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Hamid Amir, Yvon Cavaloc, Thomas Crossay, Alexandre Bourles, Simon Gensous, Alexandre Lagrange, Valérie Burtet-Sarramegna, Linda Guentas

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1 **Importance and roles of arbuscular mycorrhizal fungi in New Caledonian**
2 **ultramafic soils**

3

4 Hamid Amir, Yvon Cavaloc, Thomas Crossay, Alexandre Bourles, Simon Gensous, Alexandre
5 Lagrange, Valérie Burtet-Sarramegna, and Linda Guentas

6

7 Institut des Sciences Exactes et Appliquées (ISEA), Université de la Nouvelle-Calédonie, Noumea
8 98851, New Caledonia

9

10 Contact Hamid Amir : hamid.amir@unc.nc; <https://orcid.org/0000-0001-9777-4050>

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12

13 **ABSTRACT**

14

15 Our knowledge about New Caledonian serpentine ecosystems has increased greatly during the past
16 half-century, mainly thanks to Jaffré's group. However, research on soil microflora and plant
17 symbionts started only in the nineties and was mainly published during the last two decades. We
18 aimed to synthesize these studies, focusing particularly on arbuscular mycorrhizal fungi (AMF).
19 Research on AMF consisted firstly of a global and inventory approach aiming to produce basic but
20 essential lacking knowledge. These studies showed that AMF are abundant in ultramafic soils and
21 concerned nearly all plant species of these ecosystems. Even Ni-hyperaccumulator plants and
22 sedges, generally considered non-mycorrhizal, were found to be functionally colonized by AMF in
23 New Caledonian ultramafic soils. The adaptation of AMF communities to the extreme conditions of
24 these soils led to high levels of metal tolerance (particularly to Ni) and noticeable originality of the
25 taxa. The influence of these symbionts on plant growth and adaptation was assessed in greenhouse
26 and field conditions. An accurate selection of AMF isolates that improve plant growth, and plant
27 metal tolerance was performed. It was demonstrated that combinations of AMF isolates with
28 complementary functional traits showed high synergistic effects on plant development. Finally, a
29 partnership with a biotechnological company led to the production of an efficient commercial
30 inoculant now used in the ecological restoration of mine-degraded areas. Today studies are focused
31 mainly on the additive effects of AMF and mycorrhiza-helper bacteria.

32

33 **KEYWORDS**

34 AMF; bacteria; serpentine ecosystems; abiotic stress; toxic metals; restoration ecology; New
35 Caledonia

36

37 **Introduction**

38

39 Arbuscular mycorrhiza is among the most frequent plant-microbe mutualistic symbiosis, established
40 with 80% of vascular plants (Wang and Qiu 2006; Smith and Read 2008; Strullu-Derrien et al.
41 2017). This symbiosis is also one of the most ancient, initiated probably when plants have colonized
42 terrestrial areas more than 400 million years ago (Karatygin et al. 2006; Humphreys et al. 2010;
43 Strullu-Derrien et al. 2014). Arbuscular mycorrhizal fungi (AMF) act fundamentally on different
44 mechanisms of plant development, including mineral nutrition, drought resistance and toxic metal
45 tolerance (Smith and Smith 2011; Amir et al. 2014; Augé et al. 2015; Ferrol et al. 2016). Their use
46 in environmental remediation and ecological restoration is then particularly appropriate (Göhre and
47 Paszkowski 2006; Amir et al. 2019; Valliere et al. 2020). Moreover, these targeted environmental
48 applications are among the most advanced for large-scale mycorrhizal inoculation practices today
49 (Hart et al. 2017).

50 Serpentine ecosystems developed in ultramafic soils are generally characterized by extreme
51 conditions: macronutrient deficiency, unbalanced Ca/Mg ratio, metal toxicity and frequent drought
52 stress. These conditions have contributed to promoting original flora (Brooks 1987; Proctor 2003;
53 Jaffré and L'Huillier 2010; Isnard et al 2016). It is particularly the case in New Caledonia, a Pacific
54 island biodiversity hot spot (Myers et al. 2000, Marchese 2015), characterized by endemism of 96.7
55 % of the ultramafic obligate flora (Isnard et al. 2016). This precious biodiversity is threatened by
56 mining activities, fires, and other anthropogenic influences (Jaffré et al. 1998; L'Huillier et al.
57 2010).

