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1 **Litter species richness and composition effects on fungal richness and community**
2 **structure in decomposing foliar and root litter**

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Abstract

Litter species richness influences fungal diversity because of resource heterogeneity. Litter species composition effects on decomposition have been studied mostly in aboveground litter. However, little is known about the effects of litter diversity of roots and litter type effect on fungal diversity in general. We addressed litter species composition and richness effects on diversity of ectomycorrhizal (EcM), saprotrophic and pathogenic fungi in decomposing foliar and root litter in the Satakunta forest diversity experiment by varying litter species richness from one to four species in 560 litter bags incubated under tree canopies. After one year of decomposition, there were no significant non-additive effects of litter mixtures on mass loss. Litter species composition was the strongest predictor for saprotroph and plant pathogen community structure in foliar litter, but its effect on root litter fungal composition was much weaker. Litter diversity strongly enhanced fungal richness in foliar but not in root substrate. We found no evidence for host litter preferences in host-specific EcM fungi. Our study suggests that litter species richness and especially certain litter species may influence decomposition through modifying fungal community composition both in foliar and root litter.

Key words: fungal community, fungal richness, foliar litter, root decomposition, litter mixture, litter mass loss.

33 **1. Introduction**

34 Functioning of above- and belowground components of terrestrial ecosystems are influenced
35 by feedbacks between plants, root associated organisms and decomposers (Wardle et al.,
36 2004). In mixed forest ecosystems, individual trees affect decomposition directly through
37 species-specific litter quality (McClaugherty et al., 1985; Hobbie, 1992; Silver and Miya,
38 2001) and indirectly through modified micro-environmental conditions and soil biota
39 composition (Joly et al., 2017). In particular, Hobbie et al. (2006) showed that tree species
40 identity affects decomposition via both litter chemistry and effects on soil temperature. The
41 strength of feedback to plants depends on plant traits and interactions between root- and litter-
42 associated microbes (Cairney and Meharg, 2002; Ke et al., 2015).

43 Together with environmental variables such as temperature and moisture, plant traits such as
44 leaf nutrient and lignin concentration are strong predictors of litter decomposition in forest
45 ecosystems (Hättenschwiler, 2005; Cornwell et al., 2008; Bani et al., 2018). Due to litter
46 quality effects, broadleaf litter is expected to decompose faster than coniferous litter (Prescott
47 et al., 2000). Plant litter is often decomposed more rapidly in the vicinity of the mother plant
48 due to specialized decomposer community, termed as 'home-field advantage effect' (Ayres et
49 al., 2009; Veen et al., 2015). Home-field advantage has been found to be common in forest
50 ecosystems and may cause an average 8% faster litter mass loss in 'home' than 'away'
51 habitats (Ayres et al., 2009). Home-field advantage in decomposition communities has been
52 found to be related to chemical similarity in litter quality rather than related to associations
53 between specific species (Gholz et al., 2000; Veen et al., 2015). Ke et al. (2015) showed that
54 litter decomposability through soil nitrogen (N) availability may determine the strength of
55 plant-soil feedback in communities dominated by arbuscular mycorrhizal fungi.

56 In forest ecosystems, foliar litter from different plant species becomes usually mixed because
57 of wind and roughly simultaneous litter fall in the autumn (Staelens et al., 2003; Ťupek et al.,
58 2015). Similarly, root litter is mixed, because roots of plant species commonly intermingle
59 and their turnover is usually synchronous (Fogel, 1983; Brassard, 2010). Most root systems of
60 trees in boreal forest ecosystem have been shown to stop activity after leaf-drop in the fall
61 (Burke and Raynal, 1994). Mixing litter of different plant species may cause shifts in
62 microbial communities that may affect decomposition rates (Chapman et al., 2013). In
63 particular, chemically diverse litter mixtures provide decomposers with a varied diet that has
64 strong effects on microbial communities and functional diversity and hence may increase or
65 decrease decomposition rates with positive or negative feedbacks to plants (Gartner and
66 Cardon, 2004; Hättenschwiler et al., 2005). Decomposition patterns of leaf litter mixtures are
67 usually 'non-additive', i.e. not directly predictable based on the biogeochemical processes in
68 parent litter, whereas 'additive' responses in mixtures are predictable from component species
69 (Gartner and Cardon, 2004). Most studies have revealed that litter species composition has a
70 stronger effect on decomposition rates than litter richness *per se* (Wardle et al., 2006; Hoorens
71 et al., 2010; Cuchietti et al., 2014; Handa et al., 2014; Setiawan et al., 2016).

72 Litter mixing affects microbial abundance and community structure and tends to result in
73 synergistic or antagonistic effects where decomposition rates are faster or slower,
74 respectively, than expected based on decomposition rates of litter of component species
75 (Gartner and Cardon, 2004). However, linking microbial community changes directly to these
76 non-additive patterns in litter mixtures has been elusive (Chapman et al., 2013). It has been
77 shown that litter species composition determines the direction of non-additive effect in the
78 litter mixture (De Marco et al., 2011). It has been suggested that synergistic effects in litter
79 mixtures are caused by fungi-driven nutrient transfer from higher quality litter to the poor one,
80 and antagonistic effects are due to release of inhibitory compounds (Chapman et al., 1988).

81 Berglund and Ågren (2012) showed that the litter mixture decomposes faster than parent
82 litters alone when the litter of the higher quality mineralizes nitrogen fastest. More diverse
83 and patchy plant litter may promote niche specialists and hence support higher microbial
84 diversity (Kubartová et al., 2009; Chapman and Newman, 2010; Santonja et al., 2017). Litter
85 of different tree species develop distinct microbial communities, however, microbial changes
86 may not translate to predictably altered litter decomposition (Aneja et al., 2006; Chapman and
87 Newman, 2010).

88 Root litter represents an important C source for microbial communities (Rasse et al., 2005)
89 and plays a substantial role in plant-soil feedback (Freschet et al., 2013). Due to lower
90 nutrient concentration and higher lignin content, roots are considered to be more recalcitrant
91 than foliar litter and this might have an effect on their microbial degradability (Berg and
92 McClaugherty, 2014; Jacobs et al., 2018). To date most studies on litter decomposition have
93 focused on the foliar component and little attention has been given to understanding the
94 patterns and drivers of the large source of carbon that is found in roots, partly because of the
95 challenges of studying belowground litter. Little is known about the community composition
96 of microbial decomposers of dead roots. For example, Herzog (2017) and Kohout et al. (2018)
97 studied the composition of dead root associated decomposer communities over a two-year
98 period; Fisk et al. (2011) investigated fungal community development on dead roots in
99 disturbed rhizosphere conditions. Several studies have been conducted to analyze if fungal
100 community composition varies between litters of different diversity (Kubartová et al., 2009;
101 Chapman and Newman, 2010; Chapman et al., 2013). However, the effects of foliar litter
102 diversity and particularly root litter diversity on fungal functional groups in forest ecosystems
103 remain largely unknown.

104 Saprotrophs, endophytes, plant pathogens and EcM fungi are the major fungal guilds
105 inhabiting foliar and root litter (Lindahl et al., 2007; Voříšková and Baldrian, 2013; Kohout et

106 al., 2018). While saprotrophic fungi are the primary decomposers of C-rich biopolymers
107 (Cooke and Rayner, 1984; Talbot et al., 2013), some plant pathogens (Baker and Bateman,
108 1978; Osono, 2007) and endophytes (Müller et al., 2001; Korkama-Rajala et al., 2008;
109 Kohout et al., 2018) are also potentially important in the initial stages of decomposition, as
110 they often express saprotrophic activity after leaf senescence. EcM fungi take part in organic
111 matter decomposition through mobilizing organically bound nitrogen (Lindahl and Tunlid,
112 2015), which may lead to direct competition for resources with saprotrophs and result in an
113 overall decrease in decomposition rate (Fernandez and Kennedy, 2016).

