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1 **Opposing effects of plant-community assembly maintain constant**
2 **litter decomposition over grasslands aged from 1 to 25 years**

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14 **Highlights :**

- 15 • Plant-community assembly impacts plant afterlife traits and decomposer communities
16 • Plant-community assembly drives litter decomposition at a given successional stage
17 • Effects of traits and decomposers on decomposition mutually cancel out each other

18 **Short title:** Community assembly drives litter decomposition

19

20 **Corresponding author:** Lou Barbe (+33 6 67 44 06 56)

21 **Authors' contributions:** All authors contributed to the conception of the experiment and the data
22 collection. LB analyzed the data, with help of AP, CM and VJ. LB wrote the manuscript, with help of
23 all authors.

24

25 **SUMMARY**

26 Litter decomposition is central to ecosystem functioning and depends, under constant abiotic
27 conditions, on litter quality and decomposer activity. During the assembly of a plant
28 community following disturbance, litter quality is expected to decrease, due to an increasing
29 proportion of resource-conservative species, whereas decomposer activity is expected to
30 increase, due to the establishment of decomposer populations and their response to local
31 vegetation ("Home-Field Advantage", HFA). To date, the combined effect of these processes
32 remains poorly understood. We studied 27 semi-natural grasslands in western France, ranging
33 from 1 to 25 years since last cultivation. We measured the functional composition of plant
34 communities using litter traits (Specific Leaf Area, Leaf Dry Matter Content, C:N ratio,
35 phenolics), characterized the entire community of decomposers (macrofauna, mesofauna,
36 microbes) and performed reciprocal litter transplants to quantify HFA. We found that, overall,
37 decomposition was rapid, and HFA was not evident. While there was substantial among-
38 grassland variation in decomposition and HFA, neither changed with grassland age. Litter
39 quality and decomposer efficiency also remained, overall, unchanged. However, grassland
40 age determined all measured litter traits, and caused soil microbial C:N ratio to decline. While
41 these changes impacted decomposition individually, together they cancelled out each other,
42 resulting in constant decomposition across the chronosequence. Our results suggest that
43 processes driving decomposition differ during grassland succession, and suggest that HFA
44 may be lower in communities with high litter quality. Moreover, simultaneous assembly
45 processes have opposing, and therefore stabilizing effects on decomposition, possibly
46 explaining the outstanding resilience of primary production in temperate grassland
47 ecosystems.

48 *Key-words:* plant-community assembly, decomposers and detritivores, Home-Field
49 Advantage, grasslands, litter decomposition, plant functional traits

50 INTRODUCTION

51 The decomposition of plant litter is one of the main bottlenecks regulating carbon storage and
52 nutrient cycling in terrestrial ecosystems (Swift and others 1979). Under a given set of abiotic
53 conditions, litter decomposition is controlled by two main biotic parameters and their
54 interaction (Coûteaux and others 1995): litter quality (Cornelissen and others 1999;
55 Makkonen and others 2012), decomposer community (Petersen and Luxton 1982; Bardgett
56 and van der Putten 2014), and response of decomposers to local litter quality (Austin and
57 others 2014; Veen and others 2015). These biotic factors contribute to differences in
58 decomposition among biomes, and among successional stages (e.g., grassland versus forest),
59 however, it remains unclear whether and how they operate during the assembly of a given
60 successional stage. Grasslands are the most widespread successional stage of temperate
61 terrestrial biomes, and the largest terrestrial ecosystems in the globe. Although the
62 successional stage of grasslands is maintained by agricultural practices (grazing or mowing),
63 community assembly processes still operate, from young, species-poor grasslands dominated
64 by the sown species to old grasslands dominated by spontaneous species (i.e. grassland
65 succession, Cramer and others 2008). In grasslands, between 50 and 90% of plant primary
66 production ends up as litter (Cebrian 1999). In contrast to temperate forest ecosystems, the
67 production of litter in temperate grasslands may be sustained through the year, due to
68 continuous growth and senescence of graminoid species. Consequently, litter decomposition
69 is a central ecosystem process in natural and semi-natural grasslands, providing many
70 ecosystem services, including nutrient mineralization for plant regrowth.

71 Throughout the assembly of a grassland plant community, litter decomposition might
72 decrease, due to decreasing litter quality of plant species. Litter quality is determined by the
73 digestibility and the nutritional quality of litter for decomposers, which depends on functional
74 traits of plants (Cornelissen and Thompson 1997). For instance, litter quality decreases with

75 high phenol content or high C:N ratio (Hättenschwiler and Vitousek 2000; Quested and others
76 2007; Bakker and others 2011). Along a succession sequence, these functional traits are likely
77 to differ among successional stages, because traits are involved in plant-plant interactions and
78 community assembly (Hättenschwiler and Vitousek 2000; Garnier and others 2004; Violle
79 and others 2009; Barbe and others 2017). Specifically, resource-conservative traits, which
80 cause litter quality to decline (for instance, high C:N or high leaf dry matter content [LDMC])
81 may only be expressed in late-succession stages, where plant species are already established
82 and competition is high (Wright and others 2004). During the community assembly of a given
83 successional stage, similar mechanisms might occur and plant species present in older
84 communities might display resource-conservative traits rather than resource-acquisitive traits.
85 These dynamics could result in litter quality, and hence litter decomposition, decreasing with
86 grassland community assembly.

87 The abundance of grassland detritivores and decomposers and their ability to decompose local
88 litter might increase with time because of processes such as adaptation, plasticity, or
89 ecological sorting, thereby increasing litter decomposition. Both detritivore macrofauna
90 (earthworms) and mesofauna (Collembola, Acari and Enchytraeidae) fragment litter,
91 accelerating the mineralization and respiration of carbohydrates by fungi and bacteria
92 (Petersen and Luxton 1982; Coûteaux and others 1995; Bardgett and van der Putten 2014).
93 Many decomposers are largely immobile and have slow population growth rates. At the onset
94 of grassland community assembly, low decomposer abundance might limit litter
95 decomposition, because grasslands might inherit few decomposers from prior land use: the
96 abundance of detritivores and decomposers decreases considerably in row-crop agriculture,
97 which is considered a major anthropogenic disturbance (Ponge and others 2003, 2013;
98 Chauvat and others 2007). Consequently, time might be required to recover decomposer
99 populations, from the same patch or from adjacent patches (Decaëns and others 2008).

100 Moreover, decomposer communities are able to adapt to locally-derived litter: the
101 communities sometimes break down litter more efficiently from "Home" compared to other
102 places, with this phenomenon being called Home-Field Advantage (HFA, Freschet and others
103 2012; Austin and others 2014; Veen and others 2015). This phenomenon occurs due to
104 species sorting or selecting particular genotypes, which increase the decomposition rate of a
105 particular type of litter through time. However, there is mixed evidence about the consistency
106 and prevalence of HFA (Giebelmann and others 2011; Veen and others 2015). Of note, the
107 response of decomposers to litter quality may have a lag time, depending on particular litter
108 traits or decomposer assemblages, and might more likely to occur in plant communities with
109 low litter quality (Milcu and Manning 2011; Veen and others 2018). Overall, the net effect of
110 changes to decomposer abundance and response to litter quality might therefore depend on the
111 duration of the assembly of grassland plant community, and might increase litter
112 decomposition in old grasslands, counteracting the effects of changes to litter quality.

113 In this study, we investigated how litter traits, decomposer community, and their interactions
114 affect litter decomposition during community assembly using semi-natural grasslands as a
115 model system. We used a 25-years grassland chronosequence to test whether and how litter
116 decomposition changes with grassland age. Specifically, we tested the following hypotheses:
117 (i) grassland age slows down litter decomposition because litter quality declines and, (ii)
118 grassland age accelerates litter decomposition because decomposer abundance increases or
119 HFA emerges or increases. The chronosequence consisted of 27 grasslands in an agricultural
120 landscape in western France (Brittany), ranging from 1 to 25 years since the last crop. We
121 measured four functional traits aggregated at the plant community level; namely, specific leaf
122 area (SLA), LDMC, C:N ratio, and phenolic concentration. We characterized the entire
123 decomposer community (macrofauna, mesofauna and microbes). We performed a reciprocal

124 litter transplant experiment, to quantify the response of decomposer communities to local
125 litter quality (HFA).