58 The origin and pedological classification of new Caledonian ultramafic soils and their
59 physicochemical features have been subject of many studies from the seventies (Jaffré et al. 1971;
60 Jaffré and Latham 1974; Latham 1975; Latham et al. 1978; Jaffré and L'Huillier 2010). Metal
61 concentrations and their bioavailability in these soils were also investigated in relation to their
62 potential toxicity on plants (L'Huillier and Edighoffer 1996, Quantin et al. 1997; L'Huillier et al
63 1998). However, their microbiology has not been investigated until the nineties, and this was also
64 true for other countries, with rare exceptions (Lebedeva et al. 1978). In particular, AMF survival
65 and activity, and their relationships with plants in these extreme conditions, with very low

66 phosphorus availability (Dubus and Becquer 2001; Jaffré and L’Huillier 2010) and high potentially
67 toxic metal concentrations constituted an original unexplored research subject.

68 The first study on mycorrhizal associations in ultramafic soils worldwide concerned AMF
69 spore densities and mycorrhizal colonization of 13 endemic plant species in different New
70 Caledonian sites (Amir et al. 1997). From the year 2000, several publications showed the high
71 interest of these extreme soils to investigate the role of mycorrhizal symbiosis in the adaptation to
72 edaphic and environmental stresses of plants (Boulet et al. 2005; Jourand et al. 2010a; Lagrange et
73 al. 2011; Orłowska et al. 2011; Amir et al. 2013). The adaptive traits of fungal symbionts were also
74 highlighted (Turnau and Mesjasz-Przybyłowics 2003; Amir et al. 2008; Jourand et al. 2010b;
75 Branco and Ree 2010; Majorel et al. 2012).

76 Studies on ectomycorrhizas (EM) in New Caledonian ultramafic ecosystems were not detailed
77 here. EM are important particularly in forests (Carriconde et al. 2019) and in maquis dominated by
78 *Tristaniopsis* and *Sannantha* (Myrtaceae) species or *Acacia spirorbis* (Fabaceae) (Pillon et al.
79 2021). They are present on trees belonging to Myrtaceae, Fabaceae, Casuarinaceae and
80 Nothofagaceae families (Perrier 2005; Amir and Ducouso 2010; Carriconde et al. 2019). A recent
81 list of EM plants was reported in Pillon et al. (2021). Their role is then complementary with AMF,
82 root system of some plants (*Tristaniopsis* and *Nothofagus* (Nothofagaceae) species for example)
83 being simultaneously colonized by the two symbiont groups (Perrier et al. 2006). EM have also a
84 good potential for their use in ecological restoration of mined areas (Houlès et al. 2022).

85 In New Caledonia, studies on AMF were taken over mainly by the University of New
86 Caledonia. This review synthesizes those focused on ultramafic soils, particularly the ecological
87 aspects and their practical consequences for the ecological restoration of mine-degraded areas. Are
88 these symbionts able to maintain their spores and colonize root systems in these extreme soils, and
89 how AMF diversity is shaped by these conditions? Are the most frequent plants in ultramafic
90 maquis, particularly those used in restoration programs, arbuscular mycorrhizal? What are the main
91 functions of AMF in plant nutrition, and how could they participate to plant adaptation to highly
92 stressed conditions? These questions are relevant not only for science, but also for their potential
93 use in ecological restoration of mined areas.

