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MISS ANNE-KRISTEL BITTEBIERE (Orcid ID : 0000-0002-9882-968X)

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**Past spatial structure of plant communities determines arbuscular mycorrhizal fungal community assembly**

Anne-Kristel Bittebiere<sup>a,b,\*</sup>, Philippe Vandenkoornhuys<sup>a</sup>, Elodie Maluenda<sup>a</sup>, Agnès Gareil<sup>a</sup>, Alexandra Dheilly<sup>c</sup>, Sophie Coudouel<sup>c</sup>, Mathieu Bahin<sup>d</sup>, Cendrine Mony<sup>a</sup>.

<sup>a</sup>Université de Rennes 1, CNRS UMR 6553 Ecobio, Av. du Général Leclerc, 35042 Rennes Cedex, France; <sup>b</sup>Université of Lyon 1, CNRS UMR 5023 LEHNA, 43 Boulevard du 11 Novembre 1918, 69622 Villeurbanne Cedex, France; <sup>c</sup>Université de Rennes 1, CNRS UMS 3343 OSUR, Av. du Général Leclerc, 35000 Rennes, France; <sup>d</sup>Université de Rennes 1, CNRS UMR 6074 IRISA, Av. du Général Leclerc, 35000 Rennes, France;

\*corresponding author: Anne-Kristel Bittebiere, UMR CNRS 5023 'Ecologie des Hydrosystèmes Naturels et Anthropisés', Phone: +33 472 431 330; Fax: +33 472 431 141. Anne-kristel.bittebiere@univ-lyon1.fr

26 **Abstract**

27 1. Due to the importance of arbuscular mycorrhizal fungi (AMF) in ecosystem productivity, a key  
28 ecological question is how do their communities assemble? As plant spatial patterns constitute a  
29 mosaic of AM fungi habitats, we hypothesized that AM fungal community assembly is determined  
30 by plant community structure, both in space and time.

31 2. We tested our hypothesis by sampling individuals of two host-plant species, *Brachypodium*  
32 *pinnatum* and *Elytrigia repens*, from experimental communities cultivated in mesocosms, and  
33 assessed their AM fungal root colonizers by mass-sequencing. We related AM fungal community  
34 structure to the distribution of neighbouring plant species at different spatio-temporal scales.

35 3. We demonstrated that AM fungal community assembly depends mostly on past plant spatial  
36 patterns at a small spatial scale (5 cm), indicating that plants growing at given locations leave a  
37 footprint on the AM fungi community. This spatial scale of response was also influenced by the  
38 host-plant species, probably by its clonal propagation.

39 4. *Synthesis*. Overall, we highlighted that processes involved in AM fungal community assembly  
40 do not operate at the rough scale of the overall plant community mosaic but are instead locally  
41 determined, delineating the AM fungal “eye-view” of the host-plant community.

42

43 **Keywords**

44 Assembly mechanisms; clonal host-plant; community dynamics; Glomeromycota; Plant-soil  
45 (belowground) interactions; spatio-temporal scale; symbiosis.

## 46 Introduction

47 Arbuscular mycorrhizal fungi (AM fungi) are present in soils of all ecosystems (Öpik, Moora,  
48 Liira, & Zobel 2006) and form symbiotic interactions with about 80% of all terrestrial plant  
49 species (Wang & Qiu, 2006; Brundrett, 2009; Davison et al., 2015). The symbiotic interactions  
50 between plants and AM fungi are known to drive ecosystem productivity (*e.g.* van der Heijden,  
51 Boller, Wiemken, & Sanders 1998; Wagg, Jansa, Stadler, Schmid, & van der Heijden 2011), in  
52 particular through their contribution to soil nutrient transfers (*e.g.* Duhamel & Vandenkoornhuysen,  
53 2013) and their influence on resource sharing between plants (Klironomos, McCune, Hart, &  
54 Neville 2000). Because of the considerable importance of AM fungi and their key role in  
55 ecosystem functioning, the mechanisms driving AM fungal communities' assembly have been a  
56 hot topic in recent years (see *e.g.* Davison et al., 2016; Lekberg & Waller, 2016; López-García et  
57 al., 2017; Sepp, Jairus, Vasar, Zobel, & Öpik 2018).

58 Patterns of AM fungi relative abundance and diversity are highly heterogeneous across  
59 multiple spatial scales (Bahram, Peay, & Tedersoo 2015). Indeed, fungal assemblages vary at a  
60 local scale (Brundrett & Abbott, 1995; Carbalho, Correia, Ryel, & Martins-Loucao 2003; Wolfe,  
61 Mummey, Rillig, & Klironomos 2007) and an autocorrelation of AM fungal species has been  
62 detected within a few meters (Bahram et al., 2015). Drivers of such local heterogeneity include a  
63 patchy distribution of nutrients (Oehl et al., 2005) and heterogeneous microedaphic and  
64 microclimatic conditions (Vályi et al., 2016). Besides, AM fungal assemblages have been  
65 suggested to be either independent (the Independence hypothesis) or to co-vary with the  
66 composition of the aboveground vegetation (Zobel & Öpik, 2014). Under variable environmental  
67 conditions, the Habitat hypothesis assumes that plant and AM fungal communities vary in parallel  
68 relatively to varying habitat conditions. In steady environments however, the relationship between  
69 AM fungal assemblages and aboveground vegetation would be related to the Driver-Passenger  
70 hypothesis (Hart, Reader, & Klironomos 2001; Zobel & Öpik, 2014). AM fungi would act as  
71 "passengers" of plant species, which favor their best symbionts by preferentially allocating carbon  
72 to these cooperators (Kiers et al., 2011). This process leads to a host-plant preference effect  
73 (Vandenkoornhuysen et al., 2002; Vandenkoornhuysen, Ridgway, Watson, Fitter, & Young 2003,  
74 Gollotte, van Tuinen, & Atkinson 2004). This plant filtering may also be fine-tuned by the plant  
75 species' requirements over time (Vandenkoornhuysen et al., 2002). Conversely, AM fungi have  
76 been assumed to act as "drivers" of plant community structure (van der Heijden et al., 1998;  
77 Klironomos et al., 2000; Zobel & Öpik, 2014), and to promote some plant species over others

78 (Hartnett, Hetrick, Wilson, & Gibson 1993; van der Heijden et al., 1998). Both processes suggest  
79 the existence of a spatial relationship between plant and AM fungi, which would change over  
80 time. Despite the support for the existence of a spatial relationship between plant and AM fungi  
81 (Horn, Hempel, Verbruggen, Rillig, & Caruso 2017), the hypothesis of a spatio-temporal  
82 relationship has never been thoroughly tested.

83 Studies dealing with the effect of plant communities on AM fungal assemblages should  
84 consider that plant individuals are not randomly distributed within communities but instead form  
85 aggregated patterns of different size and composition (Watt, 1947; Herben & Hara, 2003). This  
86 spatial aggregation results from seed dispersal (Zobel, Moora, & Herben 2010) and clonal  
87 propagation (Benot, Bittebiere, Ernoult, Clément, & Mony 2013), as in both processes, the  
88 offspring are preferentially produced close to the mother plants. Plant spatial patterns form a  
89 complex matrix of spaces for AM fungi growth, and can therefore be considered as a mosaic of  
90 potential habitats. A better understanding of the scale of plant influence on the AM fungal  
91 community could be obtained from spatial analyses of their relationships. Because the spatial  
92 structure of the plant community is defined very locally (Benot et al., 2013), the AM fungal  
93 community may respond to the overlying plant composition on a few centimetres scale, which  
94 would lead to considerable variability in AM fungal composition at the plant community level  
95 (meter).

96 Plant spatial patterns are dynamic due to species mobility, *i.e.* local extinctions or  
97 emergence through seeds or clonal growth (Watt, 1947; Thórhallsdóttir, 1990; Herben & Hara,  
98 2003). The local turnover of plant species should subsequently result in changes in the spatial  
99 distribution of potential AM fungal habitats. Hausmann & Hawkes (2010) manipulated the order  
100 of plant species establishment experimentally and demonstrated that the first-established plant  
101 species filtered the initial AM fungal pool, thereby determining the symbiotic AM fungal  
102 assemblages of later-established plant species. This temporal sorting process would be reinforced  
103 by the effects of plant phenology and growth on AM fungal colonization rate, spore diversity and  
104 relative abundance (Johnson-Green, Kenkel, & Booth 1995; Schalamuk, Velazquez, Chidichimo,  
105 & Cabello 2006). Since AM fungal propagules (hyphae and spores) can survive and colonize plant  
106 roots even after one year of residence in the soil (McGee, Pattinson, Heath, Newman, & Allen  
107 1997), we examined the hypothesis that the AM fungal community responds to past or present  
108 spatial patterns of the plant community.

