hypothesis that environmental heterogeneity occurring during the dry phase of intermittent rivers can promote the chemical diversification of accumulated leaf litter and thus, affect its decomposition in downstream rivers, once lotic conditions are re-established. To this aim we first simulated the preconditioning of a single leaf litter species (*Alnus glutinosa*) under various environmental conditions typically found during the dry phase of intermittent rivers. Then, we measured the decomposition of leaf litter mixtures assembled using an increasing number of preconditioning situations. We predict that the increase of chemical diversity in mixtures of preconditioned leaves will accelerate decomposition in aquatic conditions (Fig. 1).

Materials and methods

Leaf litter preconditioning and preparation of mixtures

We collected fresh leaves of *Alnus glutinosa* (alder) directly from several trees along the Löcknitz river (Brandenburg, Germany) and let them air-dry for two weeks. Following preconditioning through seven treatments (Table 1), we prepared fine- and coarse-mesh bags (0.5 and 8 mm, respectively, 15 x 15 cm size) containing leaves of single treatments (7 treatments x 4 replicates) and mixtures of leaves of increasing treatment richness in all possible combinations of 2, 4, and 6 treatments. This design resulted in 4 richness levels comprising a total of 91 bags (28 single-treatments + 21 2-treatment combinations + 35 4-treatment combinations + 7 6-treatment combinations) for each mesh size. We filled each litterbag with 12 leaves. In mixtures, the 12 leaves were evenly partitioned across the component treatments. All leaves were scanned prior to bag assembly to later measure treatment-specific leaf areas by digital image analysis (ImageJ, https://imagej.nih.gov/ij/) and compute the exact contributions of component treatments on a dry mass (DM) basis. For this, we established conversion factors of leaf area to DM (48h, 105 °C) for each treatment from 20 leaves.

Leaf litter chemical composition and calculation of chemical diversity

Following preconditioning, sub-samples of all treatments were freeze-dried, ground using a ball mill and analyzed for C- and N-content (Elementar vario EL C/N elemental analyzer, Germany), other nutrients such as P, Ca, Mg and K by ICP-OES (Thermo Scientific, iCAP 6500, USA), and macromolecular organic C moieties by Fourier-transform infrared spectroscopy (FTIR) (Duboc et al. 2012; Liu et al. 2016; see detailed methods in Supplementary Information). We combined information from FTIR peaks and elemental analysis to perform a single principal component analyses (PCA) using z-standardized data. Average scores of each treatment on the first two PCA axes served as a 2-dimensional proxy of chemical composition. To capture composition of leaf mixtures we computed community-weighted means from the average of each involved treatment´s PCA scores weighted by its relative abundance in the mixture (see Stoler et al. 2016). As a proxy of the chemical diversity of leaf litter, we computed Rao's quadratic entropy (RaoQ; Stoler et al. 2016), a measure of functional diversity, using the package FD (Laliberte & Legendre 2010) in R 3.2.1 (R Core Team 2015). RaoQ is the mean Euclidean distance among treatments in the chemical space weighted by their relative abundance in the mixture. RaoQ was considered 0 for litterbags containing single treatments.

Aquatic decomposition experiment

To measure aquatic decomposition of single treatments and mixtures, we incubated all litterbags in the Löcknitz River (52°24'43.7"N, 13°49'33.6"E) for 23 days in August 2014. Löcknitz is a forested, 3rd-order lowland river in the Elbe catchment (Germany). Litterbags were tied to iron rods and fixed on the riverbed in four reaches of 50 m with running water and homogeneous substrate, depth and flow conditions. During incubation the water temperature oscillated between 13 and 17 °C, average dissolved oxygen concentration was always above 6.5 mg L^{-1}, conductivity and pH averaged 560 µS cm^{-1} and 7.5, respectively.

