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Abstract

It has been predicted that land use change will pose the main threat to biodiversity worldwide (Sala et al. 2000). A recent meta-analysis shows that, at local scale, conversion and degradation of habitats promote on average a global decline of 8.1 % of species richness and 10.1 % of abundance (Newbold et al. 2015). These human-mediated changes in biodiversity strongly affect ecosystem stability (Hautier et al. 2015). Given the importance of biodiversity on ecosystem functions and services, studies on the effects of land use on species assemblages are highly relevant in current global context.

Keywords (separated
by “ - ”)

Glomeromycota - Life history strategies - Biodiversity - Disturbance

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Chapter 7 1
Taxonomic and Functional Response 2
of Arbuscular Mycorrhizal Fungi to Land Use 3
Change in Central Argentina 4

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7.1 Introduction 7

It has been predicted that land use change will pose the main threat to biodiversity 8
 worldwide (Sala et al. 2000). A recent meta-analysis shows that, at local scale, con- 9
 version and degradation of habitats promote on average a global decline of 8.1 % of 10
 species richness and 10.1 % of abundance (Newbold et al. 2015). These human- 11
 mediated changes in biodiversity strongly affect ecosystem stability (Hautier et al. 12
 2015). Given the importance of biodiversity on ecosystem functions and services, 13
 studies on the effects of land use on species assemblages are highly relevant in 14
 current global context. 15

Despite that soil is an important reservoir of biodiversity (van der Heijden 16
 et al. 2008) and that belowground communities are important drivers of aboveg- 17
 round communities and ecosystem processes (Wardle et al. 2004), soil biota is 18
 generally underrepresented in studies linking land use–biodiversity–ecosystem 19
 processes. 20

Arbuscular mycorrhizal fungi (AMF) (Phylum Glomeromycota) are one of the 21
 main components of the soil biota. They are present in most terrestrial ecosystems 22
 and establish obligate symbiosis with more than the 80 % of land plants (Smith and 23
 Read 2008). These fungi depend on plant photosynthetic carbon while providing 24

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25 them with soil nutrients, among other benefits (Smith and Read 2008). The outcome
26 of the plant–fungus interaction highly depends on the fungal and plant identity and
27 the environmental context.

28 It has been widely documented that AMF affects plant community structure
29 (e.g., van der Heijden et al. 1998) and ecosystem processes such as productivity
30 (e.g., Klironomos et al. 2000), decomposition (e.g., Urcelay et al. 2011), and soil
31 aggregation (e.g., Rillig and Mummey 2006). Then, local decline of AMF diversity
32 under land use would have consequences on plant communities and ecosystem
33 functioning.

34 It has been recognized that not only richness or diversity per se but also
35 functional traits of species are important for understanding the response of
36 biotic communities to land use change as well as their impacts on ecosystem
37 processes and services (e.g., Díaz et al. 2007). This trait-based approach has
38 also been recognized as a useful framework to understand fungal ecology (e.g.,
39 van der Heijden and Scheublin 2007; Koide et al. 2014; Aguilar-Trigueros
40 et al. 2014).

41 The functional characteristics of AMF are considered phylogenetically fairly
42 conserved (Hart and Reader 2002; Powell et al. 2009; Maherali and Klironomos
43 2012). Based on C–S–R triangle (competitor, stress tolerator, ruderal) frame-
44 work (Grime 1979), Chagnon et al. (2013) recently assigned life history strate-
45 gies to the three main lineages of AMF (Gigasporaceae, Glomeraceae, and
46 Acaulosporaceae). Accordingly, Gigasporaceae are considered “competitors”
47 characterized by high soil hyphal densities, late production of spores in the
48 growing season, and higher nutritional benefits to hosts. In contrast, Glomeraceae
49 are “ruderals” characterized by higher growth rates, higher intraradical coloni-
50 zation, early production of spores, and low soil hyphal densities. The higher
51 intraradical colonization rates and lower soil hyphal densities imply less nutri-
52 tional benefits to hosts (e.g., Maherali and Klironomos 2007). In turn,
53 Acaulosporaceae is considered “stress tolerators” with low growth rates, long-
54 lived mycelium, resistance to acidity and low temperature among other stress-
55 ors, and probably more investment in constitutive defense (Chagnon et al. 2013).
56 These life history strategies could also be useful to explain fungal assemblages
57 in successional dynamics and their response to disturbances imposed by land
58 use change (Chagnon et al. 2013).