126 **MATERIALS AND METHODS**

127 *Study Site and Grassland Selection*

128 We carried out the study at the Long Term Ecological Site (LTER) «*Zone Atelier*
129 *Armorique* », which is a 150 km² research area in Brittany, France (48°36'N, 1°32'W). Row
130 crops and pastureland cover approximately 90% of the landscape, which is intersected by a
131 well-developed hedgerow network ranging from 50 to 100 m.ha⁻¹ (Thomas and others 2016).
132 We used ground-truthed aerial photos, which were taken every year since 1990, to construct a
133 detailed land-use history for all sites, allowing us to determine the time since cultivation for
134 each grassland precisely. Based on this land-use history and verification with grassland
135 owners, we selected 27 grasslands ranging from one to 25 years since last row cropping. The
136 grasslands were similar with respect to the initial species that were sown (*Lolium perenne* (L.)
137 and *Trifolium repens* or *pratensis*) and management practices (annual mowing and extensive
138 grazing, approximately 60 cows for two days once per month). The grasslands were also
139 similar regarding environmental conditions (mesophilic grasslands) and the type of soil
140 (brown soil that drained freely with well-developed organic and mineral horizons). The total
141 soil C:N ratio of parcels, measured on the top 15 cm of parcels with a 20 cm diameter
142 stainless steel hand corer, was 13.4 ± 1.7 . Parcels were $3 \text{ ha} \pm 1.4 \text{ ha}$.

143 *Characterization of Plant Community and Plant Functional Traits*

144 We characterized the percentage coverage of plant species in each grassland during spring
145 2015 using 10 quadrats of 1m² that were evenly distributed within the grassland. We
146 identified the most abundant species (*i.e.* species accounting for 80% of the total abundance of
147 the community; Pakeman and Quested 2007), which represented from two to five species for

148 each grassland (total richness from 8 to 27). For these species, we measured four functional
149 traits related to litter quality; namely, specific leaf area (SLA), leaf dry matter content
150 (LDMC), leaf C:N ratio and leaf phenolic concentration. These traits mainly reflect the
151 physical and chemical properties of the litter (Hättenschwiler and Vitousek 2000; Pérez-
152 Harguindeguy and others 2000; Santiago 2007; Quested and others 2007). To obtain a
153 representative mean value for each trait from each species, we measured the traits of 10
154 individuals that were collected from randomly selected grasslands in our experiment. Phenolic
155 concentration was measured colorimetrically, according to the Folin-Ciocalteu colorimetric
156 method (Folin and Denis 1915) modified by Santonja and others (2015), using gallic acid as a
157 standard. A 0.25 g litter sample was dissolved in an aqueous methanol solution, that was
158 shaken for 1-h and then filtered. The filtered extract was mixed with Folin-Ciocalteu reagent,
159 a color-reaction stabilizer (Na_2CO_3), and distilled water. After 1-h, phenolics concentration
160 was measured at 765 nm on a spectrophotometer (Thermo Scientific[®], USA). We measured
161 SLA and LDMC following the standard protocols of Pérez-Harguindeguy and others (2013),
162 and we measured C:N ratio using an elemental analyzer (FLASH EA 1112 Thermo Finnigan,
163 Waltham, Massachusetts, USA). For each grassland, we aggregated the values of species
164 traits to obtain an abundance-weighted mean for each trait (see Appendix Table S1 for species
165 trait values). Correlations between traits (Appendix Table S2), with only two significant
166 correlations being detected among the six trait correlations that we tested for, indicates low
167 multicollinearity among traits.

168 *Characterization of the Decomposer Community*

169 We sampled detritivore macrofauna (*i.e.* earthworms) in each grassland during spring 2016,
170 according to the method of Ponge and others (2013) and Cluzeau and others (2012). In brief,
171 three 1x1m quadrats were watered three times with 10 l formalin at increasing concentration
172 every 15 min (0.075, 0.075 and 0.12% formaldehyde solution), and a soil block (25x25cm and

173 20cm depth) was extracted at the end of sampling and hand sorted. Earthworms that were
174 expelled to the surface by the irritant solution, or were recovered during the sorting of the soil
175 block, were collected. Identification was done in the laboratory following the identification
176 key of Cluzeau and others (unpublished, available upon request), based on Bouché (1972).
177 Earthworms were characterized by abundance and biomass (fresh weight) and were grouped
178 into ecological categories: epigeic or anecic – we excluded endogeic earthworms as they do
179 not directly influence decomposition of surface litter (Bouché 1977). Then, we sampled soil
180 detritivore mesofauna using a cylindrical soil corer (5 cm diameter × 8 cm depth; three soil
181 cores per grassland on two sampling dates). Mesofauna was extracted from the soil cores
182 using the Tullgren funnel method (Berlese 1905) over a 10-day period. Collected organisms
183 were stored in 95% ethanol, counted using a binocular scope and separated into three groups:
184 Acari (Oribatids), Collembola and Enchytraeidae. Finally, we measured soil microbial C:N
185 ratio, as a proxy of the composition of the microbial community, illustrating dominance of
186 fungi or dominance of bacteria (Paul and Clark 1996; Van Elsas and others 2006). We
187 measured the microbial C:N ratio using the fumigation-extraction method from Brookes and
188 others (1985) and Vance and others (1987). We collected and aggregated 15 soil cores from
189 the top 10 cm layer for each grassland to obtain a representative soil sample. From this
190 sample, we used a 30 g soil sample that was passed through a 2-mm sieve, and was then hand-
191 sorted to remove any visible organic material (plant roots, litter fragments). Before and after
192 fumigation-extraction, we measured microbial C concentration using a Wet Oxidation Total
193 Carbon Analyzer 1010 (OI-Analytical, USA) and microbial N concentration using a
194 continuous flux AutoAnalyzer (measuring total dissolved N, AA3 Bran & Luebbe, USA). The
195 microbial C and N concentrations were obtained by subtracting the values obtained before
196 fumigation-extraction from the values obtained after. Microbial C:N ratio was then calculated
197 by dividing microbial C concentration with microbial N concentration.

198 *Abiotic Parameters and Local Landscape and Management*

199 Abiotic parameters such as soil moisture and soil pH can also affect plant traits, decomposer
200 community and litter decomposition (Coûteaux and others 1995). Thus, we quantified soil
201 moisture and pH in each grassland during spring 2016 using soil samples from the top 15 cm
202 layer collected with a 20 cm diameter stainless steel hand corer. After the manual removal of
203 rocks and roots > 2 mm, soil moisture (ω) was determined by mass loss at 105°C for 24 h
204 according to the formula: $\omega = \frac{(W-D)}{D} \times 100$, where W is the wet soil mass on the sampling
205 date and D is the dry soil mass. Soil pH was determined with a 1:10 soil, de-ionized water
206 suspension, following standard methods (Robertson and others 1999). We also accounted for
207 the local landscape surrounding the selected grasslands, which might influence plant traits and
208 decomposer community. Using the database of historical land-use data, we quantified the
209 percentage of each grassland perimeter that was in contact with grasslands older than 5 years,
210 which are adjacent grasslands that represent a significant source of propagules and fauna for
211 the selected grasslands.