After retrieving the litterbags at approximately 50% average mass loss, leaves were washed individually in the laboratory with tap water above a 250 µm sieve to collect invertebrates, which were preserved in 70% ethanol. Individuals were counted, identified to family level and classified by guilds. The density of shredders was expressed as number of individuals per DM of leaf litter. The leaves from each litterbag were dried (105 °C, 48h), weighed, and leaf litter mass loss computed as the difference between initial and final litterbag DM divided by initial DM.

From leaves in fine-mesh bags we cut a set of 12 discs with a cork borer (10 mm) to measure fungal biomass as ergosterol according to Gessner et al. (2005) (Supplementary Information). Values of ergosterol were expressed as µg g^{-1} DM.

Microbial respiration assay

Parallel to the decomposition experiment, we measured oxygen consumption rates of preconditioned leaves as a proxy for microbial respiration. We incubated 12 leaf discs by mixture or single treatment in 250 mL sealed bottles filled with mineral water (Volvic) at room temperature in a water bath. As microbial inoculum we used 10 mL of river water filtered by 0.7 µm pre-combusted glass fiber filters (Whatman GF/F, Maidstone, UK). Dissolved oxygen concentrations were measured 13 times over 24 days with a needle-based micro-optode (PM-PSt7 on a Microx 4 trace meter; PreSens, Germany). 10 bottles were filled with plain water as a control. Oxygen consumption rates (day^{-1}) were computed as first order oxygen decay rates from log-linear regression models.

Data analysis

To analyze the response of leaf litter decomposition to the increase of treatment richness in mixtures we used generalized additive models for location, scale and shape (GAMLSS) (Rigby & Stasinopoulos 2005). Models were built using the treatment richness (1, 2, 4, 6 treatments) as explanatory variable and for the response variables mass loss, fungal biomass, shredder density and microbial respiration. GAMLSS allow to model effects on the average values (μ) of the response as well as its variance (σ). We also applied GAMLSS to test for the relationship between treatment richness and chemical diversity in mixtures.

We estimated expected values of all response variables for each mixture using observed values in single treatments, and compared those to observed values in mixtures. Expected values were computed as the weighted average of observed values of component treatments on a DM basis. Non-additive effects of mixing were considered synergistic when observed values were significantly higher than expected based on paired Wilcoxon signed rank tests (Gartner & Cardon 2004).

Finally, to analyze the influence of chemical diversity and chemical composition on the decomposition of both single treatments and mixtures we used general linear models that included RaoQ (chemical diversity), PC1 and PC2 (summary of the chemical composition traits) as predictors. For each response variable, we built an initial model that included all main effects and first-order interactions between RaoQ and each PCA axis and then selected a top set of most parsimonious models with a multi-model inference approach (Grueber et al. 2011) using the R package MuMIm (Bartón 2016). This top set kept all models with delta AICc < 2 to the best model. Finally, using the natural method of model averaging we generated an average model from the top set. This way we obtained a robust, weighted mean for each predictor coefficient and its errors based on AIC weights (Grueber et al. 2011). All explanatory variables were z-standardized to obtain scaled, comparable average predictor coefficients. We finally evaluated the effect of chemical diversity and chemical composition on leaf litter decomposition by comparing the absolute magnitude and direction of the averaged predictor coefficients and checking whether their 95% confidence intervals spanned zero.

Results and discussion

The dry phase of intermittent river as promotor of leaf litter chemical diversity