59 In central Argentina (Fig. 7.1), land uses such as fire, grazing, and forest frag-
60 mentation are among the most important environmental changes (Zak et al. 2004).
61 In the last 15 years, some studies were performed to assess the impact of those
62 anthropogenic activities on AMF communities. Here we review those studies to
63 analyze the response of AMF to land use. We particularly aimed to assess whether
64 grazing, fire, and forest fragmentation (a) promote a decline of AMF taxonomic
65 diversity and (b) negatively affect Gigasporaceae and Acaulosporaceae lineages’
66 spore abundance and Glomeraceae remains unaffected as predicted by the C–S–R
framework (Fig. 7.2).

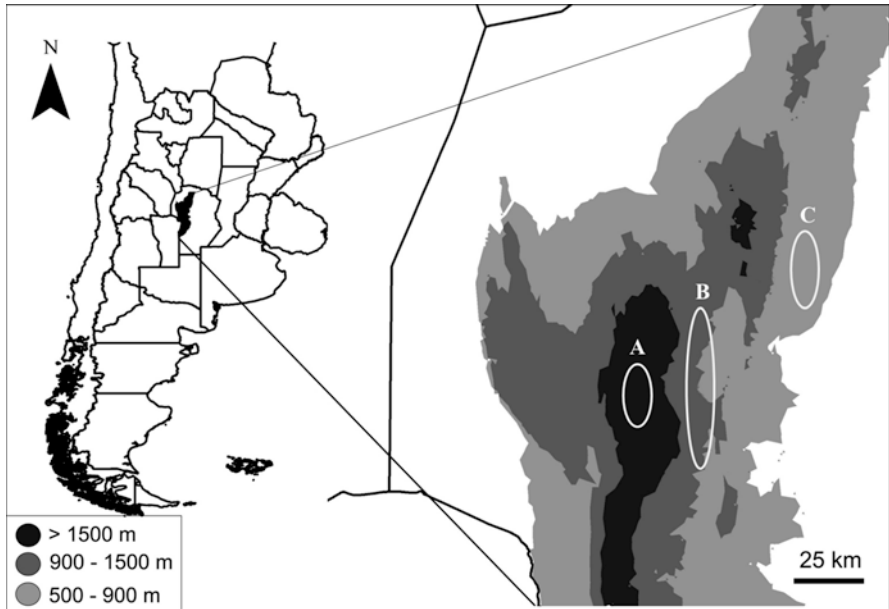


Fig. 7.1 Location of studied areas with each land use in Córdoba, central Argentina. (a) Mountain Grasslands (grazing). (b) Chaco Serrano Forests (fire). (c) Chaco Forests (forest fragmentation)

7.2 Effects of Land Use on Diversity and Abundance of AMF Spores

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To evaluate the effect of grazing on AMF spore communities, Lugo and Cabello (2002) conducted a study located in altitudinal grasslands in central Argentina. Six sampling sites were selected: three grazed and three ungrazed for a minimum of 20 years. Samplings were carried out over four seasons. The main findings of this study revealed no differences in spore richness, diversity, and abundance.

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Instead, Longo et al. (2014) found that fire severely affects AMF diversity. In this landscape-level study, five locations were selected in Chaco Serrano Forests. In each location, five nearby burned and unburned sites were studied in two seasons (autumn and spring). Results showed that diversity, richness, and evenness of AMF spores consistently decreased in the five burned sites and in some cases nearly half. However, spore abundance was not significantly affected by the fire.

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It has been widely documented that habitat loss promoted by human-mediated forest fragmentation strongly affects biological community's dynamics (e.g., Saunders et al. 1991). In this context, area size is an important factor affecting biodiversity (Haddad et al. 2015). Grilli et al. (2012) aimed to evaluate the relationship between area size of forest remnants and AMF spore communities at the

