Oikos 000: 001–013, 2015
doi: 10.1111/oik.01917

Subject Editor: Michael Scherer-Lorenzen. Editor-in-Chief: Dustin Marshall. Accepted 21 November 2014

Functional dissimilarity across trophic levels as a driver of soil processes in a Mediterranean decomposer system exposed to two moisture levels

Mathieu Coulis, Nathalie Fromin, Jean-François David, Jordane Gavinet, Alexandre Clet, Sébastien Devidal, Jacques Roy and Stephan Hättenschwiler

M. Coulis, N. Fromin, J.-F. David, A. Clet and S. Hättenschwiler (stephan.hattenschwiler@cefe.cnrs.fr), Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, CNRS – Univ. de Montpellier – Univ. Paul-Valéry Montpellier - EPHE, 1919 route de Mende, FR-34293 Montpellier Cedex 5, France. – J. Gavinet, IRSTEA, UR EMAX, 3275 route de Cézanne CS 40061, FR-13182 Aix en Provence Cedex / IMBE, UMR Aix-Marseille Univ. - CNRS - IRD – Univ. d'Avignon, Campus St Charles, Case 4, FR-13331 Marseille Cedex 03, France. – S. Devidal and J. Roy, European Ecotron of Montpellier, UMS 3248, CNRS, 1 Chemin du Rioux, campus de Baillarguet, FR-34980 Montferrier-sur-Lez, France.

The role of biodiversity for soil processes remains poorly understood. Existing evidence suggests that functional diversity rather than species richness is relevant for soil functioning. However, the importance of functional diversity has rarely been assessed simultaneously at more than one trophic level, critically limiting the prediction of consequences of biodiversity loss for soil functioning. In a laboratory microcosm experiment, we tested the hypothesis that increasing functional dissimilarity of both litter-feeding soil fauna and litter mixtures interactively affects the rates of five different soil processes related to litter decomposition. We created trait-based functional dissimilarity gradients using five assemblages of two detritivore species and five mixtures of two plant litter species commonly found in Mediterranean shrubland ecosystems of southern France. With increasing drought periods predicted for Mediterranean ecosystems in the future, we additionally included two different watering frequencies to evaluate the impact of drought on soil processes and how drought interacts with functional dissimilarity. The different fauna assemblages and litter mixtures showed strong effects on litter mass loss, soil organic carbon and nitrogen leaching, as well as on soil microbial activities. Up to 20% of the variation in response variables was explained by functional dissimilarity, suggesting an ecologically relevant impact of functional diversity on soil process rates. Detritivore functional dissimilarity tended to have stronger effects when combined with increasingly dissimilar litter mixtures, suggesting that trait dissimilarity interacts across trophic levels. Drought affected several soil processes but did not modify the relationships between functional dissimilarity and process rates. Our results indicate that trait diversity of detritivore assemblages and litter mixtures is an important predictor of soil process rates. The common and easily measurable traits used in our study suggest straightforward application across different types of ecosystems and environmental conditions.

Biological diversity is a major driver of ecosystem functioning and numerous studies indicated positive diversity effects on ecosystem processes such as primary productivity (Balvanera et al. 2006, Cardinale et al. 2011, Hooper et al. 2012) and decomposition (Cardinale et al. 2011, Handa et al. 2014). Underlying mechanisms for these biodiversity effects are multifaceted and can vary depending on the trophic level of communities of organisms and the specific processes considered (Hättenschwiler et al. 2005, Duffy et al. 2007, Cardinale et al. 2011). Moreover, biodiversity is a multidimensional concept that can be quantified in different ways (Purvis and Hector 2000, Cadotte et al. 2011). Species richness is often used but does not account specifically for functional differences among species, making mechanism-driven predictions of biodiversity–functioning relationships difficult. An increasing number of species does not necessarily reflect a parallel increase in functional differences among species (Epps et al. 2007, Cadotte et al. 2011) and can even decrease ecosystem process rates due to antagonistic interactions (e.g. competition), as shown experimentally with bacterial communities (Jousset et al. 2011). Another widely used concept for the quantification of biodiversity is the number of functional groups, which however has the drawback of ignoring potentially important differences among species within these groups and to rely on arbitrary a priori decisions for group creation (Petchey and Gaston 2006). An alternative approach of functional diversity aims at defining the value and range of organismal traits that directly influence ecosystem processes (Tilman 2001, Cadotte et al. 2011). Villéger et al. (2008) distinguished functional richness, functional divergence and functional evenness as distinct components of functional diversity.

Soil process rates typically tend to saturate at low levels of species richness (Setälä and McLean 2004, Hedde et al. 2010), suggesting an important degree of redundancy and a relatively weak impact of taxonomic richness on process rates, at least under constant environmental conditions. Similarly, no soil fauna species richness effects on soil process rates were observed in the study by Heemsbergen et al. (2004). However, when these authors expressed fauna diversity as functional dissimilarity rather than taxonomic richness, a clear positive relationship was found between fauna diversity and process rates (Heemsbergen et al. 2004). Functional dissimilarity of communities of soil organisms appears to be more relevant than richness to capture how soil biodiversity affects soil processes. Functional dissimilarity is independent of the number of species, describing the unshared functional space among species in a community (Botta-Dukát 2005). Communities comprising species with similar functional attributes are more likely to show competitive interactions than communities with functionally dissimilar species, because component species are expected to process and acquire resources in similar ways. In contrast, in communities composed of functionally dissimilar species, facilitation and/or complementary resource use among species are more likely to occur (Heemsbergen et al. 2004).

Soil fauna is a critical component of the complex soil food web (Lavelle and Spain 2001). Fauna has a major impact on litter decomposition (García-Palacios et al. 2013, Handa et al. 2014), both when feeding directly on plant litter and through complex interactions with microbial decomposers (Lavelle and Spain 2001, David 2014). The effect of litter detritivores on decomposition can depend on the species identity of fauna (Vos et al. 2011), but the role of diversity within the trophic level of litter detritivores is poorly understood (Gessner et al. 2010). When different animal species interact, their effects on decomposition and associated soil processes are not easily predictable from the sum of the effects of component species (Heemsbergen et al. 2004, De Oliveira et al. 2010, Hedde et al. 2010). For example, detritivorous snails can more easily feed on fresh litter material than millipedes, and their co-occurrence leads to an overall synergistic interaction and increased decomposition (De Oliveira et al. 2010). The mechanisms of facilitation or complementary resource use by diverse detritivore communities should be particularly effective with diverse resources. Complementary resource use by detritivores is discussed as a major mechanism explaining the synergistic litter diversity effects observed in the majority of studies comparing litter mixture decomposition with that of the component litter species decomposing singly (Hättenschwiler et al. 2005). The few studies that assessed decomposition of litter mixtures with and without the presence of fauna, generally found that litter-feeding animals amplified litter mixture effects on decomposition (Hättenschwiler and Gasser 2005, De Oliveira et al. 2010, Vos et al. 2011, Jabiol et al. 2013). These findings highlight the importance of interactions between trophic levels and the need to incorporate diversity at several trophic levels for the understanding of diversity effects on ecosystem processes (Duffy et al. 2007, Gessner et al. 2010). However, experimental manipulations of diversity across trophic levels to explore how they affect litter decomposition are rare (but see Jabiol et al. 2013, Handa et al. 2014).

Here we assessed the interactive effects of changing diversity at two trophic levels on a range of soil processes related to litter decomposition of a Mediterranean garrigue ecosystem. In a fully factorial laboratory experiment, we manipulated functional dissimilarity while keeping species number constant at both the litter (resource) and the detritivore (consumer) levels. We did not vary species numbers because species richness per se usually accounts for very little or none of the variation observed in litter diversity experiments (Gessner et al. 2010, Handa et al. 2014). Also, establishing the relationship between biodiversity and decomposition processes based on traits of contributing species seems to be most promising towards a general predictive framework of how biodiversity affects soil processes across different types of ecosystems (Handa et al. 2014). We hypothesized that 1) rates of soil processes differ according to detritivore assemblages, and more specifically that process rates increase with increasing functional dissimilarity of detritivore assemblages. We also hypothesized that 2) these detritivore effects depend on litter mixture identity, with stronger effects in more dissimilar litter mixtures.

Water availability is a key factor for decomposition in Mediterranean ecosystems, in which the activity periods of detritivores and microorganisms typically peak in the most humid periods during fall and early spring (de Dato et al. 2010). These optimal periods of decomposer activity are likely to be affected by ongoing climate change. In the Mediterranean region, climate models predict a modification of the frequency of precipitation that will increase the probability of extreme events like flood or drought (Gao et al. 2006). In addition, the amount of precipitation is predicted to decrease over the next decades (Giorgi and Lionello 2008). Drier conditions should limit decomposer activity and consequently affect decomposition and related soil processes. Whether or not the relationship between soil processes and functional dissimilarity in the decomposer food web changes under drier conditions is difficult to predict. To our knowledge the impact of changing functional detritivore diversity on decomposition under contrasting humidity treatments has not been tested experimentally before. Here we do so by including two different watering frequencies in our experiment in order to simulate optimal and more limiting moisture conditions.