109 We worked on two co-occurring Poaceae species, namely *Elytrigia repens* L. and  
110 *Brachypodium pinnatum* L., common in temperate grasslands. Individuals of both species were  
111 sampled from controlled experimental plant communities encompassing a large range of spatial  
112 structures. By accurately mapping the spatial distributions of plant species in each 1.7 m<sup>2</sup>  
113 mesocosm on several dates, we were able to relate the past and present spatial patterns of plant  
114 communities to the current structures of the *E. repens* and *B. pinnatum* AM fungal communities. A  
115 thorough analysis of the AM fungal communities associated with the roots of sampled individuals  
116 was carried out to test the following hypotheses:

- 117 (i) Past and present spatial patterns of the plant community drive the structure of the AM  
118 fungal community.
- 119 (ii) The AM fungal community responds to the overlying plant composition at a very local  
120 scale (centimetre).

121

## 122 **Materials & Methods**

### 123 *Host-plant species*

124 *Elytrigia repens* (L.) Desv. (syn. *Elymus repens* or *Agropyron repens*) and *Brachypodium*  
125 *pinnatum* (L.) Beauv. (syn. *Bromus pinnatus*) are two common, co-occurring perennial Poaceae  
126 species of grasslands in western Europe. These species grow laterally by producing sympodial  
127 plagiotropic rhizomes from which buds develop into erect shoots (ramets) [CLO-PLA database,  
128 (Klimešová & De Bello, 2009)]. *E. repens* and *B. pinnatum* respectively display long and short  
129 lateral dispersal (mean internode lengths of 2.8 cm and 1.0 cm respectively, Benot et al., 2013) *i.e.*  
130 either guerilla (loose clonal architecture) or phalanx growth (a packed front of ramets) (Lovett  
131 Doust, 1981). Both species produce roots of similar length (mean length = 6.9 cm  $\pm$ 2.5 in *E.*  
132 *repens* and 7.8 cm  $\pm$ 3.5 in *B. pinnatum*) and thickness (mean diameter = 0.05 cm  $\pm$ 0.005 in *E.*  
133 *repens* and 0.05 cm  $\pm$ 0.010 in *B. pinnatum*) as measured on individuals from our experimental  
134 design. These two target species are known to develop symbioses with AM fungi species and  
135 display a positive growth response (Rydlová & Vosátka, 2001; van der Heijden, Wiemken, &  
136 Sanders 2003). Literature studies have demonstrated different levels of mycorrhizal colonization  
137 in these species ranging from intermediate (*E. repens*, about 15% of root length) to high (*B.*  
138 *pinnatum*, about 50% of root length) (Rydlová & Vosátka, 2001; van der Heijden et al., 2003)

139 although root colonization levels can considerably vary within a growing season (Bohrer, Friese,  
140 & Amon 2004; Mandyam & Jumpponen, 2008).

141

Accepted Article

142 *Mapping plant community spatial structure over time*

143 The spatio-temporal scale, at which the AM fungal community structure responds to the spatial  
144 patterns of the overlying plant community, was determined by randomly selecting experimental  
145 plant communities (*i.e.* 19 per host-plant species) of varying spatial structures from a wider  
146 outdoor mesocosm design (Fig. 1). This mesocosm design had been set up in 2009 in the  
147 experimental garden of the University of Rennes 1, to determine the effect of plant clonal growth  
148 strategies on spatial patterns (see Benot et al., 2013 for details).

149 The sampled plant communities were composed from a set of 12 species that are widely  
150 distributed in temperate grasslands in Western France (des Abbayes, Claustres, Corillion, &  
151 Dupont 1971) (*E. repens*, *B. pinnatum*, *Agrostis stolonifera* L., *Holcus mollis* L., *Ranunculus*  
152 *repens* L., *Festuca rubra* L., *Agrostis tenuis* Sibth., *Anthemis nobilis* L., *Holcus lanatus* L.,  
153 *Dactylis glomerata* L., *Lolium perenne* L., and *Centaurea nigra* L.), and known to form symbioses  
154 with arbuscular mycorrhizal fungi (West, 1996; Pawlowska, Blaszkowski, & Rühling 1997;  
155 Gollote et al., 2004; Wearn & Gange, 2007). These plant communities varied in both richness and  
156 composition (ranging from one to a mixture of all 12 selected plant species) (Tables 1, 2). Forty-  
157 eight plant units (one mature shoot with one internode of maternal connection – Stuefer & Huber,  
158 1999) were initially transplanted 16 cm apart in a hexagonal pattern in each mesocosm of 1.30 ×  
159 1.30 × 0.25 m (Birch, Oom, & Beecham 2007). The 48 transplanted plant units consisted of equal  
160 numbers of all the co-occurring species (including the host-plant species), and their positions  
161 within the plantation pattern were randomized for each mesocosm. The plants were grown on a  
162 homogeneous unsterilized substrate (initial chemical composition: C/N = 7.2 ±3.2, NO<sub>3</sub><sup>-</sup> = 32.5  
163 ±18.6 µg.g<sup>-1</sup> dry soil, PO<sub>4</sub><sup>2-</sup> = 28.5 ±16.7 µg.g<sup>-1</sup> dry soil), composed of sand (20%) and soil from  
164 Western France (80%, collected in March 2009 and previously stored outside for a week). The  
165 mesocosms (boxes) were placed on a tarpaulin to isolate the substrate from the ground soil (Fig.  
166 1). Weeds were regularly removed, and the mesocosms were watered every two days during the  
167 dry season. Above-ground vegetation was mown once a year at the end of summer and flowers  
168 were cut off to suppress sexual reproduction. The present spatial structure of the plant community  
169 was therefore solely due to vegetative growth, without any addition of new species or individuals  
170 through sexual reproduction, and directly resulted from the past structure.

171 Species cover changed over time due to the ongoing dynamics of the plant communities.  
172 The spatial distributions of the plant species in all mesocosms were recorded after two and three  
173 years of cultivation (early March 2011, and in May 2012 right before the host individual sampling)



174 (Fig. 2), by centring a  $80 \times 80$  cm square lattice on the mesocosm. Presence/absence data were  
175 recorded in  $5 \times 5$  cm cells of the lattice (256 cells total) and a plant species was considered present  
176 when at least one individual was rooted in the target cell, a given individual belonging to one cell  
177 only. Several plant species can co-occur in a cell. We then based our work on the hypothesis that  
178 aboveground plant species distribution can be a proxy of the belowground root distribution (the  
179 accuracy of this proxy is discussed in the Discussion section). The numbers of cells that were  
180 colonized by each plant species at different scales surrounding the positions of AM fungal  
181 community sampling, were calculated in 2011 (past) and 2012 (present) (Tables 1, 2) by GIS  
182 (ArcGIS ver. 9.3., ESRI) [Bittebiere & Mony (2015) for more details on the method]. The  
183 following spatial scales *i.e.* 5, 10, 15, 20, and 25 cm from the sampled host individual, were tested  
184 (Fig. 2).

185 As a preliminary step, we checked for the absence of collinearity in our plant species  
186 abundances at the different spatial and temporal scales by testing pairwise correlations using non-  
187 parametric Spearman's rank correlation tests. No strong correlations were found between the  
188 abundances of the different species at all spatial and temporal scales tested (*i.e.* correlation  
189 coefficients  $< 0.7$  when significant) (Dormann et al., 2013).

190

#### 191 *Sampling, DNA extraction and amplicon preparation*

192 In May 2012, one individual (a mature shoot and the associated roots) of the host-plant species,  
193 either *E. repens* or *B. pinnatum*, was randomly sampled from the centre of each mesocosm (Fig.  
194 2). These sampled plant individuals had been initiated and grown in the mesocosms. The age of  
195 sampled roots was standardized by only harvesting roots directly attached to the shoot base. All  
196 individuals were sampled from independent plant communities. Nineteen samples of *E. repens* and  
197 as many of *B. pinnatum* were used in this study. The roots were separated from the rest of the  
198 plant, washed with a stringent detergent solution (Triton X100, 1% V/V), then rinsed with ultra-  
199 pure water before storage at  $-80^{\circ}\text{C}$  and subsequent analysis of the root endosphere compartment  
200 (*e.g.* Lê Van et al., 2017).