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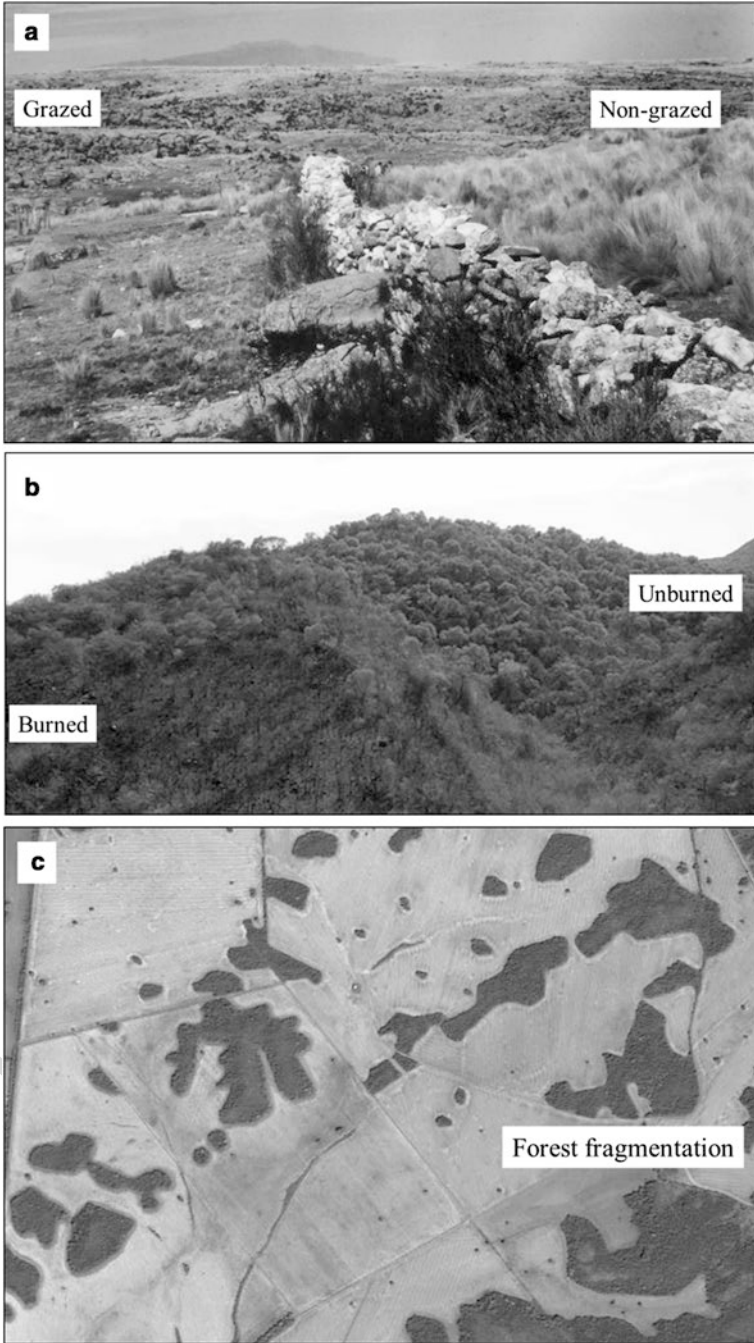


Fig. 7.2 Photographs of the three studied land uses. (a) Grazing in mountain grasslands; (b) fire in Chaco Serrano forests; (c) forest fragmentation in Chaco

landscape level. To this end, eight forest fragments with different sizes (0.86–1000 ha) immersed in an agricultural matrix in the Chaco region were selected. In this study, diversity of spores decreased with decreasing area size, while abundance marginally did it.

In Table 7.1 we summarized the direction of the response of each species (positive, neutral, or negative) to each land use *per* sampling season in those studies. Two species occurred in more than one study: *Entrophospora infrequens* and *Scutellospora biornata*. They were negatively affected in one case (by fire in spring) but not affected in the other five. The remaining species were analyzed within each particular study.

Grazing significantly decreased the abundance of *Scutellospora* sp. in one out of four seasons (winter). In contrast, the following species increased in response to grazing in one season: *Acaulospora laevis* (winter), *A. mellea* (autumn), and *Glomus* sp. (autumn). The remaining species showed neutral response to grazing.