Material and methods

Plant and animal material

We collected leaf litter of five typical and widely distributed Mediterranean plant species: the four evergreen woody shrubs *Quercus coccifera*, *Rosmarinus officinalis*, *Ulex parviflorus* and *Cistus albidus*, and the conifer tree *Pinus halepensis*. All five species typically co-occur in shrubland ecosystems of southern France. Shrub litter was collected at the Massif de l'Etoile near Marseille (5°25′E, 43°22′N), and *Pinus* needle litter in the surroundings of Montpellier (3°52′E, 43°40′N). All material was collected on the ground in March–April 2011, before peak litter fall, aiming for the roughly one-year-old leaf litter cohort. The small amount of very fresh leaf litter and the leaf litter cohorts older than one year could

relatively easily be distinguished and were not collected. We did not take freshly fallen leaf litter because soil detritivores generally prefer litter that is already well colonized by microbial communities. Litter was air-dried, sorted into species and adhering soil particles were brushed off.

We collected five common detritivore species that are often highly abundant in the same type of garrigue ecosystem: two species of Diplopoda, *Glomeris marginata* and *Ommatoiulus sabulosus*, two species of Isopoda, *Armadillidium vulgare* and *Armadillo officinalis*, and the prosobranch snail *Pomatias elegans*. Three weeks before the start of the experiment 250 adult or sub-adult individuals of each species were collected at the Massif de l'Etoile and in the surroundings of Montpellier in fall 2011, then were kept in large plastic containers at constant temperature (16°C) and day length (12 h), and fed with a mixture of the five litter species chosen for the experiment.

Trait measurements and functional dissimilarity

Trait selection is a critical step in the calculation of diversity indices (Petchey and Gaston 2006, Villéger et al. 2008). Traits must be selected according to their relevance to the ecological processes while avoiding redundancy among traits. Five litter traits were retained among the ten we initially measured (Table 1): the concentrations of nitrogen (N) and lignin, as typically good predictors of litter decomposition rates (Zhang et al. 2008); the concentration of condensed tannins, which controls the activity of decomposers (Coq et al. 2010); the concentration of organic carbon in the water-soluble litter fraction as a critical energy source for decomposers that strongly influences soil processes (Fanin et al. 2012); and finally the water holding capacity of litter, a potentially important attribute for detritivores when water is limiting and a good predictor of decomposition, especially in Mediterranean ecosystems (Makkonen et al. 2012). We used standard methods to determine these litter traits as described in Coq et al. (2010) and Coulis et al. (2013).

We also selected five traits for each detritivore species, which were related to their ability to transform leaf litter and influence its subsequent decomposition in their feces (Table 2): consumption rate and assimilation efficiency, which are directly related to the impact of detritivores on litter mass loss and determine the amounts of feces they transfer to the soil; surface area of fecal pellets and size of litter particles within fecal pellets, which are good measures of the surface available for microbial colonization in feces (Lavelle and Spain 2001, Hedde et al. 2007); and hygroscopicity of feces, due to the importance of water availability in this material for subsequent microbial activity. Consumption and assimilation were determined at constant temperature (16°C) and day length (12 h) using well-moistened leaf litter of *C. albidus* as a single food source for detritivores. *Cistus* leaf litter was the only one of the five litter types that was readily consumed by all five detritivore species in preliminary tests of food preferences (from 73 to 96% of the total consumption). Constant environmental conditions and the preferred litter species were chosen to standardize trait determination. The use of *Cistus* for trait measurements was unlikely to greatly affect the relative differences in trait values among detritivore species and the resulting dissimilarity indices. Although consumption rate and assimilation efficiency are known to vary greatly depending on the food source, taken together they situate each detritivore species along a continuum ranging from species that consume large amounts with a low assimilation efficiency (high feces production), to species that consume less and assimilate more (low feces production). These opposite feeding strategies largely depend on anatomical and physiological characteristics of species (Wieser 1978) and are largely conserved over a range of food sources. Fecal pellet dimensions and fecal particle sizes depend directly on morphological characteristics of species (mouthparts, hindgut), and different hygroscopic properties in fecal pellets derived from the same leaf litter also reflect species-specific gut processes, which are unlikely to change with changing food source. Consumption rates (mg of dry litter consumed per g of live animal per day) and assimilation efficiencies were calculated according to David and Gillon (2002). Width, length and height of 50 fecal pellets from each species were measured and used to estimate the mean surface area. The mean particle size in feces was calculated according to Hedde et al. (2007). To determine hygroscopicity of feces, the water content of 50 fecal pellets was measured after enclosing them for five hours in a saturated atmosphere.

To determine the functional dissimilarity gradients of litter mixtures and detritivore assemblages, we calculated Rao's quadratic entropy as an index of functional dissimilarity (Botta-Dukát 2005) for all possible combinations of two species of plant litter and soil animals. At each trophic level, there were ten possible combinations of two species and we chose five among them according to the following criteria: 1) maximizing the functional dissimilarity gradient, i.e. the range of Rao's index values, and 2) including each species exactly twice in the five combinations in order to avoid confounding by unbalanced species presence. The five litter mixtures retained for the experiment were, in increasing order of functional dissimilarity (Rao's quadratic entropy based on equal biomass of the two species, in parentheses), *Quercus*/*Rosmarinus* (0.33), *Rosmarinus*/*Ulex* (0.40), *Cistus*/*Ulex* (0.43), *Cistus*/*Pinus* (0.69) and *Quercus*/*Pinus* (0.81). For the detritivore assemblages we

Table 1. Litter traits used to calculate the functional dissimilarity (Rao index) of litter mixtures (mean ± SE, n = 5).

Plant species	N (mg g^{-1})	Lignin (mg g^{-1})	Condensed tannins (mg g^{-1})	Water-soluble carbon (mg g^{-1})	Water holding capacity (%)
Cistus albidus	6.4 ± 0.2	249 ± 8	5.8 ± 1.95	3.8 ± 0.9	178 ± 10
Pinus halepensis	4.0 ± 0.3	224 ± 13	33.2 ± 0.17	7.8 ± 0.1	98 ± 6
Quercus coccifera	10.3 ± 0.3	148 ± 8	6.0 ± 0.27	10.6 ± 1.3	132 ± 5
Rosmarinus officinalis	6.5 ± 0.3	155 ± 6	0.7 ± 0.06	5.2 ± 0.5	146 ± 12
Ulex parviflorus	10.9 ± 0.4	230 ± 18	0.9 ± 0.16	5.0 ± 1.1	97 ± 5

Table 2. Traits for the calculation of functional dissimilarity (Rao index) of detritivore assemblages (mean ± SE, n = 5). In addition, mean initial biomass (after 24 h starvation) per capita of all individuals used in the experiment (n = 200 per species) are shown in the last column (*Pomatias* biomass without shell).

Detritivore species	Consumption rate (mg g^{-1} d^{-1})	Assimilation efficiency (%)	Feces surface area (mm^2)	Feces hygroscopicity (%)	Feces particle size (µm)	Individual biomass (mg)*
Armadillidium vulgare	77 ± 1	50 ± 1	7.2 ± 0.3	28.8 ± 1.8	262 ± 1	151 ± 3.5
Armadillo officinalis	88 ± 7	65 ± 3	8.7 ± 0.4	28.4 ± 1	200 ± 10	211 ± 3.5
Glomeris marginata	126 ± 34	12 ± 3	40.0 ± 1.2	15.2 ± 0.9	274 ± 4	138 ± 3.6
Ommatoiulus sabulosus	117 ± 12	23 ± 4	8.2 ± 0.1	29.9 ± 0.7	165 ± 8	145 ± 3.4
Pomatias elegans	26 ± 4	43 ± 5	7.6 ± 0.5	19.7 ± 0.7	98 ± 1	255 ± 2.9

*Ranges between the smallest and the largest individuals were as follows: *A.v.*: 51–283 mg, *A.o.*: 121–353 mg, *G.m.*: 63–305 mg, *O.s.*: 71–305 mg, *P.e.*: 172–410 mg.

kept the combinations of *Armadillidium*/*Armadillo* (0.03), *Armadillidium*/*Ommatoiulus* (0.21), *Pomatias*/*Armadillo* (0.37), *Glomeris*/*Ommatoiulus* (0.58) and *Pomatias*/*Glomeris* (0.70). Microcosm-specific Rao's indices were calculated based on the relative biomass of species in each microcosm (Barantal et al. 2011). For litter mixtures these calculations were done with initial litter mass of the two species of each microcosm. For detritivore assemblages we calculated Rao's indices using the average of initial and final biomass of both species of each microcosm. Overall, there was a mortality rate of 5% during the experiment, and when possible, we took the approximate date of death into account for the calculation of dissimilarity indices. When the date of death was unknown, it was set at the middle of the experiment. For the snail biomass we excluded the heavy shell as described in De Oliveira et al. (2010).

