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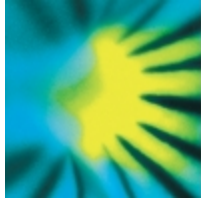
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# New Phytologist

**Misdiagnosis and uncritical use of plant mycorrhizal data are not the only elephants in the room: A response to Brundrett & Tedersoo (2018) 'Misdiagnosis of mycorrhizas and inappropriate recycling of data can lead to false conclusions'.**

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Manuscripts

1 **Misdiagnosis and uncritical use of plant mycorrhizal data are not the only elephants in the**  
2 **room: A response to Brundrett & Tedersoo (2018) ‘Misdiagnosis of mycorrhizas and**  
3 **inappropriate recycling of data can lead to false conclusions’.**

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25 There is increasing interest in using plant mycorrhizal traits – characteristics related to a plant’s  
26 ability to form mycorrhizal symbiosis – to understand the role of mycorrhizas within and across  
27 communities, ecosystems and biogeographical regions (Moora, 2014; Tedersoo, 2017). Recent  
28 studies incorporating plant mycorrhizal traits, mainly mycorrhizal type (e.g. ecto-, ericoid-,  
29 arbuscular-, and non-mycorrhizal; ECM, ERM, AM, NM) and mycorrhizal status (obligately and  
30 facultatively mycorrhizal; OM, FM; e.g. Correia et al. 2018; Gerz et al. 2018), have assigned trait  
31 values from published empirical data for plant species of interest. Dedicated efforts to build  
32 and improve databases of empirical plant mycorrhizal traits (e.g. Chaudhary et al. 2016; Bueno  
33 et al. 2017) are making these resources increasingly comprehensive, transparent and  
34 accessible.

35 A recent viewpoint paper by Brundrett and Tedersoo (2019) highlights several challenges  
36 connected with assigning mycorrhizal traits to plant species and criticizes the use of mycorrhizal  
37 trait databases. The authors argue that the use of such trait databases (which they refer to as  
38 “recycled data”) is ‘inappropriate’ due to two underappreciated problems: the databases (i)  
39 may include ‘mycorrhizal trait allocation errors’ due to misidentification of root mycorrhizal  
40 structures; or (ii) may contain data derived using diagnostic criteria that are flawed. They  
41 propose instead (1) diagnostic criteria for defining mycorrhizas that make specific assumptions  
42 about the biology of the interaction, and (2) checking databases against their curated list,  
43 derived from prior experience of assigning mycorrhizal traits to plant species (hereafter  
44 referred to as a 'standard reference', Brundrett, 2009; Tedersoo, 2017). Although we fully agree  
45 that standard protocols are required, there are several questions raised by the Brundrett and  
46 Tedersoo (2019) viewpoint that deserve critical consideration if consensus is to be reached  
47 among researchers in the field: 1) should the presence of minimum number of arbuscules  
48 define the AM symbiosis; 2) does plant taxonomy accurately predict plant mycorrhizal traits  
49 (i.e. high phylogenetic trait conservatism); 3) should the results of published studies be  
50 considered ‘incorrect’ when they do not match this, or any proposed, ‘standard reference’?  
51 Below, we discuss these three questions and address an additional topic that arises from  
52 consideration of Brundrett and Tedersoo’s criticisms of prior research: 4) the level of

53 transparency involved in building plant mycorrhizal trait databases and directions for future  
54 research.

55 **Point 1. Should the presence of arbuscules define AM plants?**

56 Symbiosis describes any intimate association of two organisms, while mutualism is an  
57 association that provides benefits for both. Mycorrhizal symbiosis is often interpreted as a  
58 mutualism, but depending on the environmental conditions in nature, the association varies  
59 along a continuum from mutualism to parasitism (Johnson *et al.*, 1997; Johnson & Graham,  
60 2013). The nutritional benefit of mycorrhizal interactions to plants has received most attention,  
61 but non-nutritional benefits, such as improved biotic and abiotic stress tolerance for host plants  
62 (Delavaux *et al.*, 2017) and habitat for the fungal partner (Brundrett, 2002), can occur and are  
63 also potential drivers of the symbiosis. Thus, in our opinion, the criterion proposed by Brundrett  
64 and Tedersoo, which focuses solely on the nutritional exchange, is too limited. Furthermore,  
65 Brundrett and Tedersoo argue that AM plant species should be defined by mycorrhizal  
66 structures devoted to nutrient exchange: the presence of arbuscules. While the presence of  
67 arbuscules could indicate P-transfer (if arbuscules are functional), the absence of arbuscules  
68 does not necessarily mean that nutrients are not transferred. For example, nutrient exchange in  
69 AM also occurs through hyphal coils (Paris colonization type) with no arbuscules involved  
70 (Dickson, 2004), or even in the absence of coils and arbuscules (Manjarrez *et al.*, 2010). Besides,  
71 the lifetime of arbuscules is short, and their presence depends on plant developmental stage  
72 (Montero & Paszkowski, 2018), meaning that detection of arbuscules is context dependent and  
73 practically challenging (Vierheilig *et al.*, 2005). Therefore, the distinction between AM plants  
74 (with arbuscules) and non-mycorrhizal (NM) plants with 'Glomeromycotan Fungal Colonization'  
75 (with no arbuscules or non-functional ones) based on potential nutritional function or lack  
76 thereof (Brundrett and Tedersoo 2019), is inconsistent with published observations. Also, any  
77 criterion that is based on terms such as "few", "many" and "low" (Table 1, Brundrett and  
78 Tedersoo 2019) is subjective. Based on this, we think it is premature to use the definition of AM  
79 proposed by Brundrett and Tedersoo 2019 and advocate for the more inclusive morphological  
80 criterion previously proposed by Smith & Read (2008), which is based only on root intracellular  
81 colonization by glomeromycotinan fungi. This definition is widely applicable to the different