94

95 **Exploration and inventory studies**

96

97 When research on ultramafic soil microbiology started in New Caledonia, the abiotic
98 characterization of these substrates in relation to ecosystem functions was relatively advanced (Jaffré

99 et al. 1971; Jaffré and Latham 1974; Lee et al. 1977; Becquer et al. 1995). Microbiological studies
100 were then focused first on a global approach that can help to explain some ecological specificities of
101 the studied ecosystems. Quantitative and qualitative analyses of soil microbiota and its activity in
102 relation with plants and soil metal concentrations were assessed (Amir and Pineau 1998; Saintpierre
103 2001; Amir and Pineau 2003a, 2003b). These publications showed different specificities of
104 ultramafic soil microbiology, with low level of activity but high metal tolerance of the microbiota,
105 part of which being responsible of the release of different metals, including Ni and Co. *Frankia*
106 symbiosis with Casuarinaceae is frequent in New Caledonian ultramafic ecosystems (Navarro et al.
107 1999; Gauthier et al. 1999) and may play an important role in nitrogen enrichment of these soils. A
108 global approach on plant growth promoting rhizobacteria was initiated (Mercky 1999). More
109 recently, it was shown that ultramafic soil properties do not limit their microbial diversity (Bordez et
110 al. 2016; Carriconde et al. 2019). However, this rich diversity showed wide variations in relation to
111 environmental conditions (Bordez et al. 2016; Gourmelon et al. 2016). The vegetation cover,
112 particularly its density, seemed to play a major role. Among soil properties, pH, nitrogen and
113 calcium influenced the distribution patterns of microbial communities.

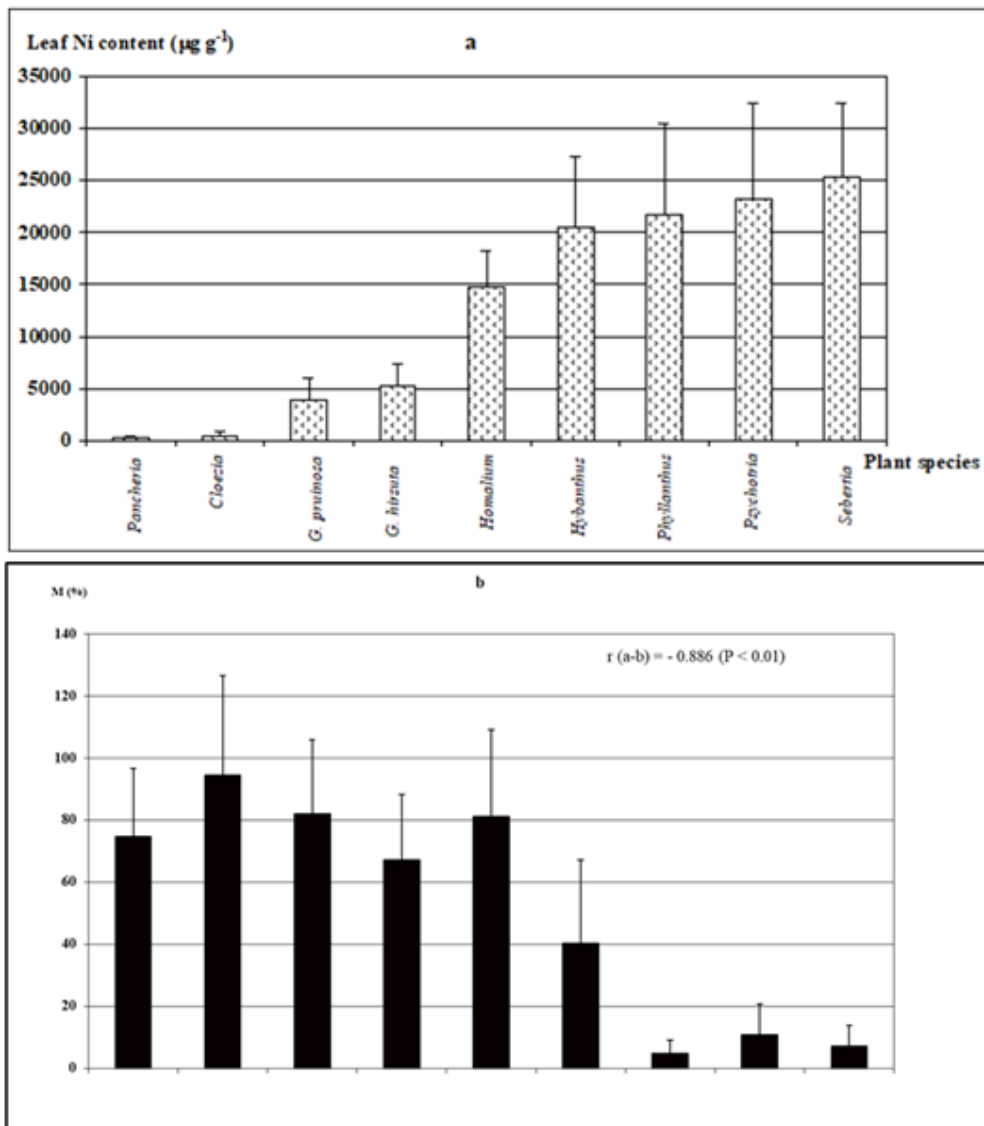
114 After exploratory works on mycorrhizas (Amir et Pineau 1997; Perrier 2005; Perrier et al.
115 2006), it was clear that AMF are abundant in New Caledonian ultramafic soils. Most of the plant
116 species tested were found to be arbuscular mycorrhizal, and AMF spore densities were globally
117 similar to those of non-ultramafic soils (Perrier et al. 2006; Amir and Ducouso 2010). If AMF root
118 colonization does not generally induce changes in root morphology, Duhoux et al. (2001) showed
119 that *Gymnostoma* trees (Casuarinaceae) produce small root nodules called myconodules, colonized
120 by AMF related to *Glomus*. Similar small nodules rich in AMF structures were found in roots of
121 *Podocarpus* trees (Podocarpaceae) in New Zealand (Russel et al. 2002), and were confirmed to be
122 present with the same characteristics in *Araucaria* trees in New Caledonia (Amir, unpublished
123 data). A correlation between AMF spore abundance and soil global activity was detected (Perrier et
124 al. 2006) probably due to negative effect on AMF development of high phosphorus deficiency of
125 the poorest soils (Lagrange et al. 2013; Amir et al. 2021). A list of over 60-studied plant species,
126 particularly those used in ecological restoration, presenting their affinity with AMF or
127 ectomycorrhizal fungi was then published (Amir and Ducouso 2010).