114 Host preference has been observed in endophytes, plant pathogens, saprotrophs and
115 mycorrhizal fungi (Molina et al., 1992; Zhou and Hyde, 2001; Põlme et al., 2018). Of these
116 four groups, mycorrhizal fungi exhibit a high degree of host specificity which is thought to be
117 a result of their coevolution with plants (Brundrett, 2002). Thus, the diversity of belowground
118 organisms who are intimately associated with plant roots (e.g. EcM fungal taxa) are predicted
119 to create stronger aboveground effects (influence on plant productivity, composition, and
120 diversity) compared with saprotrophs with low specificity (Wardle et al., 2004). Also,
121 community composition of EcM fungi might respond strongly to the aboveground
122 communities through litter chemistry (Conn and Dighton, 2000). Tedersoo et al. (2008)
123 showed that EcM fungal community composition in dead wood responds to tree species of
124 woody litter that probably results from chemical differences in substrate. Given the
125 specialization of many EcM fungal species to certain plant host genera (Kennedy et al., 2015;
126 Molina and Horton, 2015), we predict that the relative proportion of host-specific EcM fungi
127 is greater in their host plant's litter than in other tree species' litter due to their long
128 evolutionary history of being exposed to the host plant's litter.

129 The aim of this study was to determine the ecological relationships between fungal diversity
130 and plant diversity via feedbacks to foliar and root litter. We hypothesized that mass loss rate

131 increases with increasing litter diversity (H1); litter from a single tree species decomposes
132 more rapidly under the trees where it originated (H2); composition of saprotrophs, plant
133 pathogens and EcM fungi is mainly driven by litter species composition (H3); litter species
134 richness enhances fungal richness (H4); and the relative proportion of host-specific EcM
135 fungi is greater in the litter of their intimate host plant (H5).

136

137 **2. Materials and Methods**

138 *2.1. Study site and experiment set up*

139 To study litter diversity effects on fungal community composition and richness, a litter
140 decomposition experiment was set up in the Satakunta forest diversity experimental area
141 (www.sataforestdiversty.org) in Finland (61.714°N, 21.983°E). The forest diversity
142 experiment was established in 1999 to study the effects of tree species richness and
143 composition on ecosystem functioning. Experimental plots in three different areas were
144 planted with monocultures, two-, three- and five-species mixtures of silver birch (*Betula*
145 *pendula*), black alder (*Alnus glutinosa*), Siberian larch (*Larix sibirica*), Scots pine (*Pinus*
146 *sylvestris*) and Norway spruce (*Picea abies*). Each 20 m x 20 m plot contains 13 rows with 13
147 trees per row planted at 1.5 m intervals. In mixed species plots, all tree species were planted
148 in equal proportions. In 2013, one replicate of each treatment per area was thinned with tree
149 density reduced by half. In 2014-2015, the annual precipitation was 567-673 mm and annual
150 temperature was 6.7-6.9 °C (www. ilmatieteenlaitos.fi – Pori meteorological station).

151 In order to minimize spatial effects, we selected two five-species mixture plots (plots 18 and
152 22 in area 1) to test the effects of tree species identity, foliar and root litter species
153 composition and richness on microbial diversity and litter mass loss. Our block design
154 included 20 tree individuals per plot with a total of 40 focal trees (blocks). Within each of the
155 two plots, we randomly selected 5 individual trees of each tree species except the non-native
156 larch and placed litter bags (see next paragraph) under these trees. Each tree (block) received
157 eight bags of single-species foliar and root litters, two bags of two-species (the same random
158 combination for both foliar and root litters) and two four-species foliar and root litter
159 mixtures. In each block, we used two extra bags of single-species foliar and root litter to
160 increase the power for 'home' versus 'away' comparisons.

161 Foliar litter was collected by use of litter traps from neighboring monoculture plots and air-
162 dried at room temperature in September, 2014. Roots of the four tree species were excavated
163 from the edges of the two selected plots in order not to disturb the rest of the plot. We selected
164 an equal proportion of fine (≤2 mm diam.) and coarse roots (2-3 mm diam.). All roots were
165 dried at 65 °C for 48 hours to eliminate living EcM fungi, whereas leaves were dried at room
166 temperature to better mimic natural conditions. Heating may eliminate most fungi (Langley et
167 al., 2006) and affect nutrient form, distribution and availability in plant litter (Gray and
168 Dighton, 2006), which renders foliar and root litter effects incomparable in our study.

169 Litter bags (10 x 10 cm) were prepared of polyester (500 μm mesh size) that allowed root and
170 mycelium ingrowth and migration of meiofauna. 1 g of litter was weighed into each bag, with
171 litter species mixes pooled in equal proportion. Both litter substrates were kept as intact as
172 possible. Litter bags were installed above soil surface by use of nails and wire. Ground
173 vegetation and natural litter were cleared to ensure contact with the soil. Litter bags were
174 placed to one side of the tree (directing to a tree of same species), approximately 0.5 m from
175 the tree trunk and 5 cm distance between the bags.

176 For studying the effect of litter richness of one-, two- and four-species mixtures, 400, 80 and
177 80 litter bags were used, respectively. In October 2014, altogether 560 litter bags were
178 installed including 280 bags of foliar and 280 bags of root litter. Litter bags were harvested
179 after 12 months of decomposition in October 2015. We were unable to retrieve four of the
180 litter bags. The litter bags were carefully freed from the adhering soil particles and air-dried at
181 room temperature for 48 hours. Then, the decomposed litter was weighted in sterile conditions
182 and manually crushed in zip-lock plastic bags. 0.20 g of material from each sample was
183 further powdered in 2-ml Eppendorf tubes using two 3-mm tungsten carbide beads in Mixer
184 Mill MM400 (Retsch GmbH, Haan, Germany) at 30 Hz for 5 min for molecular analysis.

185 Initial C, N and phosphorus (P) concentrations in four foliar and four root litter species
186 samples were determined according to Tedersoo et al. (2012) to compare the differences in
187 litter quality between foliar and root litter, and broadleaf and coniferous litter. Litter species
188 and chemical parameters are given in Supplementary Table S1.

189 *2.2. Molecular analysis*

190 DNA was extracted from litter samples using PowerSoil DNA Isolation Kit (MoBio,
191 Carlsbad, CA, USA) following the manufacturer's protocols. PCR was carried out using a
192 mixture of five forward primers ITS3mix1-5 (CANCGATGAAGAACGYRG) (Tedersoo et
193 al., 2014) in equimolar concentration and a degenerate reverse primer ITS4ngsUni (Tedersoo
194 and Lindahl, 2016). The ITS4ngsUni (CCTCCSCTTANTDATATGC) primer was tagged
195 with one of the 110 identifier barcodes (10–12 bases) (Supplementary Table S2) that were
196 modified from those recommended by Roche (Basel, Switzerland) to differ by >3 bases, to
197 start only with adenosine and to comprise similar proportions of adenosine and thymidine
198 (between 30 and 70%) to equalize their affinities in an adapter ligation step (Tedersoo et al.,
199 2014). The PCR mixture comprised 1 µl DNA, 0.5 µl each of the primers (20 µM), 4 µl 5×
200 HOT FIREPol Blend Master Mix (Solis Biodyne, Tartu, Estonia) and 14 µl double-distilled
201 water. PCR was carried out in two replicates in the following thermocycling conditions: an
202 initial 15 min at 95 °C, followed by 30 cycles of 95 °C for 30 s, 55 °C for 30 s, 72 °C for 1
203 min, and a final cycle of 10 min at 72 °C. PCR products (typically 350–400 bp) from replicate
204 samples were pooled and their relative quantity was estimated by running 5 µl DNA on 1%
205 agarose gel for 15 min. DNA samples with no visible bands were re-amplified with 35 cycles
206 and DNA samples with strong bands were re-amplified with only 25 cycles. Both negative
207 (sterile water used for PCR mixture) and positive controls (Australian truffles *Reddellomyces*
208 *donkii* specimen MURU5473 and *Dingleya* sp. specimen MURU5844) were included in PCR
209 and sequencing runs. PCR products were pooled at approximately equimolar ratios as

210 determined by gel band strength, with the exception of negative controls, from which 5 μl were
211 added. Samples were combined into six libraries (foliar and root litter were kept separate).
212 Libraries were purified by FavorPrep™ Gel/PCR Purification Kit (Favorgen-Biotech Corp.,
213 Austria), following the manufacturer's instructions. DNA from each library was quantified
214 using Qubit® 2.0 Fluorometer (Invitrogen, Life Technologies, CA, USA) and dsDNA High
215 Sensitivity assay kit (ThermoFisher Scientific, Waltham, USA). DNA concentrations for each
216 library ranged from 63 ng μl^{-1} to 231 ng μl^{-1}. Amplicons were subjected to adaptor ligation
217 and Illumina MiSeq sequencing in the Estonian Genome Center (Tartu, Estonia).