212 *Litter Decomposition and Transplant Experiment*

213 In each grassland, we collected litter in the fall of 2015 for the 2–5 species accounting for
214 80% of total plant abundance. We did not collect stems. For all species, we collected green
215 material for litter as in semi-natural grasslands the main portion of plant material contributing
216 to the litter pool is green material, not senesced litter (due to mowing and grazing, Mazzanti
217 and others 1994; Sanaullah and others 2010). The duration of leaf decomposition is very short
218 for the main grassland species in our experiment (especially *Lolium perenne* and legumes
219 from the genera *Trifolium*, see Results for mass losses) such their leaves decompose before
220 achieving complete senescence. Litter was cleaned, air-dried, and placed into 8x8 cm mesh
221 bags. Litterbags had 2 mm mesh on the upper side to avoid contamination by allochthonous

222 litter, and 5 mm mesh on the lower side to allow numerous detritivores to shuttle between the
 223 soil and litter to freely access the litter – during the period of exposure. Litter always
 224 remained moist and was never brittle. Litterbags were positioned on bare ground by gently
 225 pushing aside grasses (*i.e.* without removing any plants). Each litterbag contained 1g of litter,
 226 that was oven-dried equivalent (air-dry/oven-dry ratio calculated from subsamples that were
 227 oven-dried but not exposed to decomposition), and were constructed with the relative
 228 proportion of species from the grassland. We constructed 15 litterbags for each grassland, five
 229 of which were placed in the original grassland (“Home” decomposition) and 10 of which we
 230 randomly placed in 10 other grasslands of the experiment (“Away” decomposition) to
 231 measure HFA. We performed decomposition experiments during early spring 2016 and
 232 litterbags were collected 10 days later, when they reached 30-60% mass loss. Mass loss was
 233 measured on all 15 samples per grassland after cleaning the litter, and were oven-dried at 65
 234 °C for three days. Mass loss (%) was calculated as $(1 - \frac{m_1}{m_0}) \times 100$, where m_0 is the initial
 235 oven-dried equivalent dry weight and m_1 is the oven-dry weight at collection.

236 We calculated HFA, litter quality and soil ability (*i.e.* abiotic conditions and decomposer
 237 efficiency) for each grassland by running the Decomposer Ability Regression Test (Keiser
 238 and others 2014) using SAS University Edition (SAS Institute, Cary, NC). This analysis
 239 disentangles, for a given mass loss, the effects of HFA, litter quality, and soil ability,
 240 estimated respectively by the parameters η_h , β_l and γ_s in the following equation:

$$Y_i = \alpha + \sum_{l=1}^N \beta_l \text{Litter}_{l_i} + \sum_{s=1}^M \gamma_s \text{Soil}_{s_i} + \sum_{h=1}^K \eta_h \text{Home}_{h_i} + \varepsilon_i$$

242 where Y_i is the decomposition of observation i , and Litter_l , Soil_s , and Home_h are dummy
 243 variables that equal 1 or 0, respectively, depending on the presence or absence of the litter
 244 mixture (from the litter mixture 1 to N), soil community (from soil community 1 to M) and

245 home combination (from home combinations 1 to K). The average decomposition in the data
 246 set is α (*i.e.* the intercept of the model) and ε is the error term. β_1 and γ_s were restricted to
 247 prevent perfect collinearity. The value of a given parameter that was estimated (η_h , β_1 and γ_s)
 248 indicated, as a single percentage per grassland, the difference to the mean decomposition of
 249 the dataset due to this parameter. These single parameters per grassland will be further
 250 correlated with grassland age, because there is no variation of age within grasslands.

251 To explore whether and how HFA is driven by litter traits and detritivore and decomposer
 252 descriptors, we calculated the HFA for the five “Home” replicates of each grassland, because
 253 plant traits vary within grasslands (similar to Veen and others 2018). We used the following
 254 equations (Giebelmann and others 2011, Pérez and others 2013):

255 (1) $HFA_{a1} = HDD_{a1} - ADD_a - H$

256 (2) $HDD_{a1} = \sum(D_{a1a} - D_{ia})$

257 (3) $ADD_a = \sum(D_{ai} - D_{ii})$

258 (4) $H = \sum HDD / (n - 1)$

259 HFA_{a1} represents the Home-Field Advantage for litter replicate 1 of grassland a. Positive
 260 values indicated, as a percentage, faster home decomposition than expected, while negative
 261 values indicated slower home decomposition than expected. HDD_{a1} represents the Home
 262 Decomposition Difference for litter replicate 1 from grassland a. This value was the sum of
 263 the differences between the decomposition of this litter in its original grassland a (D_{a1a}) and
 264 the decomposition in this grassland of litters from other grasslands i (D_{ia}). ADD_a represents
 265 the Away Decomposition Difference for grassland a. This value was the sum of the
 266 differences between the decomposition of litter from grassland a in other grasslands i and the
 267 home decomposition of grasslands i. H represents the sum of all HDD for all litters divided by
 268 amount of litters minus one. Overall, we quantified HFA per litter bag, as established in the

269 literature (see above), however, we stress that quantification per grassland (*i.e.* using means)
270 led to very similar results and are hence not presented.

271 To explore the role of litter traits and decomposer community on litter decomposition *per se*,
272 we calculated three mass loss values for each grassland, by averaging mass loss within the
273 three treatment types: home litter at home, home litter away, and away litter at home. This
274 approach allowed us to test for the numerous effects of plant traits and decomposer
275 communities, that may vary within a grassland (similar to Veen *et al.* 2018). Analyses based
276 on all values within grasslands led to the same conclusions (except that explained variance
277 was slightly smaller and *P*-values were even more significant, due to the larger sample) and
278 are therefore not presented.

279 *Statistical Analyses*

280 Before all the statistical tests, we center-scaled all variables (*i.e.* transformed variables by
281 subtracting their mean and dividing by their standard deviation) to permit comparisons of
282 regression coefficients within and among models. We used multiple ordinary least square
283 (OLS) regression models to test the effect of grassland age on plant functional traits (SLA,
284 LDMC, C:N ratio, phenolics) and decomposer community (soil microbial C:N ratio,
285 abundance and biomass of epigeic earthworms and anecic earthworms, and abundance of
286 Acari, Collembola and Enchytraeidae), accounting for abiotic parameters and local landscape
287 (soil moisture, soil pH and percentage of adjacent grasslands). We used simple OLS
288 regression models to test the effect of grassland age on HFA, soil ability, litter quality, and
289 litter mass loss. We used multiple OLS regression models to test the effect of plant functional
290 traits and decomposer community on litter mass loss and HFA (as calculated in Gießelmann
291 and others 2011, Pérez and others 2013) also accounting for abiotic parameters, local
292 landscape and grassland age. Of note, in the model explaining mass loss we also included the

293 transplantation treatment (home litter at home, home litter away, away litter at home),
294 however, this factor was not significant and we do not present the results. To summarize the
295 results of the individual regression analyses, we conducted a path analysis (Wright 1934),
296 which allowed us to visualize the strength of the indirect effects of grassland age on litter
297 mass loss and HFA, which were effects mediated by plant functional traits and decomposer
298 community. For each indirect effect, we calculated a compound path by multiplying: (i) the
299 standardized regression coefficient from the model that related grassland age to plant
300 functional traits or decomposer community with (ii) the standardized regression coefficient
301 from the model that related plant functional traits or decomposer community to litter mass
302 loss. Finally, we compared, for litter mass loss and HFA, the sum of the indirect effects of
303 grassland age with the single overall effect of grassland age. We graphically examined
304 residuals using probability plots and predicted versus residual plots, indicating that all residual
305 distributions fulfilled the assumption of normality and homogeneity. All statistical analyses
306 were performed with R 3.0.3 (R Development Core Team 2016).

307 **RESULTS**

308 *Plant Functional Traits and Decomposer Community Depend on Grassland Age*

309 We observed large differences in the functional traits of the plant community and in the
310 composition of the decomposer community among entire grasslands. Grassland age strongly
311 explained all functional traits of the plant community (simple regression analyses, Figure 1).
312 Specifically, age increased leaf C:N ratio ($F_{18}=11.07$, $P=7.10^{-4}$, $\text{adj-R}^2=0.50$), leaf phenolic
313 concentration ($F_{18}=4.19$, $P=0.03$, $\text{adj-R}^2=0.24$), and SLA ($F_{19}=3.71$, $P=0.04$, $R^2=0.20$), while
314 it decreased LDMC ($F_{25}=31.64$, $P=7.10^{-6}$, $\text{adj-R}^2=0.52$). Old grasslands hence harbored a
315 plant community with mainly thin, moist leaves; however, these leaves contained lower
316 nitrogen concentration and higher phenolic content. Grassland age also increased soil

317 microbial C:N ratio ($F_{20}=5.32$, $P=0.03$, $R^2=0.17$, Figure 1), as well as the abundance of Acari
318 ($F_{23}=9.20$, $P=6.10^{-3}$, $R^2=0.25$, Figure 1). Earthworm abundance, as well as the abundance of
319 Collembola and Enchytraeidae, was not associated with grassland age; however, the
320 percentage of adjacent grasslands increased the abundance of anecic earthworms (Figure S1).
321 Despite multiple relationships between age and either litter traits or decomposer community,
322 we found one significant correlation between litter traits and detritivore and decomposer
323 community (Acari vs LDMC, $r=-0.54$, $P<0.05$, see Table S2).

