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

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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 m²
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, NO₃⁻ = 32.5
163 ±18.6 µg.g⁻¹ dry soil, PO₄²⁻ = 28.5 ±16.7 µg.g⁻¹ 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 80×80 cm square lattice on the mesocosm. Presence/absence data were
175 recorded in 5×5 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°C and subsequent analysis of the root endosphere compartment
200 (*e.g.* Lê Van et al., 2017).

201 The 38 root samples (~ 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, γ -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).

358

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 cm² (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),
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

Accepted Article

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*.

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
<i>E. repens</i>				
Richness [†]	Past	5 cm	0.70***	5.53 – 0.07 Hmol – 0.29 Dglo – 0.06 Hlan
	Past	10 cm	0.70***	5.54 – 0.03 Hmol – 0.15 Dglo – 0.03 Hlan
	Past	15 cm	0.75***	5.52 – 0.02 Hmol – 0.09 Dglo – 0.27 Cnig + 0.14 Anob
Equitability	Past	5 cm	0.14 ^t	0.80 – 0.02 Hlan
	Past	10 cm	0.06 ^{ns}	0.80 – 7.0 × 10⁻³ Hlan
	Past	15 cm	0.27*	0.80 – 0.11 Cnig – 9.0 × 10⁻³ Dglo + 0.05 Anob
<i>B. pinnatum</i>				
Richness [†]	Past	5 cm	0.58**	5.41 – 0.05 Hmol – 0.06 Frub + 0.03 Erep
Equitability	Past	5cm	0.59***	0.84 – 0.02 Frub – 0.03 Rrep – 0.006 Aten

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.