218 *2.3. Bioinformatics analysis*

219 Illumina sequencing provided 14,564,313 raw reads. Raw reads were processed using
220 PipeCraft 1.0 platform (Anslan et al., 2017). Paired-end reads were merged and quality
221 trimmed using VSEARCH v1.1.11 (Rognes et al., 2016) (trimming options: maximum
222 expected error rate = 1). The resulting 9,947,496 sequences were re-assigned to samples based
223 on the tags using mothur v1.36.1 (Schloss et al., 2009). Chimera filtering of the sequences
224 was performed using VSEARCH based on UNITE v6 reference database (Abarenkov et al.,
225 2010b) and *de novo* option. To extract the full-length ITS2 subregion for clustering purposes,
226 reads were processed with ITSx 1.0.9 (Bengtsson-Palme et al., 2013) to remove flanking gene
227 fragments. Full-length ITS2 reads were assigned to operational taxonomic units (OTUs) by
228 clustering at 97% similarity threshold with CD-Hit v4.6 (Fu et al., 2012). All OTUs
229 represented by a single sequence (singletons) were removed. The most abundant sequence of
230 each cluster was selected as a representative for BLASTn sequence similarity search (word
231 size=7; gap open=1; gap extension=2; revard=1; penalty=-1) against both INSDc
232 (International Nucleotide Sequence Databases Collaboration) and UNITE. Also, BLASTn
233 searches were run against reference sequences of fungi in 99.0% similarity species hypothesis

234 (SH) that include third-party taxonomic and metadata updates (Kõljalg et al., 2013; Nilsson et
235 al., 2014) as implemented in the PlutoF workbench (Abarenkov et al., 2010a).

236 Further filtering of the dataset was performed manually. We used BLASTn output (similarity,
237 e-value and match length/sequence length ratio) for taxonomic assignment as well as positive
238 and negative controls to remove low quality sequences, tag switching errors and
239 contaminants. We considered 10 best matching references for each OTU to annotate taxa as
240 accurately as possible and ran manual BLASTn searches against the INSDC if no reliable
241 taxonomy was revealed. BLASTn e-values $<e^{-50}$ were considered reliable to assign OTUs to
242 kingdoms, whereas OTUs with e-values $>e^{-20}$ were treated as 'unknown' taxa. E-values
243 between e^{-20} and e^{-50} were manually checked against the 10 best matches for accurate
244 assignment. We relied on 98%, 90%, 85%, 80%, and 75% sequence identity as a criterion for
245 assigning OTUs to species, genus, family, order or class level, respectively (Tedersoo et al.,
246 2014). OTUs with sequence length <250 base pairs (over the entire amplicon length) and
247 match/sequence length <70% were excluded as potential artefacts. Each fungal genus, family
248 or order was assigned to functional categories based on FUNGuild (Nguyen et al., 2016). All
249 Glomeromycota were considered to be arbuscular mycorrhizal (AM). Taxa were considered
250 to be EcM if they matched to any sequences belonging to EcM lineages and exhibited
251 sequence blast score/sequence length above predetermined lineage-specific thresholds
252 (Tedersoo and Smith, 2017). Annotated sequence data and detailed metadata are given in
253 Supplementary Table S3 and Table S4, respectively. In order to evaluate putative host-
254 specific associations in EcM fungi, we used literature-based search for the recovered species
255 and UNITE database third-party metadata annotations at the level of SH.

256 *2.4. Statistical analysis*

257 We analyzed species richness and community composition of taxa that belonged to the
258 kingdom Fungi, focusing on EcM, saprotrophic and plant pathogenic fungi. Endophytes were
259 not analyzed separately, because they were underrepresented in the OTU matrix (<50 OTUs).
260 PERMANOVA+ (Anderson et al., 2008) was used to generate community composition
261 models for individual fungal groups and litter types (foliar and root litter). We tested the
262 effect of litter species composition, litter species richness, focal tree species identity, plot
263 (fixed factors) and block (random factor), and mass loss (covariate) on fungal community
264 composition in foliar and root litter samples. The OTU matrix was subjected to Hellinger
265 transformation using vegan package (Oksanen et al., 2017) in R prior to community analysis.
266 We compared the performance of Bray-Curtis distance and Hellinger distance (D17) metric
267 for the abundance data (including OTUs with frequency > 1) (Tedersoo et al., 2015). We
268 chose Bray-Curtis metric as models generated based on the resemblance matrices had higher
269 adjusted coefficients of determination (R^2_{adj}) values. Euclidean distance was applied to
270 generate environmental distance matrices. The best community composition model for each
271 group and litter type was constructed using PERMANOVA function in PERMANOVA+. The
272 factor block was nested in tree species and plot. Type I test and 999 permutations were used
273 for the unbalanced sampling design with nested effects. Statistical significance level was at α
274 $= 0.05$.

275 We used the phyloseq package (McMurdie and Holmes, 2013) in R for visualizing taxonomic
276 assignments at the order level in foliar and root litter. We used the vegan package to construct
277 Nonmetric Multidimensional Scaling (NMDS) plots for saprotrophs, plant pathogens and
278 EcM fungal group in foliar and litter samples. NMDS graphs were constructed to assess
279 differences in fungal community composition among litter species. The function metaMDS
280 with Procrustes analysis and 200 iterations was used to perform NMDS. In metaMDS, raw

281 sequence abundance matrix was square-root-transformed and subjected to Wisconsin double
282 standardization. Bray-Curtis dissimilarity was used to calculate community matrix.

283 For richness analyses of foliar and root litter biota, we calculated the standardized residuals of
284 OTU richness in relation to the square-root of the number of obtained sequences to account
285 for differences in sequencing depth (Tedersoo et al., 2014). Standardized residuals were
286 obtained from multiple regression analysis performed in STATISTICA 12 (StatSoft Inc.,
287 Tulsa, OK, USA). We used the vegan package to calculate Shannon diversity index and
288 evenness. Using the previously described nested design, mixed effects models for fungal
289 standardized residuals of OTU richness were calculated in STATISTICA. We used type I sum
290 of squares (SS) to construct the models. To test the non-additivity of decomposition rates in
291 two- and four-species mixtures, we calculated expected mass losses based on the average of
292 single species decomposition, and compared with the observed rates. We also tested if mass
293 loss was described by litter species composition, litter species richness, tree species identity,
294 plot or block. Using one-way and two-way analysis of variance (ANOVA), we performed
295 Tukey's post hoc tests to distinguish among statistically significantly different groups, using
296 the R package agricolae (De Mendiburu, 2014). To test the host-specific EcM fungal
297 preferences towards the litter of their host plant litter species, we extracted host-specific
298 fungal OTU and their sequence abundance as a relative proportion to all EcM fungi. Only
299 monospecific litter was included in testing the differences between 'home' and 'away'
300 treatments. We considered single litter species under the same tree species the 'home'
301 combination. We tested the differences in host specific EcM fungal composition in four
302 'home' combinations and 12 'away' combinations using one-way ANOVA.