324 *Litter Decomposition and Home-Field Advantage Differ Among Grasslands and Depend on*
325 *Plant Functional Traits and the Decomposer Community*

326 We observed large among-grassland differences in litter mass loss and HFA (Figure S2).
327 Overall, across all of the litters in our experiment, we did not observe a positive mean HFA
328 (no significant difference from a mean of 0, $t=1.41$, $df=133$, $P=0.16$). Grassland age did not
329 directly influence litter mass loss ($F_{25}=0.29$, $P=0.60$, Figure 2), HFA ($F_{25}=0.41$, $P=0.53$,
330 Figure 2), soil ability ($F_{25}=0.71$, $P=0.41$, Figure 2) nor litter quality ($F_{25}=0.22$, $P=0.4$, Figure
331 2). However, several plant functional traits and the soil microbial C:N ratio, related to
332 grassland age, strongly explained litter mass loss ($F_{56}=12.43$, $P=7.10^{-9}$, $adj-R^2=0.53$, Figure
333 3): the leaf C:N ratio decreased litter mass loss, as did LDMC and SLA (Figure 3). Decrease
334 in soil microbial C:N was associated with decrease in litter mass loss (Figure 3). Moreover,
335 soil moisture decreased litter mass loss (Figure S3). None of the plant functional traits
336 influenced HFA, but HFA increased when anecic earthworms were more abundant (Figure
337 S1, $F_{101}=6.37$, $P=0.044$, semi-partial $R^2=0.06$) and when soil moisture was low (Figure S3,
338 $F_{101}=6.37$, $P=0.013$, semi-partial $R^2=0.03$). We also note that, when explaining litter mass
339 loss by functional traits and decomposer community, a positive, direct effect of grassland age
340 on litter mass loss was detected after removal of all other significant effects (Figure S4).
341 Finally, as plant functional traits and soil microbial C:N were influenced by grassland age, we

342 obtained the following indirect effects of grassland age on litter mass loss (Figure S4): -0.42
343 via leaf C:N ratio, -0.26 via SLA, 0.53 via LDMC, -0.15 via the soil microbial C:N ratio and
344 0.22 via an unmeasured parameter. The sum of all indirect effects of grassland age on litter
345 mass loss was -0.08, indicating no significant total effect, which was consistent with the lack
346 of an overall effect of grassland age on litter mass loss that we initially observed (Figure 2).

347 **DISCUSSION**

348 Grassland age influenced all measured functional traits of the plant community, as well as the
349 soil microbial C:N ratio. These changes, in turn, impacted litter mass loss, but they cancelled
350 each other out, resulting in constant litter decomposition across the chronosequence. Litter
351 overall mass loss, litter quality (*i.e.* litter decomposability), decomposer efficiency, and HFA
352 did not change with grassland age.

353 *Plant Functional Traits Change with Age, but not towards Resource-Conservatism*

354 The four functional traits that we measured on plant communities strongly responded to
355 grassland age. Specifically, the plant communities of old grasslands displayed a higher leaf
356 C:N ratio and phenolic concentration, along with higher SLA and lower LDMC. Thus,
357 grassland assembly favored resource-conservative trait values as much as resource-acquisitive
358 trait values. This result contrasted with what we expected from other studies (Wright and
359 others 2004; Quested and others 2007). These changes in functional traits were probably due
360 to plant turnover during grassland assembly, with new species establishing and dominating
361 initial species that had higher C:N and phenolic concentration (for instance, *Ranunculus*
362 *repens* or *Dactylis glomerata*, Figure S5). These characteristics might enhance the resistance
363 of these new species against herbivores (Bernays and others 1989). Moreover, high SLA and
364 low LDMC might facilitate high resource acquisition and hence regrowth to compensate for
365 herbivory (Briske 1996). This observed plant succession during grassland assembly might be

366 attributed to the immigration of new plant species from the surrounding landscape or by the
367 germination of seeds already present in the soil seed bank. Overall, these results show that
368 shifts to plant afterlife traits arise during the assembly of a successional stage (*i.e.* grasslands),
369 not only across successional stages, for example after grassland abandonment (Kahmen and
370 Poschlod 2004; Quested and others 2007).

371 *Offsetting Effects of Plant Traits on Litter Decomposition*

372 Individually, each of these changes to plant traits (except changes to phenolics) influenced
373 litter decomposition, but they did not reduce litter decomposition, which remained unchanged
374 with grassland age overall: an increase in SLA and C:N ratio decreased litter decomposition,
375 but this was compensated by a decrease in LDMC which increased litter decomposition.
376 While the effects of the C:N ratio and LDMC are consistent with the literature (Bakker and
377 others 2011; Pakeman and others 2011), the negative effect of SLA on mass loss was
378 inconsistent with the literature (Santiago 2007; Makkonen and others 2012). However, studies
379 on SLA usually focus on SLA values distinctly smaller than ours. This negative relationship
380 might be explained by the higher compaction of litter with very thin leaves (*i.e.* high SLA),
381 slowing down the colonization of litters by detritivores and decomposers. Alternatively,
382 compensatory feeding (*i.e.* enhanced consumption rate on poor-quality litter to ensure
383 sufficient resource assimilation to meet metabolic needs; Gessner and others 2010) on litter
384 with low SLA might also explain the negative effect of SLA on mass loss. Finally, the lack of
385 influence of leaf phenolic concentration on decomposition was possibly due to the lower leaf
386 phenolic concentration of grassland plants compared to other systems (Hättenschwiler and
387 Vitousek 2000) which might have prevented the effects from being detectable. Taken
388 together, our results suggest, contrary to what we expected, that community assembly
389 processes result in similar litter quality during grassland succession, likely due to
390 compensatory effects on afterlife traits and litter quality.

391 *Little Impact of Grassland Age on Detritivores and Decomposers*

392 Only some components of decomposer communities responded to grassland age, partially
393 supporting our predictions. Anecic and epigeic earthworms (macrofauna) did not respond to
394 grassland age; however, the abundance of anecic earthworms increased in grasslands that
395 shared more edges with other grasslands, suggesting the immigration of anecics from the
396 surrounding landscape, consistently with their high dispersal ability (Caro and others 2013).
397 Considering mesofauna and microbes, we observed two shifts: the abundance of Oribatids
398 (Acari, detritivore mesofauna) increased with grassland age, as did the soil microbial C:N
399 ratio. The increase in the abundance of Oribatids might be attributed to the recovery of
400 populations of these soil organisms after land-use turnover and the disruptive agricultural
401 practices before the sowing of grasslands (Hülsmann and Wolters 1998). Recovery might be
402 permitted by the immigration of new species from an adjacent landscape, or by the
403 demographic development of the remaining initial species. Finally, the increase in soil
404 microbial C:N ratio with grassland age might be attributed to a reduction in mineral N input
405 after cropping, ultimately causing the depletion of microbial N (Wardle 1992).