Experimental design

Microcosms were constructed from lidded boxes of transparent polystyrene (175 × 115 × 65 mm). The bottom of each box was lined with 1 cm thick inert plastic composite (polyamide and polyethylene terephthalate) to improve drainage of the system. This drainage layer was covered with 700 g of air-dried soil sieved through a 2 mm screen, resulting in a 3-cm deep soil layer within each box. The soil used for the experiment was collected from the top layer (top 10 cm) of an experimental agricultural field at Grignon, France (1°56′E, 48°50N). We chose this particular soil because the field had been cultivated with C_4 plants for 40 years and we intended to take advantage of the difference in isotopic labeling between soil organic matter and the C_3 litter species used, to distinguish between soil and litter respiration (data not shown here). The soil was a Luvisol developed on loess over limestone, with a total C content of 13.9 g kg^{-1} and a total N content of 1.27 g kg^{-1}. Eight grams of leaf litter (target of 4 g of each species) were distributed on top of the soil. At the start of the experiment each microcosm was watered with deionized water to reach 80% of field capacity in the soil and to approach water holding capacity of litter (see below for actual litter water content). After watering, two individuals of each of the two animal species, previously starved for 24 h and weighed, were added in each treatment-specific microcosm. The total of 200 individuals needed of each species were chosen from the initial pool of 250 individuals based on individual biomass that varied among and within species (Table 2). Different sized individuals were put together in order to minimize variability in initial biomass within each species. This resulted in an average (± SE, n = 50) total detritivore assemblage biomass of 706 ± 7 mg (*Armadillidium*/*Armadillo* treatment), 587 ± 11 mg (*Armadillidium*/*Ommatoiulus* treatment), 918 ± 9 mg (*Pomatias*/*Armadillo* treatment), 548 ± 13 mg (*Glomeris*/*Ommatoiulus* treatment), and 757 ± 13 mg (*Pomatias*/*Glomeris* treatment).

In addition to the five litter mixtures and five detritivore assemblages in all possible combinations plus a litter treatment of all mixtures without fauna, we included two different watering regimes. Each treatment combination was replicated five times resulting in a total number of 300 microcosms (5 litter treatments × 6 animal treatments × 2 watering regimes × 5 replicates). An additional five replicates per watering regime without any litter and fauna were included, yielding a grand total of 310 microcosms. Each of the five replicates per treatment combination was kept in one of five incubators in the CNRS Montpellier European Ecotron, with microcosms distributed randomly within incubators and positions changed every three days according to a randomized complete block design. Microcosms were incubated for 11 weeks, at constant temperature (20°C), relative air humidity (50%), and day length (12 h). The 12-h daylight conditions were created by bands of white LEDs attached vertically along the walls of each incubator. Microcosms of the humid treatment were remoistened weekly, whereas those of the dry treatment were remoistened every two weeks or after a three-week interval during the last drying–rewetting cycle (Fig. 1). Microcosm lids were initially pierced with five 1.3 mm diameter holes to allow CO_2 and water vapor exchanges (phase I, Fig. 1). As the desiccation rate was rather low, an additional 14 holes were pierced (a total of 19) for phases II and III (Fig. 1). The amount of water added compensated for evaporation losses and reset litter and soil moisture to initial conditions in both the humid and the dry treatments. This resulted in roughly the same total amount of water added to microcosms of both treatments (96.6 ± 1.8 and 95.5 ± 2.2 ml in the humid and dry treatments, respectively) over the course of the experiment. However, as a result of the different watering frequencies, soil water content was on average 81 ± 0.1% of field capacity in the humid treatment, and 77 ± 0.1% in the dry treatment ($p < 0.001$). Soil moisture content in the dry treatment decreased to 67%, and even 58% of the field capacity during the last drying-rewetting cycle, while it never dropped below 75% in the humid treatment (Fig. 1). Litter water content just after watering was on

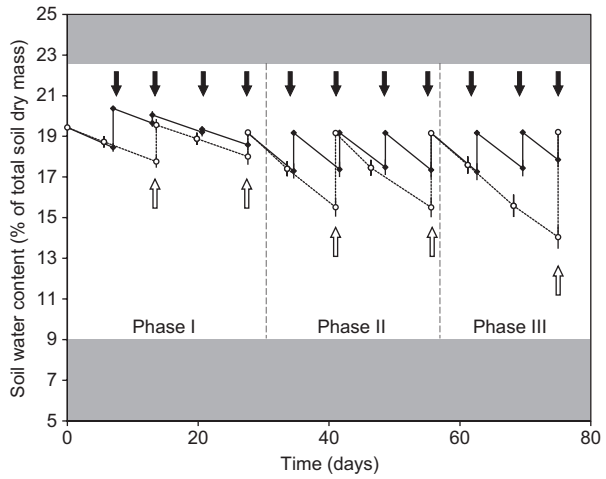

Figure 1. Soil water content (means ± SE, n = 150) in microcosms from the dry treatment (open circles) and the humid treatment (filled circles) over the duration of the experiment. Arrows indicate rewetting events. Shaded zones correspond to water contents above the field capacity and below the wilting point.

average 120% of air dry weight for *Cistus*, 72% for *Quercus*, 71% for *Rosmarinus*, 67% for *Pinus*, and 54% for *Ulex*. Litter water content decreased rapidly to reach 26% for *Cistus*, 24% for *Quercus*, 25% for *Rosmarinus,* 24% for *Pinus* and 19% for *Ulex* after six days, just before rewetting the microcosms of the humid treatment. Litter water content remained roughly at these low levels during the rest of the second (and third) week in the dry treatment (Supplementary material Appendix 1 Fig. A1 for more details).

Microcosms with fauna were checked for animal mortality every three days, without disturbing the litter and soil layers. Thirty-two dead animals were replaced by individuals of similar mass within the first half of experimental duration, and 23 additional dead individuals were recorded at the end of the experiment. Mortality was not influenced by litter mixture identity ($p = 0.21$) nor by moisture treatment ($p = 0.99$).

Response variables

At the end of the 11-week experiment, animals were taken out of the microcosms, kept for 24 h without any food, and then weighed. The remaining litter material was collected from the microcosms separately by species, rinsed in 200 ml distilled water for 5 min to remove soil particles, and immediately freeze-dried before weighing for mass loss determination (expressed in % of initial litter dry mass, corrected with a conversion factor to account for the difference between air-dry and freeze-dry litter mass). The water used for litter rinsing was added to the corresponding microcosm in order to simulate a rain event leading to soil drainage (i.e. a single 10 mm precipitation event). After water addition, microcosms were allowed to drain for 20 min and leachates were collected from the bottom of the microcosms underneath the drainage layer, filtered at 0.45 µm (cellulose nitrate membrane) to remove microorganisms and particulate soil matter, and immediately stored at –80°C until analysis. Dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) in leachates were determined using a TOC analyzer equipped with a supplementary module for N detection.

Microcosms were then kept at 25°C for 48 h to allow moderate drying before the soil was sieved through a 2 mm screen and dried at 25°C for five days. Representative samples of soil were used to measure substrate induced respiration (SIR) following Beare et al. (1990), and potential cellulose decomposition (PCD) by the soil microbial community according to Wardle et al. (1999). Briefly, cellulose paper disks (filter paper qualitative 410, VWR, 55 mm diameter) were enclosed between two nylon 2 mm mesh nets and incubated with 20 ± 0.5 g of treatment-specific soil watered to 80% of field capacity in petri dishes. After three weeks at 25°C in the dark, cellulose disks were recovered, gently cleaned with a brush in deionized water, and oven dried (65°C) to determine remaining cellulose dry mass and cellulose mass loss (expressed in % of initial cellulose mass).

Statistical analyses

The main effects and interactions of litter mixture identity, detritivore assemblage identity and watering frequency on the response variables (litter mass loss, DOC leaching, TDN leaching, soil SIR and PCD) were tested using ANOVA for randomized complete block designs. Data from control boxes (no litter and no fauna) were not included in these tests. Incubators were included in the analyses as a random blocking factor and the main effects and interactions of the three fixed factors were tested over their interactions with blocks. Post hoc pairwise comparisons were performed using Tukey's method.

Relationships between the same five response variables and functional dissimilarity of litter mixtures or detritivore assemblages were determined by ordinary least squares (OLS) regression, with litter and detritivore functional dissimilarity indices as continuous independent variables. We used ANCOVA to test the relationships between functional dissimilarity (co-variable) and process rates with the moisture treatment as a categorical variable. Interaction terms between functional dissimilarity and watering frequency were used to compare the slopes of the regression lines at the two watering frequencies.