303 *2.5. Accession numbers*

304 The sequence data has been submitted to the SRA database under accession number

305 SRP133556.

306

307 **3. Results**

308 *3.1. Mass loss*

309 Within one year of decomposition, the average mass loss of foliar and root litter were 30.4%
310 (± 8.1%, SD) and 19.2% (± 6.8%), respectively. Litter species richness had no significant
311 effect on mass loss of foliar litter ($F_{2,272} = 0.38$; $P = 0.682$; Fig. 1a) or root litter ($F_{2,275} = 0.51$;
312 $P = 0.599$; Fig. 1b). Instead, litter species composition was the best predictor for
313 decomposition rate of both foliar litter ($F_{10,264} = 6.58$; $P < 0.001$; Fig. 1c) and root litter
314 ($F_{10,267} = 57.47$; $P < 0.001$; Fig. 1d). We did not detect any significant non-additive effects of
315 foliar (Fig. 1c) and root litter (Fig. 1d) mixtures on decomposition rates. Unexpectedly, the
316 slowest decomposing foliar litter combinations included deciduous litter (treatments: birch
317 birch–spruce and alder–birch) and the fastest decomposing foliar litter treatments included
318 coniferous litter (treatments: spruce, pine–spruce and alder–spruce) which is assumed to be
319 more recalcitrant than deciduous litter and thus expected to decompose slower (Fig. 1c). Of
320 root litter, coniferous litter (treatments: pine–spruce, pine and spruce) decomposed fastest,
321 whereas deciduous litter (treatments: birch, alder–birch and alder) decomposed slowest (Fig.
322 1d). We detected significant differences in decomposition rates of foliar and root litter of
323 conifers and broadleaf trees. Foliar litter of birch decomposed significantly slower than foliar
324 litter of pine ($F_{1,95} = 37.18$; $P < 0.001$), spruce ($F_{1,95} = 52.28$; $P < 0.001$) and pine–spruce
325 treatments ($F_{1,53} = 10.94$; $P = 0.002$). Mass loss of coniferous (treatments: pine–spruce, pine
326 and spruce) root litter was significantly higher than that of broadleaf root litter (treatments:
327 birch, alder–birch and alder; $F_{1,210} = 572.11$; $P < 0.001$).

328 There were no significant overall differences between 'home' and 'away' treatments in foliar
329 litter ($F_{1,194} = 0.04$; $P = 0.851$) or root litter ($F_{1,196} = 0.007$; $P = 0.934$). Also, we found no
330 significant 'home' vs 'away' effects for root litter species ($F_{3,190} = 0.73$; $P = 0.535$; Fig. 2b).

331 However, we detected a weak ‘home’ vs ‘away’ effect for foliar litter species ($F_{3,188} = 2.69$; P
332 $= 0.048$; Fig. 2a). Foliar litter of birch tended to decompose 4% faster in ‘home’ than ‘away’
333 treatment.

334 *3.2. Identification of litter biota*

335 The 8,044,053 high-quality reads were clustered into 14,963 OTUs. Based on sequence
336 distribution in negative and positive controls, we excluded OTU sequence counts=1 per
337 sample to remove most of the potential tag-switching errors. After removal of samples with
338 <500 sequences (three samples) and OTUs with poor BLASTn values, the final data set
339 comprised of 10,042 OTUs, 7,532,808 sequences and 553 samples. In all, 29.0% of OTUs
340 occurred only in one sample. Each sample was comprised of 566 to 45,105 reads (median:
341 12,641 reads) and 45 to 1107 OTUs (median: 421 OTUs).

342 Altogether 91.1% of OTUs were assigned to Fungi, 5.3% to Viridiplantae (mostly Bryophyta,
343 Chlorophyta and Magnoliophyta), 1.4% to Metazoa (mostly Nematoda), 0.9% to Alveolata
344 (mostly Ciliophora), 0.6% to Rhizaria (mostly Cercozoa), 0.6% to Stramenopila (mostly
345 Chrysophyceae) and 0.1% to Apusozoa. Of the 9,148 fungal OTUs, 48.2% were identified as
346 Ascomycota, 20.2% as Basidiomycota, 1.3% as Chytridiomycota, 0.7% as Mucoromycota,
347 0.6% as Mortierellomycota, 0.2% as Glomeromycota, 0.2% as Rozellomycota, whereas
348 28.5% remained unclassified at phylum level. Helotiales (1,926,859 reads, 1647 OTUs),
349 Agaricales (616,174 reads, 460 OTUs), and Rhytismatales (429,495 reads, 183 OTUs) were
350 dominant orders; *Lophodermium* (404,960 reads, 127 OTUs), *Mollisia* (325,480 reads, 101
351 OTUs) and *Mycena* (226,043 reads, 107 OTUs) were dominant genera. Helotiales was
352 relatively more abundant in root litter samples, whereas Agaricales and Rhytismatales were
353 relatively more abundant in foliar litter samples, the latter especially in pine needle samples.

354 At fungal order level, the composition of fungal communities was not litter species
355 composition specific (Fig. 3).

356 Respectively, saprotrophs, plant pathogens and EcM fungi accounted for 66.1%, 16.8% and
357 11.0% of OTUs that could be assigned to functional guilds. The average number of EcM
358 OTUs was 5.5 ± 11.2 (SD) in foliar litter samples and 4.2 ± 3.6 (SD) in root litter samples.
359 The average number of plant pathogens was 45.1 ± 23.2 (SD) in foliar litter samples and 17.3
360 ± 10.9 (SD) in root litter samples. The average number of saprotrophs was 121.9 ± 64.5 (SD)
361 in foliar litter samples and 84.7 ± 37.2 (SD) in root litter. In foliar and root litter samples,
362 altogether 344 and 163 EcM fungal OTUs were recognized. The EcM fungal community
363 included an estimated 9.7% of host-specific OTUs that corresponded to 33.8% of total EcM
364 fungal sequences. Among these, alder-specific fungi comprised 16 OTUs (42% of host-
365 specific EcM fungal OTUs) with 20,569 sequences (87% of host-specific fungal sequences).

366 *3.3. Fungal community structure*

367 Community structure of all fungi, saprotrophic and plant pathogenic fungi was best described
368 by litter species composition and litter species richness in foliar litter (Table 1). Litter species
369 composition had the strongest effect on the community structure of saprotrophs (F_{pseudo} =
370 10.87; $R^2_{adj} = 0.210$; $P < 0.001$; Fig. 4a) and plant pathogens ($F_{pseudo} = 16.64$; $R^2_{adj} = 0.292$; P
371 < 0.001; Fig. 4c), but negligible effect on EcM fungi in foliar litter ($F_{pseudo} = 1.47$; R^2_{adj} =
372 0.003; $P < 0.001$; Fig. 4e). In root litter, no clear influence of litter species composition was
373 evident for fungal composition (Table 1). Community composition of all fungi in root litter
374 was marginally influenced by litter species richness ($F_{pseudo} = 3.18$; $R^2_{adj} = 0.011$; $P < 0.001$).
375 Saprotrophs were weakly affected by litter species composition ($F_{pseudo} = 2.92$; $R^2_{adj} = 0.048$;
376 $P < 0.001$; Fig. 4b), whereas plant pathogens were slightly affected by plot ($F_{pseudo} = 4.51$;
377 $R^2_{adj} = 0.017$; $P < 0.001$; Fig. 4d) and EcM fungi were affected by focal tree species identity

378 (F_{pseudo} = 2.50; R^2_{adj} = 0.025; P < 0.001; Fig. 4f). Focal tree species identity and interaction
379 term between tree and litter species composition had a significant but weak effect on
380 composition of most fungal guilds both in foliar and root litter (Table 1).