201 The 38 root samples ( $\sim 10$  g each) were ground to powder using a pestle and mortar under  
202 liquid nitrogen. The total DNA was then extracted from a 100 mg sub-sample using the DNeasy  
203 plant kit (Qiagen) according to the manufacturer's recommendations. A 520 bp DNA fragment of  
204 the AM fungi SSU rRNA gene was specifically amplified by PCR using NS31/AM1 primers  
205 (Simon, Lalonde, & Bruns 1992; Helgason, Daniell, Husband, Fitter, & Young 1998) with

206 PuReTaq Ready-to-go PCR beads (GE Healthcare). True technical amplicon replicates were  
207 obtained for each of the 38 samples (*i.e.* for a given DNA extract, two independent PCRs were  
208 never mixed together in any of the molecular studies). Each amplicon was tagged using a  
209 multiplex identifier (*i.e.* index). The 76 amplicons were purified using AMPure XP – PCR kit  
210 (Agencourt/Beckman-Coulter).

211

#### 212 *Amplicon libraries preparation and sequencing*

213 The sequencing libraries were prepared by measuring the DNA concentration of each amplicon  
214 using a Picogreen assay (Invitrogen) and digital PCR (Fluidigm EP1). After equimolar mixing of  
215 the 76 purified amplicons, emPCR amplification (GS FLX Titanium emPCR Kit Lib-L) and  
216 sequencing (GS FLX Titanium Sequencing Kit XL+) were performed with a 454/Roche GSflx+  
217 instrument, according to the manufacturer's instructions. The 520 bp SSU rRNA fragments were  
218 fully sequenced.

219

#### 220 *Sequence trimming and bioanalyses*

221 The sequence production and trimming strategy has been published previously (*e.g.* Ciobanu et al.,  
222 2014; Ben Maamar et al., 2015; Lê Van et al., 2017). Sequences shorter than 300 bp in length,  
223 with homopolymers longer than 8 bp or with ambiguous nucleotides, were removed from the  
224 dataset. Sequences containing errors in the MID (*i.e.* multiplex identifier) or primer sequences  
225 were discarded. The technical replicates were sequenced to filter sequencing errors. Only full  
226 length 100% identical sequences found in both technical replicates were kept in the dataset  
227 (Ciobanu et al., 2014; Lê Van et al., 2017). In addition to this first stringent filtering process, each  
228 sample was subjected to a search for chimeric sequences with the chimera.uchime command in  
229 MOTHUR (Kozich, Westcott, Baxter, Highlander, & Schloss 2013). Operational Taxonomic  
230 Units (OTUs) were delineated at a 97% identity threshold using DNACLUSt, similarly to QIIME.  
231 After these steps, OTUs found in more than 10.5% of the samples (*i.e.* four samples) were kept.  
232 Thus an OTU was kept only if this one contained a minimum of eight identical sequences obtained  
233 independently (four sequences in each of the two independent PCR). The sequencing data were  
234 organized in a contingency matrix. Because of the different numbers of sequences per sample, the  
235 dataset was normalized to the lowest number (*i.e.* 1500 sequences for each sample) using the  
236 VEGAN package in R (Oksanen et al., 2016) and the frequencies of each OTU per sample were  
237 calculated. The resulting rarefied matrix was used for the statistical analyses (see below). The

238 most abundant sequence within each OTU was selected as the representative sequence for the  
239 phylogenetic analyses and taxonomic assignation using Phymyco-DB, a curated SSU rRNA fungal  
240 database (Mahé et al., 2012). At the last release this database contained 1400 non-redundant  
241 Glomeromycota SSU rRNA sequences and hundreds to thousands of sequences from other fungal  
242 phyla (see <http://phymycodb.genouest.org/>). All the OTUs detected belonged to the  
243 Glomeromycota. Nevertheless, taxonomic affiliations of OTU with a match at high taxonomic  
244 level only (*i.e.* phylum) remain speculative with no consequences for our analyses and results as  
245 they only represent 2% of all OTU. The taxonomic affiliation of the OTUs is summarized in Fig.  
246 3. A Ward clustering analysis, using the Bray-Curtis dissimilarity index, was performed with  
247 SEED (Beck, Dennis, & Foster 2015). This analysis allowed us to compare the fungal  
248 communities between samples and more precisely, to determine their composition similarity.

249

#### 250 *OTUs phylogenetic analysis*

251 The representative sequences of the 173 most abundant OTUs (*i.e.* 80% of the sequences) were  
252 aligned using SINA aligner v1.2.11 (Pruesse, Peplies, & Glöckner 2012) and imported into the  
253 non-redundant SILVA SSURef ARB database (release 115) (Ludwig et al., 2004). Alignments of  
254 the representative OTU sequences and their 15 closest phylogenetic relatives were exported from  
255 ARB. A putative Choanoflagellate, *Acanthoeca spectabilis*, was used as outgroup. Gaps and  
256 ambiguous positions were excluded by manually refining the alignments. The best possible model  
257 to explain the matrix (*i.e.* GTR+I+G), based on jModelTest v2.1.4 (Darriba, Taboada, Doallo, &  
258 Posada 2012) was used to compute the Maximum likelihood phylogeny in TREEFINDER (Jobb,  
259 von Haeseler, & Strimmer 2004) (Fig. S1). GenBank accession numbers of the most abundant  
260 OTU (Fig. S1) are MH429633 – MH429779.

261

262 *Data analyses*

263 The spatio-temporal scale of the AM fungal community response to the spatial distribution of  
264 overlying plant species, was determined from the AM fungal community indexes, and AM fungal  
265 species occurrences (*i.e.* identities) and relative abundances.

266 AM fungal community indexes were calculated using the VEGAN package in R (Oksanen  
267 et al., 2016): (i) the AM fungal richness (S, *i.e.* the number of OTUs), (ii) the Simpson diversity  
268 index (H'), and (iii) the equitability index (J). Pairwise correlations between AM fungal  
269 community indexes were tested using non-parametric Spearman's rank correlation tests. OTU  
270 richness and equitability were poorly correlated (*i.e.* correlation coefficients < 0.65) while OTU  
271 Simpson diversity was strongly correlated with the two other indexes (correlation coefficients  
272 between OTU Simpson diversity and equitability > 0.9, and between OTU Simpson diversity and  
273 richness > 0.7). We therefore removed OTU diversity from subsequent analyses to avoid  
274 collinearity between the AM fungal community indexes.

275 The influence of plant community spatial patterns on AM fungal community indexes in *B.*  
276 *pinnatum* and *E. repens* at all spatial and temporal scales was determined by multiple regression  
277 analyses with plant species abundances as explanatory variables in linear model (LM) procedures.  
278 Data was log-transformed, when necessary, to satisfy the assumption of a normal distribution of  
279 model residuals. One model was developed for each date and spatial scale. Thus, ten models were  
280 constructed per index, each of which was optimized by backward stepwise selection of the  
281 explanatory variables. The information-theoretic model comparison approach based on Akaike's  
282 Information Criterion (AIC) was used to compare all the optimized models for each index through  
283 second-order AIC corrected for small sample sizes (AICc) (Burnham & Anderson, 2002). In our  
284 analyses, those models with smaller AICc values and with a substantial level of empirical support  
285 (*i.e.*, a difference of AICc > 2 compared to other models) were considered the most probable  
286 (Burnham & Anderson, 2002). The coefficients and the proportion of index variation that was  
287 accounted for by the regression ( $R^2$ ) were then calculated for these most probable models. The  
288 significance of each explanatory variable was determined by ANOVA analyses.

289 AM fungal OTUs occurrences and relative abundances were used as two response matrices  
290 in Canonical Correlation Analyses (CCA) with the plant species abundances as the environmental  
291 matrix. These CCA were performed at all spatial and temporal scales tested with the VEGAN  
292 package (Oksanen et al., 2016), to determine the effects of plant species abundances on the AM  
293 fungal community composition *i.e.* the identities and relative abundances of the fungal species

294 present. One model was developed for each date and spatial scale. Thus, ten models were  
295 constructed per response matrix, each being optimized by backward stepwise selection of the  
296 explanatory variables. The percentage of variance of the AM fungal species occurrences explained  
297 by the environmental matrix was calculated (constrained CCA inertia) and an ANOVA was  
298 carried out based on permutation test to determine the significance of the CCA.