Fire significantly decreased the abundance of several species. *Acaulospora rehmi*, *A. scrobiculata*, *Gigaspora gigantea*, *Gigaspora* sp. 1, and *Gigaspora* sp. 3 consistently decreased their abundance in burned sites in both seasons. In turn, *Ambispora jimgerdemannii*, *Entrophospora infrequens*, *Dentiscutata heterogama*, *Scutellospora biornata*, and *Scutellospora* sp. declined with fire in spring, while *Racocetra gregaria* and *Acaulospora* sp. 1 did it in autumn. In contrast, *Septoglomus constrictum* consistently increased in abundance in burned sites over both seasons, while *Glomus* sp. 4 and *Glomus* sp. 5 only did it in spring.

In fragmented forest, three unidentified species of *Glomus* significantly declined their abundance with decreasing area size. The remaining species were not affected.

These results show that the response of AMF depends on the land use type. While fire and reduction of area size seem to strongly decrease AMF diversity, no important differences between grazed and non-grazed sites were observed.

In comparison to fire and forest size reduction, grazing might not strongly affect soil properties and plant diversity. Indeed, despite that livestock grazing removes plant biomass they increase plant diversity in the studied mountain grasslands (e.g., Pucheta et al. 1998). In contrast, fire imposes great impacts to soils such as reduction or elimination of the aboveground and belowground biomass, loss of soil organic horizon, and increase in soil temperature and ash deposition (Neary et al. 1999; Certini 2005), at least in the short term (Neary et al. 1999). Regarding forest fragmentation, it has been shown in the studied area that reduction in area size is accompanied by a decrease in plant diversity (Cagnolo et al. 2006). Then, different impacts on soil properties and plant communities might explain the differential response of AMF communities to the studied land uses.

When looking at particular AMF, several species were not affected by land use while others consistently decreased or increased. Examples of these last cases are some *Gigaspora* species that decreased their abundance in burned sites in both seasons, while *Septoglomus constrictum* behaved in the opposite way (Table 7.1). These species could be considered as indicators of land use in the studied region (Oehl et al. 2003).

t1.1 **Table 7.1** Response of AMF spore species to land use (+: increased, -: decreased, and =: did not
t1.2 change)

t1.3	<i>Land use type</i>							
t1.4		Fire	Fire	Grazing	Grazing	Grazing	Grazing	Area
t1.5		spring	autumn	summer	autumn	winter	spring	size
t1.6	Acaulosporaceae							
t1.7	<i>Acaulospora alpina</i>							
t1.8	<i>A. bireticulata</i>							
t1.9	<i>A. cavernata</i>	=	=					
t1.10	<i>A. excavata</i>							
t1.11	<i>A. foveata</i>							
t1.12	<i>A. lacunosa</i>							
t1.13	<i>A. laevis</i>			=	=	+	=	
t1.14	<i>A. mellea</i>			=	+	=	=	
t1.15	<i>A. rehmi</i>	-	-					
t1.16	<i>A. rugosa</i>							
t1.17	<i>A. scrobiculata</i>	-	-					
t1.18	<i>A. spinosa</i>							
t1.19	<i>A. undulata</i>							
t1.20	Ambisporaceae							
t1.21	<i>Ambispora</i>							
t1.22	<i>appendicula</i>							
t1.23	<i>A. jimgerdemannii</i>	-						
t1.24	<i>A. leptoticha</i>							
t1.25	Claroideoglomeraceae							
t1.26	<i>Claroideoglomus</i>	=	=					
t1.27	<i>claroideum</i>							
t1.28	<i>C. luteum</i>							
t1.29	Entrophosporaceae							
t1.30	<i>Entrophospora</i>	-	=	=	=	=	=	
t1.31	<i>infrequens</i>							
t1.32	Gigasporaceae							
t1.33	<i>Dentiscutata</i>	-	=					
t1.34	<i>heterogama</i>							
t1.35	<i>Gigaspora gigantea</i>	-	-					
t1.36	<i>G. margarita</i>							
t1.37	<i>G. rosea</i>							
t1.38	<i>Racocetra gregaria</i>	=	-					
t1.39	<i>Scutellospora</i>	-	=	=	=	=	=	
t1.40	<i>biornata</i>							
t1.41	Glomeraceae							
t1.42	<i>Funneliformis badium</i>							
t1.43	<i>F. geosporum</i>							
t1.44	<i>F. mosseae</i>							

(continued)

Table 7.1 (continued)