To assess the magnitude of the effect of watering frequency, we calculated the standardized difference between mean process rate in humid (μ_{humid}) and dry (μ_{dry}) conditions (drought effect size) using Cohen's d formula (Cohen 1992):

$$d = \frac{\mu_{humid} - \mu_{dry}}{\sqrt{\left(\left(\sigma_{humid}\right)^2 + \left(\sigma_{dry}\right)^2\right)/2}}$$

Relationships between drought effect sizes (independent variables) and mean process rates in humid conditions (dependent variables) were tested by OLS regression.

Prior to statistical analyses, data were log (mass loss, DOC, TDN) or power (PCD) transformed to meet the requirements of normality and heteroscedasticity. All statistical analyses were performed using R software ver. 2.15.2.

Results

Litter mixture and detritivore assemblage effects

The identity of litter mixtures and/or detritivore assemblages significantly affected the five soil processes measured (Table 3). Averaged across the moisture treatments, litter mass loss varied among litter mixtures from $14.7 \pm 1.0\%$ in *Quercus/Pinus* to $23.1 \pm 1.0\%$ in *Quercus/Rosmarinus* when no detritivores were present (Supplementary material Appendix 1 Table A1). The presence of detritivores nearly doubled these values, but also changed the ranking of litter mixture specific mass loss. Across all detritivore treatments (excluding the controls without fauna) and moisture treatments, litter mass loss ranged from $29.0 \pm 0.6\%$ in *Quercus/Pinus* to $43.9 \pm 1.3\%$ in *Cistus/Ulex* (Fig. 2). Detritivore assemblage identity also significantly affected litter mass loss, which ranged from $31.0 \pm 0.7\%$ with *Pomatias/Armadillio* to $46.1 \pm 1.5\%$ with *Glomeris/Ommatoiulus* (all litter and moisture treatments combined) (Fig. 2). However, the detritivore assemblage effect on mass loss differed among litter mixtures, as shown by the significant litter × fauna interaction (Table 3). The *Pomatias/Armadillo* assemblage, in particular, had a comparatively weaker effect on *Cistus/Ulex* mass loss, and a stronger effect on *Quercus/Romarinus* mass loss compared to the other detritivore assemblages.

Dissolved organic carbon (DOC) leached from the soil of the microcosms at the end of the experiment was mostly driven by decomposing leaf litter, as shown by the roughly six-fold higher amount of leached DOC when litter was present in the microcosms (on average 2.7 ± 0.1 mg kg^{-1} in the absence of detritivores) compared to control microcosms without any litter material (0.4 ± 0.1 mg kg^{-1}) (Supplementary material Appendix 1 Table A2). The amount of DOC in leachates differed significantly among litter mixtures, ranging from 1.7 ± 0.1 mg kg^{-1} in *Cistus/Ulex* to 3.5 ± 0.1 mg kg^{-1} in *Quercus/Rosmarinus* (all detritivore and moisture treatments combined, but excluding the no fauna control) (Fig. 2). The presence of detritivores slightly decreased DOC leaching in comparison with microcosms without fauna, and the amount of DOC differed significantly among detritivore assemblages, ranging from 2.3 ± 0.1 mg kg^{-1} with *Pomatias/Glomeris* to 2.8 ± 0.1 mg kg^{-1} with *Armadillidium/Armadillo* (all litter and moisture treatments combined) (Fig. 2). We detected no significant interactions between main factors on leaching of DOC (Table 3).

Litter mixture identity significantly affected the total dissolved nitrogen (TDN) content in leachates (Table 3). Across all detritivore treatments (excluding the control without fauna) and moisture treatments, TDN ranged from 1.34 ± 0.07 mg kg^{-1} in *Quercus/Rosmarinus* to 2.06 ± 0.09 mg kg^{-1} in *Quercus/Pinus* (Fig. 2, Supplementary material Appendix 1 Table A3). Although the presence of detritivores did not significantly affect nitrogen leaching compared to microcosms without fauna, the amount of TDN differed significantly among detritivore assemblages, ranging from 1.42 ± 0.07 mg kg^{-1} with *Pomatias/Glomeris* to 1.72 ± 0.08 mg kg^{-1} with *Armadillidium/Armadillo* (all litter and moisture treatments combined) (Fig. 2). Leaching of TDN varied distinctively among litter mixtures and detritivore assemblages compared to DOC leaching (Fig. 2). There were no interacting effects among the main factors on TDN leaching (Table 3).

Substrate induced respiration (SIR) of soil microbial communities did not significantly differ among litter treatments, but varied among detritivore assemblages (Table 3, Supplementary material Appendix 1 Table A4). Soil SIR ranged from 4.32 ± 0.05 μg CO_2 g^{-1} h^{-1} with *Pomatias/Armadillio* to 4.61 ± 0.07 μg CO_2 g^{-1} h^{-1} with *Glomeris/Ommatoiulus* (all litter and moisture treatments combined). Overall, average soil SIR with detritivores was higher (4.46 ± 0.03 μg CO_2 g^{-1} h^{-1}) compared to microcosms in which only litter was added (3.97 ± 0.07 μg CO_2 g^{-1} h^{-1}). While there was no effect of litter mixture identity on soil SIR, soil SIR varied among litter mixtures depending on watering frequency (significant litter mixture × watering frequency interaction, Table 3). No other interacting effects on soil SIR were observed.

In contrast to soil SIR, the potential cellulose decomposition (PCD) differed significantly among litter

Table 3. Results of ANOVAs to test for the effects of litter mixture identity, detritivore assemblage identity, and moisture treatment on the five response variables.

	Litter mass loss			DOC leaching			TDN leaching			Soil SIR			Soil DCP		
	DF	S.Sq	F-value	DF	S.Sq	F-value	DF	S.Sq	F-value	DF	S.Sq	F-value	DF	S.Sq	F-value
Block (B)	4	3.4	–	4	0.6	–	4	13.3	–	4	10.8	–	4	19.1	–
Litter mixture identity (L)	4	42.5	183***	4	65.4	267***	4	16.9	21***	4	6.3	2	4	4.6	5*
L × B	16	0.9	–	16	1.0	–	16	3.3	–	16	10.9	–	16	4.0	–
Detritivore assemblage identity (D)	4	31.2	50***	4	4.5	9***	4	3.3	5**	4	5.9	9***	4	0.7	1
D × B	16	2.5	–	16	2.0	–	16	2.7	–	16	2.5	–	16	2.9	–
Moisture level (M)	1	1.2	12*	1	2.4	8*	1	2.5	2	1	5.6	12*	1	2.6	3
M × B	4	0.4	–	4	1.2	–	4	5.4	–	4	1.8	–	4	3.8	–
L × D	16	6.4	7***	16	1.9	1	16	4.0	1	16	4.5	1	16	7.5	2
L × D × B	64	3.5	–	64	8.4	–	64	20.2	–	64	17.5	–	64	19.7	–
L × M	4	0.4	1	4	0.5	1	4	0.3	0	4	2.3	4*	4	1.3	2
L × M × B	16	1.2	–	16	1.9	–	16	2.5	–	16	2.1	–	16	3.2	–
D × M	4	0.4	2	4	0.4	1	4	0.9	1	4	1.1	1	4	0.7	0
D × M × B	16	0.6	–	16	1.2	–	16	3.0	–	16	4.8	–	16	6.4	–
L × D × M	16	1.1	1	16	2.1	1	16	5.8	1	16	2.2	0	16	3.4	1
L × D × M x B	64	4.1	–	62	6.6	–	63	16	–	61	21.6	–	58	20.1	–

