1   Decomposition disentangled: a test of the multiple mechanisms by which nitrogen enrichment alters

2   litter decomposition

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Summary

1. Nitrogen (N) enrichment has direct effects on ecosystem functioning by altering soil abiotic conditions and indirect effects by reducing plant diversity and shifting plant functional composition from dominance by slow to fast growing species. Litter decomposition is a key ecosystem function and is affected by N enrichment either by a change in litter quality (the recalcitrance of the plant material) or through a change in soil quality (the abiotic and biotic components of the soil that affect decomposition). The relative importance of soil and litter quality and how the direct and effects of N alter them remains poorly known.

2. We designed a large grassland field experiment manipulating N enrichment, plant species richness and functional composition in a full factorial design. We used three complementary litter bag experiments and a novel structural equation modelling approach to quantify the relative effects of the treatments on litter and soil quality and their importance for total decomposition.

3. Our results indicate that total decomposition was mostly driven by changes in litter quality rather than soil quality. Litter quality was affected by the nutrient contents (N and calcium) and structural components of the litter (leaf dry matter content, fibres). N enrichment increased litter decomposition mostly indirectly through a shift in functional composition toward faster growing plant species producing higher quality litter. N enrichment also had effects on soil, by directly and indirectly affected vegetation cover, but this had relatively few consequences for the total decomposition rate.

4. *Synthesis*. Our approach provides a mechanistic tool to test the drivers of litter decomposition across different ecosystems. Our results show that functional composition is more important than richness or soil quality in determining litter decomposition and that N enrichment effects mainly occur via above- rather than belowground processes. This highlights the importance

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52   of considering shifts in plant species composition when assessing the effects of N enrichment

53   on decomposition.

Introduction

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56   Soil nitrogen enrichment is one of the major global changes ecosystems are currently facing

57   (Galloway et al., 2008). Nitrogen (N) enrichment alters ecosystem functioning directly and through

58   several indirect mechanisms. It directly alters functions related to nutrient stocks and fluxes by

59   changing soil abiotic conditions, stoichiometry and pH (Sardans, Rivas-Ubach, & Peñuelas, 2012;

60   Laliberté & Tylianakis, 2012). In addition N enrichment indirectly affects ecosystem functioning by

61   altering biotic community properties such as plant diversity and composition. N enrichment typically

62   reduces the number of plant species able to coexist (Suding et al., 2005) and this loss of diversity could

63   affect ecosystem functioning as much as N addition per se. (Hooper et al., 2012; Tilman, Reich, & Isbell,

64   2012). However, plant community change, following N enrichment, does not only involve a loss of

65   species it also involves compositional turnover and in particular a shift towards faster growing plant

66   species (Isbell et al., 2013; Lavorel & Grigulis, 2012; de Vries et al., 2012). This shift is indicated by an

67   increase in mean values of trait linked to the leaf economics spectrum, such as specific leaf area and

68   leaf N content, (Wright et al., 2004) and this shift is a key driver of ecosystem functioning (Lavorel &

69   Grigulis, 2012). However, we still have little mechanistic insight into the relative importance of these

70   direct (abiotic) and indirect (plant richness and composition) effects of N enrichment on ecosystem

71   functioning. Observational studies have separated direct effects of N from indirect effects mediated

72   through species richness (Isbell et al., 2013) and/or functional composition (Allan et al., 2015).

73   However, observational studies struggle to separate effects of correlated drivers, such as diversity loss

74   and compositional turnover. Experimental approaches are therefore needed to separate these effects

75   and to fully understand and predict the mechanisms by which N addition affects ecosystem

76   functioning.

77   The decomposition of plant litter is a key ecosystem function that influences rates of soil

78   biogeochemical cycling and which is strongly affected by N deposition (Finn et al., 2015; Knorr, Frey,

79   & Curtis, 2005; Hobbie et al., 2012). Depending on the ecosystem, the enrichment level and duration,

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80   N can have either positive or negative effects on decomposition (Bardgett & Wardle, 2012; Knorr et

81   al., 2005; Hobbie et al., 2012; Riggs, Hobbie, Bach, Hofmockel, & Kazanski, 2015) and to understand

82   this variation we need to better understand the mechanisms behind them. Plant litter decomposition

83   is determined by multiple mechanisms: it depends principally on the physical and chemical properties

84   of the litter and on soil biotic and abiotic conditions (Cebrian, 1999; Handa et al., 2014; Cornwell et

85   al., 2008). To distinguish these two main drivers of litter decomposition, we will refer to "litter quality",

86   as the physical and chemical properties of litter that affect its decomposition and to "soil quality", as

87   the soil biotic and abiotic factors which determine decomposition rates. Both soil and litter quality are

88   key determinants of litter decomposition but their relative importance, especially following N

89   enrichment, is not well known (but see Cleveland et al., 2014; García-Palacios, Prieto, Ourcival, &

90   Hättenschwiler, 2016b; Maaroufi, Nordin, Palmqvist, & Gundale, 2017). N enrichment could influence

91   decomposition by directly or indirectly changing both soil quality (i.e. by altering soil properties and

92   fauna), and litter quality. To understand the impacts of N enrichment on decomposition we need

93   experimental and analytical approaches that can separate these different, cascading mechanisms.

94   N enrichment is likely to directly and indirectly alter litter quality and therefore decomposition

95   rates. Litter quality is largely determined by its chemical properties (nutrient contents and the

96   presence of defence compounds) and by physical factors such as leaf dry matter and fibre contents

97   (Garnier et al., 2004; Cornwell et al., 2008). With higher soil N availability, plants will produce more

98   rapidly degradable tissues with higher N contents and fewer fibres. In addition to N, macronutrients

99   like Ca and Mg may also influence litter decomposability (García-Palacios, McKie, Handa, Frainer, &

100   Hättenschwiler, 2016a) and their availability could also be altered by N addition (Aber et al., 1998).

101   Indirect effects of N are also likely to be important: a shift to fast growing plant communities further

102   enhances litter quality because fast growing plants have generally higher leaf N and lower fibre

103   contents. Fast growing plants also invest less in defences against herbivores and pathogens

104   (Blumenthal, Mitchell, Pysek, & Jarosík, 2009) and have fewer chemicals such as tannins that reduce

105   decomposition. However, other indirect effects of N may reduce decomposition. A reduction in

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106 species and functional diversity could reduce decomposability (Handa et al., 2014). Although some

107 aspects of litter quality are well characterised, we lack a comprehensive picture of how N enrichment

108 alters these different aspects simultaneously.