381 *3.4. Fungal richness*

382 The mean OTU richness of all fungi in foliar and root litter samples was 426.3 ± 167.0 (SD)
383 and 345.1 ± 145.7 (SD), respectively. Mixed effects models for standardized residuals of
384 OTU richness indicated that the best predictors differed among functional groups of fungi
385 depending on litter type (Table 2). Litter species richness was one of the two strongest
386 predictors for total fungal (positive effect; $F_{2,195}$ = 83.38; R^2_{adj} = 0.229; P < 0.001; Fig. 5a),
387 saprotroph (positive effect; $F_{2,195}$ = 22.27; R^2_{adj} = 0.099; P < 0.001) and plant pathogen
388 richness ($F_{2,195}$ = 87.99; R^2_{adj} = 0.251; P < 0.001) in foliar litter, but none of the tested factors
389 affected richness of EcM fungi. In foliar litter, litter species composition had a significant
390 additional effect on richness of all fungi (positive effect; $F_{8,195}$ = 16.82; R^2_{adj} = 0.209; P <
391 0.001), plant pathogens (positive effect; $F_{8,195}$ = 24.68; R^2_{adj} = 0.284; P < 0.001) and
392 saprotrophs (positive effect; $F_{8,195}$ = 6.96; R^2_{adj} = 0.118; P < 0.001). Shannon diversity index
393 of all fungi was significantly affected by litter species composition ($F_{10,264}$ = 15.31; P < 0.001)
394 and litter species richness ($F_{2,272}$ = 14.62; P < 0.001) in foliar litter. The Shannon diversity
395 index showed that fungal diversity increased with increasing number of litter species in a
396 mixture. In foliar litter, the evenness values were similar at the three levels of litter richness
397 ($F_{2,272}$ = 0.60; P = 0.549), but differed by litter species composition ($F_{10,264}$ = 8.12; P < 0.001).
398 We detected significant non-additive effects of foliar litter mixtures on fungal richness (Fig.
399 5c). Three out of the seven foliar litter mixtures showed significant synergistic effects: two-
400 species mixtures alder–birch (t = 2.11; P = 0.037) and birch–spruce (t = 2.61; P = 0.011) and
401 the four-species mixture alder–birch–pine–spruce (t = 9.36; P < 0.001).

402 Richness of root litter had weaker effects on fungal OTU richness than richness of foliar litter
403 (Fig. 5b). Richness of root litter increased OTU richness of saprotrophs ($F_{2,233}$ = 11.15; R^2_{adj} =
404 0.058; P < 0.001), plant pathogens ($F_{2,233}$ = 7.71; R^2_{adj} = 0.039; P < 0.001) and EcM fungi
405 ($F_{2,198}$ = 5.42; R^2_{adj} = 0.024; P = 0.005). Litter species composition had a significant positive
406 effect on richness of EcM fungi ($F_{8,198}$ = 2.25; R^2_{adj} = 0.023; P = 0.026), plant pathogens
407 ($F_{8,233}$ = 2.62; R^2_{adj} = 0.035; P = 0.009) and saprotrophs ($F_{8,233}$ = 2.15; R^2_{adj} = 0.022; P =
408 0.032) in root litter. In root litter, the Shannon diversity index of all fungi was significantly
409 affected by litter species composition ($F_{10,267}$ = 2.89; P = 0.002), but remained unaffected by
410 litter species richness ($F_{2,275}$ = 1.55; P = 0.213). The evenness was influenced by litter species
411 richness ($F_{2,275}$ = 6.50; P = 0.002) and litter species composition ($F_{10,267}$ = 6.22; P < 0.001) in
412 root litter. We detected significant non-additive effects of root litter mixtures on fungal
413 richness (Fig. 5d). Two out of the seven root litter mixtures showed significant synergistic
414 effects: the two-species mixtures alder–birch (t = 2.24; P = 0.028) and birch–spruce (t = 2.37;
415 P = 0.020).

416 *3.5. EcM specificity analysis*

417 We assigned OTUs of EcM fungi into host-specific and promiscuous taxa to test preferences
418 of fungi for the litter of their intimate hosts. Relative sequence abundance and OTU
419 abundance of host-specific EcM fungi in 'home' combinations were similar to 'away'
420 combinations in both foliar ($F_{1,145}$ = 0.00004; P = 0.995 and $F_{1,145}$ = 0.42; P = 0.518,
421 respectively) and root litter ($F_{1,118}$ = 0.86; P = 0.355 and $F_{1,118}$ = 1.34; P = 0.249,
422 respectively). Taken separately, the four 'home' and 12 'away' combinations had no
423 significant effect on relative sequence abundance of host-specific EcM fungi in either foliar
424 litter ($F_{15,131}$ = 1.56; R^2 = 0.12; P = 0.093; Supplementary Fig. S1a) or root litter ($F_{15,104}$ =
425 0.63; R^2 = 0.07; P = 0.842; Supplementary Fig. S1b). By contrast, these combinations had a
426 weak but significant effect on relative host-specific EcM fungal OTU abundance in foliar

427 litter ($F_{15,131}$ = 2.50; R^2 = 0.14; P = 0.003; Supplementary Fig. S1c) but not in root litter
428 ($F_{15,104}$ = 1.23; R^2 = 0.11; P = 0.264; Supplementary Fig. S1d). Alder-specific fungal taxa
429 contributed most to the relative OTU and sequence abundance both in foliar and in root litter,
430 but these taxa showed no evidence for preference of alder litter.

431

432 **4. Discussion**

433 *4.1. Litter mass loss*

434 Decomposition rates of both foliar and root litter remained unaffected by litter species
435 richness, providing no support to the first hypothesis. Non-additive patterns of mass loss are
436 common (Gartner and Cardon, 2004; Lecerf et al., 2011; Cuchietti et al., 2014; Santonja et al.,
437 2015), by contrast this finding is in agreement with studies that have reported additive
438 decomposition rates (Prescott et al., 2000; Hoorens et al., 2010; Guerrero-Ramírez et al.,
439 2016), suggesting that mass loss dynamics of monospecific treatments can be used to predict
440 the dynamics of mixed species treatments. Mass loss of foliar and root litter was most
441 strongly affected by litter species composition, supporting the view that litter quality may play
442 a strong role in decomposition (Hoorens et al., 2010; Coq et al., 2011; Cuchietti et al., 2014;
443 Handa et al., 2014; Setiawan et al., 2016; Dawud et al., 2017). Broadleaf litter usually
444 decomposes faster than coniferous litter (Prescott et al., 2000; Silver and Miya, 2001), but this
445 may strongly depend on studied species (Cornelissen et al., 2001; Hobbie et al., 2010, 2006).
446 In line with Heim and Frey (2004), we found that decomposition of coniferous root litter was
447 more rapid than decomposition of broadleaf root litter. This may indicate some home-field
448 advantage in these plantations as much of the litter on the forest floor is dominated by needle
449 litter of the three conifers from previous years (personal observations). However, we detected
450 no clear home-field advantage effects, with no support to the second hypothesis. Although
451 tree effects are found to be largest close to the trunk (Saetre and Bååth, 2000), all five tree
452 species, growing together for 15 years, may have had effects on soil properties and microbial
453 community and may not have allowed ‘away’ to distinguish from ‘home’ in this study system.

454 *4.2. Fungal richness and composition*

455 We found that saprotrophs and putative plant pathogens dominated both foliar and root litter,
456 which is consistent with previous findings in Pinaceae-dominated forests (Herzog, 2017;
457 Kyaschenko et al., 2017). Within one year of decomposition, many of the typical leaf
458 pathogenic fungi were evident, indicating that part of the decomposer community most
459 probably originated from the living tissue. Plant pathogens have strong preferences for litter
460 species, with particularly strong patterns between coniferous and broadleaf foliage (Zhou and
461 Hyde, 2001; Arnold, 2007; Prescott and Grayston, 2013).

462 Consistent with the third hypothesis, foliar litter species composition affected the composition
463 of associated fungal communities. We detected that the effect was stronger on communities of
464 saprotrophic and plant pathogenic fungi compared with EcM fungi. Plant pathogens and
465 especially saprotrophs exhibit higher specialization for acquisition of nutrients from
466 recalcitrant plant-derived biopolymers (Zhou and Hyde, 2001; Baldrian, 2016). In root litter,
467 species composition effect was much weaker, which could be related to our heating treatment,
468 more similar root chemistry or lower specificity of soil-borne root decomposers. In root litter,
469 broadleaved trees differed from conifers in their fungal composition that may be explained by
470 different chemistry or its confounding phylogeny effect (Betulaceae *vs*. Pinaceae).