<i>Land use type</i>		Fire spring	Fire autumn	Grazing summer	Grazing autumn	Grazing winter	Grazing spring	Area size
t1.45	<i>Glomus aggregatum</i>	=	=					
t1.46	<i>G. brohultii</i>							
t1.47	<i>G. dimorphicum</i>			=	=	=	=	
t1.48	<i>G. fuegianum</i>			=	=	=	=	
t1.49	<i>Rhizophagus clarus</i>							
t1.50	<i>R. intraradices</i>							
t1.51	<i>Sclerocystis coremioides</i>	=	=					
t1.52	<i>Sclerocystis rubiformis</i>			=	=	=	=	
t1.53	<i>Septoglomus constrictum</i>	+	+					
t1.54	<i>Septoglomus constrictum</i>							
t1.55	Unidentified							
t1.56	(Longo et al. 2014)							
t1.57	<i>Glomus</i> sp. 1	=	=					
t1.58	<i>Glomus</i> sp. 2	=	=					
t1.59	<i>Glomus</i> sp. 3	-	=					
t1.60	<i>Glomus</i> sp. 4	+	=					
t1.61	<i>Glomus</i> sp. 5	+	=					
t1.62	<i>Glomus</i> sp. 6	=	=					
t1.63	<i>Glomus</i> sp. 7	=	=					
t1.64	<i>Glomus</i> sp. 8	=	=					
t1.65	<i>Glomus</i> sp. 9	=	=					
t1.66	<i>Glomus</i> sp. 10	=	=					
t1.67	<i>Glomus</i> sp. 11	=	=					
t1.68	<i>Claroideoglomus</i> sp.	-	=					
t1.69	<i>Acaulospora</i> sp. 1	=	-					
t1.70	<i>Acaulospora</i> sp. 2	=	=					
t1.71	<i>Acaulospora</i> sp. 3	=	=					
t1.72	<i>Gigaspora</i> sp. 1	-	-					
t1.73	<i>Gigaspora</i> sp. 2	=	=					
t1.74	<i>Gigaspora</i> sp. 3	-	-					
t1.75	<i>Scutellospora</i> sp.	-	=					
t1.76	Unidentified							
t1.77	(Grilli et al. 2012)							
t1.78	<i>Glomus</i> sp. 1							=
t1.79	<i>Glomus</i> sp. 2							-
t1.80	<i>Glomus</i> sp. 3							=
t1.81	<i>Glomus</i> sp. 4							=
t1.82	<i>Glomus</i> sp. 5							=

(continued)

Table 7.1 (continued)

<i>Land use type</i>		Fire spring	Fire autumn	Grazing summer	Grazing autumn	Grazing winter	Grazing spring	Area size
t1.85	<i>Glomus</i> sp. 7							–
t1.86	<i>Glomus</i> sp. 8							=
t1.87	<i>Glomus</i> sp. 9							=
t1.88	<i>Glomus</i> sp. 10							=
t1.89	<i>Sclerocystis</i> sp.							–
t1.90	<i>Gigaspora</i> sp. 1							=
t1.91	<i>Gigaspora</i> sp. 2							=
t1.92	Unidentified (Lugo and Cabello 2002)							
t1.93								
t1.94	<i>Acaulospora</i> 2			=	=	=	=	
t1.95	<i>Acaulospora</i> 3			=	=	=	=	
t1.96	<i>Glomus</i> spp.			=	+	=	=	
t1.97	<i>Glomus</i> sp. 7			=	=	=	=	
t1.98	<i>Glomus</i> sp. 3			=	=	=	=	
t1.99	<i>Scutellospora</i> sp.			=	=	–	=	

131 **7.3 Effects of Land Use on AMF Spores: A Functional Group**
 132 **Approach**

133 Arbuscular mycorrhizal fungi were grouped into three functional groups according to their traits (*sensu* Chagnon et al. 2013): Gigasporaceae, Acaulosporaceae
 134 (Acaulosporaceae + Ambisporaceae + Entrophosporaceae), and Glomeraceae (Claroideoglomeraceae + Glomeraceae + Pacisporaceae). Then, the number of cases
 135 in each functional group that evidenced negative, neutral, or positive response to land use was computed and a Chi-square analysis on absolute frequency was
 136 applied (Table 7.2).
 137