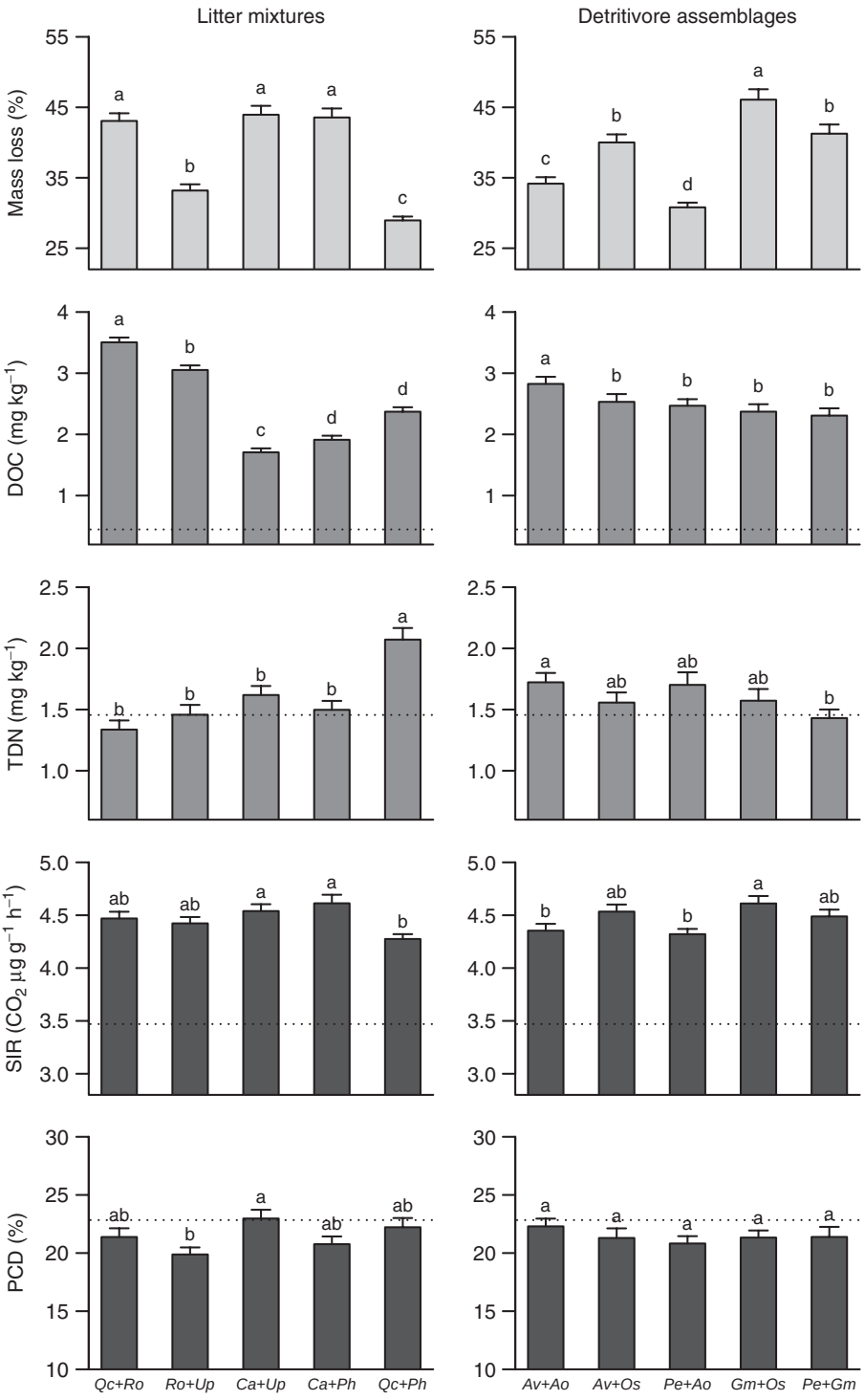

Figure 2. Effects of litter mixtures and detritivore assemblages on litter mass loss, DOC leaching, TDN leaching, soil SIR, and soil PCD (mean ± SE, n = 50, pooled across the two humidity treatments). Tukey's post hoc tests were performed to evaluate pairwise differences between litter mixtures across all detritivore treatments (left) and between detritivore assemblages across all litter treatments (right). Different letters indicate significant differences among bars within each graph. Dotted lines indicate mean process rates in microcosms without leaf litter.

mixtures, but not among detritivore assemblages (Table 3, Supplementary material Appendix 1 Table A5). Soil PCD ranged from 20.0 ± 0.6% in *Rosmarinus/Ulex* to 22.9 ± 0.7% in *Cistus/Ulex* (mean across all detritivore treatments, excluding the no fauna control, and both moisture treatments combined). No interacting effects among main factors were observed for soil PCD (Table 3).

The role of functional dissimilarity

The functional dissimilarity of detritivore assemblages contributed to the detritivore effects observed for litter mass loss and soil DOC leaching. Litter mass loss across all litter mixtures increased with increasing functional dissimilarity of detritivore assemblages with little difference between the two moisture treatments (Fig. 3). In contrast, soil DOC leaching decreased with increasing functional dissimilarity of detritivore assemblages, regardless of moisture treatment (Fig. 3). The slopes of these relationships remained positive for litter mass loss and negative for DOC leaching when each litter mixture was analyzed separately (across both moisture treatments - data not shown), although they were not always significantly different from zero. Apart from the *Quercus/Pinus* treatment that showed no significant relationship between mass loss and detritivore assemblage dissimilarity ($p = 0.51$), the slope of the regression line (b) was steeper in the two more dissimilar litter mixtures (*Cistus/Ulex:* $b = 0.16$, $R^2 = 0.25$, $p < 0.001$; *Cistus/Pinus:* $b = 0.14$, $R^2 = 0.21$, $p < 0.001$) compared to the two less dissimilar litter mixtures (*Quercus/Rosmarinus:* $b = 0.10$, $R^2 = 0.11$, $p = 0.009$; *Rosmarinus/Ulex:* $b = 0.08$, $R^2 = 0.11$, $p = 0.01$). When each litter treatment was analyzed separately, DOC leaching was negatively related to increasing detritivore dissimilarity only in the two most dissimilar litter mixtures (*Cistus/Pinus:* $b = -0.70$, $R^2 = 0.18$, $p = 0.001$; *Quercus/Pinus:* $b = -0.88$, $R^2 = 0.24$, $p < 0.001$). The relationship was not significant for the three less dissimilar litter mixtures.

Both, litter mass loss and DOC leaching were negatively related with functional dissimilarity of litter mixtures across

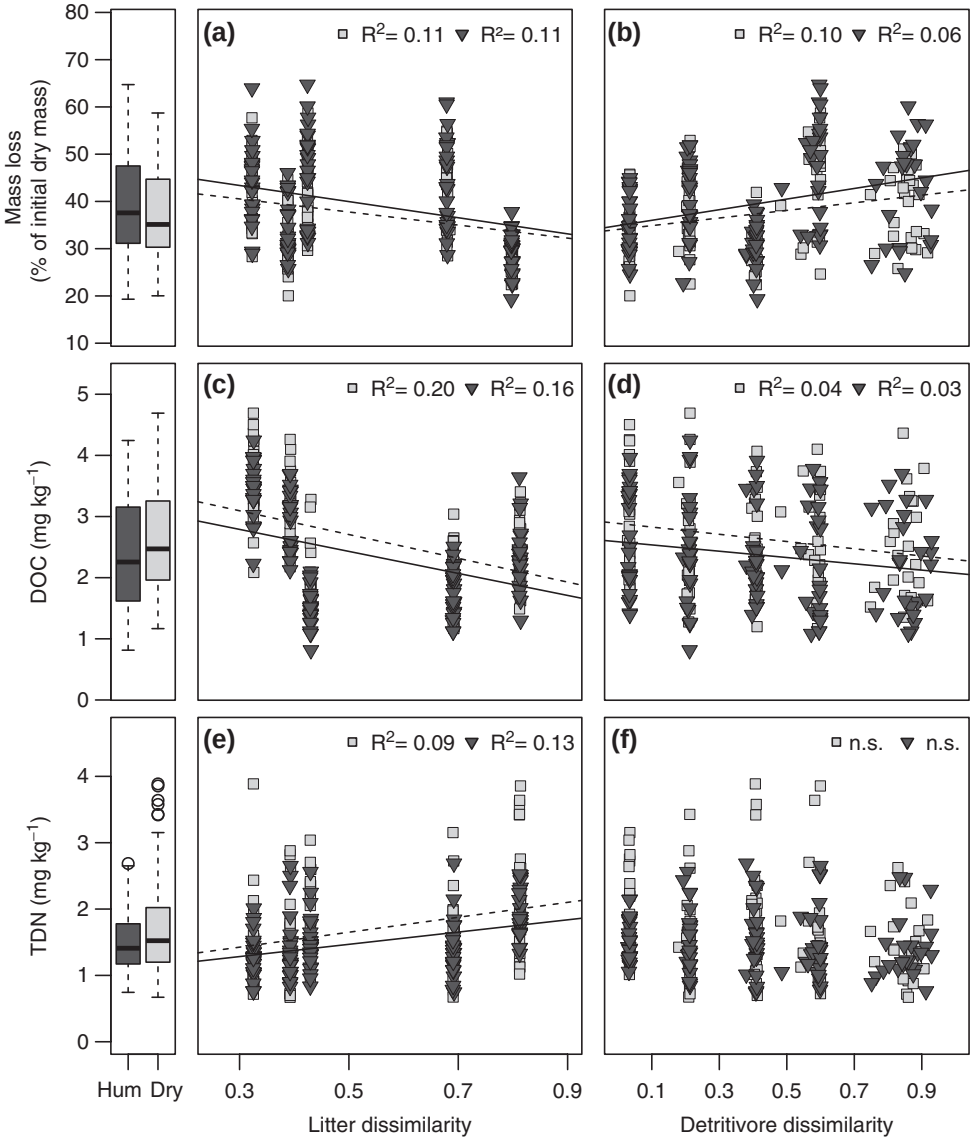

Figure 3. Relationships between functional dissimilarity of litter mixtures or detritivore assemblages and mass loss (a, b), DOC leaching (c, d), and TDN leaching (e, f). For each process, data are shown either grouped by humidity treatment in a boxplot (left), expressed as a function of litter mixture dissimilarity (center) or as a function of detritivore assemblage dissimilarity (right). Treatments without detritivores are not shown. Dark triangles represent humid treatments and ligth grey squares dry treatments. When linear regressions are significant ($p < 0.05$), regression lines are drawn with their respective R^2-values.