109   Enriching soils with N is likely to alter their quality for litter decomposition both directly and

110 indirectly. The abundance and composition of the soil macro, meso and microfauna are key

111 determinants of soil quality (Milcu & Manning, 2011) as macrofauna fragment large litter pieces,

112 which accelerates decomposition by smaller organisms (Milcu, Partsch, Scherber, Weisser, & Scheu,

113 2008). N enrichment could increase soil quality if it causes a shift towards bacterial dominated

114 communities (from fungal dominated ones), either through direct effects of N or through changes in

115 plant functional composition, which is likely to lead to increased decomposition rates (Fierer,

116 Strickland, Liptzin, Bradford, & Cleveland, 2009; Bardgett & McAlister, 1999; Bardgett & Wardle, 2012;

117 de Vries, Hoffland, van Eekeren, Brussaard, & Bloem, 2006). However, N enrichment might indirectly

118 reduce soil quality if a loss of plant diversity loss results in a loss of soil organism diversity (Milcu et al.,

119 2013). In addition, N addition will directly increase plant biomass (in N limited systems), but might

120 indirectly reduce it by reducing diversity (van der Plas, 2019; Isbell et al., 2013), and a change in

121 biomass will alter microclimatic conditions such as soil temperature and moisture, which are

122 important drivers of decomposition (Hättenschwiler, Tiunov, & Scheu, 2005; Blankinship, Niklaus, &

123 Hungate, 2011). The various direct and indirect effects of N enrichment are therefore likely to have

124 complex and potentially opposing effects on soil quality and therefore on litter decomposition rates.

125   In this study, we tested the effects of N enrichment on litter decomposition and disentangled

126 its direct effects on soil and litter quality from its indirect effects mediated by plant richness and

127 functional composition. We created experimental plant communities to realise a full factorial cross of

128 plant functional composition, plant species richness and N enrichment. Plant functional composition

129 was manipulated by creating a gradient in community mean specific leaf area and leaf N as these traits

130 are key indicators of resource economics and plant growth strategy. Three complementary litter bag

131   experiments were used to test direct and indirect effects of N addition on litter quality, on soil quality

132   and on both combined. We also looked at the effect of macro and mesofauna on decomposition by

133   using different mesh sized litter bags. This framework enabled us to test the following questions:

134   What is the relative importance of direct effects of N enrichment on decomposition relative to indirect

135   effects mediated through changes in the plant community (species richness and functional

136   composition)?

137   Is decomposition determined more by changes in litter quality or soil quality?

138   How important are meso and macro fauna in determining decomposition and how does their relative

139   importance change with N enrichment?

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Material and methods

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The PaNDiv Experiment

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145   The PaNDiv Experiment is located in Münchenbuchsee near the city of Bern (Switzerland,

146   47°03'N, 7°46'E, 564 m.a.s.l.). It has a mean annual temperature of 9.2 ± 0.61°C and mean annual

147   precipitation of 1051.78 ± 168.42 mm y^{-1} (mean over the last 30 years, data from the Federal Office of

148   Meteorology and Climatology MeteoSwiss). The soil is characterized as 0.7 to 1m deep brown earth

149   (Cambisol), according to the Geoportal of the Canton Bern (http://www.geo.apps.be.ch). We

150   measured total soil N and carbon (C) concentrations and pH in the top 20 cm of soil at the start of the

151   experiment and found concentrations of 2.3-4.2% C, 0.26-0.43% N and a pH of 7.4. The field site had

152   been extensively managed (without fertilization) for at least 10 years before the start of the

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153   experiment and had been used for fodder production and grazing. The vegetation was cleared and the

154   area ploughed before the experimental plots were established.

155   The species sown were selected from a pool of 20 species commonly found in both extensively

156   and intensively managed Central European grasslands. We divided our 20 species into 10 fast and 10

157   slow growing species according to their Specific Leaf Area (SLA) and leaf N content, which are related

158   to resource use strategy (see Figures S1 and S2) (Wright et al., 2004). The fast growing pool therefore

159   corresponds to species found in N enriched sites, whereas the slow growing pool comprises species

160   found in less productive sites. We excluded legumes from the species pool as few legume species will

161   grow well at high N levels and including legumes only in the slow growing pool would have caused an

162   additional and large difference between the species pools. We realised several combinations of fast

163   and slow growing species, so effects of changes in mean traits are independent of particular species

164   effects.

165   In order to separate direct and indirect effects of N enrichment, we established a factorial

166   cross of treatments representing the direct (N enrichment) and indirect effects (plant diversity loss

167   and change in functional composition) on 2x2m plots. Fertilised plots received N in the form of urea

168   twice a year in April and late June (beginning of the growing season and following the first cut, see

169   below), for an annual addition of 100 kg N $ha^{-1}y^{-1}$, which corresponds to intermediately intensive

170   grassland management (Blüthgen et al., 2012). To manipulate diversity, we established plots with 1,

171   4, 8 or all 20 species. To manipulate functional composition and diversity we established plots with

172   only fast growing, only slow growing or a mix of fast and slow growing species. This allowed us to

173   realise a large gradient in community weighted mean trait values, which is crossed with functional

174   diversity, as mixed plots have higher diversity than single strategy plots. Functional composition,

175   functional diversity and species richness were all completely crossed at the 4 and 8 species levels

176   (monocultures and 20 species plots could only contain one functional composition). We sowed all

177   plants in monoculture and we established four replicates of the 20 species together. At the four and

178   eight species levels we randomly selected species compositions: we selected 10 species compositions

179   for each combination of richness (4 and 8), times functional composition (fast, slow mixed). This meant

180   we had a total of 20 monocultures, 30 four species compositions, 30 eight species compositions and

181   four replicates of 20 species composition. We constrained the random selection to ensure that all

182   polycultures contained both grasses and herbs. The 84 different species compositions were grown

183   once in control conditions and once with N addition. In addition to the N treatment, we also applied

184   a fungicide treatment and a fungicide x N treatment, resulting in 336 plots in total. However, for

185   logistical reasons the litter bag experiment was only conducted on the 168 control (no fungicide) plots

186   (see Table S1). The whole field was divided into four blocks. Each block contained all 84 compositions

187   but the particular N x fungicide treatment was randomly allocated per block. A regularly mown 1m

188   path sown with a grass seed mixture consisting of *Lolium perenne* and *Poa pratensis* (UFA-

189   Regeneration Highspeed) separated the plots.

190   All species within a plot were sown at equal density in October 2015, with proportions corrected by

191   species specific germination rates, to obtain a total density as close as possible to 1000 seedlings m^{-2}.

192   The seeds were obtained from commercial suppliers (UFA Samen, Switzerland, and Rieger-Hofmann,

193   Germany). Some species were resown once in spring 2016 because of poor establishment (*Heracleum*

194   *sphondylium, Anthriscus sylvestris, Daucus carota, Salvia pratensis, Prunella grandiflora, Plantago*

195   *media*), because they were mixed with other seeds to begin with (*Helictotrichon pubescens, Bromus*

196   *erectus*) or because their seedlings froze in autumn or spring (*Holcus lanatus, Dactylis glomerata,*

197   *Anthoxanthum odoratum*). No resowing was done after spring 2016. In order to maintain the diversity

198   levels, the plots were weeded three times a year in April, July and September. This regime was highly

199   successful and most plots contained very low weed covers in the following season (Figure S3). The

200   whole experiment was mown twice a year in mid-June and mid-August which corresponds to

201   intermediate to extensive grassland management.