406 *Strong Functional Redundancy of Detritivores and Decomposers in Grassland Ecosystems?*

407 Unexpectedly, the abundance of macrofauna and mesofauna did not influence decomposition
408 (Milcu and others 2008), suggesting that microbial and fungal decomposition were not limited
409 by the fragmentation of leaves. The only decomposer-mediated effect we could identify was
410 the increase in soil microbial C:N ratio that was associated with decreasing litter mass loss.
411 Possibly, high soil microbial C:N also reflected a change in the composition of the microbial
412 community, from a dominance of bacteria to a dominance of fungi (Paul and Clark 1996; Van
413 Elsas and others 2006), which might be less efficient at decomposing labile litter (Santonja
414 and others 2018). This slight, microbial C:N-mediated, decrease in litter mass loss was

415 probably compensated for by a slight increase of litter mass loss due to a statistically direct
416 effect of grassland age in the full model; this effect was necessarily that of age on one or
417 several parameters that we did not measure (and it may be a biologically indirect effect, like
418 the effects of plant traits and decomposers that we observed), and it explains why soil ability,
419 which represents decomposer efficiency and abiotic conditions, remained globally similar
420 among grasslands. Overall, the lack of relationships between detritivores and decomposers
421 with decomposition might be attributed to the high functional redundancy of these groups for
422 decomposing grassland litter (Gessner and others 2010). Despite variation in the abundance of
423 detritivores and decomposers in our grasslands, there was no effect of any particular group on
424 decomposition. Given the high decomposability of litter in grasslands, the effects of
425 detritivores and decomposers on decomposition might be particularly redundant, with this
426 feature being very stable across time.

427 *No Impact of Grassland Age on Home-Field Advantage, Due to High Litter Decomposability?*

428 We found, overall, a low HFA, with a substantial variation across grasslands. We found only
429 one significant relationship between the numerous plant traits and detritivores and
430 decomposers that we sampled, not indicating ecological sorting or abundance shifts of
431 detritivores and decomposers in response to litter traits. Overall, we found no relationship
432 between grassland age and HFA: grassland age did not influence HFA, nor did plant
433 functional traits and soil microbial C:N ratio. Besides, litter decomposition rates were very
434 high in our experiment, resulting from the very high decomposability of the green litter of
435 graminoids and *Trifolium sp.* (Sanaullah and others 2010 for similar decomposition rates).
436 High decomposition also resulted from the humid and relatively warm, frost-free winter in the
437 study region which increases decomposer activity (this rapidity is also illustrated by the
438 absence of a distinct litter layer in the grasslands). Therefore, our results support that strong
439 HFA may only arise when home litter is very recalcitrant or very dissimilar to other litter

440 (Milcu and Manning 2011; Li and others 2017; Lu and others 2017; Palozzi and Lindo 2018;
441 Hoyos-Santillan and others 2018). Only increased abundance of anecic earthworms triggered
442 some HFA. This interesting phenomenon might reflect, for instance, the response of digestive
443 enzymes of anecic earthworms to local litter (Eisenhauer and others 2012): the digestive
444 metabolism of earthworms could acclimate to home litter, and then secrete more enzymes that
445 are adapted to home litter, which would increase digestion and hence litter consumption.
446 Alternatively, in their permanent galleries, the mucus of anecic earthworms might have been a
447 durable, high quality substrate for decomposer microorganisms, giving them time to adapt to
448 local litter, ultimately triggering HFA. Finally, high soil moisture triggered a slight Home-
449 Field Disadvantage. This might be due to waterlogging triggering anoxia in the top soil,
450 decreasing bacterial and fungal activity (thus decreasing mass loss per se) especially in soft,
451 easily hydratable and compactable litters produced within the home environment. Overall,
452 these results show that grassland maturation did not drive HFA, and that HFA might only
453 occur when litter is very recalcitrant or dissimilar, which was not the case in our system.
454 Hence, HFA did not require experience of local decomposers with local plants, but rather
455 environments favorable for macrofauna and aerobic decomposition. Earthworms might have a
456 role in this process, despite being quite generalist organisms, with microbes not being the only
457 biotic drivers of HFA (Freschet and others 2012; Austin and others 2014). Further studies,
458 including the sampling of detritivore and decomposer traits, and including the exclusion of
459 fauna, are required to elucidate the precise role of fauna and microbes on HFA.

460 **CONCLUSIONS**

461 We found that community assembly maintained similar litter decomposition along a 25-years
462 chronosequence, and that HFA was not associated with plant community assembly or age.
463 HFA was quite low and was only associated with the macrofauna community and soil
464 moisture, which were not related to grassland age. However, our results showed that several

465 plant functional traits and the soil microbial C:N ratio changed during community assembly.
466 In turn, these changes acted on decomposition, but cancelled out each other, resulting in the
467 same decomposition rate across succession. These results also suggest that in temperate
468 grassland ecosystems, where decomposition is very fast, numerous and important changes in
469 plant and decomposer communities lead to the same levels of ecosystem functions, possibly
470 explaining the outstanding resilience of many grassland ecosystems despite being often a
471 transitional stage.

472

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658 **Figure captions**

659 **Figure 1.** Grassland age significantly influenced all aggregated functional traits of the plant
660 community (phenolics, leaf C:N ratio, Leaf Dry Matter Content, and Specific Leaf Area) as
661 well as the abundance of soil Acari (mesofauna) and soil microbial C:N ratio. Green points
662 represent plant trait values, orange points represent values of decomposer and detritivore
663 indicators. See Results for all model parameters.

664 **Figure 2.** Grassland age did not influence Home-Field Advantage (HFA), soil ability
665 (illustrating soil conditions and decomposer efficiency), litter quality (*i.e.* litter
666 decomposability) nor litter overall mass loss (calculated as the mean per grassland across all
667 litters). See Material and Methods for the transplantation treatment and calculations.

668 **Figure 3.** Three aggregated functional traits of plant community and soil microbial C:N ratio
669 decreased litter mass loss. Each graph presents partial residuals, so accounts for the
670 simultaneous effect of the other variables in the model. SP-R² represents semi-partial
671 residuals. Green points represent plant trait values, and orange points represent values of
672 decomposer and detritivore indicators. The three data points per grassland are the mean of the
673 three treatments (home litter exposed at home, home litter exposed away, and away litter
674 exposed at home; the factor containing these treatments did not significantly interact with age
675 in the statistical model explaining mass loss). See Material and Methods for the
676 transplantation treatment and calculations, and Results for all model parameters.