The PCA based on the chemical traits of leaf litter clearly separated the various treatments (Fig. 2AB), evidencing a strong chemical diversification of leaf litter by the various treatments, that were intended to mimic the environmental heterogeneity typically emerging in intermittent rivers during drying. The observed chemical alterations of leaf litter agree with previous works (Dieter et al. 2013; del Campo et al. 2019; Mora-Gómez et al. 2019). The greatest chemical differentiation observed along PC1 (56 % of the total variance; Fig. 2B) was achieved between distinct terrestrial and aquatic habitat conditions (Abril et al. 2016). Leaf litter in terrestrial-like habitats (T1: leaves entering the riverbed shortly before flow resumption and T2: leaf litter exposed to UVB radiation) retained labile carbohydrates, likely because of the limitation of microbial activity by water scarcity (Abril et al. 2016). Conversely, leaves in aquatic habitats with high temperature and nutrient concentration (T6 and T7) lost carbohydrates due to leaching and microbial degradation (Dieter et al. 2013, Abril et al. 2016), while gained in nutrients and phenols by microbial immobilization (Mora-Gómez et al. 2019). Separated from other treatments along PC2, leaf litter immersed in stagnant pools (T5) increased in structural polysaccharides such as cellulose, which might result from the (relative) loss of more soluble C compounds by leaching due to limited microbial degradation in acidic and anoxic conditions (Dieter et al. 2013).

Chemical diversity accelerates decomposition of leaf litter mixtures after flow resumption

In litter mixtures, such chemically diversified leaf litter experienced accelerated decomposition under fully aquatic conditions through synergistic effects on the activity of both microbial decomposers and detritivores, in a similar way as reported for mixtures of riparian leaf litter species (Gessner et al. 2010; Lecerf et al. 2011). Increasing preconditioning treatment richness in leaf litter mixtures significantly increased mass loss in coarse- and fine-mesh bags, fungal biomass and microbial respiration (Fig. 3A and Fig. 4), while this was not the case for expected values computed from single treatments for any response variable (data only shown for mass loss in Fig 3B). Shredder density did not increase significantly along the gradient of treatment richness; but higher than expected shredder densities in leaf litter mixtures (Fig. S1I) indicated a positive effect of leaf litter diversity on the detritivore community as well.

Increasing treatment richness of leaf litter mixtures also caused a decrease of the variability in fungal biomass and mass loss in fine-mesh bags (Fig. 4A and 4C). This often-observed outcome of manipulating resource (or species) richness emerges by dampening of extreme contributions in more complex mixtures (Dang et al. 2005; Lecerf et al. 2007). A reduced variability in fungal-mediated decomposition with higher diversity of preconditioned leaf litter translates to decreased spatial variability and increased stability of this ecosystem process in downstream aquatic systems. Such a decrease in variance with treatment richness was not found for shredder density or mass loss in coarse-mesh bags. This result may point to strong influence of individual leaf litter types on the consumption of detritivores, which usually tend to preferentially consume leaf litter species richer in labile C compounds or nutrients when present in mixtures (Swan & Palmer 2006; López-Rojo et al. 2020).

Synergistic effects of leaf litter mixing on decomposition usually arise from facilitative interactions among litter components with contrasting chemical composition. With our experimental design, we cannot identify which precise mechanism drives the acceleration of leaf litter decomposition by mixing; however, our results suggest chemical diversity as the main factor stimulating decomposition. The increase in treatment richness in mixtures implied an increase in chemical diversity (Fig. 2C). More importantly, chemical diversity was the main predictor in averaged-models explaining mass loss in coarse-mesh bags, microbial respiration and fungal biomass (Fig. 5). These results are in line with previous studies where chemical diversity had a predominant influence on the decomposition of leaf litter mixtures (Lecerf et al. 2011; Stoler et al. 2016). We suggest that chemical diversity in mixtures of preconditioned leaves enhanced the activity of microbial communities by facilitating the acquisition of essential nutritional components for their growth and metabolism from multiple sources, such as nutrients, labile C compounds like carbohydrates, or long-lasting resources like cellulose (Gessner et al. 2010).

Besides chemical diversity, the chemical composition of leaf litter strongly influenced microbial decomposition of mixtures (Frainer et al. 2015; López-Rojo et al. 2020). The chemical composition of leaf litter was the main predictor explaining mass loss in fine-mesh bags (significantly positive effect of PC2) and microbial respiration (significantly negative effect of

PC1) (Fig. 5, Table S1) in averaged-models. The positive effect of PC2 scores on the mass loss in fine-mesh bags may indicate a higher microbial activity associated with leaf litter rich in cellulose (Talbot & Treseder 2012). On the other hand, the negative effect of PC1 on microbial respiration could be due to either inhibition by lignin or phenolic compounds (Talbot & Treseder 2012; Chomel et al. 2016) and/or positive influence of carbohydrates (Stoler et al. 2016).