299 All statistical tests were performed using R 3.2.3 (R Development Core Team, 2008).

300

## 301 **Results**

### 302 *AM fungi in E. repens and B. pinnatum roots, $\gamma$ -diversity*

303 After the trimming steps, the rarefied dataset contained 58 920 sequences corresponding to 602  
304 OTUs (*i.e.* formed with a minimum of eight sequences). Only 21 OTUs were present in more than  
305 80% of the samples, and 113 OTUs were found in more than 50% of the samples, showing that  
306 our samples contained a majority of rare OTUs. 544 and 22 OTUs were found within the  
307 Glomerales and Diversisporales orders respectively (Fig. 3). No sequence belonging to other  
308 Glomeromycota orders (*i.e.* Archaeosporales, Paraglomerales) was detected (Fig. 3). At higher  
309 taxonomic ranks, 24 and 12 OTUs could not be identified at the class and phylum levels,  
310 respectively (Fig. 3). *Rhizophagus* and unclassified Glomerales were dominant, accounting for  
311 93.6 % of the total number of sequences and 87.0 % of all the OTUs (Fig. 3). Phylogenetic  
312 analysis of the OTUs representing 5/6 of the sequences dataset (*i.e.* the 173 most abundant OTUs)  
313 demonstrated that 39 of these OTUs could not be identified at the order level (*i.e.*  
314 Glomeromycetes). The 30 most abundant OTUs accounted for 46.7% of the sequences (Fig. S2).

315 In these AM fungal communities, Glomeromycota OTU richness per sample ranged from  
316 59 to 128 in *E. repens*, and from 61 to 123 in *B. pinnatum* with no difference in the mean  
317 Glomeromycota richness (mean=95,  $\pm$ SD=17) or equitability (mean=0.56,  $\pm$ SD=0.04) between the  
318 host-plants. However, the Ward clustering analyses demonstrated that the AM fungal communities  
319 colonizing the roots of one of these two host-plant species were closer to each other than to those  
320 of the other host-plant species ( $P<0.05$ ) (Fig. S3), although only 10 OTUs were host-plant species  
321 specific.

322

### 323 *Response of AM fungal community indexes to plant community spatial structure*

324 Our procedure of model selection based on the AICc allowed us to delineate the most probable  
325 models adjusted to our data. These models were described in Table 3, while all other models were

326 discarded from further analyses. These most probable models indicated that the richness and  
327 equitability of the AM fungal community associated with *E. repens* and *B. pinnatum* (with the  
328 exception of AM fungal equitability in *E. repens* at 5-10 cm scale) were significantly determined  
329 by plant community spatial patterns (Table 3, Fig. 4). Our results demonstrated that past plant  
330 spatial patterns alone explained about 70% and 58% of the variations in AM fungal richness in *E.*  
331 *repens* and *B. pinnatum* roots respectively, and from 27% to 59% of the equitability variations,  
332 depending on the host-plant species.

333 Overall, the AM fungal community indexes responded at a rather small scale to past plant  
334 spatial patterns (*i.e.* 5 cm radius, except for AM fungal equitability in *E. repens*) (Table 3, Fig. 4).  
335 An effect of past plant spatial patterns was also observed at a larger spatial scale (10-15 cm radius)  
336 on the AM fungal richness recorded in *E. repens* roots.

337 AM fungal community indexes were influenced by the presence and abundance of only  
338 two to four plant species (Table 3, Fig. 4). These plant species decreased the richness and  
339 equitability of the AM fungal communities associated with both host species, with the exception  
340 of *Anthemis nobilis* and *E. repens*. These latter species had positive effects on the richness and  
341 equitability of the *E. repens* symbiotic community at 15 cm, and on the richness of the *B.*  
342 *pinnatum* symbiotic community at 5 cm, respectively.

343

#### 344 *Response of AM fungal occurrences and relative abundances to plant community spatial structure*

345 Canonical Correlation Analyses demonstrated that the abundances of the overlying plant species  
346 did not drive AM fungal species occurrences and relative abundances in the roots of  
347 *Brachypodium pinnatum* (ANOVAs,  $p$ -values  $> 0.05$  for all CCA). In *Elytrigia repens* however,  
348 both AM fungal species occurrences and relative abundances responded to plant community  
349 spatial structure (Table 4). Our CCA results demonstrated in this host-plant species that past plant  
350 spatial patterns explained at least 30% and 20% of the variations in AM fungal occurrences and  
351 relative abundances respectively, with an additional effect of the present plant spatial patterns.

352 Overall, the AM fungal community structure responded at a fine spatial scale to plant spatial  
353 patterns (*i.e.* from 5 cm to 15 cm radius) (Table 4) although an effect of present plant spatial  
354 patterns was also observed at a larger spatial scale (20 cm radius) on the AM fungal relative  
355 abundances in *E. repens* roots. AM fungal occurrences and relative abundances were influenced  
356 by the presence and abundance of only two to five plant species in particular *Holcus lanatus*  
357 (Table 4).

359 **Discussion**360 ***Plant landscape affects fungal community structure***

361 Our results are consistent with the Passenger hypothesis (Hart et al., 2001; Zobel & Öpik, 2014)  
362 and previous studies demonstrating that AM fungal community structure can be related to the  
363 composition of the overlying plant community (*e.g.* Bever, Morton, Antonovics, & Schultz 1996;  
364 Eom, Hartnett, & Wilson 2000; Vandenkoornhuysen et al., 2002; 2003; Pivato et al., 2007;  
365 Davison, Öpik, Daniell, Moora, & Zobel 2011; Ji, Gehring, Wilson, Miller, & Johnson 2013).  
366 Additionally, those results newly indicated that the heterogeneous spatial distributions of plant  
367 individuals, forming a mosaic of potential habitats, determine the species pool and competitive  
368 balance of the AM fungal community. Indeed, in both host-plant species, we found an effect of  
369 plant spatial patterns on the AM fungal richness and equitability, with an additional effect on AM  
370 fungal species occurrences and relative abundances recorded in *E. repens*. The discrepancy in the  
371 responses of AM fungal community descriptors in *B. pinnatum*, would indicate a fungal pool with  
372 a varying number of rare species and subsequently a varying equitability, but with no shift in the  
373 dominant species identities and insignificant variations in their relative abundances.

374 In the two host-plant species studied, AM fungal communities responded to the plant  
375 aboveground spatial patterns, which were used as a proxy of belowground root distribution. The  
376 accuracy of this proxy would vary with the plant species. Plant species richness can be 1.5 times  
377 higher belowground than aboveground due to the root distribution of rhizomatous species  
378 (Hiiesalu et al., 2014), for example *E. repens*, *B. pinnatum* or *H. mollis* in our system. Based on  
379 their aboveground spatial patterns, the actual root distributions of these three plant species may  
380 have been underestimated in our study. Future investigations relating the spatial patterns of AM  
381 fungi and plant species should therefore be based on spatially explicit root sampling to improve  
382 precision.

383 Our findings strongly suggest that the processes involved in the coexistence of AM fungal  
384 species (OTUs) are spatially determined locally. By analogy with the work of Turkington &  
385 Harper (1979) on plant communities, this allows us to determine the AM fungal “eye-view” of the  
386 host-plant community. Landscape ecological studies (*e.g.* Burel & Baudry, 1999) have clearly  
387 shown that the biodiversity of macro-organisms is strongly influenced by the habitat mosaic (*i.e.*  
388 composition and relative abundances of habitat types, *e.g.* forests or crops) defined at the square  
389 kilometre scale (*e.g.* Michel, Burel, Legendre, & Butet 2007). By analogy, we argue that the

390 spatial structure of plant communities can similarly be considered as a mosaic of AM fungal  
391 potential habitats and would therefore constitute a centimetric “plant landscape”. Hereafter, we  
392 refer to this conceptual analogy to investigate the assembly processes in action within the AM  
393 fungal community.

394 Our results emphasize the importance of the host-plant species in modulating the strength  
395 of the plant landscape effect on AM fungal community assembly. The processes involved in AM  
396 fungal community assembly therefore result from an interplay between the plant landscape and the  
397 host-plant species identity.

398  
399 ***Spatio-temporal scale of AM fungal community response to plant landscape***

400 In *E. repens*, AM fungal occurrences and relative abundances were shown to depend on present  
401 but also on past plant landscape. Moreover, in the two host-plant species, OTU richness and  
402 equitability depended on the past, rather than the present plant landscape. While there is literature  
403 support for the existence of a spatial relationship between present plant landscape and AM fungal  
404 community structure (Horn et al., 2017), we demonstrated for the first time that this spatial  
405 relationship varies through time with a dominant effect of the past plant landscape.