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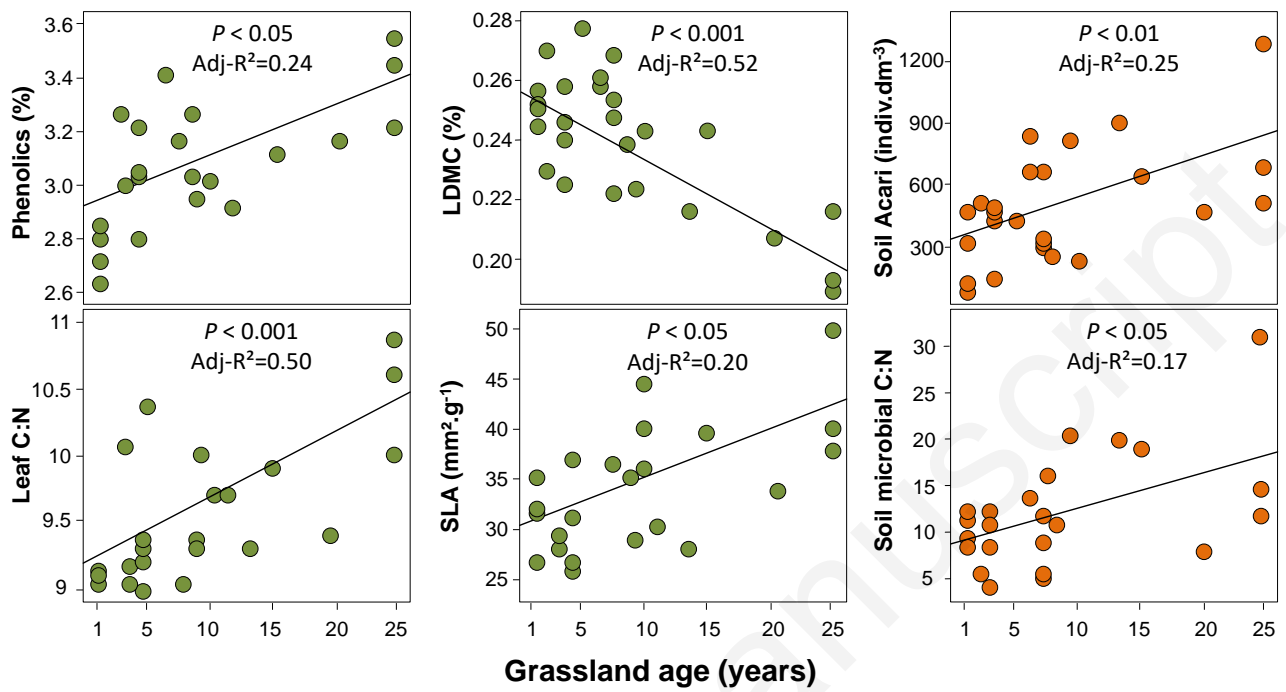
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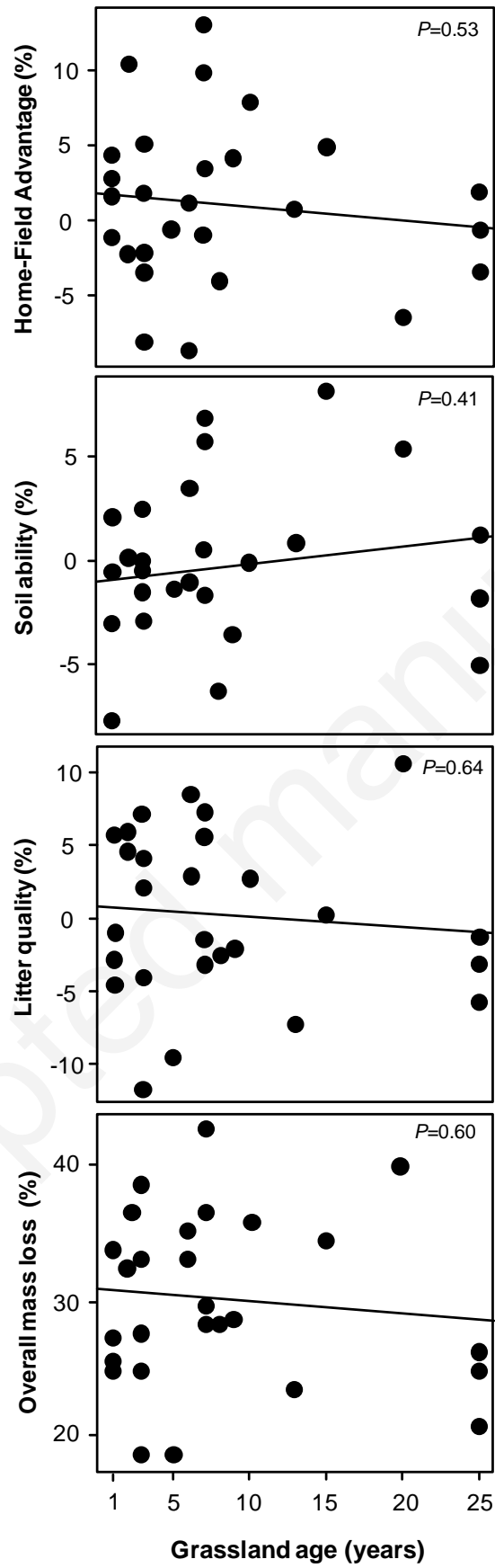
681 **FIGURES**

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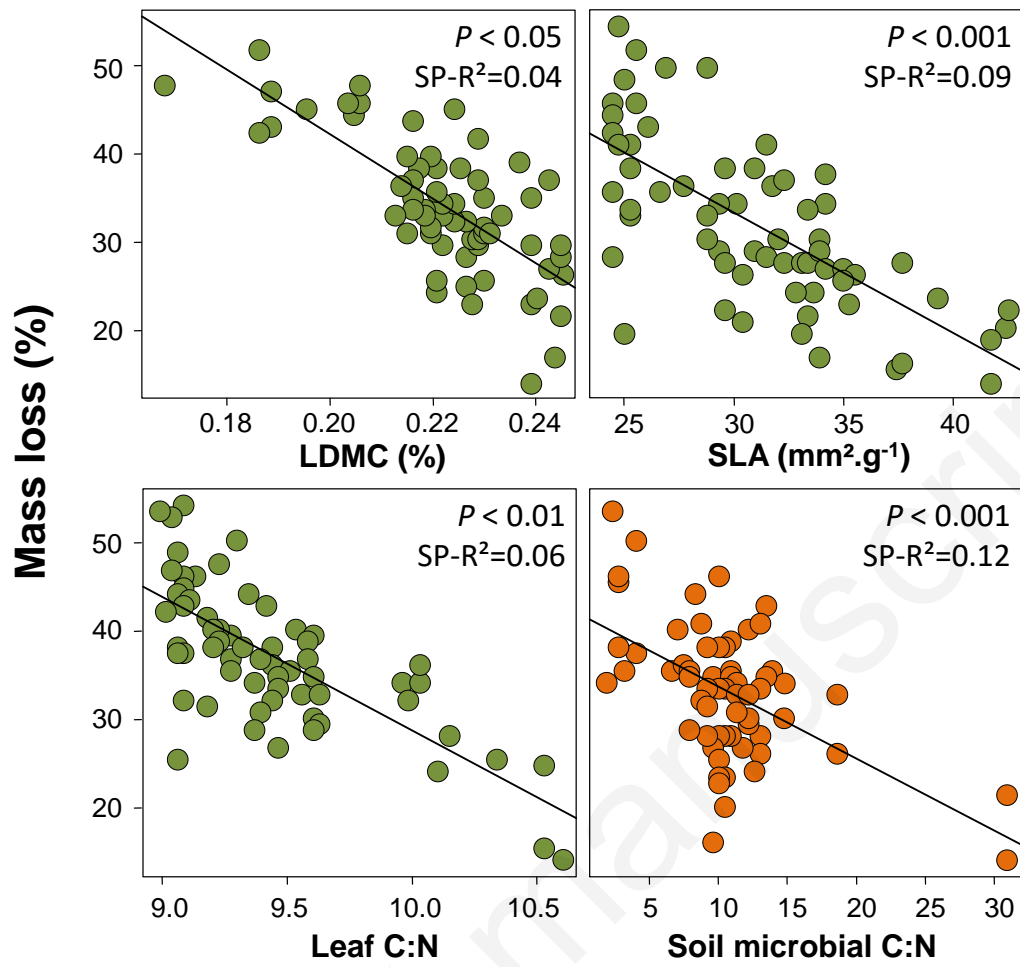
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684 **Figure 1.**



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686 **Figure 2.**



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688 **Figure 3.**

689 **SUPPORTING INFORMATION**

690 **Table S1.** Mean values of functional traits measured on plant species representing 80% of the
 691 grassland communities in our experimental design (see Material and Methods) and that were
 692 accounted for in the decomposition experiment. Phenolics and LDMC (Leaf Dry Matter
 693 Content) are in %, SLA (Specific Leaf Area) is in $\text{mm}^2\cdot\text{g}^{-1}$, and C:N ratio has no unit.

Species	Functional traits							
	Phenolics		C:N ratio		LDMC		SLA	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<i>Agrostis stolonifera</i>	3.32	0.19	10.78	1.35	21.67	2.09	36.22	3.38
<i>Agrostis tenuis</i>	3.02	0.07	10.36	0.07	32.90	0.66	22.60	1.23
<i>Dactylis glomerata</i>	3.58	0.27	10.47	0.30	16.81	1.19	37.48	8.03
<i>Holcus lanatus</i>	2.92	0.09	9.79	0.16	19.92	2.40	43.53	9.50
<i>Lolium italicum</i>	2.56	0.12	9.30	0.09	22.11	1.78	36.25	5.65
<i>Lolium perenne</i>	2.80	0.10	9.17	0.05	25.00	2.78	22.81	2.71
<i>Ranunculus repens</i>	3.58	0.30	12.22	0.51	14.79	2.62	31.70	7.61
<i>Trifolium pratense</i>	3.82	0.15	9.36	0.20	21.31	1.45	18.90	4.59
<i>Trifolium repens</i>	3.76	0.16	8.93	0.09	20.22	2.01	29.45	5.64

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704 **Table S2.** Correlations between plant functional traits, between decomposers and between
 705 plant functional traits and decomposers (Leaf Dry Matter Content, LDMC; Specific Leaf
 706 Area, SLA). For each correlation, the given parameter is the Pearson's or Spearman's
 707 coefficient (depending on the normality of variable distribution) with its significance (*:
 708 $P<0.05$; ***: $P<0.001$).