Ecological implications at river-network scale

Evidence highlighting the role of intermittent rivers in the processing of terrestrial organic matter in drainage networks is continuously growing. Intermittent rivers are the most predominant lotic ecosystem worldwide and they trigger hot moments of microbial processing of C during rewetting events due to their capacity to accumulate large amounts of organic matter during the dry phase (Datry et al. 2018; Marcé et al. 2019; Shumilova et al. 2019). Our results demonstrate that, beyond the accumulation of organic matter, its chemical alteration and diversification during the dry phase may have river-network scale implications. Our results suggest that flow re-establishment in intermittent rivers triggers not only a pulse of organic matter, but a pulse of chemical diversity, which is transported downstream across the river network, and consequently may alter organic matter fluxes at regional, river-network scale. As mixing of variously preconditioned leaf litter accelerates its decomposition, the length of organic matter transport along the river network decreases. This means a spatial compression of organic matter processing along the river continuum, which, in fact, counteracts the classical view of intermittent rivers as pulsed bioreactors (Larned et al. 2010), where the organic-matter processing length is considered to increase due to the little decomposition activity during the dry phase and the far-reaching transport by flashy flow during rewetting events. Certainly, the experimental character of our study precludes a strong assessment of implications. Future studies will have to achieve this under natural conditions, also considering the influence of other factors acting at larger spatial scale such as land use, climate or vegetation types. Here, we demonstrate that environmental heterogeneity can promote chemical diversity, which in turn may accelerate C processing in intermittent river networks. Our results reinforce the potential relevance of intermittent rivers in global C cycling and the necessity (and difficulties) of integrating them in larger scale modelling efforts.

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Tables

Table 1. Summary of the preconditioning treatments used in the study to mimic the terrestrial-aquatic habitat mosaic appearing in intermittent rivers during the dry phase.

Treatments	Riverbed habitat during the dry phase	Laboratory simulation	Physicochemical conditions in aquatic habitats
T1 Untreated	Vertical input of leaf litter shortly before flow resumption	Initially collected leaves, air-dried and kept at room temperature and in darkness.	
T2* UV	Dry riverbed exposed to intense solar irradiation	Irradiation for 12 h/day with a UV lamp (Cosmedico Arimed B6, Osram Biolux 965, Germany; with 31% UVB of total UV) at room temperature.	
T3 Moist	Shaded and humid riverbed habitats	Container with soil from the Löcknitz river floodplain moistened with 500 mL of tap water every 4 days and kept at room temperature.	
T4 Cold pool	Pool connected to hyporheic flow paths with cold and nutrient-poor water supporting limited algal growth	Aquarium filled with mineral water and stones with biofilm from the Löcknitz river. The aquarium was continuously illuminated, oxygenated by air-bubbling and kept at constant low temperature.	T = 15.3 °C DO = 9.45 mg L^{-1} pH = 7.94 Cond = 925 µS cm^{-1}
T5 Anoxic pool	Anoxic, stagnant pool	Container filled with mineral water and 8 mg of Na_2SO_3 per mg dissolved oxygen to create anoxic conditions, kept at room temperature and in darkness.	T = 24.6 °C DO = 0.15 mg L^{-1} pH = 5.5 Cond = 1650 µS cm^{-1}
T6* Wet/dry	Habitats subjected to wet/dry cycles associated to rain events	Alternating T2 and T3 every 7 days.	
T7 Hot pool	Disconnected pool with warm and nutrient-rich water supporting algal growth	Same conditions as T4, except that the aquarium was kept at room temperature and a nutrient solution (0.6 g L^{-1} of $NaNO_3$ and 0.3 g L^{-1} of KH_2PO_4) was added.	T = 25.1°C DO = 6.72 mg L^{-1} pH = 7.66 Cond = 800 µS cm^{-1}

T: water temperature, DO: dissolved oxygen, Cond: water conductivity. *The duration of preconditioning treatments was 21 days except for T2 and T6, which extended for 60 days, since terrestrial decomposition processes occur at a longer time scales than aquatic ones.

