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Latitudinal constraints in responsiveness of plants to arbuscular mycorrhiza: The 'sun-worshipper' hypothesis.

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7 Latitudinal constraints in responsiveness of plants to arbuscular mycorrhiza: The
8 ‘sun-worshipper’ hypothesis.

9

10 Stavros D. Veresoglou^{1,2*}, Baodong Chen^{3,4}, Matthias M. Fischer¹, Thorunn Helgason⁵,
11 Andreas P. Mamolos², Matthias C. Rillig^{1,6}, Antonio Roldán⁷, David Johnson⁸

12

13 ¹ *Freie Universität Berlin, Institut für Biologie, Plant Ecology, D-14195 Berlin, Germany*

14 ² *Faculty of Agriculture, Laboratory of Ecology and Environmental Protection, Aristotle*
15 *University of Thessaloniki, 541 24 Thessaloniki, Greece.*

16 ³ *State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-*
17 *Environmental Sciences, Chinese Academy of Sciences, Beijing, China*

18 ⁴ *University of Chinese Academy of Sciences, Beijing, China*

19 ⁵ *Department of Biology, University of York, York, YO10 5DD, UK*

20 ⁶ *Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), D-14195 Berlin,*
21 *Germany*

22 ⁷ *CSIC-Centro de Edafología y Biología Aplicada del Segura, Department of Soil and Water*
23 *Conservation, P.O. Box 164, Campus de Espinardo, 30100 Murcia, Spain*

24 ⁸ *School of Earth and Environmental Sciences, The University of Manchester, Manchester,*
25 *M13 9PT. UK.*

26 * Email address: sveresoglou@zedat.fu-berlin.de, telephone: +49 30 838-53172

27

28 **Keywords**

29 Arbuscular mycorrhiza; eco-evolutionary processes; environmental filtering;

30 Glomeromycotina; mycorrhizal responsiveness; phenotypic adaptation; plant biogeography;

31 the sun-worshipper hypothesis

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35 Most terrestrial plants depend strongly on associations with arbuscular mycorrhizal (AM)
36 fungi (Subphylum: Glomeromycotina) to establish and survive (Bever, 2002; van der Heijden
37 *et al.*, 1998; Klironomos *et al.*, 2011; Veresoglou *et al.*, 2017), and have evolved a nutritional
38 mutualism. In this mutualism, the plant provides carbon to the fungus, usually subject to the
39 availability of light (Hayman 1970; Heinemeyer *et al.*, 2003; Shi *et al.* 2014; Konvalinkova &
40 Jansa, 2016), and the fungus provides the plant with mineral nutrients acquired from soil.
41 Because of light constraints, it is expected that latitude exerts a strong influence on reciprocal
42 exchange of resources between mycorrhizal plants and fungi, and this could have
43 consequences on the responsiveness of plants to mycorrhizal fungi. Latitude induces changes
44 in the amount of solar energy and the timing when this is made available to primary producers
45 during the year and in the day. At the same time, there is a strong negative relationship
46 between latitude and temperature that may also impact the functioning of the mycorrhizal
47 symbiosis, and in some cases (e.g. in north temperate systems), a general relationship between
48 latitude and several edaphic factors (Read and Perez-Moreno 2003).

49 There is compelling evidence that the alpha-diversity of Glomeromycotan fungi,
50 which form AM symbioses, decreases with latitude (Davison *et al.*, 2015). This finding can be
51 partially explained by the transition from ecosystems dominated by AM host plants in the
52 tropics, to ectomycorrhizal and ericoid mycorrhizal dominated ecosystems at higher latitudes
53 (Smith & Read, 2008). We know less about the extent to which latitude impacts the
54 functioning of AM symbioses, which could occur either through latitudinal differences in
55 solar radiation or resulting changes in temperature (Clarke & Gaston, 2006; Schluter, 2016).
56 Here, we propose the ‘sun-worshipper’ hypothesis that discriminates three different types of
57 underlying responses of latitudinal gradient-induced changes in plant host mycorrhizal
58 responsiveness (Fig. 1). Changes in abiotic conditions may allow plants to derive more
59 benefits from the symbiosis at lower latitudes through phenotypic plasticity (mechanism one –
60 Fig.1). A likely example of phenotypic plasticity might involve changes in the expression of
61 genes that allow crosstalk with AM fungi when light availability is low as has been shown for
62 drought (Li *et al.*, 2016). Abiotic conditions more favourable for the symbiosis close to the
63 tropics could further exclude, via competition, species less dependent on AM fungi, resulting
64 in distinct plant communities from a perspective of AM fungal-associating behaviour; such a
65 process can be described as environmental filtering (mechanism two – Fig. 1). Finally, we
66 know that AM plants at high latitudes encounter a less diverse pool of potential symbiotic
67 partners (e.g. because of the observed latitudinal gradient in Glomeromycotan diversity;
68 Davison *et al.*, 2015) and at the same time communities at high latitudes are in general