471 Litter species richness and litter species composition were two major predictors for explaining
472 species richness of saprotrophs and plant pathogens in foliar litter. In foliar litter, we detected
473 non-additive effects of two and four litter species mixtures on fungal richness, whereas in root
474 litter, litter species mixtures had non-additive effect on fungal diversity only in two-species
475 mixture, which is only partly consistent with our fourth hypothesis. Several authors have
476 reported enhanced fungal diversity with increasing foliar litter diversity (Kubartová et al.,
477 2009; Chapman and Newman, 2010; Santonja et al., 2017). This can be explained by higher
478 niche and resource availability or fine-scale resource heterogeneity (Chapman and Newman,
479 2010). The lack of positive root litter richness effect can be partly explained by the initial

480 heating treatment for endophytes and pathogens, or the paucity of specialist fungi for fine root
481 decomposition, because roots naturally decompose in the soil matrix (Štursová et al., 2012).

482 Our fifth hypothesis predicted that host-specific EcM fungi are more litter species-specific
483 than generalists, preferring the litter of their host plant. Based on high host-specificity and
484 restricted EcM fungal community of alders (Tedersoo et al., 2009; Põlme et al., 2013), we
485 expected that alder-specific fungi, in particular, occur in relatively greater abundance in alder
486 litter. Although the preference of EcM fungi to certain litter species has been previously
487 demonstrated (Conn and Dighton, 2000), we found no support to this hypothesis. No
488 differences in litter species preference in EcM fungi in general or preference for intimate
489 host's litter in particular was detected. However, it cannot be excluded that fresh litter is
490 unsuitable substrate for EcM fungi or the scale of our study is too small.

491

5. Conclusions

Our results showed that litter species composition was the main driver of decomposition rate and saprotroph and pathogen community composition in foliar litter. However, EcM fungal communities both in foliar and root litter were only marginally affected by litter species composition. Also, we found no evidence for the positive feedback of host litter on performance of EcM fungi specific to particular hosts. These results collectively suggest that growth of EcM fungal hyphae into fresh litter is rather opportunistic and unspecific. Litter species composition and litter species richness were two major factors underlying fungal richness in foliar litter. In particular, we detected strong synergistic effect of four-species foliar litter mixture on fungal richness. This study demonstrates that the fungal community in both foliar and root litter is affected by litter species richness and composition.

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Author contributions

L.T., J.K., S.B and E.O. designed the experiment; E.O. conducted fieldwork and molecular analysis; S.A. performed bioinformatic analysis; E.O. annotated metadata, analyzed the data, and wrote the first draft of the manuscript; all authors contributed to writing of the manuscript.

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853

854 **Fig. 1.** Litter mass loss (%) of (a, c) foliar and (b, d) root litter described by (a, b) litter species
855 richness (1, monospecific; 2, two-species mixtures; 4, four-species mixture), and (c, d)
856 observed and expected decomposition rates (%) for litter species composition (A, alder; B,
857 birch; P, pine; S, spruce; AB, alder–birch; AP, alder–pine; AS, alder–spruce; BP, birch–pine;
858 BS, birch–spruce; PS, pine–spruce; ABPS, alder–birch–pine–spruce). Data represents the
859 means of all samples with standard errors. Different letters denote significant differences
860 among factor levels. Expected litter mass loss rates are displayed with white and observed
861 with black.

862 **Fig. 2.** 'Home' versus 'away' treatment effect on mass loss (%) in (a) foliar and (b) root litter
863 described by litter species identity. Data represents the means of all samples with standard
864 errors. Different letters denote significant differences among factor levels. 'Away' treatments
865 are displayed with white and 'home' treatments with black.

866 **Fig. 3.** Abundances of major fungal orders in (a) foliar and (b) root litter. The data represents
867 the mean values of the relative abundances of ITS2 amplicons expressed as percentages. A,
868 alder; B, birch; P, pine; S, spruce; AB, alder–birch; AP, alder–pine; AS, alder–spruce; BP,
869 birch–pine; BS, birch–spruce; PS, pine–spruce; ABPS, alder–birch–pine–spruce.

870 **Fig. 4.** NMDS ordination plots describing the relative importance of litter species composition
871 in explaining the community structure of (a, b) saprotrophs, (c, d) plant pathogens and (e, f)
872 EcM fungi in (a, c, e) foliar and (b, d, f) root litter. Ellipses denote 95% confidence intervals
873 around the mean values of litter species composition. Circles, monospecific litters; stars,
874 alder–birch mixture; diamonds, alder–pine mixture; upward triangles, alder–spruce mixture;
875 crosses, birch–pine mixture; pluses, birch–spruce mixture; downward triangles, pine–spruce
876 mixture; red squares, alder–birch–pine–spruce mixture. Blue, alder; green, birch; pink, pine;
877 yellow, spruce.

878 **Fig. 5.** Variation in standardized residual richness of all fungi in (a, c) foliar and (b, d) root
879 litter described by (a, b) litter species richness (1, monospecific; 2, two-species mixtures; 4,
880 four-species mixture) and (c, d) litter species composition (A, alder; B, birch; P, pine; S,
881 spruce; AB, alder–birch; AP, alder–pine; AS, alder–spruce; BP, birch–pine; BS, birch–spruce;
882 PS, pine–spruce; ABPS, alder–birch–pine–spruce). Data represents the means of all samples
883 with standard errors. Different letters denote significant differences among factor levels.
884 Expected standardized residual richness of all fungi is displayed with white and observed with
885 black.

886 **Table 1.** Multivariate models for community composition of all fungi, EcM, plant pathogen

887 and saprotroph group in foliar and root litter

Foliar litter				Root litter			
variable	R^2 adj	Pseudo-*F*	*P*-value	variable	R^2 adj	Pseudo-*F*	*P*-value
1 Fungi (total)							
Litter composition	0.209	11.00	<0.001	Litter richness	0.011	3.18	<0.001
Litter richness	0.020	5.45	<0.001	Litter composition	0.050	3.06	<0.001
Plot	0.006	2.21	<0.001	Plot	0.013	2.98	<0.001
Tree	0.014	2.04	<0.001	Tree	0.032	2.64	<0.001
Block (Tree*Plot)	0.016	1.66	<0.001	Block (Tree*Plot)	0.063	1.85	<0.001
Mass loss	0.000	1.31	0.010	Mass loss	0.001	1.27	0.015
Tree*Litter composition	-0.026	1.17	<0.001	Tree*Litter composition	-0.019	1.05	0.015
1.1 EcM fungi							
Plot	0.027	3.37	<0.001	Tree	0.025	2.50	<0.001
Block (Tree*Plot)	0.184	3.12	<0.001	Plot	0.004	1.64	0.027
Litter richness	0.001	1.58	<0.001	Block (Tree*Plot)	0.023	1.20	<0.001
Tree	0.029	1.47	<0.001	Litter composition	-0.004	0.93	0.803
Litter composition	0.003	1.47	<0.001	Litter richness	-0.003	0.71	0.975
Tree*Litter composition	-0.030	1.05	0.161	Tree*Litter composition	-0.017	0.92	0.965
1.2 Plant pathogens							
Litter composition	0.292	16.64	<0.001	Plot	0.017	4.51	<0.001
Litter richness	0.024	6.92	<0.001	Litter composition	0.050	3.01	<0.001
Tree	0.006	1.76	<0.001	Tree	0.025	2.72	<0.001
Block (Tree*Plot)	-0.018	1.40	<0.001	Litter richness	0.008	2.52	<0.001
Plot	0.001	1.38	0.049	Block (Tree*Plot)	0.028	1.44	<0.001
Tree*Litter composition	-0.025	1.28	<0.001	Tree*Litter composition	-0.012	1.07	0.043
1.3 Saprotrophs							
Litter composition	0.210	10.87	<0.001	Litter composition	0.048	2.92	<0.001
Litter richness	0.019	5.19	<0.001	Plot	0.009	2.49	<0.001
Tree	0.010	1.78	<0.001	Litter richness	0.007	2.34	<0.001
Plot	0.003	1.76	0.002	Tree	0.023	2.23	<0.001
Block (Tree*Plot)	0.011	1.57	<0.001	Block (Tree*Plot)	0.057	1.73	<0.001
Mass loss	0.000	1.37	0.004	Mass loss	0.001	1.36	0.008
Tree*Litter composition	-0.027	1.12	<0.001	Tree*Litter composition	-0.018	1.02	0.247