406 This ‘footprint’ of the past plant landscape on current AM fungal community structure can  
407 be explained by two non-exclusive processes. First, after a growing season, AM fungal spore  
408 composition in soil varies according to the overlying plant species (Johnson, Zak, Tilman, &  
409 Pflieger 1991; Bever et al., 1996; Eom et al., 2000). Bever (2002) showed that this differentiation  
410 increased over successive growing seasons, due to the filtering of AM fungi by their hosts. In  
411 particular, because plants are able to provide a higher carbon flux to their best cooperators (Kiers  
412 et al., 2011), the expected consequence of this selective rewarding would be a better fitness for  
413 these particular symbionts, and thus the possible exclusion of certain colonizers (Duhamel &  
414 Vandenkoornhuyse, 2013). Overall, this suggests that the very early presence of plant species  
415 within the plant landscape is important. Second, a recent study has confirmed the importance of  
416 the arrival order of AM fungal species for colonization of plant seedlings (Werner & Kiers, 2015).  
417 This ‘priority effect’, *i.e.* early arrival conferring an advantage to a particular AM fungus in  
418 occupying the root habitat, might provide an ability to exclude one that arrives later (Werner &  
419 Kiers, 2015) and thus impact the assembly processes of future AM fungal communities.  
420 Nevertheless, the persistence of past plant landscape effects could be related to the rather short  
421 period of time investigated in this study (15 months). As most fungal spores and propagules are



422 able to survive in soil, a longer term study, mapping plant communities *e.g.* five years before AM  
423 fungal community sampling, would allow to determine the temporal limits of the past plant  
424 landscape footprint on current AM fungal community structure.

425 Within each host-plant species, fungal OTU richness and equitability generally responded  
426 to plant landscape at the same very narrow spatial scale (5 cm radius). Similarly, in *E. repens*, the  
427 OTU occurrences was influenced by past and present plant landscapes within a 5 cm radius  
428 neighbourhood. This could be explained by two complementary hypotheses related to dispersal  
429 and recruitment mechanisms of AM fungi involving spores, hyphae, and colonized root fragments  
430 (Allen, 1991). First, spores are not randomly distributed in soil but can occur in patches of about 4  
431 cm<sup>2</sup> (Allen & MacMahon, 1985), in agreement with observations of dispersal limitation (Friese &  
432 Koske, 1991), in ectomycorrhizal fungi, for example (Peay, Bidartondo, & Arnold 2010). Second,  
433 the dispersal of AM fungi through hyphae and colonized root fragments may have been influenced  
434 by the clonal growth strategy of the two studied host-plants, although this hypothesis remains to be  
435 thoroughly tested with several plant species per clonal growth strategy. Indeed, the roots of  
436 daughter ramets, developing less than 5 cm from their mother and displaying the same host-plant  
437 preferences, will likely be colonized, through hyphae and root contacts, by a similar AM fungal  
438 community (*i.e.* pseudo-vertical transmission of the AM fungal community to ramets). Thus, the  
439 additional effect of a larger plant landscape (10-20 cm radius) on AM fungal community structure  
440 observed in *E. repens*, could be related to its more diffuse clonal growth (Benot et al., 2013),  
441 allowing AM fungal transmission from parent to offspring through the hyphal growth, over greater  
442 distances (Friese & Allen, 1991; Jakobsen, Abbott, & Robson 1992). Moreover, this hypothesis  
443 would suggest that clonal plant networks serve as privileged dispersal pathways for AM fungi.  
444 AM fungi will disperse step by step from the older to the younger ramets (Vannier et al., 2018).  
445 Considering the importance of clonal growth in grassland ecosystems [70% of plant species, (van  
446 Groenendael & de Kroon, 1990)], this dispersal mechanism would be of particular importance for  
447 AM fungal species fitness and thus AM fungal community dynamics.

448

#### 449 ***Determinant species of the plant landscape***

450 In our study, we were interested in the scale of AM fungal community response to the overall  
451 plant landscape. We therefore considered that the various plant species composing this landscape  
452 had similar spatial scales of influence. Actually, this might not be the case, particularly for plant

453 species with different clonal growth strategies (guerilla, phalanx or tussock – Lovett Doust, 1981),  
454 but this requires further investigation.

455 Interestingly, the AM fungal community response was triggered by only a few of the plant  
456 species composing the plant landscape, regardless of their abundances. With the exception of  
457 *Holcus mollis* for community indexes, this set of plant landscape species varied according to the  
458 host-plant species. The species in our landscapes impacted AM fungal richness or equitability with  
459 different strengths and generally negatively, except for *E. repens* and *Anthemis nobilis*. Thus the  
460 intensity of the filtering process will vary within the plant landscape, which therefore represents a  
461 mosaic of AM fungi microhabitats of heterogeneous quality. These findings are consistent with  
462 previous reports demonstrating that AM fungal diversity in *Plantago lanceolata* is dependent on  
463 the specific identity of its neighbours (Johnson et al., 2003), or is reduced by the sole presence of  
464 *Centaurea maculosa* in the plant community (Mummey & Rillig, 2006). The positive effect of *E.*  
465 *repens* and *A. nobilis* on AM fungal species coexistence likely indicates that their roots are easily  
466 reached and colonized by AM fungi. Indeed, our work with mesocosms revealed that these plant  
467 species produce superficial and diffuse roots, which increases the probability of between-root  
468 contacts (pers. obs.). This highlights the major role of interspecific differences in root architecture  
469 for root colonization (Friese & Koske, 1991) and hence micro-habitat reachability.

470

#### 471 ***AM fungal community in B. pinnatum and E. repens roots***

472 Since its publication in 1998, the primer pair NS31/ AM1 (Helgason et al., 1998) amplifying a  
473 fragment of the 18S SSU rRNA gene of Glomeromycota has frequently been used to detect and  
474 analyse AM fungal communities despite the known bias in favour of Glomerales and  
475 Diversisporales (*i.e.* Paraglomerales and Archaeosporales not being amplified) (Lee, Lee, &  
476 Young 2008). This bias was the same across all the samples studied here. Despite the stringent  
477 sequence trimming, we found a higher OTU richness within the Glomeromycota, than in other  
478 studies (*e.g.* Johansen et al., 2015; Varela-Cervero et al., 2015). However, direct comparisons  
479 between published studies of the total number of OTUs are difficult as this value depends on the  
480 number of analysed samples, the sequencing depth, the targeted sequence (*i.e.* primer used), and  
481 also the trimming strategy. Our high OTU richness is likely due to our delineation method.  
482 Application of a 97% sequence identity from the SSU rRNA gene for OTU detection and  
483 delineation, has been shown to be a good proxy of AM fungal species, but is accompanied by an  
484 increase in species richness compared to the Monophyletic Clade Approach, for example

485 (Lekberg, Gibbons, & Rosendahl 2014). Nevertheless, as confirmed by an additional multivariate  
486 cut-off level analysis (MultiCoLA) (Fig. S4) and the existing literature, our delineation method  
487 has no impact on the detected AM fungal community patterns (Lekberg et al., 2014; Hart et al.,  
488 2015), and thus on the relevance of our results. However, the number of Glomeromycota OTUs  
489 observed in this single study, which is higher than the known morphospecies (for an updated AM  
490 fungal species list see URL [http://schuessler.userweb.mwn.de/amphylo/amphylo\\_species.html](http://schuessler.userweb.mwn.de/amphylo/amphylo_species.html)),  
491 and the relationships with known taxonomic groups, suggests that our understanding of  
492 Glomeromycota diversity is still very fragmented.

493

#### 494 ***Conclusion and prospects***

495 This study demonstrated that the plant community constitutes a dynamic centimetric landscape  
496 that deeply influences AM fungi community assembly. As in macro-organisms (*e.g.* birds, insects,  
497 mammals) (Fahrig et al., 2011), the coexistence of AM fungi species is determined by the  
498 interplay between the landscape (*i.e.* spatial heterogeneity and temporal variability of habitats  
499 distribution) and the suitability of the habitat (*i.e.* host-plant identity). Clonal networks of host-  
500 plants may moreover contribute to the plant landscape permeability to AM fungi species *i.e.*  
501 facilitating their dispersal from one host species to another.