Figure legends

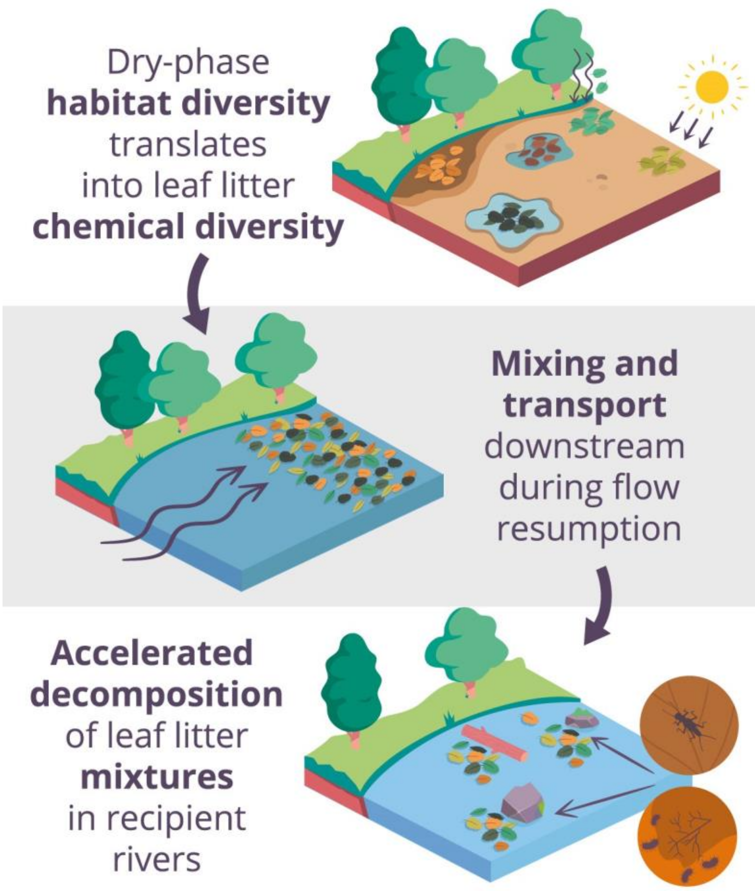

Figure 1. Conceptual figure showing the main hypothesis of the study. Environmental heterogeneity promotes a chemical diversification of accumulated leaf litter during the dry phase. After flow resumption, variously "preconditioned" leaves are mixed and transported downstream. Upon retention, chemical diversity accelerates the decomposition of leaf litter mixtures.