		<i>Plant functional traits</i>				<i>Decomposer community</i>				
		LDMC	SLA	Leaf C:N ratio	Phenolics	Microbial C:N ratio	Collembola	Acari	Enchytraeidae	Anecis
<i>Plant functional traits</i>	SLA	-0.13								
	Leaf C:N ratio	-0.07	0.45*							
	Phenolics	0.01	0.20	0.79***						
	Microbial C:N ratio	-0.34	0.26	0.26	0.18					
<i>Decomposer community</i>	Collembola	-0.22	-0.24	0.07	0.23	0.15				
	Acari	-0.54*	0.14	0.39	0.35	0.43*	0.54*			
	Enchytraeidae	-0.13	-0.16	-0.03	0.31	-0.09	-0.09	0.07		
	Anecis	0.01	-0.34	-0.10	0.22	-0.04	0.30	0.17	0.25	
	Epigeics	0.08	0.04	0.02	-0.01	-0.17	-0.23	-0.10	0.40	0.14

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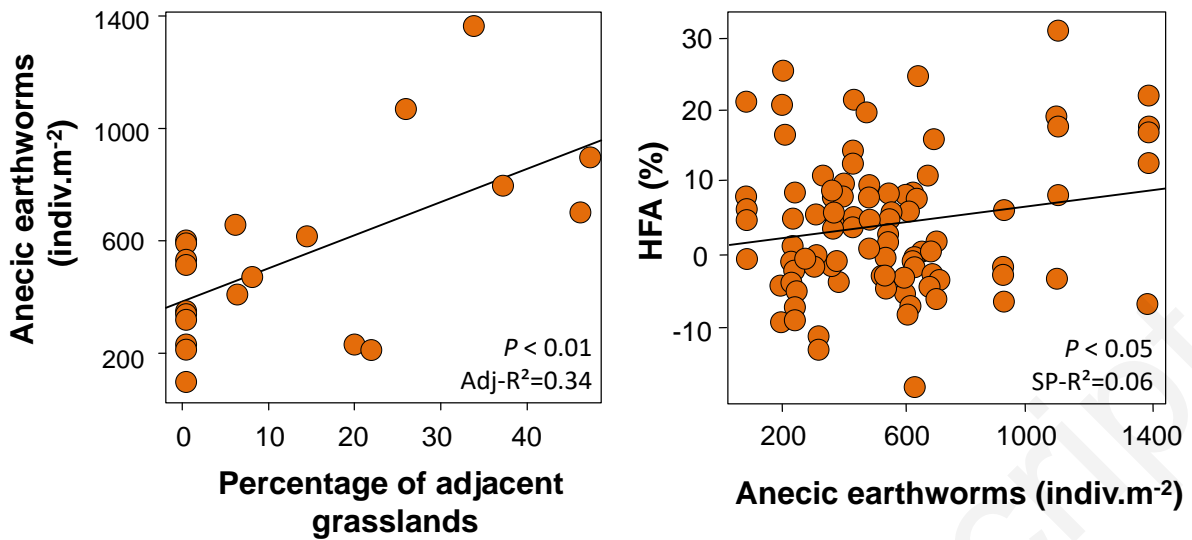
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721 **Figure S1.** Percentage of adjacent grasslands increased the abundance of anecic earthworms,
 722 which, in turn, increased Home-Field Advantage (HFA). SP-R² represents semi-partial
 723 residuals. See Figure S4 for parameters of models, and see Material and Methods for the
 724 transplantation treatment and calculations of HFA.

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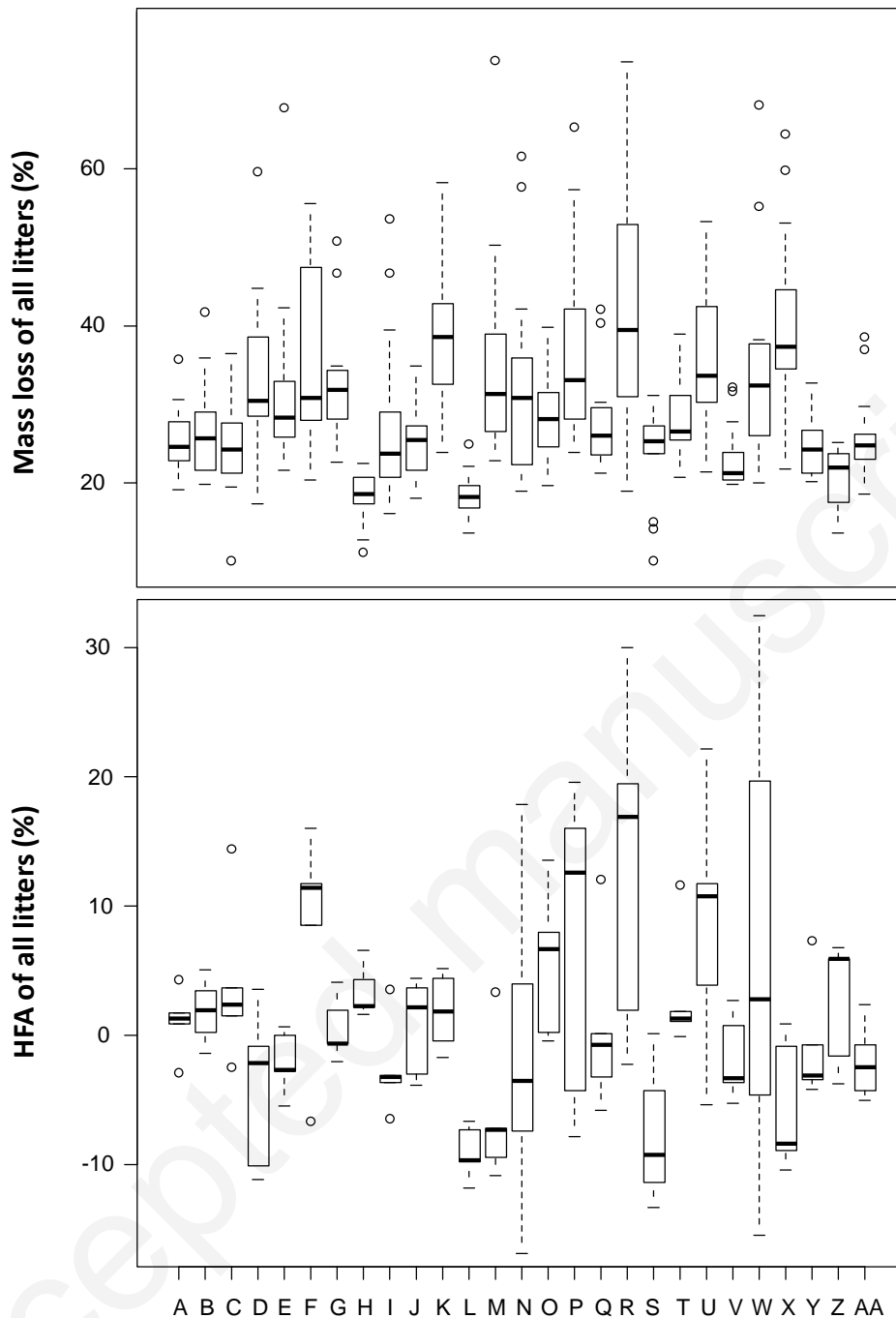
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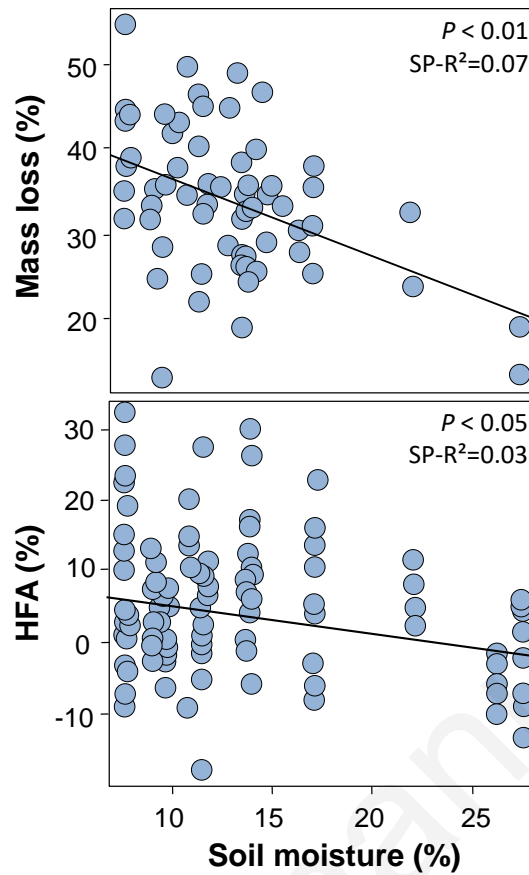
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735 **Figure S2.** Boxplot of mass loss and Home-Field Advantage (HFA) for all litters from the
 736 grasslands in our experiment. Grasslands are ordered by age, from the youngest (A, one year
 737 old) to the oldest (AA, 25 years old). We observe that, while there is substantial intra-
 738 grassland variation, there is still important inter-grassland variation for mass loss (ANOVA
 739 with grassland as explicative factor: $P < 10^{-16}$, $r^2 = 0.27$) and HFA (ANOVA with grassland as
 740 explicative factor: $P = 4.9 \times 10^{-4}$, $r^2 = 0.23$).