502 This study originally involves the use of landscape ecology concepts at a centimetric scale  
503 to address questions related to the community assembly of microorganisms. We argue that  
504 transposition of this biogeographic framework which involves powerful tools to study spatially  
505 determined processes at a very fine scale, would provide a new understanding of the community  
506 structure and dynamics of microorganisms. In particular, and for the first time, this framework  
507 provided us with an AM fungal “eye-view” of the host-plant community. Considering the spatial  
508 dimension in future studies should lead to a better appraisal of plant microorganism interactions, a  
509 current key concern in deciphering the plant-holobiont (*i.e.* the whole organism formed by the  
510 plant and the associated microbiota, see *e.g.* Vandenkoornhuyse, Quaiser, Duhamel, Lê Van, &  
511 Dufresne 2015; Vannier, Mony, Bittebiere, & Vandenkoornhuyse 2015).

512

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521

522 **Data availability statement**

523 The study accession number in the European Nucleotide Archive is PRJEB26688 (ERP108695).

Accepted Article

524 **Authors' contributions**

525 AKB, CM, PV conceived the experimental design. AKB performed the experiment. AKB, EM,  
526 AG, AD, and SC collected data. MB and Alexis Dufresne designed and ran the pipeline for  
527 amplicon sequences analyses. PV performed phylogenetic analyses. AKB and CM performed  
528 statistical analyses. AKB, CM and PV wrote the manuscript, and all authors contributed to  
529 revisions.

530

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#### 767 **Supporting Information**

768 Additional supporting information may be found in the online version of this article:

769 **Figure S1.** *Maximum likelihood phylogeny of the 173 most abundant OTUs.*

770 **Figure S2.** *Cumulated Glomeromycota OTUs frequencies from the rarified contingency matrix.*

771 **Figure S3.** *Ward clustering of the 38 AM fungal communities.*

772 **Figure S4.** *Results from the MultiCoLA.*

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**Table 1.** Mean percentages of abundance ( $\pm$ SD) of each plant species at different scales surrounding the sampling position of the AM fungal community of *E. repens* in 2011 (past) and 2012 (present). Abundance of plant species in a mesocosm was calculated as the ratio between the number of species occurrences and the number of grid cells (256). Because several plant species could occur in one cell of the grid, the summed abundances for a single mesocosm can be greater than 100%.

Spatial scales	Time scales	Erep	Asto	Hmol	Rrep	Bpin	Frub	Aten	Anob	Dglo	Hlan	Lper	Cnig
5 cm	Past	95.9 $\pm$ 11.2	20.5 $\pm$ 33.4	7.0 $\pm$ 14.4	5.8 $\pm$ 13.5	2.34 $\pm$ 7.0	<0.5	<0.5	<1.0	1.2 $\pm$ 5.1	4.1 $\pm$ 13.5	<0.5	<0.5
10 cm	Past	96.2 $\pm$ 9.2	19.8 $\pm$ 33.0	7.3 $\pm$ 13.8	7.5 $\pm$ 13.2	4.3 $\pm$ 8.1	1.3 $\pm$ 3.8	<0.5	0.5 $\pm$ 1.5	1.0 $\pm$ 4.4	3.5 $\pm$ 10.6	<0.5	<0.5
15 cm	Past	95.3 $\pm$ 9.7	20.5 $\pm$ 32.4	7.3 $\pm$ 12.5	6.4 $\pm$ 9.8	4.8 $\pm$ 10.0	2.0 $\pm$ 5.1	<0.5	0.7 $\pm$ 2.5	0.9 $\pm$ 3.7	3.1 $\pm$ 8.5	<0.5	<0.5
20 cm	Past	94.7 $\pm$ 10.7	20.7 $\pm$ 29.9	8.3 $\pm$ 12.3	7.1 $\pm$ 9.3	5.2 $\pm$ 10.2	3.0 $\pm$ 6.5	<0.5	0.7 $\pm$ 2.6	0.6 $\pm$ 2.6	2.7 $\pm$ 6.4	0.5 $\pm$ 1.3	0.9 $\pm$ 2.2
25 cm	Past	93.3 $\pm$ 13.6	21.9 $\pm$ 28.0	8.8 $\pm$ 12.7	6.7 $\pm$ 8.5	5.2 $\pm$ 9.0	3.2 $\pm$ 6.3	<0.5	<0.5	0.5 $\pm$ 1.7	2.7 $\pm$ 6.0	<0.5	0.8 $\pm$ 2.0

5 cm	Present	91.2 ±21.1	4.7 ±17.9	21.6 ±33.0	2.9 ±6.2	9.9 ±24.8	3.5 ±11.1	<0.5	<0.5	1.8 ±7.6	2.3 ±7.0	<0.5	<0.5
10 cm	Present	92.2 ±20.2	5.3 ±13.6	23.1 ±29.7	3.5 ±5.9	12.0 ±23.3	4.0 ±11.1	<0.5	<0.5	1.5 ±6.6	1.8 ±5.3	<0.5	<0.5
15 cm	Present	92.5 ±20.1	4.6 ±10.8	23.2 ±27.9	3.0 ±4.1	13.8 ±22.9	5.8 ±12.6	<0.5	<0.5	1.4 ±6.2	1.4 ±3.4	<0.5	<0.5
20 cm	Present	91.6 ±20.1	4.3 ±9.6	22.5 ±25.1	2.9 ±4.0	14.5 ±21.5	6.7 ±12.0	<0.5	<0.5	1.3 ±4.9	1.5 ±3.7	<0.5	0.5 ±1.6
25 cm	Present	92.0 ±18.4	4.0 ±8.7	21.2 ±22.7	2.8 ±3.9	15.4 ±19.5	6.6 ±10.5	<0.5	<0.5	1.6 ±3.7	1.3 ±3.4	<0.5	0.9 ±2.1

782 Notes: Erep, *Elytrigia repens*; Asto, *Agrostis stolonifera*; Hmol, *Holcus mollis*; Rrep, *Ranunculus repens*; Bpin, *Brachypodium pinnatum*; Frub,  
783 *Festuca rubra*; Aten, *Agrostis tenuis*; Anob, *Anthemis nobilis*; Dglo, *Dactylis glomerata*; Hlan, *Holcus lanatus*; Lper, *Lolium perenne*; Cnig,  
784 *Centaurea nigra*.

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**Table 2.** Mean percentages of abundance ( $\pm$ SD) of each plant species at different scales surrounding the sampling position of the AM fungal community of *B. pinnatum* in 2011 (past) and 2012 (present). Abundance of plant species in a mesocosm was calculated as the ratio between the number of species occurrences and the number of grid cells (256). Because several plant species could occur in one cell of the grid, the summed abundances for a single mesocosm can be greater than 100%.

Spatial scales	Time scales	Erep	Asto	Hmol	Rrep	Bpin	Frub	Aten	Anob	Dglo	Hlan	Lper	Cnig
5 cm	Past	34.5 $\pm$ 43.8	22.8 $\pm$ 36.8	7.6 $\pm$ 19.3	4.1 $\pm$ 8.5	49.7 $\pm$ 30.4	5.8 $\pm$ 18.3	18.1 $\pm$ 33.5	0.6 $\pm$ 2.5	<0.5	<0.5	<0.5	<0.5
10 cm	Past	35.6 $\pm$ 44.7	20.8 $\pm$ 34.3	6.8 $\pm$ 13.8	4.0 $\pm$ 9.2	46.1 $\pm$ 32.5	6.3 $\pm$ 14.6	14.8 $\pm$ 27.5	<0.5	<0.5	<0.5	<0.5	<0.5
15 cm	Past	36.7 $\pm$ 45.4	19.1 $\pm$ 31.8	6.3 $\pm$ 11.8	4.4 $\pm$ 8.7	46.1 $\pm$ 31.3	7.7 $\pm$ 12.9	12.1 $\pm$ 21.6	<0.5	<0.5	<0.5	<0.5	<0.5
20 cm	Past	36.6 $\pm$ 45.2	19.0 $\pm$ 31.1	5.9 $\pm$ 10.6	4.0 $\pm$ 7.8	46.1 $\pm$ 30.7	8.1 $\pm$ 12.0	10.4 $\pm$ 18.5	0.5 $\pm$ 1.2	<0.5	<0.5	<0.5	<0.5
25 cm	Past	35.9 $\pm$ 44.6	19.2 $\pm$ 31.1	5.5 $\pm$ 10.3	4.3 $\pm$ 7.9	45.7 $\pm$ 31.1	8.9 $\pm$ 11.6	9.8 $\pm$ 16.9	0.9 $\pm$ 2.0	0.6 $\pm$ 1.9	<0.5	<0.5	<0.5