128 **Adaptation of arbuscular mycorrhizal symbiosis to ultramafic soils**

129

130 In the past, Ni-hyperaccumulating plants were generally assumed to be non-mycorrhizal (Leyval et
131 al. 1997; Pawlowska et al. 2000). Amir et al. (2007) tested nine Ni-accumulating New Caledonian

132 plants ranging from weak accumulators to hypernickelophore species. All species were more or less
 133 mycorrhized, but mycorrhizal colonization was reduced by high levels of Ni-hyperaccumulation
 134 (Figure 1). Indeed, for the same species, the level of mycorrhizal colonization was negatively
 135 correlated with Ni-concentration in plant leaves. The main reason for classically considering Ni-
 136 hyperaccumulators as non-mycorrhizal was that the plant species generally studied for this property
 137 in Europe and USA belonged to non-mycorrhizal plant families (Brassicaceae, Caryophyllaceae).



138

139 **Figure 1.** Relationships between leaf Ni content and mycorrhizal intensity (M) of 9 Ni-
 140 accumulating plant species (means of 8-10 samples for each value); *G* = *Geissos*. The
 141 coefficient r (a-b) indicates the total linear correlation between the two parameters. From
 142 Amir et al. (2007), reprinted with the permission of Plant and Soil.

143

144 Some studies on metal-polluted soils have revealed the high tolerance to Zn and Cd of AMF
 145 isolated from this environment (Weissenhorn et al. 1994; Tullio et al. 2003). When tested for Ni
 146 tolerance, AMF from ultramafic soils were more tolerant than those from other origins (Amir et al.

147 2008). Moreover, isolates from roots of Ni-hyperaccumulating plants tolerated the highest Ni
148 concentrations (Amir et al. 2007; 2008). This last study also reported that Ni-tolerance of AMF
149 isolates could be inducted by the presence of this metal in the substrate solution during host plant
150 growth.