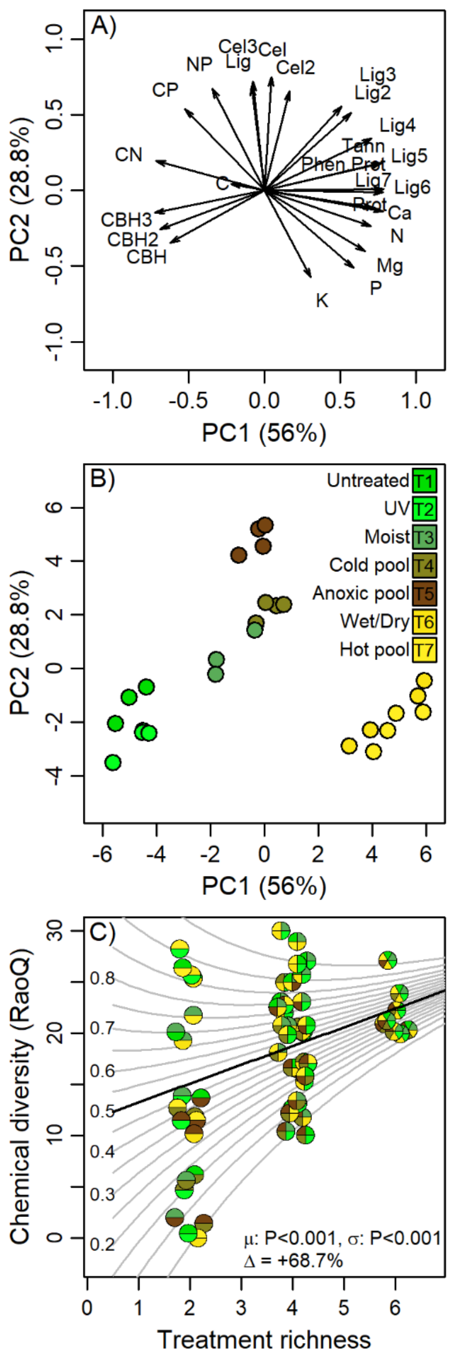

Figure 2. PCA describing changes in the chemical composition of leaf litter due to preconditioning under different treatments (A and B). (A) Variable loadings defining the PCA space. (B) Distribution of the preconditioning treatments across the PCA space. In (B), the colors of treatments represent their positions in PCA-space; similar chemical compositions of two treatments (e.g. T6 - T7) translates to similar colors and vice versa (e.g. T1 - T7) – this allows

chemical interpretation of color in subsequent figures. (C) GAMLSS identified a significant increase of the average (μ, black line) and a significant reduction of the variance (σ, grey percentile lines) of chemical diversity (RaoQ) with increasing richness or preconditioning treatments. The colors in the pie charts used as symbols for mixtures indicate chemical composition as identified in (B).

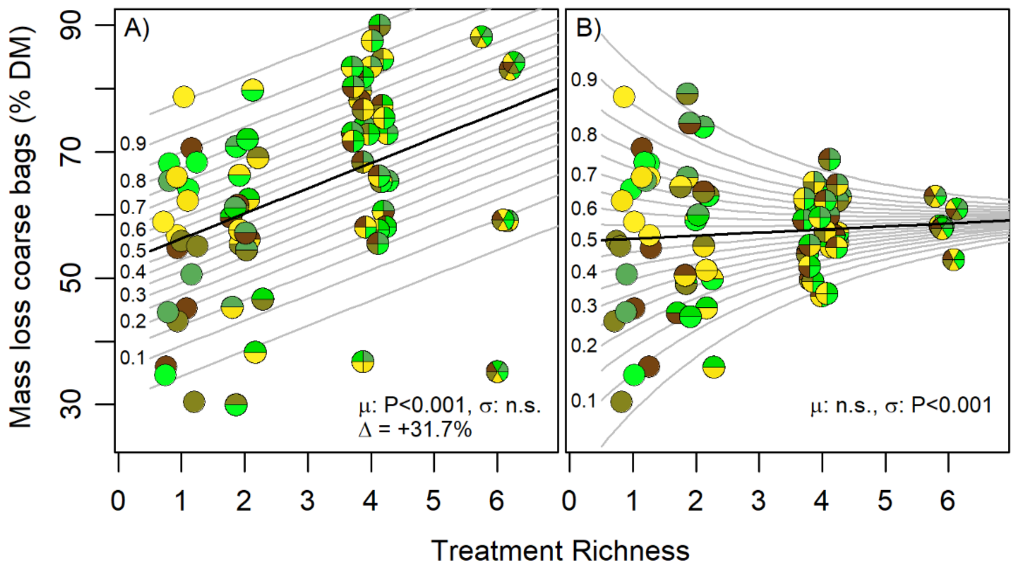

Figure 3. Observed (A) and expected (B) values of mass loss in coarse-mesh bags in single treatments and mixtures along the treatment richness gradient. GAMLSS identified a significant increase of the mean (μ, black line) but no change in the variance (σ, grey percentile lines) of observed values of mass loss with increasing richness, while there was no change in the mean but a decrease in variance of the expected values. Colors indicate the identity of single treatments (simple dots) or the treatment composition of mixtures (pie charts); color codes in Fig. 2B.