888

889

890 **Table 2.** The best predictors for standardized residuals of OTU richness of all fungi, EcM,

891 plant pathogen and saprotroph group

Foliar litter				Root litter			
variable	**R^2 adj**	***F*-value**	***P*-value**	**variable**	**R^2 adj**	***F*-value**	***P*-value**
1 Fungi (total)							
Litter richness	0.229	83.38	<0.001	Plot	0.072	15.94	<0.001
Litter composition	0.209	16.82	<0.001	Litter richness	0.005	2.09	0.127
Plot	0.017	4.51	0.040	Block (Tree*Plot)	0.050	1.61	0.020
Block (Tree*Plot)	0.037	3.19	<0.001	Tree*Litter composition	0.015	1.38	0.103
Tree*Litter composition	-0.046	1.63	0.027	Litter composition	-0.000	1.22	0.288
1.1 EcM fungi							
Litter composition	-0.013	0.50	0.855	Litter richness	0.024	5.42	0.005
Litter richness	-0.007	0.09	0.913	Block (Tree*Plot)	0.148	2.43	<0.001
Tree*Litter composition	-0.094	0.28	1.000	Litter composition	0.023	2.25	0.026
				Tree*Litter composition	-0.020	1.06	0.385
1.2 Plant pathogens							
Litter richness	0.251	87.99	<0.001	Mass loss	0.037	13.44	<0.001
Litter composition	0.284	24.68	<0.001	Litter richness	0.039	7.71	<0.001
Tree	0.014	3.60	0.022	Litter composition	0.035	2.62	0.009
Block (Tree*Plot)	-0.056	1.58	0.028	Tree*Litter composition	0.046	1.51	0.045
Tree*Litter composition	-0.069	1.11	0.330				
1.3 Saprotrophs							
Litter richness	0.099	22.27	<0.001	Litter richness	0.058	11.15	<0.001
Litter composition	0.118	6.96	<0.001	Mass loss	0.027	10.47	0.001
Block (Tree*Plot)	0.038	1.91	0.002	Litter composition	0.022	2.15	0.032
Tree*Litter composition	0.008	1.64	0.025	Tree*Litter composition	0.060	1.78	0.008

892

893

894 **Supplementary Information**

895 **Fig. S1.** Host-specific EcM fungal preferences towards foliar and root litter species.