202

Measuring decomposition of litter bags

205   We conducted three complementary litter bag experiments simultaneously to test the

206   mechanisms by which our treatments affected decomposition. The first set of bags tested the effect

207   of our treatments on the soil quality. We filled those bags with rapeseed straw (*Brassica napus*) as a

208   standard material and placed them on every plot. No Brassicaceae are present in the experiment and

209   this litter should therefore be equally foreign for all plots. To test the effect of our treatments on litter

210   quality (decomposability), we filled a second set of bags with biomass collected from each plot and let

211   them decompose in a common garden, established in the grassland surrounding the experimental

212   plots. We filled the third set of bags, called plot bags, with aboveground dry biomass from each plot

213   and let them decompose on their own plot (i.e. the plot from which the biomass was collected) to test

214   the combined effect of soil and litter quality on decomposition. By combining data from these three

215   experiments, we can disentangle the relative importance of soil and litter quality in driving overall

216   decomposition.

217   We sewed the litterbags using nylon fabric with a mesh size of 5 mm for the above part and

218   0.2 mm for the fabric in contact with the soil, to avoid loss of material during transport and

219   manipulation (Bradford, Tordoff, Eggers, Jones, & Newington, 2002). To investigate the effects of

220   different sized groups of detritivores on decomposition, we sewed two additional plot bags: a 2 mm

221   mesh size to exclude the macrofauna, and a 0.2 mm mesh size to exclude meso and macrofauna (Milcu

222   & Manning, 2011; Bardgett, 2005). By comparing decomposition rates in the bags with different mesh

223   sizes we can estimate the effect of different aspects of the soil community on the overall

224   decomposition rate.

225   The plant biomass used to fill the common garden and plot bags was collected on the field

226   before the mowing in June 2017 (with some very unproductive plots sampled again in August in order

227   to have enough material). Green litter differs in its composition from senescent litter due to nutrient

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228   resorption (Aerts, 1996), and therefore decomposes at a different rate (Sanaullah, Chabbi, Lemaire,

229   Charrier, & Rumpel, 2010). We were, however, more interested in the difference in decomposition

230   among plant communities rather than in measuring the absolute decomposition rate. In addition,

231   green litter decomposition is an important process in grasslands which are managed by cutting and

232   many similar decomposition experiments have therefore also used green litter (Sanaullah et al., 2010;

233   Vogel, Eisenhauer, Weigelt, & Scherer-Lorenzen, 2013). The biomass was dried at 65°C for 48h,

234   chopped, homogenized and split into equal parts (Biomass splitter, RT 6.5–RT 7; Retsch, Haan,

235   Germany). We filled each bag with a maximum of 20g dry material and weighed the litterbags again

236   after closing. Because some experimental communities produced only a small amount of biomass, we

237   could not include 20g in all bags and the initial biomass varied from 5 to 20g. The bags decomposed

238   on top of the soil for 2.5 months between September and December 2017. We then collected the

239   bags, cleaned them of debris and soil, dried them and weighed them again. We measured

240   decomposition rate as the percentage biomass lost between September and December, to correct for

241   differences in initial weight. Initial bag weight was included as a covariate in our models but it never

242   affected the percentage mass loss (see Table S3).

243

244   Plant traits used to calculate functional composition

245

246   To produce a continuous measure of functional composition for all our plant communities we

247   calculated community weighted means for Specific Leaf Area (SLA) and Leaf Dry Matter Content

248   (LDMC). Although plots were designed to differ in SLA, we also created a large gradient in mean LDMC,

249   which was only partially correlated with SLA. We measured SLA and LDMC in the control (unfertilised)

250   monocultures and therefore did not include any plasticity in response to N addition, in order to ensure

251   that the community weighted mean traits were as orthogonal to N addition as possible. We sampled

252   one leaf from five individuals per species and followed the protocol of Garnier, Shipley, Roumet, and

253   Laurent (2001) and measured the fresh weight and leaf area with a leaf area meter (LI-3000C, LI-COR

254   Biosciences) after a minimum of 6h and a maximum of 2 days of rehydration in the dark. We dried the

255   samples at 65°C for two days and measured their dry weight. To measure the abundances of the plant

256   species, we visually estimated the percentage cover of our target and weed species on every plot

257   before the biomass was cut. In total three people estimated cover but there was no systematic

258   difference in the species relative covers estimated by the three recorders (data not shown). We

259   calculated a Community Weighted Mean (CWM) trait measure for each plot by multiplying each

260   species' relative abundance (cover) by the mean trait value of the species in monoculture (CWM = $\sum$

261    $p_i * x_i$; with p_i the relative abundance of the species i and x_i the trait value of i).

262

263   ## Litter quality

264

265   Two key aspects of litter quality are nutrient and fibre contents. We measured the

266   concentration of several nutrients and fibre fractions in the plant biomass. We analysed biomass

267   samples of all plots from June and August 2017 using Near Infrared Reflectance Spectrometry (NIRS).

268   A minimum of 5 g of biomass per plot (pooled sample, including all species present and their relative

269   abundance) was ground with a cyclone mill to obtain a fine powder. The infrared spectrum of the

270   powder was used to estimate the nutrient and fibre contents based on calibration models developed

271   for aboveground grassland biomass by Kleinebecker, Klaus, and Hölzel (2011). We estimated acid

272   detergent fiber (ADF: cellulose, lignin and silica), neutral detergent fiber (NDF: ADF + hemicellulose)

273   and acid detergent lignin (ADL: crude lignin fraction) in the biomass, as well as concentrations of N, C,

274   phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg).

275   We could not use all nutrients and fibre fractions separately in the analyses as some of them were

276   highly correlated (e.g. Mg and Ca, see Figures S4 and S5). We decided to select a widely used set of

277   variables that did not correlate strongly and which together account for structural components and

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278   nutritional quality of litter: biomass N, fibres (ADF) and Ca content (García-Palacios et al., 2016a; Smith

279   & Bradford, 2003; Cornwell et al., 2008). We did not include ratios like C:N or lignin:N as they were

280   closely correlated with other variables and did not add more information to the model.

281   In addition to our measures of functional composition (CWMs) and mean values of litter quality, we

282   calculated a measure of litter quality diversity. For this we used the abundance weighted Mean

283   Pairwise Distance metric (MPD) (de Bello, Carmona, Lepš, Szava-Kovats, & Pärtel, 2016). This measure

284   quantified the distance between all species in a plot in their SLA, LDMC, biomass N, fibre and Ca values.