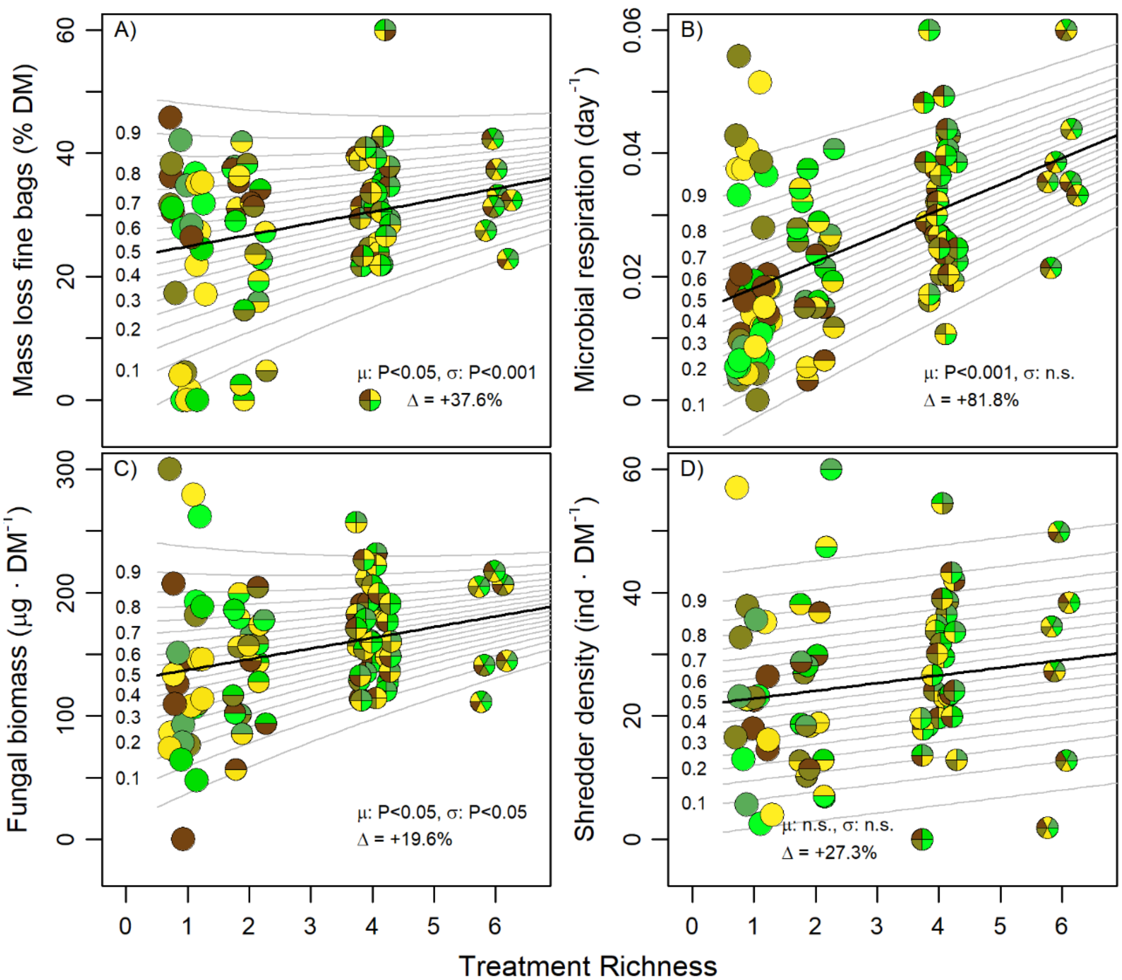

Figure 4. Observed values of mass loss in fine-mesh bags (A), microbial respiration (B), fungal biomass in leaf litter (C) and shredder density (D) in single treatments and mixtures along the treatment richness gradient. GAMLSS identified a significant increase of the mean (μ, black line) for all four variables with increasing richness, but a decrease in the variance (σ, grey lines) only for mass loss in fine mesh bags and fungal biomass. Colors indicate the identity of single treatments (simple dots) or the treatment composition of mixtures (pie charts); color codes in Fig. 2B.