5 cm	Present	29.2 ±43.1	<0.5	15.2 ±28.7	0.6 ±2.5	84.8 ±20.0	10.5 ±18.7	13.5 ±30.4	<0.5	<0.5	<0.5	<0.5	<0.5
10 cm	Present	30.8 ±44.4	0.5 ±1.5	15.8 ±28.4	1.3 ±3.1	84.0 ±17.3	10.5 ±15.5	12.5 ±24.5	<0.5	<0.5	<0.5	<0.5	<0.5
15 cm	Present	31.4 ±44.1	0.6 ±1.9	15.6 ±26.5	1.3 ±2.8	82.5 ±18.7	12.2 ±16.3	11.1 ±21.4	<0.5	<0.5	<0.5	<0.5	<0.5
20 cm	Present	31.1 ±43.0	1.5 ±3.0	15.4 ±25.1	1.5 ±3.3	80.1 ±21.0	12.4 ±14.8	10.1 ±19.2	<0.5	0.6 ±2.0	<0.5	<0.5	<0.5
25 cm	Present	32.0 ±43.1	2.0 ±3.8	14.4 ±23.9	1.7 ±3.5	77.5 ±23.2	13.6 ±14.3	10.1 ±18.3	<0.5	1.1 ±3.3	<0.5	<0.5	<0.5

790 Notes: Erep, *Elytrigia repens*; Asto, *Agrostis stolonifera*; Hmol, *Holcus mollis*; Rrep, *Ranunculus repens*; Bpin, *Brachypodium pinnatum*; Frub,  
791 *Festuca rubra*; Aten, *Agrostis tenuis*; Anob, *Anthemis nobilis*; Dglo, *Dactylis glomerata*; Hlan, *Holcus lanatus*; Lper, *Lolium perenne*; Cnig,  
792 *Centaurea nigra*.

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**Table 3.** Results from the most probable linear models ( $\Delta\text{AICc} < 2$ ) linking the indexes characterizing AM fungal community structure with plant species abundances in the neighborhood of the sampled individual (see Materials and Methods section for the model selection). The parameters represent the regression slopes associated with each explanatory variable, the model intercept, and the proportion of variance accounted for by the regression ( $R^2$ ).

	Time scale of response	Spatial scale of response (Radius)	$R^2$	Selected model formula
<b><i>E. repens</i></b>				
Richness <sup>†</sup>	Past	5 cm	<b>0.70***</b>	<b>5.53 – 0.07 Hmol – 0.29 Dglo – 0.06 Hlan</b>
	Past	10 cm	<b>0.70***</b>	<b>5.54 – 0.03 Hmol – 0.15 Dglo – 0.03 Hlan</b>
	Past	15 cm	<b>0.75***</b>	<b>5.52 – 0.02 Hmol – 0.09 Dglo – 0.27 Cnig + 0.14 Anob</b>
Equitability	Past	5 cm	0.14 <sup>t</sup>	<b>0.80 – 0.02 Hlan</b>
	Past	10 cm	0.06 <sup>ns</sup>	<b>0.80 – 7.0 × 10<sup>-3</sup> Hlan</b>
	Past	15 cm	<b>0.27*</b>	<b>0.80 – 0.11 Cnig – 9.0 × 10<sup>-3</sup> Dglo + 0.05 Anob</b>
<b><i>B. pinnatum</i></b>				
Richness <sup>†</sup>	Past	5 cm	<b>0.58**</b>	<b>5.41 – 0.05 Hmol – 0.06 Frub + 0.03 Erep</b>
Equitability	Past	5cm	<b>0.59***</b>	<b>0.84 – 0.02 Frub – 0.03 Rrep – 0.006 Aten</b>

*Notes:* As obtained through ANOVA analyses, bold indicates the significance of the model slopes *i.e.*  $P < 0.05$ , and asterisks indicate the significance level of  $R^2$ : ns = not significant; t  $0.1 > P > 0.05$ ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ . † log-transformation. The explanatory variables in the selected model formula correspond to the abundances of the plant species at the different spatial scales studied: Erep *E. repens*; Hmol *H. mollis*; Rrep *R. repens*; Frub *F. rubra*; Aten *A. tenuis*; Anob *A. nobilis*; Dglo *D. glomerata*; Hlan *H. lanatus*; Cnig *C. nigra*.

**Table 4.** Results from the significant Canonical Correlation Analyses linking the AM fungal occurrences and relative abundances with plant species abundances in the neighborhood of the sampled *E. repens* individuals. No CCA performed in *B. pinnatum* were significant. Constrained CCA inertia indicated the proportion of variance accounted for by the environmental matrix.

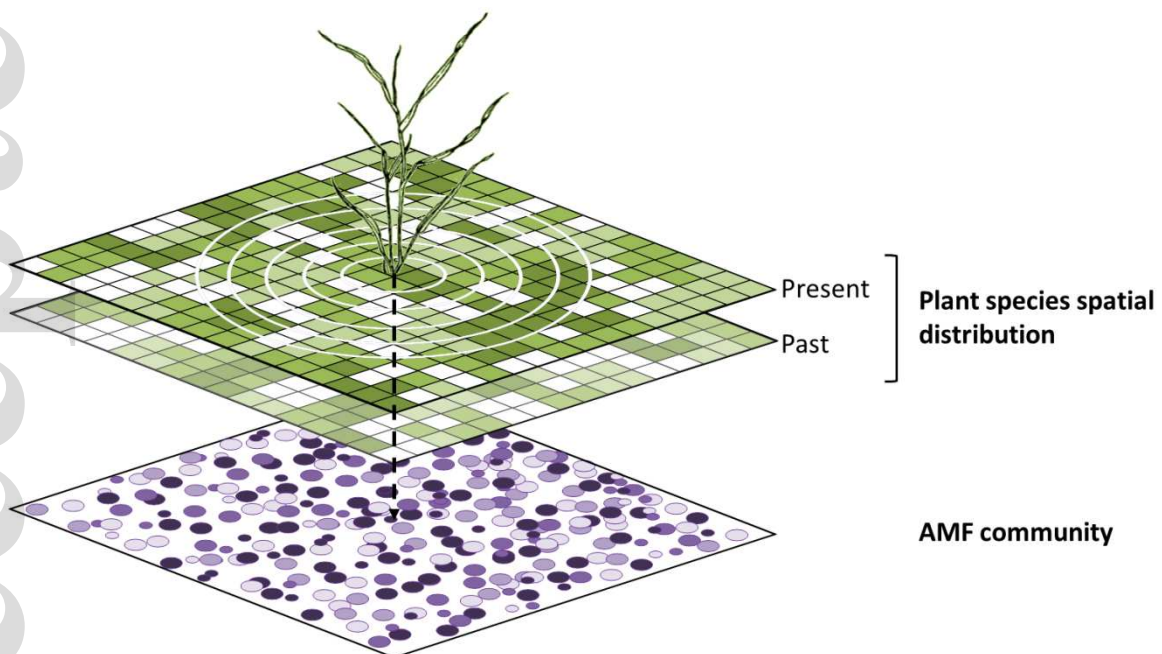
	Scale of response		ANOVA test			CCA inertia		Significant plant species
	Time	Space	Df	F	P-value	Total	Constrained	
OTU occurrences	Past	5 cm	4	1.42	*	0.75	0.30	Erep, Rrep, Anob, Hlan
OTU occurrences	Past	15 cm	5	1.45	*	0.75	0.38	Aten, Anob, Lper, Hlan, Cnig
OTU occurrences	Present	5 cm	2	1.63	*	0.75	0.18	Frub, Hlan
OTU occurrences	Present	10 cm	2	1.77	**	0.75	0.19	Erep, Hlan
OTU abundances	Past	10 cm	2	1.93	*	2.13	0.20	Anob, Hlan
OTU abundances	Past	15 cm	3	1.94	*	2.13	0.29	Anob, Hlan, Cnig
OTU abundances	Present	20 cm	3	1.91	*	2.13	0.29	Erep, Asto, Hlan

Notes: Constrained CCA Inertia is expressed as a proportion of Total CCA inertia. Asterisks indicate the significance level of the CCA: \*  $P < 0.05$ ; \*\*  $P < 0.01$ . The explanatory variables in the CCA correspond to the abundances of the plant species at the different spatial scales studied: Erep, *Elytrigia repens*; Asto, *Agrostis stolonifera*; Rrep, *Ranunculus repens*; Frub, *Festuca rubra*; Aten, *Agrostis tenuis*; Anob, *Anthemis nobilis*; Hlan, *Holcus lanatus*; Lper, *Lolium perenne*; Cnig, *Centaurea nigra*.