285   In order to derive species specific values for biomass N, Ca and fibres, we used the values from the

286   control monocultures as the species trait values, as for SLA and LDMC.

287

288   Analyses

289

290   We first used linear mixed effect models to test the effect of our treatments on litter

291   decomposition (percentage mass loss), for each bag individually and for all sets of bags combined. We

292   ran two combined models: one with plot litter, standard litter and common garden litter combined

293   and one with the three mesh sizes combined. We ran the models in R (package lme4, Bates, Mächler,

294   Bolker, & Walker, 2015; R Core Team, 2018) and simplified full models by dropping terms that did not

295   significantly improve the overall model fit, using likelihood-ratios. All models included block and

296   species composition (84 levels) as random terms. Species composition distinguished the randomly

297   assembled sets of species and was included to correct for the fact that replicated species composition

298   are pseudoreplicates for testing the species richness effects. The combined model with all the bags

299   also included plot as a random term (168 levels). We added fixed covariates for the month of biomass

300   harvest (June or August) and the initial weight of biomass put in each bag. We did not transform the

301   data since the errors were normally distributed and the variance homogenous.

13

302   The first type of models tested the effects of the treatments on each bag:

303   % mass loss ~ Nitrogen * Species richness * Functional composition + Harvest date + Initial

304   weight + (1|Block) + (1|Combination)

305   The second type of models tested for interactions between bag type (plot, standard, common garden

306   litter; or the three mesh sizes) and the treatments:

307   Common garden, Standard and Plot bags

308   % mass loss ~ Nitrogen * Species richness * Functional composition * Bag type + Harvest date

309   + Initial weight + (1|Block) + (1|Combination) + (1|Plot number)

310   Although we used categorical measures of functional composition to design the experiment, we

311   intended to create a gradient in CWM traits. We therefore replaced our three level functional

312   composition variable by a continuous measure of community weighted mean SLA and LDMC, and

313   functional diversity (MPD). For instance, in a single model:

314   % mass loss ~ Nitrogen * Species richness * (SLA + LDMC + MPD) + Harvest date + Initial weight

315   + (1|Block) + (1|Combination)

316

317   In a second step, we quantified the mechanisms by which our treatments affected decomposition

318   using Structural Equation Modelling (SEM) (Grace, 2006). We included our three decomposition

319   experiments (and the different mesh size treatments, see below) in the same model. By doing this we

320   were able to test, not only the effect of our treatments on litter or soil mediated decomposition, but

321   also the relative importance of litter and soil mediated decomposition for driving the final

322   decomposition rate measured per plot. We used the mass loss in the "plot" litter bags (i.e. litter

323   decomposing on its own plot) as a measure of the total plot decomposition rate. We then used the

324   mass loss in the common garden litter bags as a measure of the litter mediated effects on

325   decomposition, as these bags decompose on the same soil and only variation in litter quality will

326   determine variation in mass loss between the bags. We used mass loss from the standard litter bags

327   as our measure of soil mediated decomposition rates. In these bags the litter is always the same and

328   therefore only variation in soil quality between plots will determine variation in decomposition. We

329   fitted paths from common garden and standard litter mass loss to plot litter mass loss. The size of

330   these two standardised path coefficients indicates the relative contribution of litter and soil quality to

331   overall decomposition rates. In the SEM, plot litter mass loss is only affected by the mass loss

332   measured in common garden and standard litter bags, to determine if we can explain all of the

333   variation in overall decomposition rate based on our two measures of litter and soil quality.

334   We then tried to identify the traits and community properties that determined litter and soil

335   quality. To do this we included our manipulated variables, N addition and plant species richness, as

336   well as continuous measures of plant functional composition and litter quality, SLA, LDMC, biomass N,

337   fibres and Ca, in the SEM. These measures could affect functional diversity (MPD) and microclimate.

338   The microclimate measure we used in the analyses is the total plant cover on each plot. It correlates

339   with biomass production and accounts for humidity and temperature variation among plots (Figure

340   S6). To account for an effect of the soil fauna on decomposition, we included the log response ratio of

341   the big mesh to the small mesh bag decomposition rate (see Figure S7). This variable "soil fauna effect"

342   measures the relative effect of macro and mesofauna exclusion on decomposition and tests whether

343   our treatments alter their effect.

344   We fitted SEMs using the lavaan package (Rosseel, 2012). This meant we could not include random

345   effects, which could bias paths from species richness to other variables (which are not corrected for

346   species composition). However, we also fitted models using piecewiseSEM (Lefcheck, 2016), in which

347   we could include composition as a random effect, and this did not change the significance of any paths

348   (see Table S2). Our initial model was rejected. We therefore included four residual covariance terms

349   suggested by the lavaan modification indices. Including these covariances substantially improved

350   model fit and led to a well supported model, however, it did not change the significance or

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351   substantially alter the strength of any paths. The first additions were negative covariances between

352   biomass N and MPD and between LDMC and MPD. These are justified because monocultures (coded

353   as zero MPD) had a greater range in biomass N and LDMC measures than polycultures, meaning some

354   monocultures had much higher biomass N content than any of the polycultures. The two other

355   covariances were between soil fauna effect and plot decomposition, and between litter quality and

356   plot decomposition. These covariances are reasonable because we used the same litter in these

357   different bags and a residual covariance is therefore likely. The residual covariance between plot and

358   litter quality was fitted alongside a directed path and indicated the influence of unmeasured variables

359   on both terms. The theoretical model and all detailed hypothesis are described in the Supplementary

360   Information (Figure S7).

361

Results

363

Individual effects of N enrichment and plant community characteristics on litter and soil quality

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367   Decomposition rates differed significantly among bag types. Litter decomposed faster in the

368   common garden than on the experimental plots, and standard litter decomposed most slowly.

369   Decomposition rates increased with mesh size (Fig.1a and Table S3).

370   N enrichment increased the litter decomposition rate in all bags consistently (significant main effect

371   of N but no interaction between N and mesh size, Table S3 and Figure 1a). The effect was absent for

372   standard litter bags when analysed alone but was significant when different bag types (common

373   garden, standard, and plot big mesh size bags) were analysed together. There was no interaction

374   between N and mesh size, meaning that N enrichment did not change the relative effect of large fauna,