896 **Table S1.** Initial chemical composition of foliar and root litter species

897 **Table S2.** Primers used in this study

898 **Table S3.** OTU table of all taxa associated with foliar and root litter

899 **Table S4.** Detailed metadata for foliar and root litter samples

Figure 1

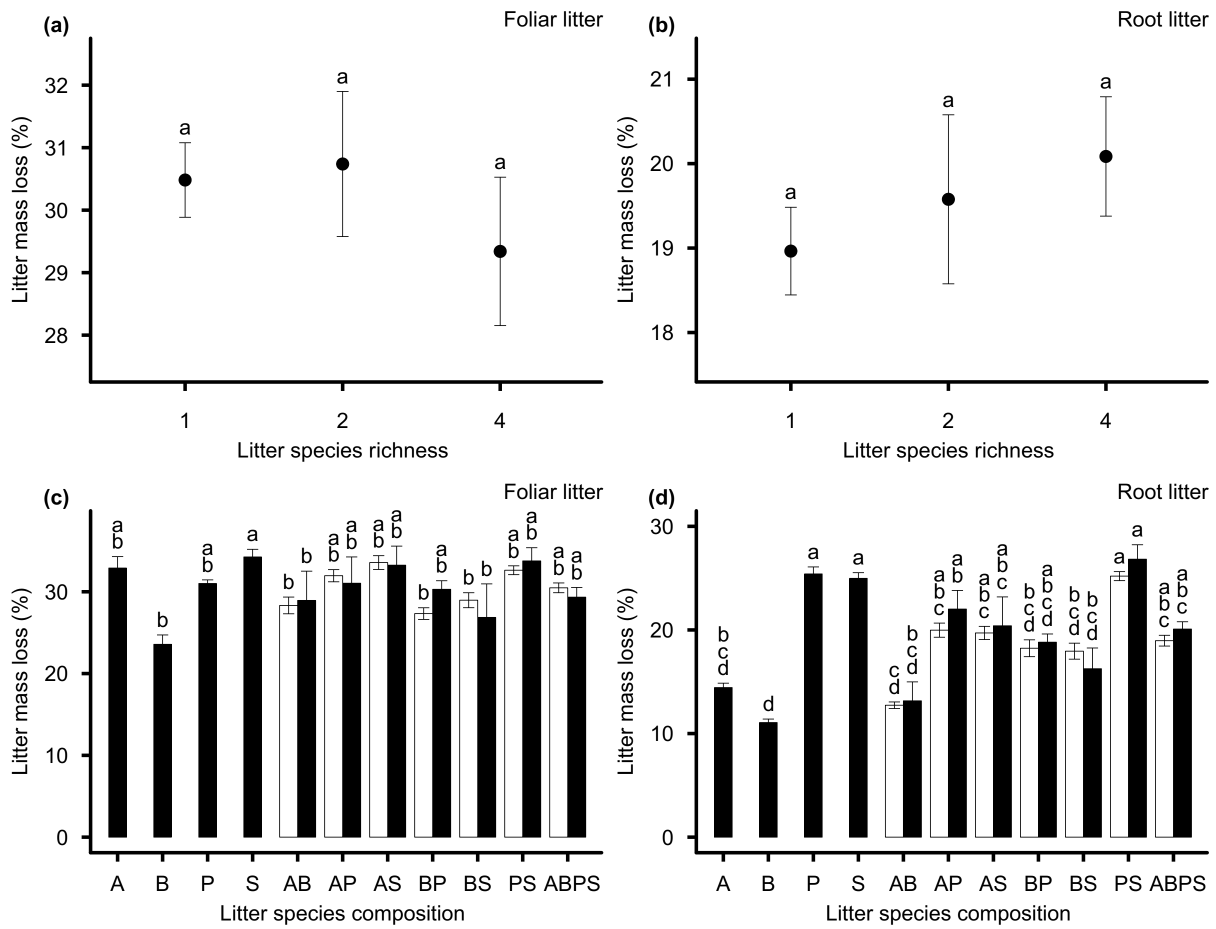

Figure 2

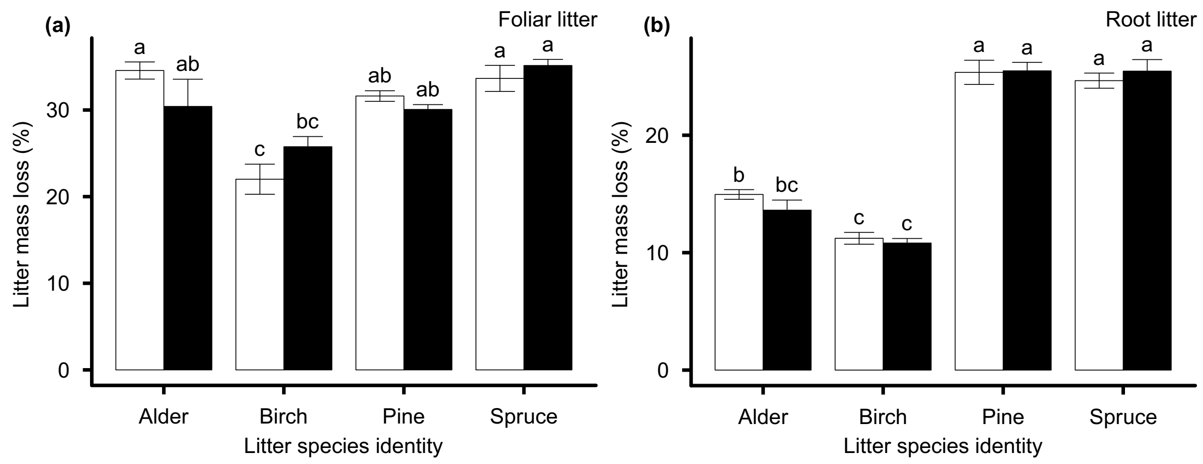

Figure 3

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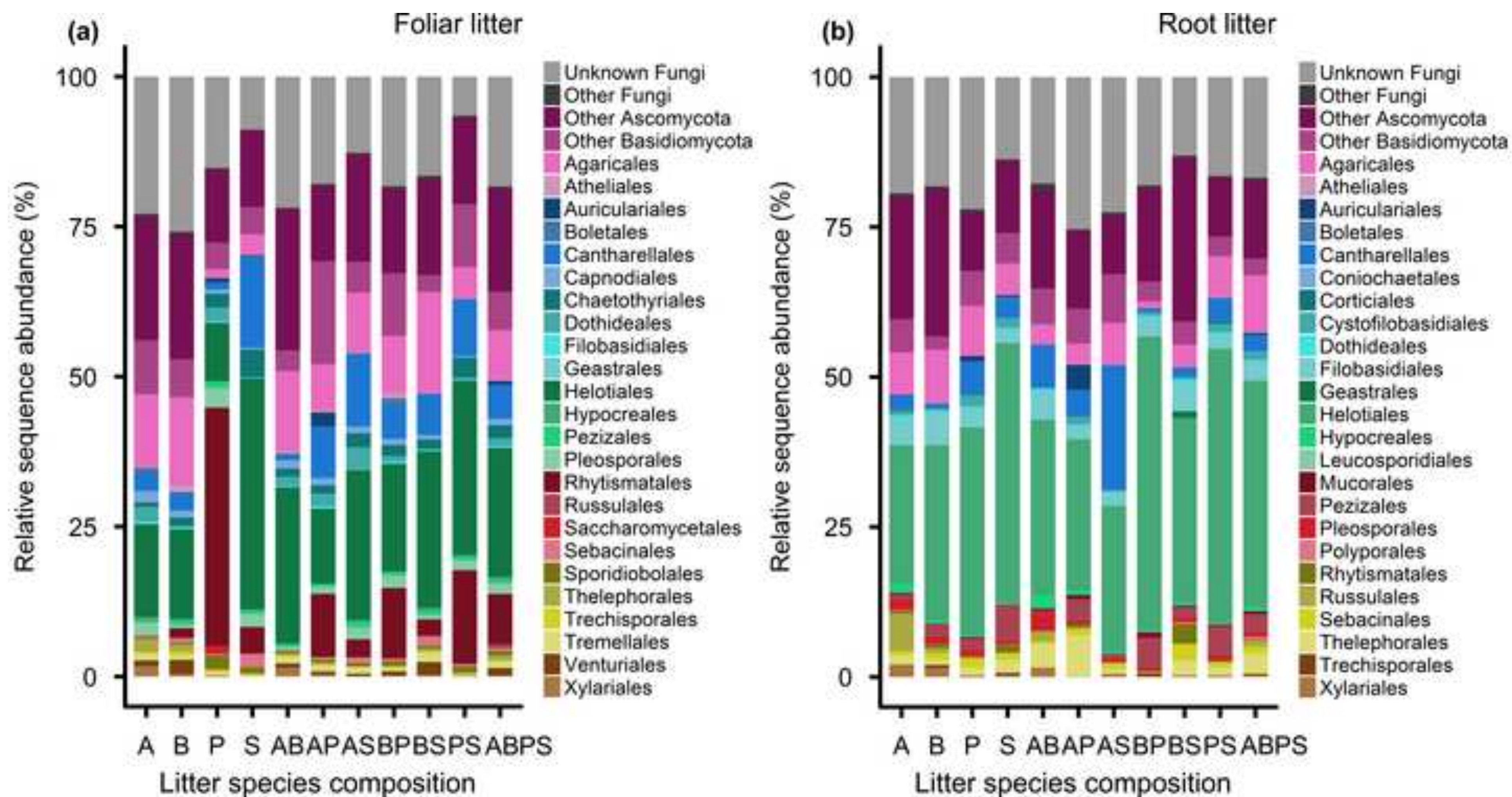

Figure 4

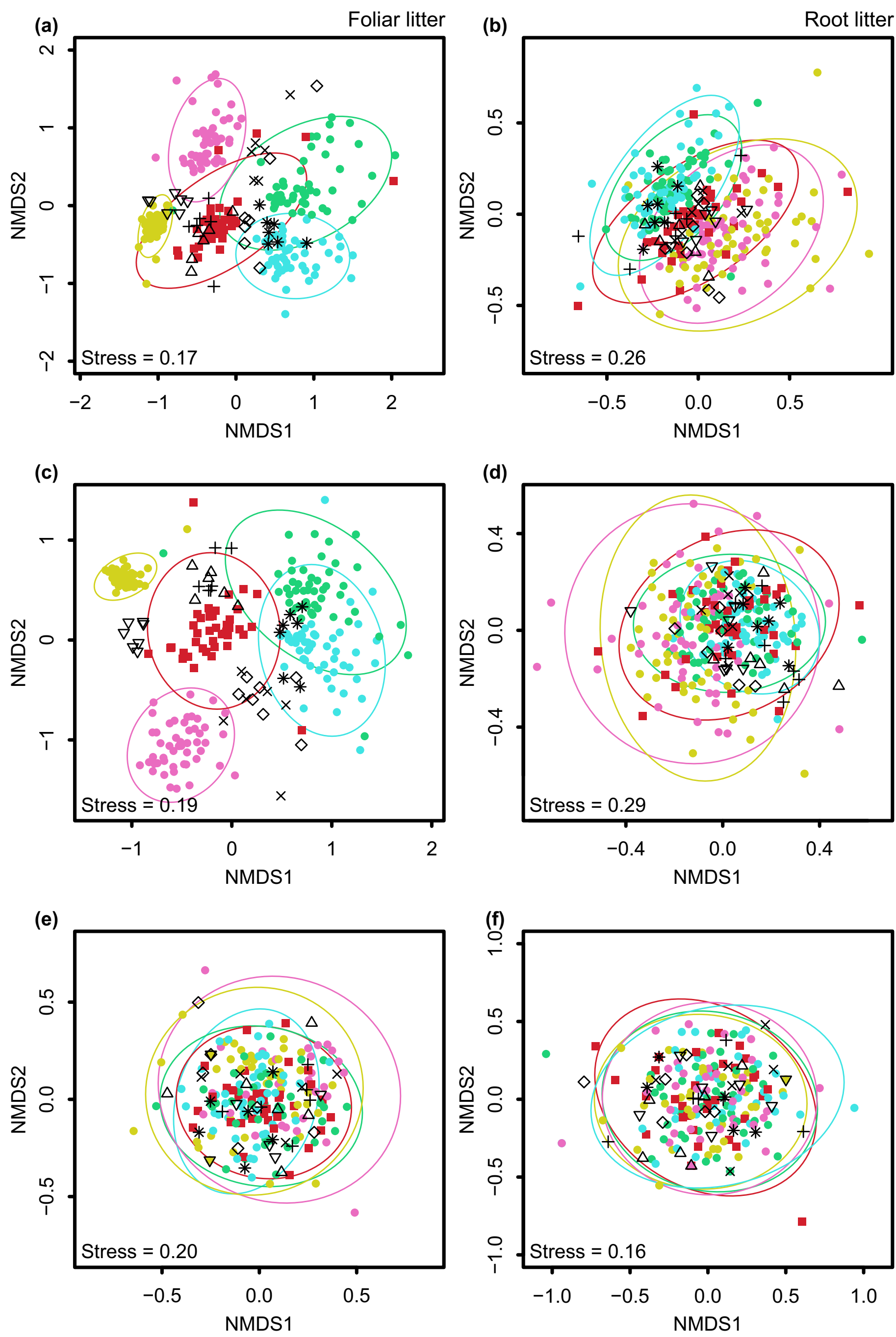

Figure 5