151 In New Caledonian ultramafic areas, the herbaceous stratum is mainly represented by
152 Cyperaceae (sedges), a family generally considered non-mycorrhizal (Brundrett, 2009). However,
153 several endemic Cyperaceae species highly adapted to ultramafic soils were colonized at low levels
154 by AMF (Perrier et al. 2006; Lagrange et al. 2011). Tested in greenhouse conditions and field
155 experiment, *Tetraria comosa*, one of the most frequent and pioneer sedge species in New
156 Caledonian maquis, was shown to be functionally mycorrhizal, even at low levels of root
157 colonization, with positive effects on plant survival rate and plant growth (Lagrange et al. 2011;
158 2013).

159

160 **Importance and role of AMF on plant adaptation to ultramafic soils**

161

162 AMF are obligate symbionts so their cultivation needs a host plant. Isolates from New Caledonian
163 ultramafic soils were obtained in a greenhouse in association with sorghum. This grass was chosen
164 not only because it has a good affinity with AMF, but also because it can grow in difficult
165 conditions with a relatively high rate, contrary to native species that grow slowly. The effects of
166 AMF isolates on plant development have then been tested with sorghum and two endemic shrubs,
167 *Alphitonia neocaledonica* (Rhamnaceae) and *Cloezia artensis* (Myrtaceae), currently used in
168 restoration programs (Amir et al. 2013). The study showed that AMF not only stimulated the
169 growth and phosphorus nutrition of these plants, but also reduced nickel absorption and its toxicity
170 (Figure 2). Similar but less important effects were obtained on *T. comosa* (Lagrange et al. 2011).



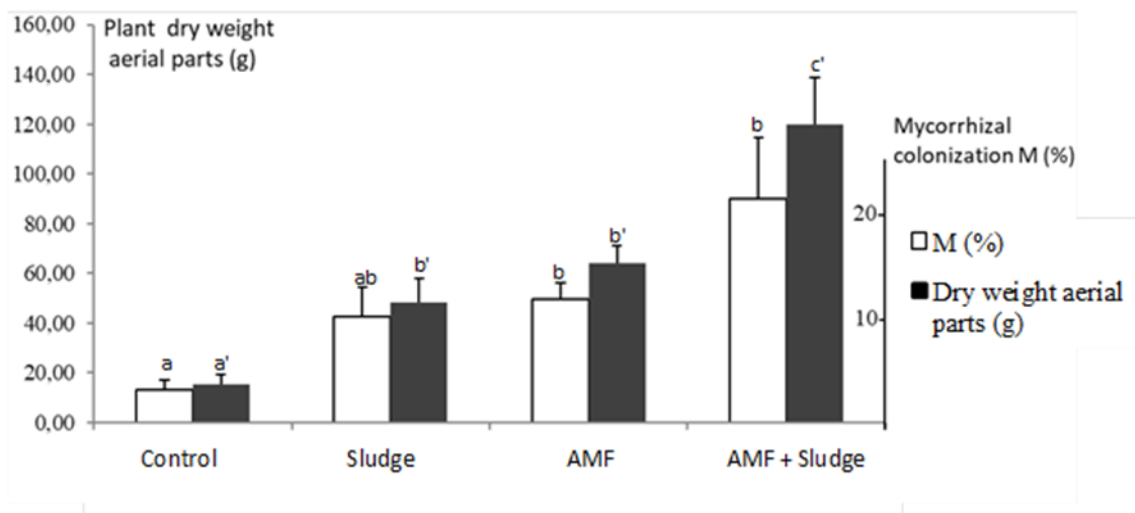
171

172 Figure 2. Aspect of *Alphitonia neocaledonica* plants in pots treated or not with nickel and
 173 inoculated or not with SFONL arbuscular mycorrhizal fungus isolate, showing Ni-toxicity
 174 symptoms. *A. neocaledonica* plants without Ni are not shown because they have the same
 175 aspect than SFONL 30 $\mu\text{g g}^{-1}$ Ni. NM: non mycorrhizal plants. From Amir et al. (2013),
 176 reprinted with the permission of Mycorrhiza.
 177