375   compared to small fauna, on decomposition.
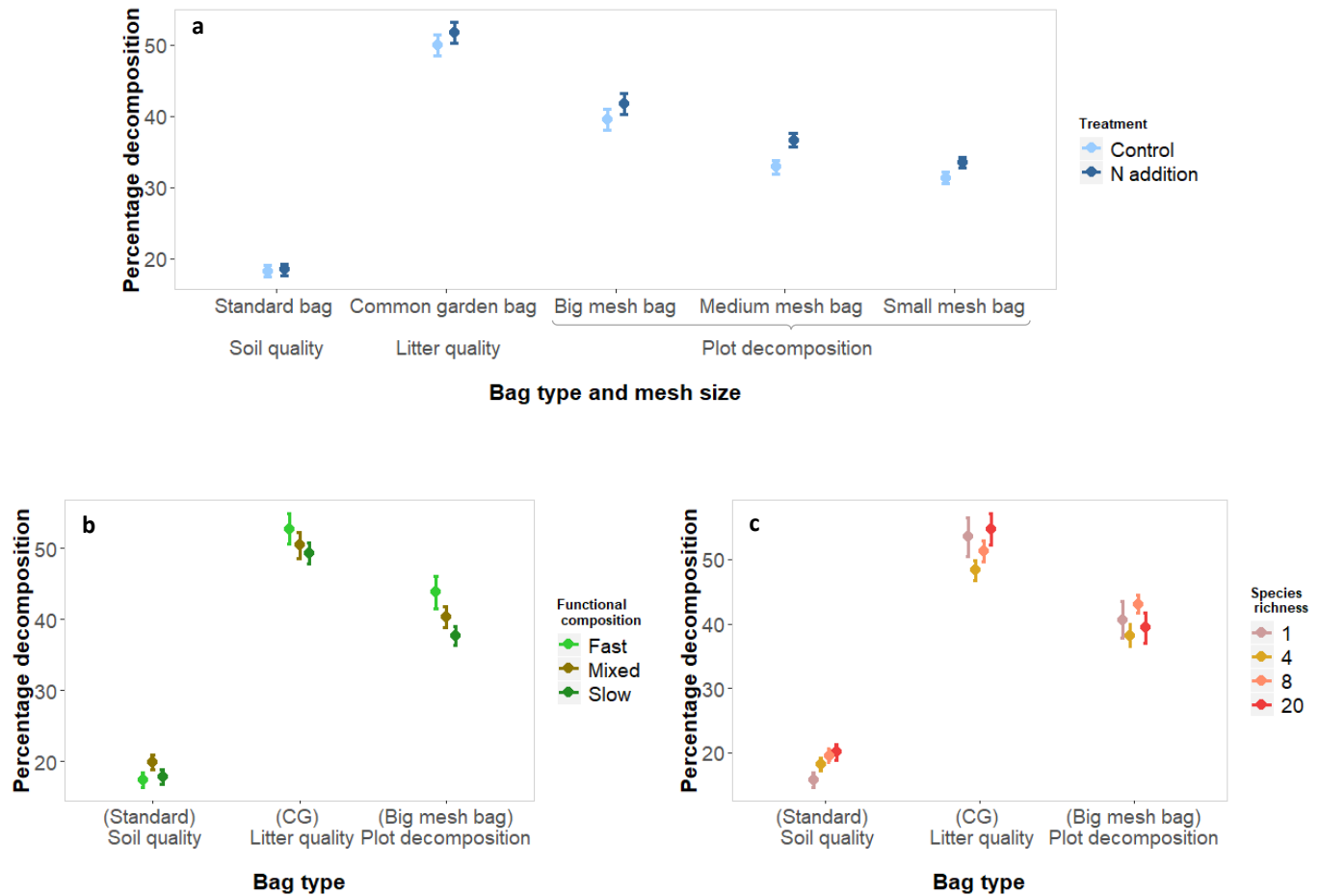
Figure 1. Effect of nitrogen addition (**a**), functional composition (**b**) and species richness (**c**) on litter decomposition depending on the litter bag type (standard, common garden and plot decomposition) and the mesh size (big, medium and small). Mean and standard error of the raw values (168 plots per bag).

376

377   Plant functional composition, expressed as a categorical variable (fast, mixed or slow growing species,

378   Fig.1b), had a significant effect on the decomposition of common garden and plot litter. Litter from

379   fast growing communities decomposed more rapidly than litter from mixed and slow communities.

380   We observed the same pattern with continuous measures of functional composition, with a non-

381   significant effect of SLA but a negative significant effect of LDMC on decomposition (Figure 2). LDMC

382   therefore seemed to be a better predictor than SLA of the effect of growth strategy on decomposition.

383   Comparing the bags with different mesh sizes, LDMC had a larger negative effect on decomposition in

384   the big mesh litter bags than in the smaller mesh sizes, suggesting a larger effect of LDMC on the

385   activity of the macrofauna than on the activity of the meso or microfauna (Fig 2b).

386   Plant species richness had a positive effect on the decomposition of standard litter bags, when

387   analysed separately (Fig.1c and Table S3). The effect of functional diversity depended on the bag type,

388   with a negative effect in plot and common garden bags and a positive effect on standard bags (Table

389   S3). These results indicate that species richness and functional diversity of communities increased soil

390   quality, whereas the functional composition of the community increased litter quality.
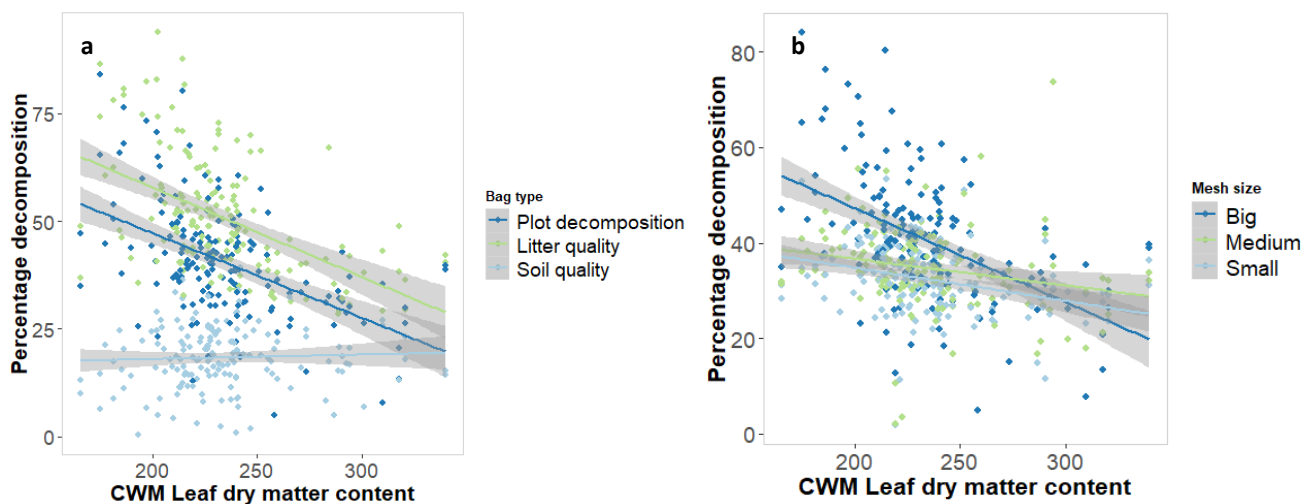
Figure 2. Effect of community weighted mean leaf dry matter content (mg g^{-1}) on decomposition depending on the bag type (**a**) and on the mesh size (**b**). Mean and standard error of the raw values (168 plots per bag).