all detritivore treatments (Fig. 3). In contrast, TDN leaching increased with increasing litter functional dissimilarity. Again, the signs of the slopes of these relationships remained the same when each detritivore assemblage was analyzed separately, although the slopes were not always significantly different from zero (data not shown). The slope between mass loss and litter mixture dissimilarity was not significantly negative for the least dissimilar detritivore assemblage (*Armadillidium/Armadillo*; $p = 0.18$), while it differed from zero for all other detritivore treatments. The negative relationship between DOC leaching and litter mixture dissimilarity was significant for each individual detritivore assemblage, but was increasingly negative with increasingly dissimilar detritivore assemblages (e.g. the least dissimilar *Armadillidium/Armadillo* combination: $b = -1.49$, $R^2 = 0.10$, $p = 0.014$; the most dissimilar *Pomatias/Glomeris* combination: $b = -2.32$, $R^2 = 0.27$, $p < 0.001$). The leaching of TDN increased with increasing functional dissimilarity of litter mixtures for the two most dissimilar detritivore assemblages (*Glomeris/Ommatoiulus*: $b = 1.40$, $R^2 = 0.14$, $p = 0.005$; *Pomatias/Glomeris*: $b = 1.41$, $R^2 = 0.30$, $p < 0.001$), and also for the least dissimilar detritivore assemblage (*Armadillidium/Armadillo*: $b = 0.95$, $R^2 = 0.09$, $p = 0.02$). However, the positive slopes for these relationships were not significantly different from zero in the remaining two detritivore assemblages. Functional dissimilarity of detritivore assemblages and litter mixtures did not correlate with soil microbial SIR or PCD (data not shown).

The slopes of the relationships between soil processes and functional dissimilarity of detritivore assemblages and that of litter mixtures were of similar magnitude (although opposite for litter mass loss) and explained a similar amount of variation. Comparisons between the sums of squares calculated from the linear regressions between process rates and functional dissimilarity, and those emerging from ANOVAs shown in Table 3, suggest that functional dissimilarity accounted for a much smaller proportion of the variance explained than that explained by community identity. For example, litter dissimilarity accounted for 16 and 20% of the variation in DOC leaching under humid and dry conditions, respectively, compared to 74 and 61% accounted for by litter mixture identity.

Moisture effects

Reduced watering frequency resulted in significantly lower litter mass loss, higher DOC leaching, and higher soil SIR (Table 3, Supplementary material Appendix 1 Table A1, A2, A5). In contrast, reduced watering frequency had no effect on TDN leaching and PCD (Table 3, Supplementary material Appendix 1 Table A3, A6). Lower watering frequency decreased litter mass loss, on average from 19.7% to 17.7% in the absence of detritivores and from 39.6% to 37.5% when detritivores were present (Supplementary material Appendix 1 Table A1). On average (across all detritivore and litter treatments), DOC leaching increased from 2.4 ± 0.1 to 2.6 ± 0.1 mg C kg^{-1} with decreasing water frequency. Soil SIR also increased from 4.36 ± 0.04 to 4.57 ± 0.04 $\mu g\ CO_2\ g^{-1}\ h^{-1}$ with less frequent watering. However, the effects of reduced watering on soil SIR differed among litter mixtures (significant litter mixture × watering frequency interaction, Table 3). This interaction was driven by weak and strong drought effects on soil SIR in *Cistus/Ulex* and in *Cistus/Pinus*, respectively (Supplementary material Appendix 1 Table A5).

The reported significant relationships between litter and detritivore functional dissimilarity and litter mass loss, DOC leaching, and TDN leaching did not differ with lower watering frequency compared to microcosms that were watered weekly (Fig. 3). However, the drought effect size on litter mass loss, DOC leaching and PCD significantly increased with increasing process rates measured in microcosms watered every week (Fig. 4). In contrast, there was no change in drought effect size on TDN leaching and soil SIR with increasing process rates under humid conditions (Fig. 4).

Discussion

By manipulating functional biodiversity simultaneously across the two trophic levels of litter feeding soil animals and

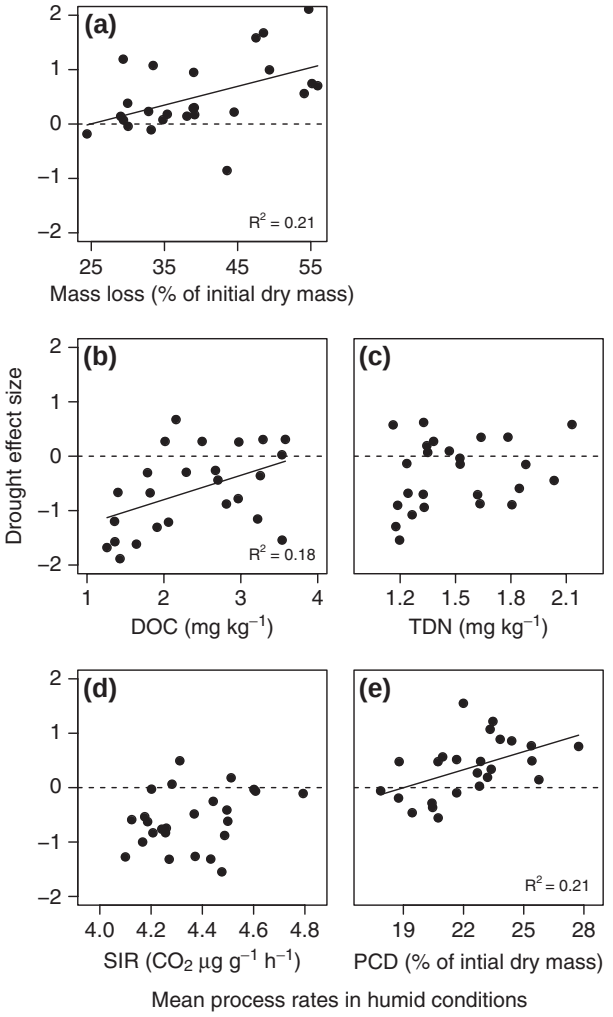

Figure 4. Drought effect size (Cohen's index d) as a function of mean process rates in humid conditions. Each point represents the mean of a particular combination of litter mixture and detritivore assemblage. Treatments without detritivores are not shown. When linear regressions are significant ($p < 0.05$), regression lines are drawn with their respective R^2-values.

plant leaf litter, we showed that changing biodiversity in the decomposer system has important consequences on a range of soil processes of a Mediterranean woody shrub ecosystem. Water availability as a critical environmental factor in the studied ecosystem additionally changed soil processes, but did not appear to modify the observed relationships between functional diversity and process rates.

Functional dissimilarity as a predictor of soil process rates

Unlike previous experiments that included species richness gradients, we exclusively varied functional dissimilarity defined on the basis of five well-described plant and detritivore traits. By keeping species number constant at two species at both trophic levels with the same abundances and similar biomass, we standardized across a number of parameters that are known to affect decomposition, such as species evenness (Dangles and Malmqvist 2004), and individual density and biomass (Frainer et al. 2014). With our design of keeping species number constant and including each species exactly twice, we also avoided confounding effects of simultaneously changing species richness and functional diversity, and species dominance effects.

Of the five different soil processes we measured, litter mass loss and leaching of dissolved organic carbon (DOC) showed significant relationships with functional dissimilarity of detritivore assemblages. In line with our initial hypothesis, our results showed that mass loss of decomposing leaf litter from Mediterranean shrub species is accelerated when detritivore assemblages are functionally more dissimilar. Increased litter mass loss was accompanied by decreased leaching of DOC. Accordingly, as detritivore dissimilarity increases there is less DOC loss from the system despite higher litter decomposition. The opposite relationships observed for DOC leaching and mass loss are rather unexpected, since decomposing litter was the major source of DOC with an average six-fold higher amount of DOC leached from soils with litter on the surface compared to bare soils. However, it has been shown previously that rates of C mineralization and DOC leaching from leaf litter do not necessarily correlate (Hagedorn and Machwitz 2007). Changes in the relative amounts of litter mass loss and DOC leaching may indicate that detritivore dissimilarity contributes to control the balance between C mineralization and DOC leaching, leading to altered soil C fluxes and potentially influencing long term C storage (Kalbitz and Kaiser 2008). Any detritivore effect on C mineralization would rather be indirect through altered microbial activity (Lavelle and Spain 2001), which concurs with our results of higher soil SIR in the presence of detritivores compared to microcosms without detritivores. However, this detritivore effect on SIR was not significantly correlated to the dissimilarity of detritivore assemblages.