178 Ultramafic soils are often highly deficient in phosphorus (P), this element being moreover
 179 strongly adsorbed to iron oxides (Dubus and Becquer 2001; Jaffré and L'Huillier 2010). It is well
 180 known that an optimal level of available P in soil generally reduces AMF root colonization
 181 (Marschner 1995; Smith and Read 2008), but the effects of high P deficiency has received less
 182 attention (Abbott et al. 1984; Lambers et al. 2009). Lagrange et al. (2011) suggested that P
 183 deficiency could explain low levels of AMF root colonization in New Caledonian ultramafic soils.
 184 A field experiment with *T. comosa* in an ultramafic area confirmed this hypothesis: it showed that
 185 AMF root colonization and arbuscules' density of non-inoculated plants were clearly enhanced by
 186 phosphorus supply, with correlatively a better mineral nutrition (Lagrange et al. 2013).

187 In the latter cited study, plants were not inoculated with AMF. More recently, a field
 188 experiment with *Metrosideros laurifolia* (Myrtaceae) plants inoculated in greenhouse with a mix of
 189 three AMF isolates was assessed in an ultramafic area in Goro (south of New Caledonia). Stored
 190 topsoil spread in this area a few years before, and characterized by a low density of AMF spores,
 191 was amended or not with sewage sludge and planted with *M. laurifolia* plantlets (Amir et al. 2019).
 192 After 528 days, the aerial dry biomass of AMF-inoculated plants was four times greater than the

193 control ones (Figure 3). Mycorrhizal colonization was increased by sewage sludge inducing a
 194 complementary effect with AMF inoculation. This resulted in better plant growth and mineral
 195 nutrition, with plant biomass 7.7 times greater than control ones. Ca/Mg ratio was also enhanced by
 196 AMF inoculation, and the translocation to aerial parts of potentially toxic metals (particularly Mn,
 197 Ni, and Co) was strongly reduced. The analysis of AMF diversity in *M. laurifolia* roots showed a
 198 higher number of operational taxonomic units (OTU) in AMF-inoculated plants grown on non-
 199 amended plots compared to non-inoculated control. However, the introduced AMF isolates
 200 constituted at most, only 9% of the detected OTUs. These results were explained by the strong
 201 increase in plant biomass of AMF-inoculated plants. This increase allowed more carbon allocation
 202 to AMF in roots, the competition between AMF communities, then inducing a relative reduction of
 203 inoculated isolates. However, the relative decrease of the introduced isolates did not weaken the
 204 positive effects of mycorrhizal inoculation on plant nutrition and growth, even after 3.5 years (Amir
 205 et al. 2019). This latter point is interesting for AMF biotechnologies, knowing that inoculum
 206 reduction after a few months to a few years is one of the drawbacks of this practice (Pellegrino et al.
 207 2012; Janoušková et al. 2013).



208

209 Figure 3. Influence of AMF inoculation, sewage sludge and their combination on growth
 210 (plant dry weight of aerial parts) and mycorrhizal colonization (M%) of *Metrosideros*
 211 *laurifolia* plants, 528 days after plantation (mean values with standard error). Bars with the
 212 same letters are non-significantly different (post-hoc Bonferroni corrected Mann-Whitney
 213 test). From Amir et al. (2019), reprinted with the permission of Science of the Total
 214 Environment.

215

216 Studies on AMF diversity of New Caledonian soils, quite recently initiated, revealed the
 217 originality and high richness of AMF communities of ultramafic soils (Gensous 2014; Amir et al.
 218 2015; Cavaloc and Amir 2019). A comparison between AMF communities associated with roots of
 219 *Psychotria* (Rubiaceae) and *Phyllanthus* (Phyllanthaceae) species from tropical rain forests