391

392

393   Relative importance of litter and soil quality in driving overall decomposition

394

395   We used structural equation models to test the relative importance of our different

396   treatments in affecting soil and litter quality and the relative importance of litter and soil in driving

397   the overall decomposition rate. Litter and soil quality both had a positive effect on total plot

18

398   decomposition, but litter quality was much more important (path coefficient of 0.96, Table S4) than

399   soil quality (path coefficient of 0.20; see Figures 3 and 4a and b). Although soil macro and mesofauna

400   increased decomposition overall, they did not contribute to variation in decomposition between plots,

401   as there was no link between the log response ratio between decomposition in big and small mesh-

402   sized bags and the overall decomposition rates.

403
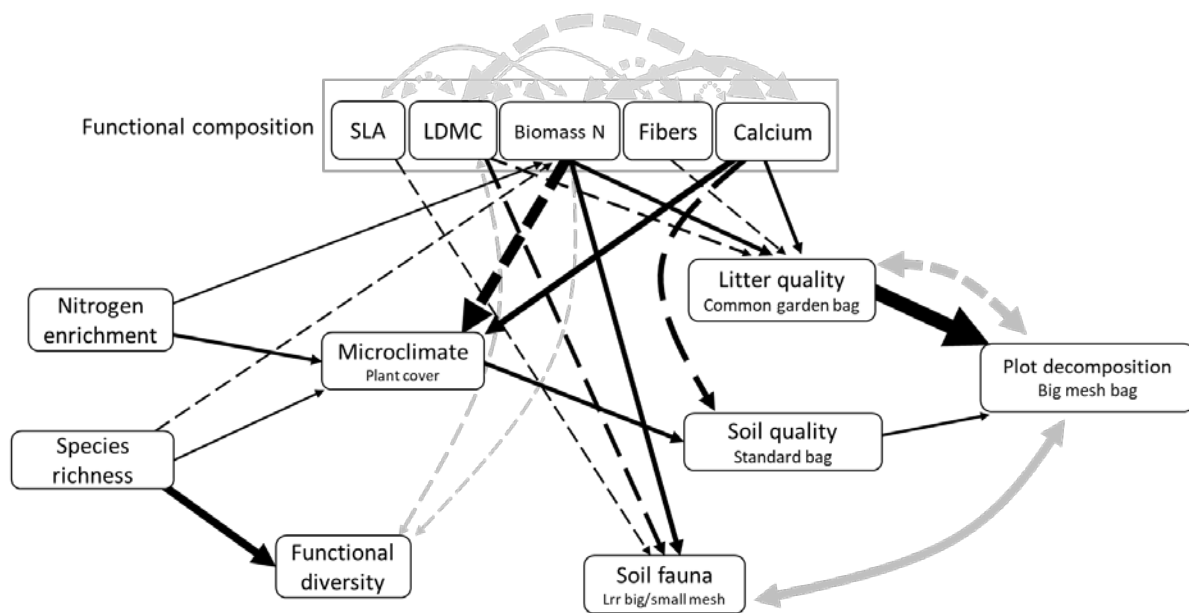
Figure 3. Final results of the structural equation model, showing effects of nitrogen enrichment, plant species richness and plant functional composition on decomposition. Dashed arrows show negative, full arrows positive path coefficients. The arrow size is proportional to the path coefficient. Double-headed grey arrows show covariances. Details of the output in Table S4. Model fit: Pvalue 0.423; Chisq 17.477; Df 17; RMSEA 0.013.

404

405   Litter quality was mainly influenced by plant functional composition. Litter from communities with a

406   high biomass N content, low LDMC and low fibre content, corresponding to our fast growing

407   communities, decomposed faster than litter from slow growing communities (Fig. 4e-h). Interestingly,

408   high Ca concentrations in the biomass also increased litter quality (path coefficient of 0.32). In

409   addition, N enrichment and plant species richness had opposite (positive and negative, respectively)

410   indirect effects on litter quality because they had opposing effects on the N content of the biomass.

411   Plant species richness increased soil quality, as observed in the mixed models (see Fig. 1b). However,

412   this effect was not direct or through effects on soil fauna, but was indirect and mediated by a change

413   in microclimatic conditions: increased plant cover in diverse communities presumably increased soil

414   moisture which increased the decomposition rate. N enrichment also increased soil quality indirectly,

415   through a change in the microclimatic conditions.

416   Plant functional composition also altered soil quality through changes in microclimatic conditions.

417   Communities with high Ca contents had higher plant cover and therefore higher soil quality. Ca-rich

418   communities were dominated by herbs, which would explain this increase in cover, as herbs

419   established better than grasses at the start of the experiment probably due to higher drought

420   resistance. Surprisingly, however, biomass N was negatively related to plant cover. This can be

421   explained either by a larger investment of the more productive plants in structural tissues (higher fibre

422   contents and a dilution of biomass N content), or by the dry conditions in the first year of the

423   experiment, which allowed the conservative species (with low N contents) to establish better than

424   faster growing species (see Figure S8). Ca also had a direct negative effect on soil quality. Ca therefore

425   had opposing effects on total decomposition through its effects on litter quality (positive) and effects

426   on soil quality (negative), with a total positive effect of 0.20. Biomass N increased, and LDMC and SLA

427   decreased, the effect of the macrofauna on decomposition, i.e. the relative differences in

428   decomposition rate in big compared to small bags (coeff. 0.31; -0.22 and -014 respectively). However,

429   the change in the effect of the soil fauna did not influence soil quality (i.e. there is no path between

430   soil fauna and soil quality).

431   Plant functional diversity had no significant effect on decomposition, despite the increase in the soil

432   quality effect in mixed communities plots found in the linear models (Fig. 1b). According to the SEM,

433   this effect seems to be mediated by mass-ratio (community-weighted traits) rather than functional

20

434   diversity effects per se. Functional diversity increased with species richness, which can also be due to