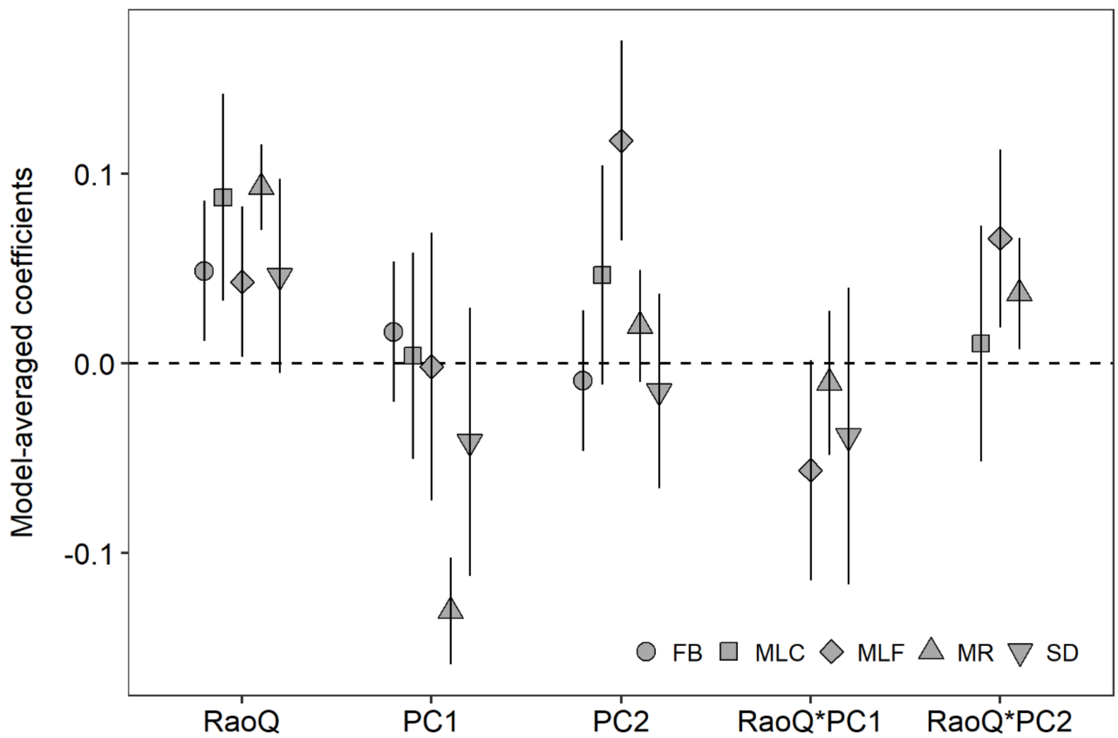

Figure 5. Model-averaged coefficients (mean ± 95% CI) of predictors explaining the mass loss, microbial respiration, fungal biomass and shredder density of single treatments and mixtures. Chemical diversity (estimated through RaoQ) was the most important predictor for mass loss in coarse-mesh bags, fungal biomass and shredder density, while chemical composition features (estimated through the average score of PC1 and PC2) were more important explaining mass loss in fine-mesh bags (PC2) and microbial respiration (PC1).

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