According to our second hypothesis, the observed effects of detritivore dissimilarity on litter mass loss and DOC leaching varied among the five different litter mixtures. Litter mass loss increased more with increasing detritivore dissimilarity in the two more dissimilar litter mixtures *Cistus/Ulex* and *Cistus/Pinus* compared to the two less dissimilar litter mixtures *Quercus/Rosmarinus* and *Rosmarinus/Ulex*. Similarly, the overall negative correlation between DOC leaching and detritivore dissimilarity remained significant for only the two most dissimilar litter mixtures (*Cistus/Pinus* and *Quercus/Pinus*) when analyzed for each litter mixture separately. Collectively, these data support the prediction that complementary resource use by a more diverse detritivore assemblage should be more effective with a more diverse diet (Gessner et al. 2010), leading to higher litter mass loss and less organic carbon leaching from the system when both detritivore assemblages and litter mixtures increase in functional dissimilarity. However, litter mass loss in the functionally most dissimilar *Quercus/Pinus* mixture did not fit this pattern. When analyzed separately, this was the only litter mixture that did not show a significant response to detritivore dissimilarity. The average mass loss was lowest in *Quercus/Pinus* litter compared to all other litter mixtures (Fig. 2), and it varied the least among detritivore treatments with a CV of 9.2% compared to an average CV of 17.0% across the other four litter mixtures. Apparently, all detritivore assemblages consumed *Quercus/Pinus* litter at similar low rates despite its highest functional dissimilarity, perhaps because additional litter traits not included in the calculation of litter functional dissimilarity, such as leaf toughness, affect the consumption by detritivores. Low *Quercus/Pinus* litter mass loss, particularly when fauna was present, also seems to be the main driver of the negative correlation we reported between litter functional dissimilarity and mass loss.

This result highlights the difficulty of the a priori choice of traits. Obviously, the specific sets of traits included in the calculation of functional diversity affect the diversity indices and consequently the relationships with process rates. As we measured some more litter traits in addition to the five traits we defined a priori, we explored additional combinations of traits to calculate different functional dissimilarity indices. The positions of the different litter mixtures included in our study remained largely the same along the functional dissimilarity gradient, and correlations with process rates were little affected (data not shown). Similarly, Barantal et al. (2011) tested a large number of trait combinations for the calculation of different functional diversity indices, but found no correlation with litter mass loss, irrespective of the different functional diversity indices and different litter traits they used. An alternative approach to the a priori selection of species traits is directly using process rates determined from single species treatments in order to calculate functional dissimilarity of multispecies communities (Heemsbergen et al. 2004). The advantage of this approach is that the relevant ecosystem processes are incorporated into community characteristics. However, they do not reflect inherent species traits in the strict sense, but context-dependent species effects on ecosystem processes. These species effects on process rates can strongly vary depending on environmental conditions, while process-independent species-specific traits that differ from response variables vary less and allow a general characterization of the community that can be used in different contexts (Hedde et al. 2010, Barantal et al. 2011, Vos et al. 2013).

The very few existing explicit tests of the role of functional diversity of detritivore communities from temperate forest ecosystems (Heemsbergen et al. 2004, Hedde et al. 2010) and our study using a different set of species from a Mediterranean shrub ecosystem, all suggest that trait

dissimilarity of litter-feeding soil animal communities is an important component of soil biodiversity that can predict some of the variation in soil process rates. However, the amount of variation explained by detritivore functional dissimilarity is relatively small compared to species identity effects and unexplained variation in all of these studies. Perhaps under field conditions with higher variability in environmental factors, functional dissimilarity might gain further in importance as it may stabilize process rates under fluctuating environmental conditions (Yachi and Loreau 1999). Here, we did not observe any differences in the relationship between functional dissimilarity and process rates at the two distinct moisture regimes, suggesting a rather robust relationship under contrasting environmental conditions. The differences in moisture conditions were small compared to naturally occurring fluctuations, and it will be an important next step to address these questions in the field and over longer time periods. Naturally established detritivore communities are also typically more uneven than in our experiment, with some species being more abundant than others. It has been shown that in such communities, ecosystem processes can often be well predicted by the community-weighted mean (CWM) trait values (Garnier et al. 2004, Bíla et al. 2014) according to the biomass ratio hypothesis (Grime 1998). In fact, using a range of isopod assemblages of varying species richness and species-specific abundances, Bíla et al. (2014) could demonstrate that CWM accounted for most of the variation in ash leaf litter mass loss, while trait dissimilarity accounted for only a relatively small part. Although very challenging, it will be ultimately needed to quantify the relative importance of trait dissimilarity and CWM across trophic levels and under different environmental conditions in order to predict the consequences of changing biodiversity on ecosystem processes in a variable environment.

The impact of drought

Although all microcosms received virtually the same amounts of water during the experiment, reduced frequency of watering in half of the microcosms clearly resulted in drier litter and soil conditions, which caused significant changes in several of the processes we measured. As expected, litter mass loss was significantly lower in the dry treatment. This result is in line with earlier studies that showed that the frequency rather than the quantity of precipitation is important for litter decomposition, because the soil surface dries out at the same rate after large or small rain events, and differences in soil moisture at greater depth are less relevant for leaf litter decomposing at the soil surface (Yahdjian and Sala 2008). Microcosms from the drier treatment leached more DOC than those maintained at a consistently high humidity. This result might appear counterintuitive, but it reflects well the pulse of DOC that is expected when microorganisms subjected to drought release osmolites upon rewetting (Schimel et al. 2007). Such drought-induced pulses of relatively labile compounds may have a positive feedback on soil microbial activity, as indicated by the higher SIR that we measured in soils from the dry treatment and as was found in previous studies (Butenschoen et al. 2011, Sherman et al. 2012).

Drought did not influence the relationships between process rates and detritivore or litter functional dissimilarity. However this conclusion was reached under a scenario of moderate drought and without taking into account potentially different extinction risks of detritivore species, and thus changing detritivore diversity, following more severe drought periods. In an earlier study, Collison et al. (2013) reported a possible effect of detritivore species richness on litter mass loss under dry compared to humid conditions, suggesting that detritivore species richness may have a positive effect on process rates when environmental conditions are getting less favorable, in line with the insurance hypothesis (Yachi and Loreau 1999). However, the results of the study by Collison et al. (2013) were not conclusive and there is a strong need for further studies addressing the consequences of fauna diversity on soil processes under varying environmental conditions.

Irrespective of detritivore or litter functional dissimilarity, we observed that drought effects tended to increase with increasing process rates measured under optimal humidity conditions. This relationship was significant for mass loss, DOC leaching and PCD, indicating that detritivore/litter communities resulting in high process rates under undisturbed conditions were more sensitive to reduced water availability. This result agrees with a study by Fromin et al. (2012) reporting that the soil microbial communities that displayed the highest rates of SIR were the most affected by a transient heat disturbance. In the type of Mediterranean ecosystem we studied, which is predicted to be exposed to severe drought under future climate scenarios, poorer performing communities may be less affected by drought in relative terms with consequently more stable process rates in the long term. Again it will be important to test this prediction based on our laboratory experiment under natural and more fluctuating environmental conditions in the field.

Conclusions

By manipulating functional diversity simultaneously at the two trophic levels of detritivores and leaf litter, but keeping species richness and biomass constant, we showed marked effects on litter decomposition, soil C and N leaching as well as soil microbial activity. In addition to the strong community identity effects, a small but significant part of the variation in process rates was explained by functional dissimilarity of detritivore assemblages and litter mixtures. Our data also tend to support the prediction that the combined higher functional dissimilarity of both detritivore assemblages and litter mixtures have a major impact on process rates. These results suggest that the community trait diversity can predict soil process rates to some degree, potentially providing a generally applicable index to assess biodiversity effect on soil processes across ecosystems.

The intensity of drought simulated in our experiment did not alter the relationships between functional dissimilarity and soil processes, suggesting some robustness of these relationships under changing environmental conditions. However, the best performing litter mixtures and detritivore assemblages under optimal humidity conditions were distinctively more affected by drought, suggesting a tradeoff between performance and resistance to disturbance for soil organisms.

Acknowledgements – We thank the team at the Ecotron (UPS CNRS 3248) for technical support, Pierre Cellier of the INRA centre Versailles-Grignon for the soil used in the experiment, Sandra Barantal, David Degueldre, Jeremy Devaux, François-Xavier Joly, Johanne Nahmani, Patrick Schevin and Anaïs Rancon for their help at setup and harvest of the microcosms, Raphaëlle Leclerc and Patrick Schevin for assistance during laboratory analyses at the Plate-Forme d'Analyses Chimiques en Ecologie, LabEx Centre Méditerranéen de l'Environnement et de la Biodiversité (France), Joële Toucet and the BioSolTrop lab (Eco&Sols, Montpellier) for TOC analyses, and Gaëlle Rolland (LEPSE, Montpellier) for her help with lyophilisation. This work benefited from the CNRS human and technical resources allocated to the ECOTRONS Research Infrastructure as well as from the State allocation 'Investissement d'avenir' ANR-11-INBS-0001. This research is part of the project "CLIMED" funded through the ANR grant 09-CEP-007.