220 developed on ultramafic and volcano-sedimentary soils, in four regions, was performed (Gensous
221 2014). AMF diversity richness did not differ significantly between the two types of forests, but
222 community composition was different. Ultramafic plants were associated mostly with the genera
223 *Rhizophagus*, *Glomus*, *Diversispora* and *Archaeospora*, whereas plants from volcano-sedimentary
224 soils were associated more frequently with *Acaulospora*, *Claroideoglomus*, and an unknown
225 Glomeraceae. Moreover, in ultramafic forest, AMF community composition differed significantly
226 between Ni-hyperaccumulating and non-accumulating plants. Cavaloc and Amir (2019) analyzed
227 the diversity of AMF in soils of 4 ultramafic open, dense and bushy maquis in south New
228 Caledonia. They reported total number of 188 Amplicon Sequence Variants (ASVs), varying from
229 72 to 104 ASVs per type of maquis, increasing with the vegetation density. Each analyzed plot
230 contained about 10 to 30 ASVs. Shannon-Wiener AMF diversity index varied from 1.5 to 3.5. Amir
231 et al. (2015) estimated AMF diversity inside roots of 4 endemic plant species collected from a dense
232 maquis in Goro (south New Caledonia). They detected 427 sequences corresponding to 54
233 Operational Taxonomic Units (OTUs), varying from 13 to 20 per plant species. These AMF
234 communities were dominated by Glomeraceae family, the genera *Rhizophagus* and *Glomus*
235 generally constituting more than 60% of the sequences (Gensous 2014; Amir et al. 2019; Cavaloc
236 and Amir 2019). The other most detected genera were *Sclerocystis*, *Acaulospora*, *Scutellospora*,
237 *Claroideoglomus*, *Diversispora*, *Redeckera*, and *Paraglomus*. Five AMF new species were
238 published (Blaszkowski et al. 2017; Crossay et al. 2018).

239 This diversity has also been the object of functional experiments. With a larger collection of
240 fungal isolates, greenhouse studies on the effects of different AMF mixes using the endemic plant
241 *M. laurifolia* grown on ultramafic soil were assessed, assuming synergistic effects would be found.
242 Indeed, combinations of co-inoculated isolates belonging to different families and having different
243 functional traits were more efficient than single ones (Crossay et al. 2019). The best mix improved
244 not only mineral nutrition with better absorption of major elements, particularly P and K, compared
245 to single isolates, but also increased Ca/Mg ratio and reduced Ni and Co translocation more clearly.
246 These effects resulted in a great growth improvement, with an aerial dry biomass 21.6 times bigger
247 than the non-inoculated plants. In contrast, the best single isolate induced a 12-fold increase of this
248 biomass. These results comfort the hypothesis stating that synergistic effects of AMF on plant
249 development are optimal when the phylogenetic distance between the mixed isolates is maximized
250 (Maherali and Klironomos, 2007), thus complementing biological niches and reducing functional
251 redundancy. Mathematical modeling of these AMF synergistic effects was produced (Crossay et al.
252 2019) explaining the experimental results with a high concordance ($R^2 = 0.90$, $p < 0.00001$).

253

254 **AMF and mycorrhiza helper bacteria**

255

256 Studies on bacteria and their communities in New Caledonian ultramafic soils have received less
257 attention than fungal symbionts (Héry et al. 2003; Herrera et al. 2007; Bordez et al. 2016;
258 Gourmelon et al. 2016). A few articles reported some of their growth promoting effects on plants
259 (Mercky 1999; Gonin et al. 2013; Bourles et al. 2019; Bourles et al. 2020a). Complementary effects
260 between bacteria and AMF have been addressed only recently (Bourles et al. 2020b). The latter
261 studied the strain BE isolated from the rhizosphere of *Tetraria* plants and screened by Gonin et al.
262 (2013) for its metal tolerance and plant growth promotion properties : phosphorus solubilization,
263 and production of indole acetic acid (IAA), siderophores, ammonium and 1-aminocyclopropane-1-
264 carboxylate deaminase (ACC deaminase). This bacterium belonging to the species *Curtobacterium*
265 *citreum* was able to form biofilm and produce an exopolysaccharide inducing Ni adsorption and
266 inactivation capacities (Bourles 2019; Bourles et al. 2019). The strain reduced Ni, Co and Cr
267 absorption by sorghum plants (Bourles et al. 2019) and strongly enhanced mycorrhizal colonization
268 (Bourles et al. 2020b). The latter study reported complementary effects on the growth and nutrition
269 parameters of *T. comosa* plants when the bacterium was co-inoculated with AMF in greenhouse
270 conditions. A field experiment testing these effects is underway.