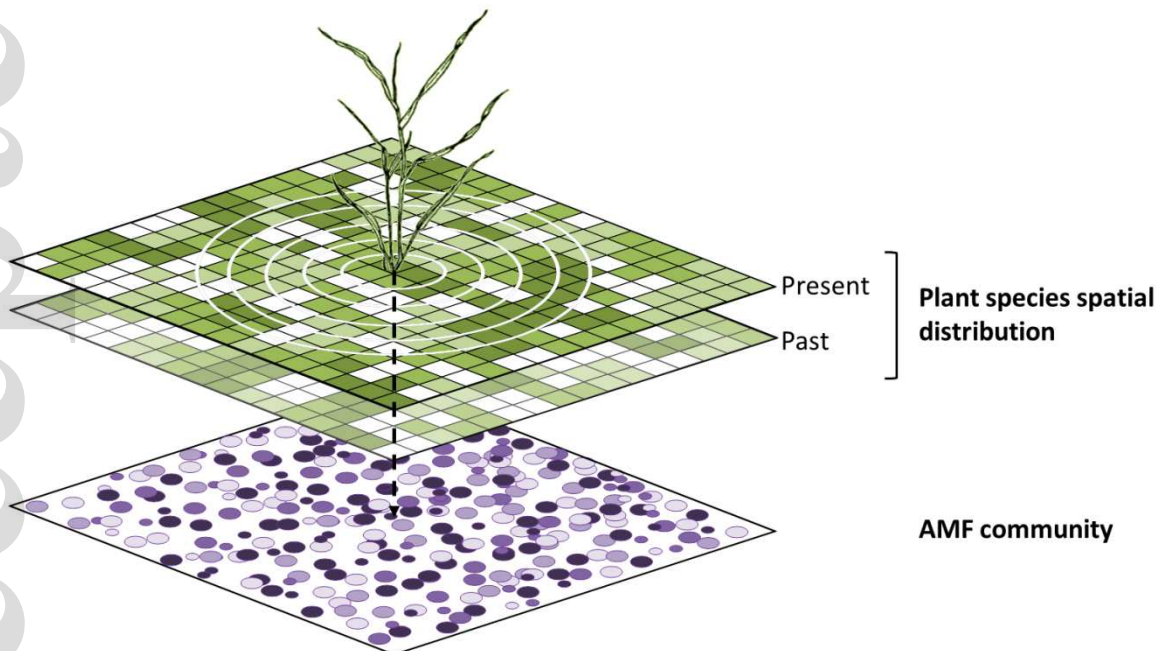


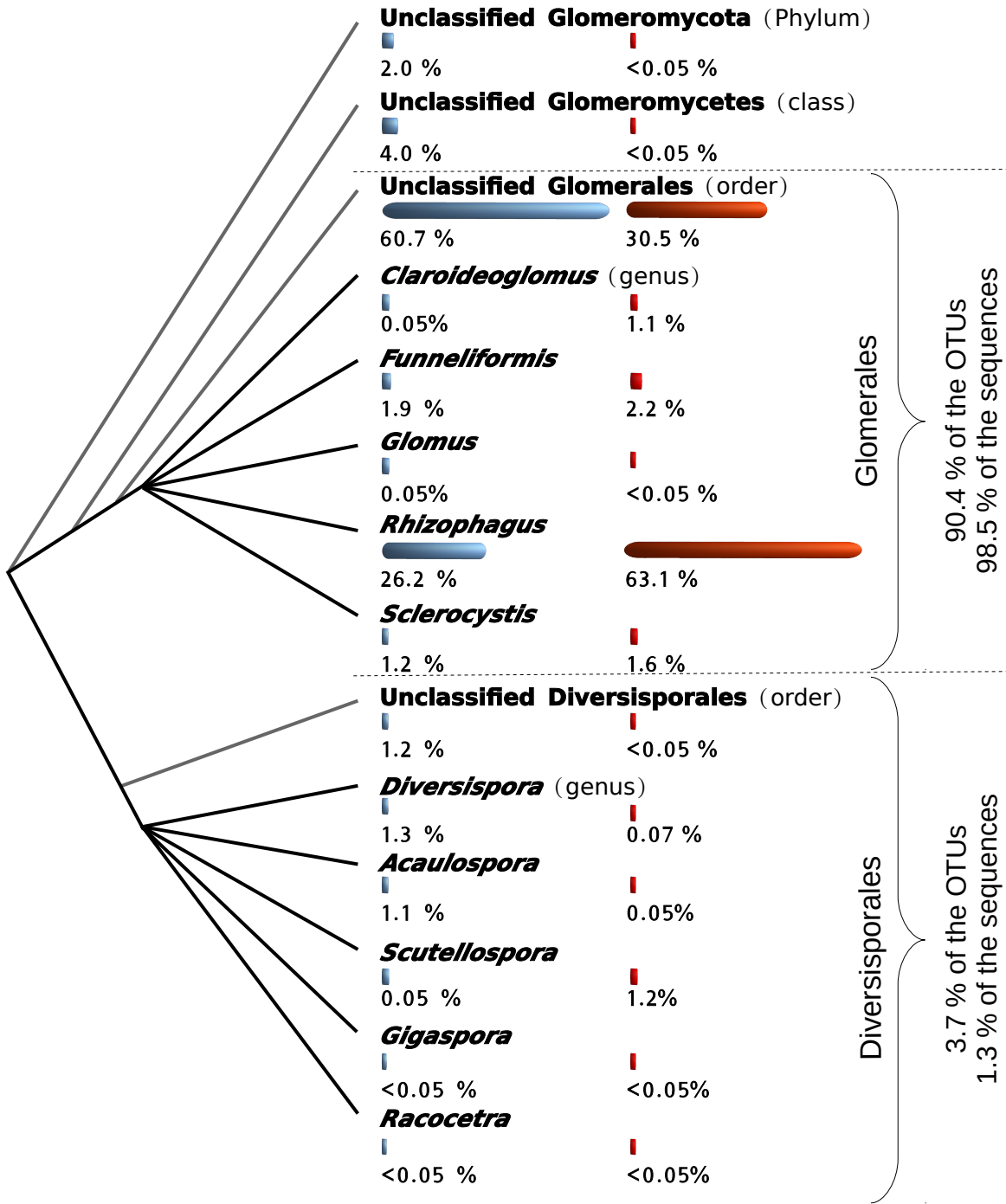
Figure 2. Characterization of the plant species spatial distributions. The black arrow represents the sampling point of the AM fungal community (in the roots of an *Elytrigia repens* or *Brachypodium*

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



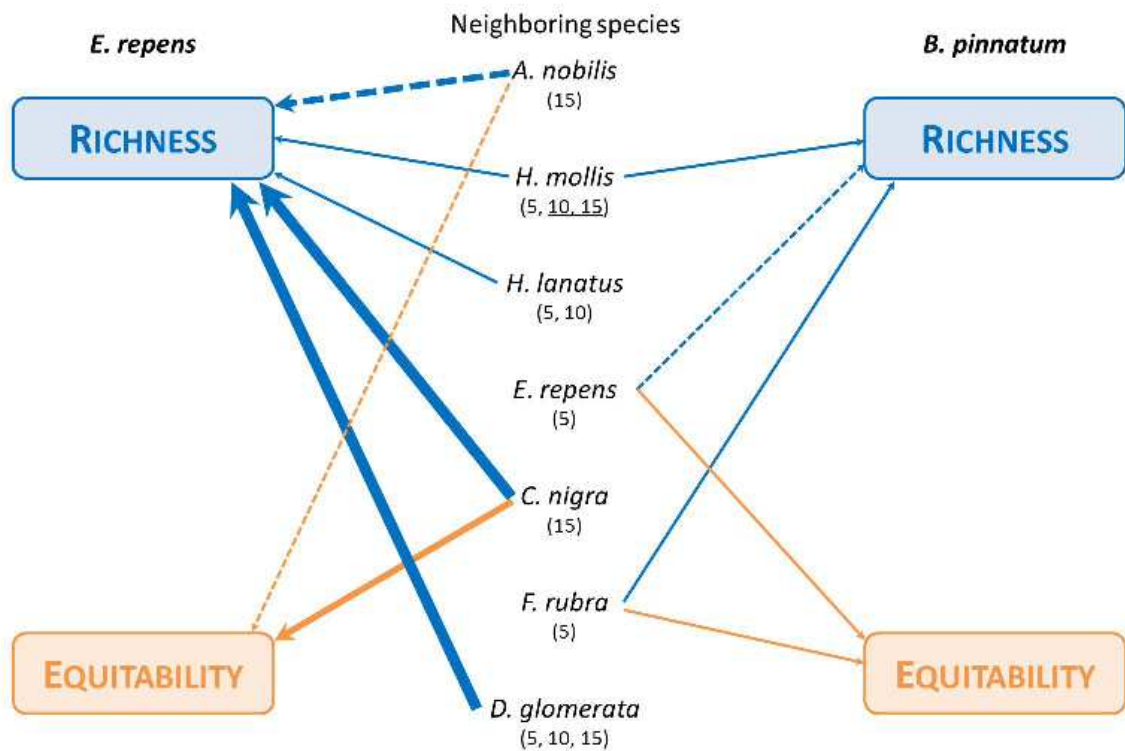


Figure 4. Past plant spatial patterns determine the AM fungal community structure. Only the most probable models describing a significant relationship between AM fungal richness or equitability and neighboring plant species abundances are plotted (neighboring species with no influence on AM fungal community 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.