82 contexts that occur in nature (e.g., during development of mycorrhizal fungal colonization,  
83 plant-specific developmental stages, seasonal and soil fertility variation) and avoids any criteria  
84 linked to a function (i.e., nutritional, non-nutritional) of the symbiosis, where the degree of  
85 mutualism may fluctuate independently from morphological structures. Moreover, in ECM  
86 plants, N-transfer does not necessarily require a Hartig net (Sa *et al.*, 2019). This demonstrates  
87 that for ECM symbiosis there are potential new discoveries that may change our understanding  
88 about the functioning of mycorrhizal symbiosis. It is our hope, however, that a definition  
89 encompassing all the complexities of the mycorrhizal symbiosis will evolve as our knowledge  
90 advances.

## 91 **Point 2. Can plant taxonomy be a reliable predictor of plant mycorrhizal traits?**

92 Brundrett and Tedersoo proposed a 'standard reference' for checking whether any new list of  
93 plant mycorrhizal traits contains potential errors. This 'standard reference' approach is based,  
94 in part, on the assumption that mycorrhizal traits can be assigned to species by extrapolating  
95 from higher taxonomic units, such as families or genera. The approach relies on the expectation  
96 that plant mycorrhizal traits are phylogenetically conserved within plant families or genera to a  
97 degree that allows predictions to be made. However, this assumption is not always justified.  
98 Taxonomy based extrapolations at lower taxonomic levels (e.g. within families and genera) may  
99 be more suitable for some mycorrhizal types (ECM, ERM, ORM), where well-studied plant  
100 groups are expected to exhibit highly conserved mycorrhizal traits. However, the approach  
101 could even yield errors in these groups because assumptions about the uniformity of  
102 mycorrhizal traits within well-studied plant groups are regularly disproved. For example, the  
103 ECM association was unexpectedly documented (based on morphology) in *Pulsatilla patens*  
104 (Hoeksema *et al.*, 2018), a species belonging to a family (Ranunculaceae) that contains a  
105 number of species, including *P. patens*, that have been shown experimentally to be highly  
106 dependent on AM symbiosis (Moora *et al.*, 2004).

107 A recent comparison of the Brundrett and Tedersoo's 'standard reference' and literature-  
108 derived databases of European plant species indicated frequently diverging mycorrhizal trait  
109 assignment. Based on the literature databases, only 19% and 6% of plant families (out of 75

110 European plant families with more than five studied species) comprised a single plant  
111 mycorrhizal type or status, respectively (Bueno *et al.*, 2019). One cause for low phylogenetic  
112 conservatism in mycorrhizal traits is that some plant species have adapted to different  
113 environmental conditions in a way that elicits changes in mycorrhizal traits (Gerz *et al.*, 2018).  
114 For instance, Osborne *et al.* (2018) recently described how adaptation to different soil  
115 conditions was accompanied by a divergence of mycorrhizal traits in sister palm species. This  
116 type of adaptation has not been systematically explored, but it may explain why phylogeny is  
117 not a consistently reliable tool for determining plant mycorrhizal traits within plant families or  
118 genera.