435   the coding of monoculture as zero diversity.
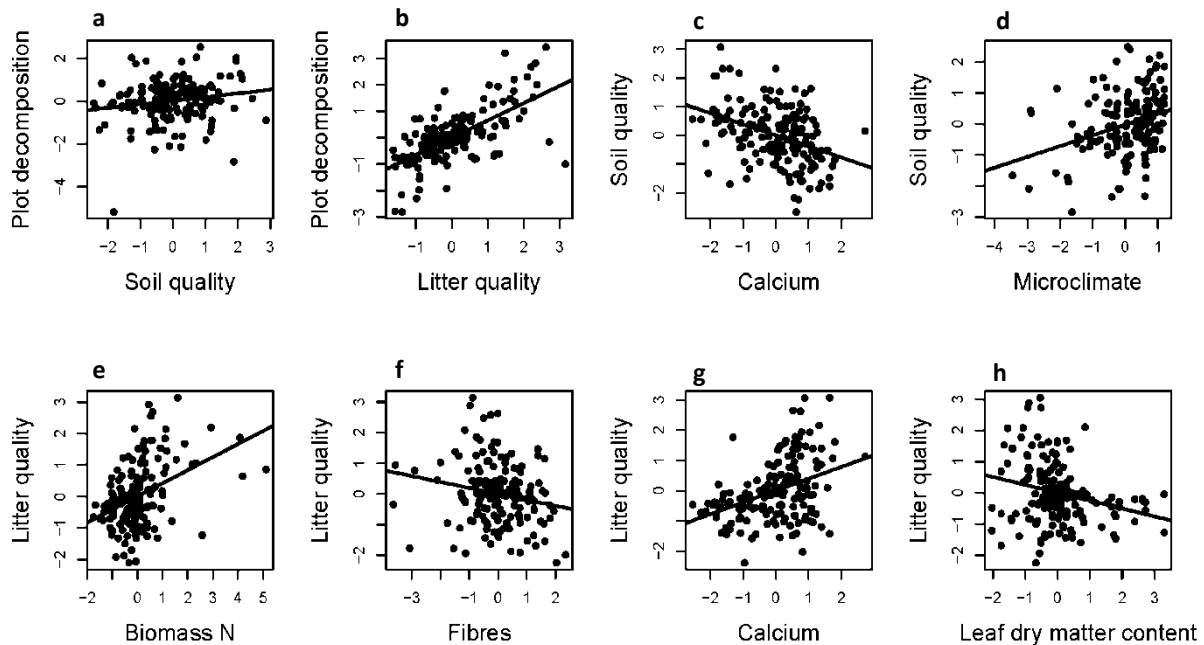
Figure 4. Partial plots visualizing SEM outputs from the Figure 3 of variables effects on overall decomposition (**a-b**), on soil quality (**c-d**) and on litter quality (**e-h**). X-axis units are standardized values, y-axis are standardized residuals of the target explanatory variable on the remaining explanatory variables.

436

437

Discussion

439

440   Here we disentangled the key drivers of litter decomposition by using data from several litter

441   bag experiments to compare the effects of soil and litter quality on decomposition. We use a new

442   approach to combine data from three types of litter bag in an experiment manipulating the direct

443   (increase in soil N) and indirect (diversity and functional composition change) effects of N enrichment.

444   Our results show that both litter and soil quality affect overall decomposition, but that litter quality is

445   most important. The key determinant of litter quality was the functional composition of the plant

446   community, which played a bigger role than plant species richness or functional diversity. It was

447   important to consider effects of multiple mechanisms and pathways because we found that some

448   factors had contrasting effects on soil and litter quality (like Ca), or contrasting direct and indirect

449   effects (species richness, biomass N), meaning that we would have missed many effects if we had

450   looked only at their overall effects on decomposition. Therefore, N enrichment increases

451   decomposition, mostly through indirect effects arising from a shift in functional composition towards

452   faster growing plant species which produce easily decomposable litter.

453

The relative importance of litter and soil quality in determining decomposition

455   The overall decomposition rate was more influenced by litter quality than by soil quality in our

456   experiment (see Figure 3). This result agrees with studies in multiple biomes showing that litter traits

457   are more important than the complexity of the decomposer community (García-Palacios, Maestre,

458   Kattge, & Wall, 2013) or soil properties in determining decomposition (García-Palacios et al., 2016b).

459   However, other studies in boreal forests experiencing long term N enrichment have found opposing

460   patterns (Maaroufi et al., 2017). Part of this variation between the outcomes of these studies might

461   be explained by differences in the relative importance of litter versus soil quality across biomes. We

462   might expect that soil quality would be more important in unproductive ecosystems, where soil biota

463   are expected to react more strongly to a change in microclimatic conditions (Blankinship et al., 2011).

464   The soil quality effect could also be stronger when N enrichment leads to a decrease in soil pH, which

465   reduces soil community diversity and abundance (Chen, Lan, Hu, & Bai, 2015; Tian & Niu, 2015). These

466   previous studies also used different approaches to quantify litter and soil effects on decomposition

467   and some of the variation among them may arise because they analysed different litter traits or

468   incorporated different measures of the soil community. By combining our different litter bag

469   experiments, we integrate all aspects of litter quality and soil quality together, allowing us to robustly

470   test for their relative importance without the need for a complete list of all the litter and soil properties

471   that could affect decomposition. Further studies using our approach could compare the effects of soil

472   and litter quality on decomposition across environmental gradients to determine the global

473   importance of these factors in determining litter decomposition.

474

Functional composition is the main driver of litter quality

476   The main determinants of litter quality in our experiment were related to the leaf economics

477   spectrum. Plant communities with an N-rich biomass, low fibre content and low LDMC produced the

478   most degradable material because this type of litter is easier for the soil fauna to break down. This

479   result agrees with a large body of literature showing that litter quality relates to leaf traits indicating

480   a fast growth strategy, like high SLA and biomass N, low LDMC, as well as low fibre content (Cornwell

481   et al., 2008; Reich, 2014; Freschet, Aerts, & Cornelissen, 2012). Interestingly, in our experiment, we

482   found that nutrient contents (N and Ca) were about twice as important as structural components

483   (LDMC and fibres) in determining litter quality (combined path coefficients of 0.61 for nutrients and -

484   0.36 for structure). Effects of N have been shown in many studies (Garnier et al., 2004; Cornwell et al.,

485   2008) and as pointed out in Mládková, Mládek, Hejduk, Hejcman, and Pakeman (2018), Ca and Mg

486   content (which were highly correlated in our case) also indicate a better digestibility and a higher

487   decomposability of the litter (García-Palacios et al., 2016a). Ca and Mg are key components of

488   invertebrate diets and can therefore increase their abundance (National Research Council, 2005),

489   which may explain their positive effects on decomposition. However, a high Ca content did not

490   increase the effect of macrofauna on decomposition perhaps suggesting that high Ca is also important

491   for microbes. In addition to the nutrients, litter structural components were important in determining

492   decomposition. We found that fibre content was important alongside LDMC in determining

493   decomposition which suggests that there are several aspects of plant structure that matter. The fibre

494   content, measured in bulk biomass, added complementary information on structure, as some species

23

495   had a low LDMC but still produced fibrous stems (see Figure S9). We did not measure plant defence

496   compounds such as tannins and phenolics, which can also be important determinants of litter quality

497   (Hättenschwiler & Jørgensen, 2010), however, these may correlate strongly with SLA if growth-

498   defence trade-offs are widespread (Blumenthal et al., 2009). Overall, our results show that nutrients

499   and structure are the key determinants of litter quality but that several different aspects are important

500   and should be considered, as single traits may not provide adequate proxies of overall litter quality.