## Figure legends



**Figure 1.** Mesocosm design set up in the experimental garden of the University of Rennes 1 in May 2009, to study the role of plant clonal traits for the spatial dynamics and functioning of prairial systems. 14 types of plant communities were tested, differing in richness, nature and number of occurring functional groups based on plant clonal traits (from one to 12 plant species in mixture). Ten replicates of each community type were randomly positioned in the experimental design, comprising 140 square mesocosms. a) the 140 mesocosms in late April 2011, b) focus on mesocosms. The experimental plant communities studied in our work are part of this wider mesocosm design: we selected for each target species *B. pinnatum* and *E. repens*, 19 mesocosms out of the 140, in which they occur.



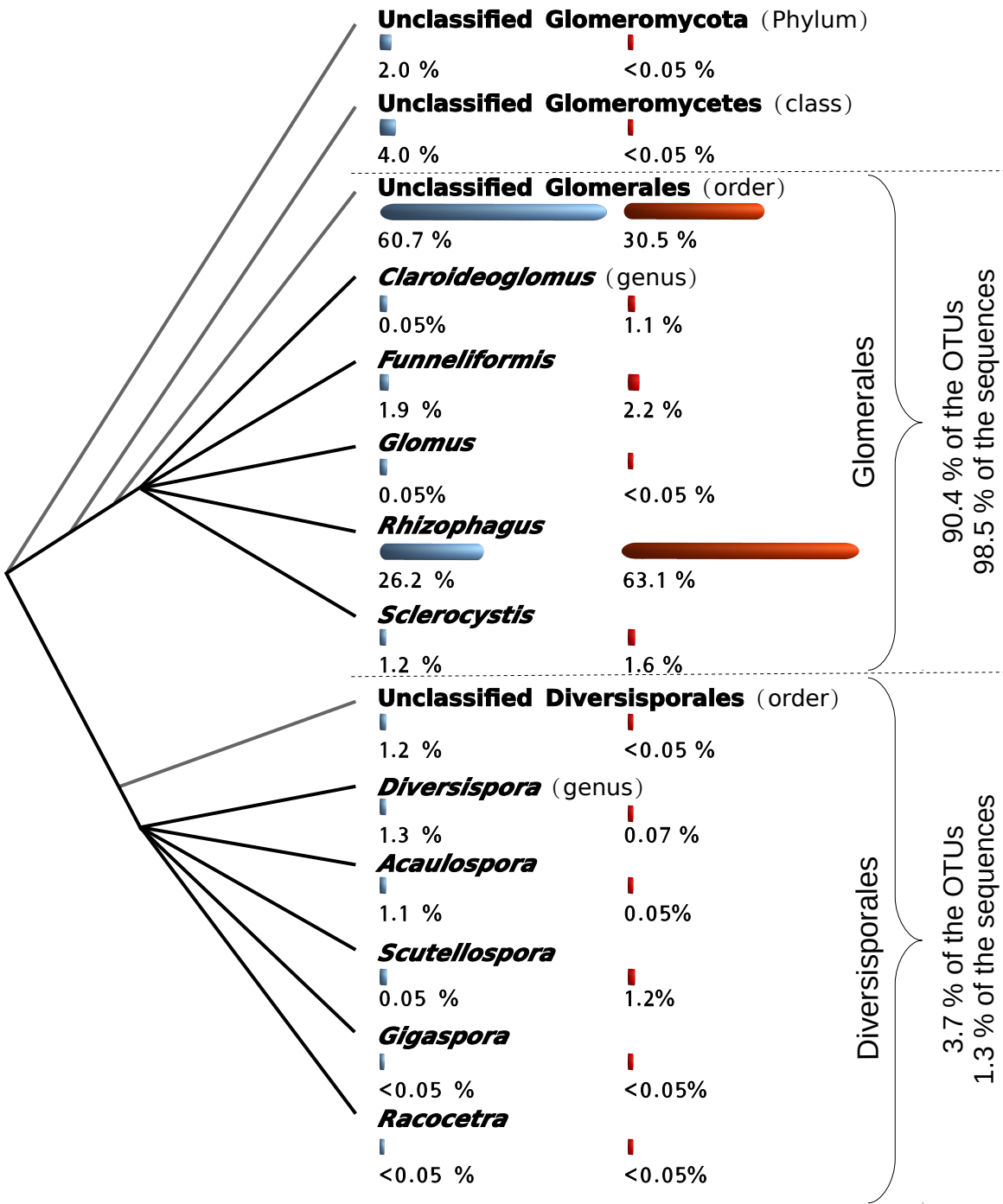
**Figure 2.** Characterization of the plant species spatial distributions. The black arrow represents the sampling point of the AM fungal community (in the roots of an *Elytrigia repens* or *Brachypodium*

*pinnatum* individual). The above two maps represent examples of the present and past spatial distributions of plant species (different species corresponding to different shades of green. Although more than one plant species can actually occur per cell, this has not been indicated here to simplify the figure. Circles surrounding the sampling point of the AM fungal community represent the different spatial scales that were tested in the analyses (5, 10, 15, 20, and 25 cm).

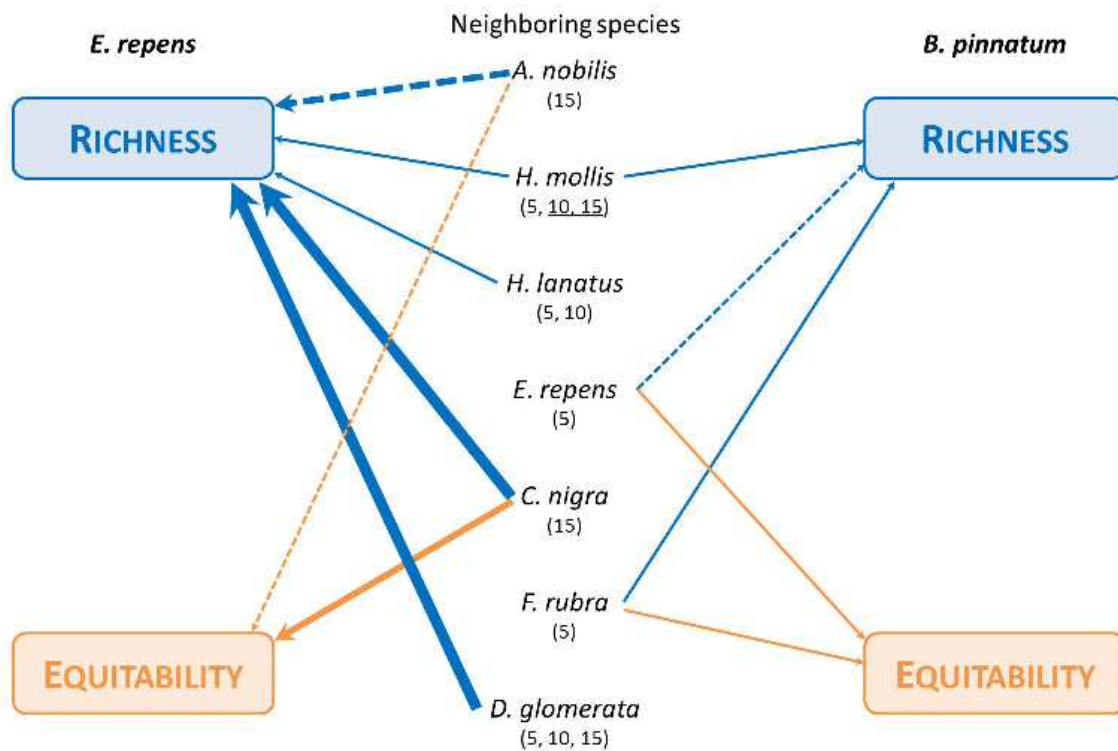
**Figure 3.** Taxonomic distribution of the sequence reads. This simplified cladogram resulted from a Maximum likelihood reconstruction using a small sample of each taxonomic group identified. The proportions of OTUs and sequences are shown beside the cladogram.

**OTUs**

**Sequences**







**Figure 4.** Past plant spatial patterns determine the AM fungal community structure. Only the most probable models describing a significant relationship between AM fungal richness or equitability and neighboring plant species abundances are plotted (neighboring species with no influence on AM fungal community indexes do not appear on this figure). Arrows thickness and style represent the significant model slopes *i.e.* respectively the strength and the sign (solid: negative; dashed: positive) of the influence of neighboring plant species abundances on *E.repens* or *B. pinnatum* AM fungal community structure. Values in brackets indicate the spatial scale of AM fungal community response (radius in cm) to neighboring plant species abundances. For *H. mollis*, underlined radius values are only for *E. repens* AM fungal community richness.