271

272 **AMF and ecological restoration of ultramafic degraded areas**

273

274 A part of AMF studies in New Caledonia concerned directly the ecological restoration of ultramafic
275 mine-degraded areas. It was shown that AMF communities of revegetated subsoils on mine-
276 degraded areas are different and functionally non-equivalent with AMF communities of non-
277 degraded related ecosystems (Cavaloc et al. unpublished data). AMF diversity seemed to adapt to
278 the new conditions of the restored ecosystem. The reuse of topsoil, generally not recuperated by
279 mine companies until the nineties, was strongly recommended (Amir et al. 2003; Bordez et al.
280 2018), but in practice, this substrate was generally stored for years before being spread for
281 revegetation. Studies showed that topsoil storage not only reduces seed bank, soil activity and
282 nutrients' reserve, but also AMF spore density and AMF diversity (Amir et al. 2015; Amir et al.
283 2022). It was then recommended to reuse the topsoil for the revegetation as soon as possible,
284 preferably not more than 6 months after its stripping (Bordez et al. 2018; Amir et al. 2022).

285 Considering the important role of AMF in plant development on ultramafic areas, a company
286 partner of the University of New Caledonia developed recently a commercial inoculum, containing
287 synergistic isolates, based on Crossay et al. (2019) results, after innovation of an aseptic method for
288 AMF culture. Today, this inoculum is used to enhance growth and adaptation of plants for the
289 revegetation of mined areas in ecological restoration perspective. It is also envisaged to develop
290 inoculants with isolates that are specific to particular lateritic soils to avoid reduction of native
291 AMF biodiversity.

292 On-going greenhouse and field experiments aim to adapt the inoculation technic to seeding
293 methods, by incorporating AMF inoculum into seed balls. These experiments also test the co-
294 inoculation of AMF and MHB. Three to ten seeds of different native species, depending on their
295 size, are incorporated with AMF powder inoculum into 8 mm balls. The balls made with a mix of
296 clay and organic matter are then sowed and followed-up for seed germination, plant growth,
297 mycorrhizal colonization and inoculum behavior.

298

299 **Conclusion**

300

301 Research on mycorrhizas' role in New Caledonian ultramafic soils during the last two decades
302 followed a progression dictated by the local context. The protection of the biodiversity of valuable
303 ecosystems geared the studies toward the ecological restoration perspective. Yet, the originality of
304 ultramafic environment and the absence of knowledge worldwide on AMF symbiosis of these soils
305 have made this subject particularly attractive to investigate plant adaptation in extreme
306 environments.

307 The abundance and importance of these symbionts in New Caledonian ultramafic ecosystems
308 were shown, and their diversity and relative originality in relation to the high plant endemism of
309 this environment was then highlighted. The ability of AMF to improve plant mineral nutrition and
310 metal tolerance in harsh conditions pointed out the central role of these symbionts in plant
311 adaptation to multi-stress environments. Greenhouse and field experiments then revealed practical
312 perspectives.

313 If an efficient AMF inoculant adapted to ultramafic mined areas is commercialized today, more
314 research on microbial ecology are needed to improve restoration technics in such extreme
315 conditions. New microbe consortia containing AMF and bacteria constitute particularly an
316 interesting target for deeper investigations.

317

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323

324 Author contributions

325 HA managed the research, designed the experiments and wrote the article; YC designed and
326 followed up biomolecular studies; TC, AB, AL and SG contributed as PhD students to significant
327 parts of the studies; TC worked as co-manager of a private company in partnership with the
328 research team for the commercial use of selected AMF; VBS and LG followed up and designed
329 biochemical and bacterial studies; all reviewed the article text.

330

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333

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339

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