501   Litter diversity, calculated from the diversity of functional traits of the species present in the plot, did

502   not have any effect on litter quality. Functional diversity might be of importance only in communities

503   containing legumes, where a transfer of nutrients from the N-rich legume litter to more recalcitrant

504   litter can increase decomposition (Handa et al., 2014). Our experimental design, which did not include

505   legumes, may therefore have underestimated the effects of diversity on decomposition rates. Our

506   results do however, agree with other studies using tree leaf litter which showed that functional

507   composition is usually a good predictor of litter decomposition rate and that functional diversity is of

508   secondary importance (see Finerty et al., 2016 and Bílá et al., 2014).

509

510   **Soil quality and soil fauna effects are indirectly mediated by biomass Ca content and**

511   **microclimate**

512   Soil quality also affected the overall decomposition rate, although it was less important than

513   litter quality. Soil quality was influenced by two factors: biomass Ca and microclimatic conditions. We

514   observed no direct effect of N enrichment, plant species richness, functional diversity or soil fauna on

515   soil quality, all their effects were mediated through changes in plant cover (microclimate; see Figure

516   2). The key indicator of increased plant cover was biomass N, which suggests that a decrease in plant

517   cover under N enrichment could decrease soil decomposition potential by decreasing humidity. N

518   addition had both direct (positive) and indirect effects (through increasing the negative effect of

519   biomass N) on plant cover. As microclimate had no impact on the relative effect of macro vs.

520 microfauna it seems likely that an increase in humidity was of equal importance for all soil

521 decomposers. In contrast to the positive effects of microclimate, biomass Ca reduced soil quality. This

522 means that plant communities producing more digestible litter, with a higher Ca (and/or Mg) content,

523 were growing on a soil which was poor at decomposing standard litter. Since we used a fairly

524 recalcitrant standard litter, this result could indicate that inputs of Ca-rich litter stimulated soil

525 communities that were less effective at decomposing recalcitrant litter. Enzymes responsible for the

526 breakdown of resistant material have been shown to be inhibited under N enrichment (Carreiro,

527 Sinsabaugh, Repert, and Parkhurst (2000), but see Sinsabaugh (2010)). Our results may indicate that

528 these enzymes are also inhibited by inputs of Ca-rich litter. Our use of one standard material may

529 therefore have underestimated some effects if there are strong interactions between litter and soil

530 quality and future studies could consider using a range of standard litters. The various direct and

531 indirect effects of N enrichment therefore had opposing effects on soil quality: a loss of species

532 diversity, expected under N enrichment, would reduce soil quality but this effect would be

533 compensated for by a direct increase of plant cover under fertilisation.

534 The relative effect of macrofauna on decomposition increased with biomass N and decreased

535 with LDMC. The macro and mesofauna contribution to decomposition was higher, relative to the

536 effect of microfauna, when litter contained more easily degradable material. This means that high

537 litter quality either increased the abundance of macrofauna, such as earthworms and isopods, or their

538 efficiency in breaking down litter. Little is known about how a change in litter quality alters the effect

539 of different soil fauna on decomposition but we can hypothesise that macrofauna are more active

540 when feeding on higher quality litter because they actively forage for nutrients and make them

541 available for microorganisms (see Smith & Bradford, 2003).

542 Our study used a new experimental and analytical approach to disentangle the complex

543 drivers of litter decomposition. However, some issues need to be considered and the most important

544 of these is probably the relatively early stage of the experiment. Overall, the lower importance of soil

25

545   quality compared to litter quality for decomposition indicates either that litter quality is indeed more

546   important than soil quality, or that the effects of N enrichment, diversity and functional composition

547   take longer to fully change soil communities (Eisenhauer et al., 2011; Boeddinghaus et al., 2019). In

548   particular, we might expect the plant species richness effect on decomposition to become more

549   important in longer experiments, as the soil biotic community becomes more closely linked to the

550   aboveground community (Eisenhauer, Reich, & Scheu, 2012). The drivers of decomposition might

551   therefore change as communities re-assemble above and belowground.

552   In our experiment we used green litter, as green litter decomposition is an important process

553   in grasslands managed by mowing and very little senescent plant material is present in these

554   grasslands. However, the factors determining decomposition of dead litter may differ. Due to its

555   higher fibre to nutrient ratio, dead litter would have taken more time to decompose and the relative

556   importance of litter quality compared to soil quality might have been lower. Although green litter

557   accounts for a large part of the decomposed material in semi-natural grasslands, the decomposition

558   of dead litter is also important and separate studies would need to explore its drivers. In addition, we

559   measured litter mass loss after 2.5 months of decomposition. While some litter bags were almost

560   empty at the end of the experiment, we have to keep in mind that the results represent a snapshot of

561   the decomposition process, for some plots only the early stage of decomposition. It would be

562   interesting to determine the drivers of litter decomposition at different stages of decomposition as

563   the relative importance of soil and litter quality, and the factors determining them, might change over

564   time (Smith & Bradford, 2003).

565

Conclusion

567

568   Decomposition was more strongly affected by litter quality rather than soil quality under N

569   enrichment. Aboveground plant traits related to structural composition as well as nutrient

570 concentrations were major determinants of high litter quality. This suggests that several traits are

571 needed to properly characterise litter quality and that stem structural composition should be

572 considered alongside leaf traits. Soil quality was mainly affected by microclimatic conditions, driven

573 by changes in plant cover. Our study suggests that, at least for the early stages of plant material

574 decomposition, N enrichment will directly increase decomposition rates by increasing litter N content

575 and by increasing biomass which promotes a microclimate favouring high soil faunal activity. It will

576 indirectly affect decomposition through a shift in plant functional composition towards faster growing

577 species, which will increase litter quality, and through a loss in plant species richness, which would

578 mainly decrease soil quality through a reduction in plant cover. The relative importance of different

579 drivers of decomposition under N enrichment might vary between ecosystems and further studies

580 could use our approach to quantify the relative importance of soil and litter quality in different

581 contexts. Nevertheless, the large effect of plant functional composition, seen in both biomass

582 nutrients and structural components, indicates that it is among the major drivers to take into

583 consideration when assessing overall N enrichment effects on decomposition.

584

Acknowledgments

592

Authors' contribution

594   NP, SC and EA designed and set up the PaNDiv Experiment. NP and SC collected the data. NP, NH, VHK

595   and TK processed and analysed the NIRS samples. NP analysed the data and wrote the first manuscript

596   with the substantial input from EA, SS and SC. All authors contributed to revisions of the manuscript.

597

Data accessibility

599   Once this manuscript is accepted, all the relevant data will be archived in figshare

600   (https://figshare.com/).

601

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