References

Balvanera, P. et al. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. – Ecol. Lett. 9: 1146–1156.

Barantal, S. et al. 2011. Long-term presence of tree species but not chemical diversity affect litter mixture effects on decomposition in a neotropical rainforest. – Oecologia 167: 241–252.

Beare, M. H. et al. 1990. A substrate-induced respiration (SIR) method for measurement of fungal and bacterial biomass on plant residues. – Soil Biol. Biochem. 22: 585–594.

Bíla, K. et al. 2014. Disentangling community functional components in a litter–macrodetritivore model system reveals the predominance of the mass ratio hypothesis. – Ecol. Evol. doi:10.1002/ece3.941

Botta-Dukát, Z. 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. – J. Veg. Sci. 16: 533–540.

Butenschoen, O. et al. 2011. Interactive effects of warming, soil humidity and plant diversity on litter decomposition and microbial activity. – Soil Biol. Biochem. 43: 1902–1907.

Cadotte, M. W. et al. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. – J. Appl. Ecol. 48: 1079–1087.

Cardinale, B. J. et al. 2011. The functional role of producer diversity in ecosystems. – Am. J. Bot. 98: 572–592.

Cohen, J. 1992. A power primer. – Psychol. Bull. 112: 155–159.

Collison, E. J. et al. 2013. Macrofauna assemblage composition and soil moisture interact to affect soil ecosystem functions. – Acta Oecol. 47: 30–36.

Coq, S. et al. 2010. Interspecific variation in leaf litter tannins drives decomposition in a tropical rain forest of French Guiana. – Ecology 91: 2080–2091.

Coulis, M. et al. 2013. Macroarthropod-microorganism interactions during the decomposition of Mediterranean shrub litter at different moisture levels. – Soil Biol. Biochem. 64: 114–121.

Dangles, O. and Malmqvist, B. 2004. Species richness–decomposition relationships depend on species dominance. – Ecol. Lett. 7: 395–402.

David, J. F. 2014. The role of litter-feeding macroarthropods in decomposition processes: a reappraisal of common views. – Soil Biol. Biochem. 76: 109–118.

David, J. F. and Gillon, D. 2002. Annual feeding rate of the millipede *Glomeris marginata* on holm oak (*Quercus ilex*) leaf litter under Mediterranean conditions. – Pedobiologia 46: 42–52.

de Dato, G. D. et al. 2010. Impact of drought and increasing temperatures on soil CO_2 emissions in a Mediterranean shrubland (gariga). – Plant Soil 327: 153–166.

De Oliveira, T. et al. 2010. Snail and millipede complementarity in decomposing Mediterranean forest leaf litter mixtures. – Funct. Ecol. 24: 937–946.

Duffy, J. et al. 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. – Ecol. Lett. 10: 522–538.

Epps, K. Y. et al. 2007. Chemical diversity – highlighting a species richness and ecosystem function disconnect. – Oikos 116: 1831–1840.

Fanin, N. et al. 2012. Distinct microbial limitations in litter and underlying soil revealed by carbon and nutrient fertilization in a tropical rainforest. – PloS ONE 7: e49990.

Frainer, A. et al. 2014. When does diversity matter? Species functional diversity and ecosystem functioning across habitats and seasons in a field experiment. – J. Anim. Ecol. 83: 460–469.

Fromin, N. et al. 2012. Spatial variability of the functional stability of microbial respiration process: a microcosm study using tropical forest soil. – J. Soils Sediments 12: 1030–1039.

Gao, X. et al. 2006. Projected changes in mean and extreme precipitation over the Mediterranean region from a high resolution double nested RCM simulation. – Geophys. Res. Lett. 33: L03706.

García-Palacios, P. et al. 2013. Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. – Ecol. Lett. 16: 1045–1053.

Garnier, E. et al. 2004. Plant functional markers capture ecosystem properties during secondary succession. – Ecology 85: 2630–2637.

Gessner, M. O. et al. 2010. Diversity meets decomposition. – Trends Ecol. Evol. 25: 372–380.

Giorgi, F. and Lionello, P. 2008. Climate change projections for the Mediterranean region. – Global Planet. Change 63: 90–104.

Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter, and founder effects. – J. Ecol. 86: 902–910.

Hagedorn, F. and Machwitz, M. 2007. Controls on dissolved organic matter leaching from forest litter grown under elevated atmospheric CO_2. – Soil Biol. Biochem. 39: 1759–1769.

Handa, I. T. et al. 2014. Consequences of biodiversity loss for litter decomposition across biomes. – Nature 509: 218–221.

Hättenschwiler, S. and Gasser, P. 2005. Soil animals alter plant litter diversity effects on decomposition. – Proc. Natl Acad. Sci. USA 102: 1519–1524.

Hättenschwiler, S. et al. 2005. Biodiversity and litter decomposition in terrestrial ecosystems. – Annu. Rev. Ecol. Evol. Syst. 36: 191–218.

Hedde, M. et al. 2007. Beech leaf degradation in laboratory experiments: effects of eight detritivorous invertebrate species. – Appl. Soil Ecol. 35: 291–301.

Hedde, M. et al. 2010. Patterns and mechanisms responsible for the relationship between the diversity of litter macroinvertebrates and leaf degradation. – Basic Appl. Ecol. 11: 35–44.

Heemsbergen, D. A. et al. 2004. Biodiversity effects on soil processes explained by interspecific functional dissimilarity. – Science 306: 1019–1020.

Hooper, D. U. et al. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. – Nature 486: 105–108.

Jabiol, J. et al. 2013. Trophic complexity enhances ecosystem functioning in an aquatic detritus-based model system. – J. Anim. Ecol. 82: 1042–1051.

Jousset, A. et al. 2011. Genotypic richness and dissimilarity opposingly affect ecosystem functioning. – Ecol. Lett. 14: 537–545.

Kalbitz, K. and Kaiser, K. 2008. Contribution of dissolved organic matter to carbon storage in forest mineral soils. – J. Plant Nutr. Soil Sci. 171: 52–60.

Lavelle, P. and Spain, A. V. 2001. Soil ecology. – Kluwer.

Makkonen, M. et al. 2012. Highly consistent effects of plant litter identity and functional traits on decomposition across a latitudinal gradient. – Ecol. Lett. 15: 1033–1041.
Petchey, O. L. and Gaston, K. J. 2006. Functional diversity: back to basics and looking forward. – Ecol. Lett. 9: 741–758.
Purvis, A. and Hector, A. 2000. Getting the measure of biodiversity. – Nature 405: 212–219.
Schimel, J. et al. 2007. Microbial stress-response physiology and its implications for ecosystem function. – Ecology 88: 1386–1394.
Setälä, H. and McLean, M. A. 2004. Decomposition rate of organic substrates in relation to the species diversity of soil saprophytic fungi. – Oecologia 139: 98–107.
Sherman, C. et al. 2012. Effects of climate change on soil respiration and carbon processing in Mediterranean and semi-arid regions: an experimental approach. – Eur. J. Soil Biol. 52: 48–58.
Tilman, D. 2001. Functional diversity. – In: Levin, S. A. (ed.), Encyclopedia of biodiversity, Vol. 3. Academic Press, pp. 109–120.
Villéger, S. et al. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. – Ecology 89: 2290–2301.

Supplementary material available online as Appendix oik.01917 at <www.oikosjournal.org/readers/appendix>). Appendix 1.

Vos, V. C. A. et al. 2011. Macro-detritivore identity drives leaf litter diversity effects. – Oikos 120: 1092–1098.
Vos, V. C. A. et al. 2013. Leaf litter quality drives litter mixing effects through complementary resource use among detritivores. – Oecologia 173: 269–280.
Wardle, D. A. et al. 1999. Plant removals in perennial grassland: vegetation dynamics, decomposers, soil biodiversity and ecosystem properties. – Ecol. Monogr. 69: 535–568.
Wieser, W. 1978. Consumer strategies of terrestrial gastropods and isopods. – Oecologia 36: 191–201.
Yachi, S. and Loreau, M. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. – Proc. Natl Acad. Sci. USA 96: 1463–1468.
Yahdjian, L. and Sala, O. E. 2008. Do litter decomposition and nitrogen mineralization show the same trend in the response to dry and wet years in the Patagonian steppe? – J. Arid Environ. 72: 687–695.
Zhang, D. Q. et al. 2008. Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. – J. Plant Ecol. 1: 85–93.