741

742 **Figure S3.** Soil moisture decreased litter mass loss and Home-Field Advantage (HFA). $SP-R^2$

743 represents semi-partial residuals. See Results and Figure S4 the model parameters, and see

744 Material and Methods for the transplantation treatment and calculations of HFA.

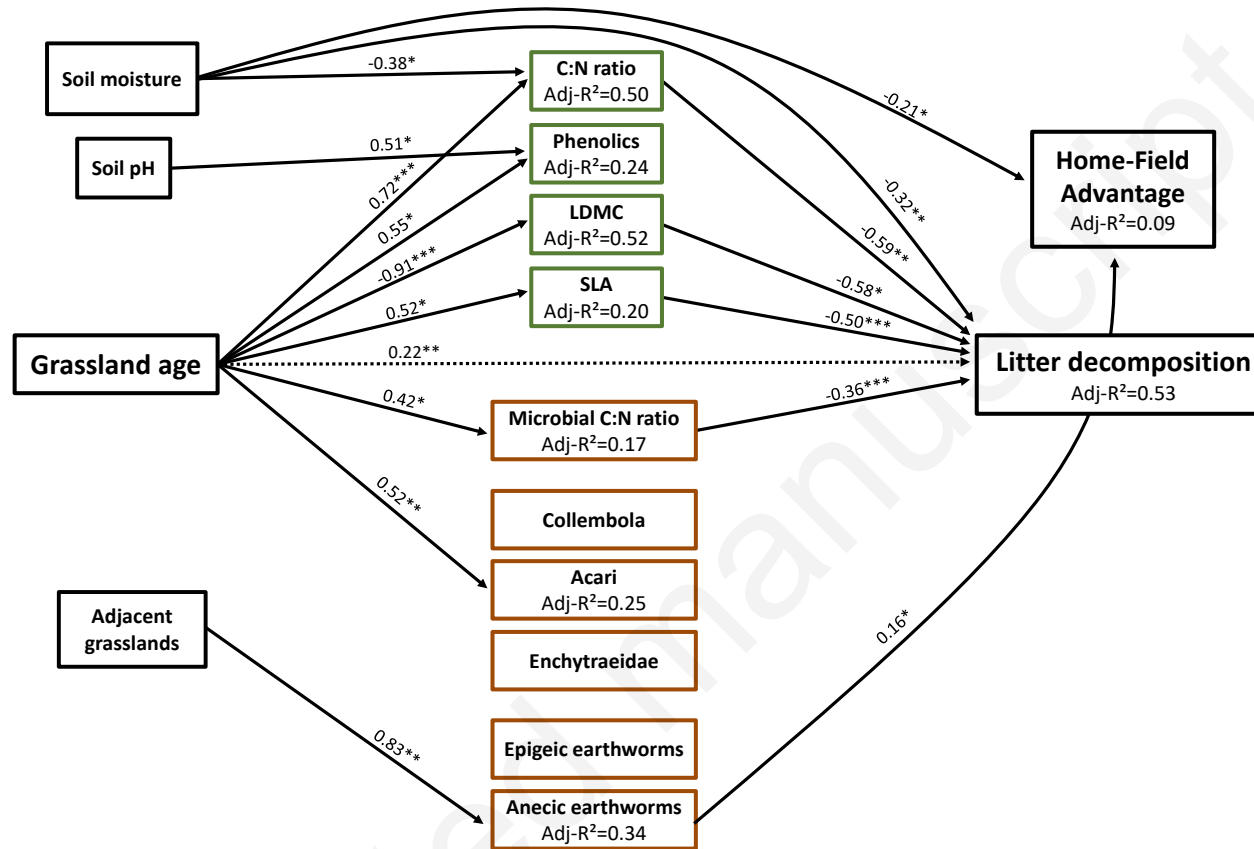
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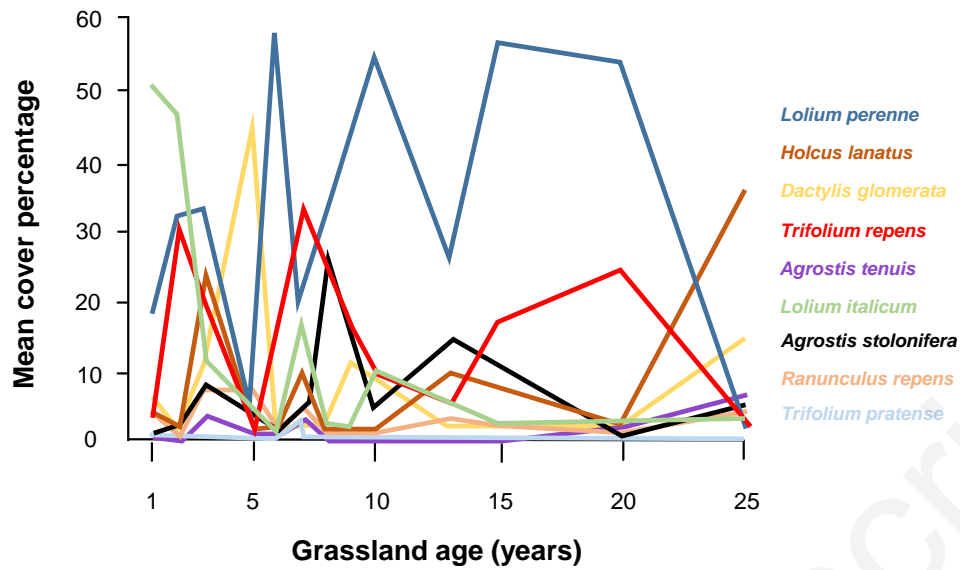
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751 **Figure S4.** Path analysis model for the indirect effects of grassland age on litter mass loss and Home-Field Advantage. These effects are
 752 mediated by the functional traits of plant community and by the decomposer community. The figure also presents the effects of abiotic and
 753 landscape variables accounted for in the models. Effects are indicated as the standardized regression coefficients of the model, that is the sign and
 754 magnitude of the effect. Explained variances are indicated in with each dependent variable, with adj-R². The dotted line represents a statistically
 755 direct effect of grassland age on litter decomposition in the model (*i.e.* a biological indirect effect of grassland age that was not mediated by any
 756 of the parameters that we measured). The relationship between soil pH and phenolics might be the least causal within the analysis.



757

758 **Figure S5.** Trend lines of mean cover percentage of the nine species used in the
 759 decomposition experiment across grassland ageing. These species represent 80% of the total
 760 abundance of the plant community. See Table S1 for species traits.