138 The AMF functional groups were differentially affected by land use ($X_2=37.69$;
 139 $p=0.0001$). Specifically, Glomeraceae was mainly unaffected (84 % of analyzed
 140 cases) and the few positive and negative responses were equally distributed in the
 141 remnant cases. In turn, 74 % of Acaulosporaceae revealed neutral responses, while
 142 20 % and 6 % were negative and positive, respectively. In contrast, Gigasporaceae
 143 showed 58 % of neutral and 42 % of negative response cases.
 144

145 It is worth to highlight that Glomeromycota as a whole seem to be fairly resistant
 146 to land use since spore abundance was mostly unaffected. Nevertheless, there were
 147 clear differences between functional groups.
 148

149 In line with the C–S–R framework for strategies in AMF (see Fig. 1.1 in Chagnon
 150 et al. 2013), Gigasporaceae and Glomeraceae represented opposite trends in their
 151 response to land use. This is consistent with the competitor–ruderal life history axis,

t2.1 **Table 7.2** Number of positive, neutral, and negative response cases regarding the spore abundance
t2.2 of species belonging to three AMF functional groups

t2.3	Functional group	Land use effect		
t2.4		Positive	Neutral	Negative
t2.5	Glomeraceae	5	53	5
t2.6	Acaulosporaceae	2	26	7
t2.7	Gigasporaceae	0	15	11
t2.8	Total	7	94	23

t2.9 Glomeraceae includes Claroideoglomeraceae, Glomeraceae, and Pacisporaceae. Acaulosporaceae
t2.10 includes Acaulosporaceae, Ambisporaceae, and Entrophosporaceae; see Table 7.1 for more details

[AU7] closely related to environmental conditions caused by disturbance intensity. In turn, 152
Acaulosporaceae showed to be in mid position of the axis. This is not fully consistent 153
with the scheme adapted by Chagnon et al. (2013). 154

The majority of Glomeraceae seems to be resistant to disturbance posed by land 155
use such as fire, grazing, and forest fragmentation. This is consistent with their 156
“ruderal” life strategy which is characterized by rapid growth, capacity to fuse 157
hypha and restore integrity of the mycelium in soil, and earlier investment in spore 158
production (Chagnon et al. 2013). On the other hand, an important proportion of 159
cases in Gigasporaceae reveal that this group is particularly sensitive to disturbance 160
and would behave as “competitors.” They need to allocate large quantities of carbon 161
to extraradical mycelia for soil exploration and sporulate later in the growing season 162
(Chagnon et al. 2013). These traits make this functional group fairly incompatible 163
with the disturbances generally associated with land use. The results suggest that 164
Acaulosporaceae have traits situated in between “ruderal–competitor” axis, but this 165
remains to be explicitly measured. 166

Overall, these results reveal that trait-based approaches, in particular the C–R–S 167
framework, provide useful insight for ecological understanding of AMF ecology in 168
face of global change. 169

7.4 Conclusions and Future Directions 170

Altogether, the results analyzed here reveal that land uses in central Argentina 171
(grazing, fire, and forest fragmentation) tend to negatively affect AMF diversity, 172
mainly those human activities that involve severe soil damaging and decrease 173
plant diversity such as fire and forest fragmentation. When considering AMF 174
functional groups, Glomeraceae seems to be resistant to these land uses, while 175
Gigasporaceae seems to be fairly sensitive. It could be predicted that these changes 176
in AMF taxonomic diversity and functional traits would have consequences on 177
successional dynamics and ecosystem processes. For example, it has been shown 178
that Glomeraceae invests more in intraradical colonization than extraradical 179
mycelium and this may imply less nutritional benefits to plant hosts. In contrast, 180

181 Gigasporaceae largely invests in extraradical mycelium allowing for better exploi-
 182 tation of soil resources, particularly P, thus enhancing benefits to plant hosts
 183 (Maherali and Klironomos 2007). In addition, the large amounts of soil mycelium
 184 might promote better soil aggregation through glomalin secretion by these fungi
 185 (Rillig and Mummey 2006).

186 Further studies using trait-based approaches would be useful to test hypothesis
 187 regarding the AMF-mediated effects of land use on successional dynamics. This
 188 seems to be a fruitful way forward to gain knowledge for making predictions about
 189 the consequences of global changes on plant community dynamics and ecosystem
 190 functioning.

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AU1	Please check if the affiliations are presented correctly.	
AU2	Please provide email address for the corresponding author.	
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