119 Given the discrepancies noted by Bueno *et al.* (2019) and the limited volume of existing plant  
120 mycorrhizal trait data (fewer than 5% of all plant species; Brundrett 2009) we argue that strong  
121 generalizations about the predictability of plant mycorrhizal traits from plant taxonomy are  
122 unwarranted. In fact, rigid adherence to this assumption could lead to misdiagnosis when newly  
123 explored plant species diverge from expectations or a new type of mycorrhizal association is  
124 discovered for a plant species. Therefore, care needs to be taken in making predictions based  
125 on plant's taxonomic placement, particularly for AM and NM types or FM status, which are less  
126 phylogenetically conserved than ECM, ERM and ORM types (Maherali *et al.*, 2016; Bueno *et al.*,  
127 2019). The amount of putative misclassification errors seems directly related to the level of  
128 taxonomy extrapolated, being higher within plant families than within genera (Bueno *et al.*,  
129 2019). Still, in contexts where the available evidence is absent for a high number of species,  
130 plant phylogenetic relationships, which are not yet fully resolved (APG, 2016), could be used as  
131 a reasonable starting point for formulating hypotheses regarding missing plant mycorrhizal  
132 traits, but those hypotheses should be tested and not be assumed to be correct in advance. We  
133 advocate for a more flexible view of mycorrhizal symbioses, where plant and fungal partners, as  
134 well as our knowledge about them, are constantly evolving (Selosse *et al.*, 2018). Overall, more  
135 empirical research, observing and analyzing mycorrhizal fungal colonization of plant species in  
136 natural systems is needed to overcome limitations, improve our extrapolations and hypotheses,  
137 and ultimately build our knowledge of mycorrhiza on more solid ground.

138 **Point 3. Constructing a 'standard reference'**

139 We agree with Brundrett and Tedersoo that detailed comparison with a critical review of  
140 knowledge accumulated in the field is necessary to contextualize new findings. However, there  
141 are unstated assumptions in the 'standard reference' proposed by Brundrett and Tedersoo that  
142 should be addressed in order for the field to advance. First, the binary evaluation ('correct' or  
143 'incorrect') of earlier studies disregards differences in the conceptual frameworks or definitions  
144 used by those studies. We are not suggesting that existing databases are error free, but genuine  
145 errors in plant mycorrhizal traits need to be distinguished from variation that is generated by  
146 using alternate, but still valid definitions of the mycorrhizal symbiosis (see point 1). Given  
147 differences in the definitions used by researchers to assign mycorrhizal traits, opinions about  
148 the conclusions of prior studies without appropriate analytical and/or empirical support should  
149 not be treated as evidence that prior conclusions were incorrect (Table 4, Brundrett & Tedersoo  
150 2019). In light of this, we do not think that researchers should be dissuaded from using curated  
151 databases, nor inherently disregard the output of analyses stemming from them without first  
152 examining the assumptions, objectives and definitions used by the authors. Second, it should  
153 be noted that the 'standard reference' cited in Brundrett and Tedersoo's viewpoint did not  
154 appear to be presented with detailed references or supporting information that could justify  
155 decisions about each family assignment to a mycorrhizal type or status (See point 4).

#### 156 **Point 4. Towards a transparent database of mycorrhizal traits and future research**

157 Any methodological approach is expected to be independently reproducible. Reproducibility is  
158 enabled by a clear methodological description that includes the criteria, background  
159 information and evidence used to justify conceptual or analytical decisions ('Towards  
160 transparency', 2014; Powers & Hampton, 2018). This is crucial if methodologies are to be  
161 assessed, discussed and improved in light of both conceptual developments and the availability  
162 of new information. To achieve this, we suggest that the research community strives to build a  
163 standard reference that represents a review of empirical evidence for all examined species,  
164 providing references and evidence to support mycorrhizal trait assignment (by morphological  
165 and ideally by functional features), and highlighting known uncertainties and knowledge gaps  
166 for which more empirical research is needed.



167 We hope that the discussion prompted by Brundrett and Tedersoo's viewpoint draws attention  
168 to a lack of consensus about core concepts in mycorrhizal ecology and provides incentive for  
169 researchers to openly discuss the various challenges, and to agree on core concepts. Moving  
170 forward, we advocate that researchers are transparent about the different conceptual  
171 frameworks used to make plant mycorrhizal trait assignments in their studies, and that readers  
172 consider such frameworks when drawing inferences from those studies. To spur expansion of  
173 the empirical knowledge base, we advocate the development of more inclusive definitions of  
174 mycorrhizal symbiosis and suggest that researchers strive to reach consensus on suitable  
175 definitions that allow us to capture features of the symbiosis that we are just beginning to  
176 discover. In this respect, meetings and forums such as ICOM (International Conference on  
177 Mycorrhiza) are ideal. A concerted effort to account for this complexity in detailed data  
178 collation will pave the way for future multidisciplinary work and enable new discoveries, such  
179 as unearthing possibly novel roles of the symbiotic partners. This approach could encompass  
180 experimental and observational studies at molecular to global scales, and could lead us towards  
181 a more comprehensive understanding of the functional roles of mycorrhizal symbioses in  
182 ecosystems.

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### 194 **Author contributions**

195 CGB and MM wrote the first draft, and all authors significantly contributed to revisions.

196

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