69 dominated by plants that associate with ectomycorrhizal and ericoid mycorrhizal fungi. Plants
70 distant from the tropics could thus form less profitable AM symbioses (but also support fewer
71 AM partners) because of a more limited pool of suitable AM fungal partners, and this
72 mechanism is analogous to the indirect eco-evolutionary causes (Pärtel, 2002) (mechanism
73 three - Fig. 1). Here, we use the term eco-evolutionary processes to describe combined effects
74 of latitude on phenotypic plasticity, environmental filtering and eco-evolutionary adaptation
75 of the host plant trait mycorrhizal dependency (e.g. Thuiller *et al.*, 2013). Even though these
76 different mechanisms are not mutually exclusive, it is important to disentangle how each of
77 them influences how host plants respond to mycorrhizal symbioses along gradients of latitude
78 and solar radiation.

79 The benefits that plants receive from the symbiosis in relation to the carbon costs vary
80 considerably depending on abiotic growth conditions (Johnson *et al.*, 1997; Hoeksema *et al.*
81 2010; Grman and Robinson, 2013), compatibility of the plant host with the local AM fungal
82 community (Klironomos, 2003) and the degree to which a plant can take advantage of non-
83 nutritional functions of mycorrhiza such as protection from pathogens (Veresoglou & Rillig,
84 2013). Resource stoichiometry of phosphorus (P), nitrogen (N) and light, in particular,
85 represents a proven tool explaining variance in growth responses of mycorrhizal hosts at
86 various spatial scales (Johnson, 2010). Latitude-related predictions could complement such
87 existing tools in understanding why mycorrhizal growth responses differ at large scales. It
88 may additionally illuminate systematic differences in mycorrhizal responsiveness such as
89 those explained by the life history of the hosts (Boerner, 1992; Roumet *et al.*, 2005). This
90 would be the case if the latitudinal effects are mediated through differences in solar radiation.
91 Annual terrestrial plants may never experience light-duration stress during winter, whereas
92 the opposite is the case for perennials that represent the majority of terrestrial plants (for
93 example over 70% of species in the LEDA database are perennials – Kleyer *et al.* 2008).
94 There is good evidence that perennial AM fungi can survive over winter in the roots of their
95 hosts (Buwalda *et al.*, 1985; Dodd & Jeffries, 1986 but see Hetrick *et al.*, 1984; Mohammed
96 *et al.*, 1988), which could affect the carbon economy of their plant hosts. During winter, plant
97 requirements for nutrients are limited and photoassimilates are in short supply; therefore,
98 plants that can confine the activity of their mycorrhizal partners may benefit through
99 improved survival rates. As a result, we expect that there is evolutionary pressure for
100 perennials to further confine mycorrhizal responsiveness when growing outside the tropics,
101 compared to annuals.

102

103 We undertook three synthesis activities to establish whether the expectations outlined
104 above are plausible for mycorrhizal systems (see Methods in supplementary material). We
105 first compiled a database on crop plant responses to mycorrhiza to identify phenotypic
106 responses to latitude (Fig. S1). To assess environmental filtering due to AM fungi with
107 regards to latitude, we synthesized data from a common garden experiment on comparative
108 mycorrhizal responsiveness of North-American annual and perennial herbaceous plants
109 (Wilson & Hartnett, 1998) with plant distribution data for the specific plants from USDA
110 (USDA, 2016). We also tested for differences in mycorrhizal responsiveness across genotypes
111 of *Zea mays* (maize) that are routinely used either in temperate or tropical systems, despite
112 that genetic variability could effectively be attributed to breeding. These syntheses activities
113 were not sufficiently robust to address the mechanistic constituents of the sun worshipper
114 hypothesis but were carried out to support the over-arching concept and encourage larger
115 syntheses or experiments exploring the hypothesis in the future.

116 Variance in the database on crop plant responses could be best explained, in our
117 models consisting of a single predictor, by photosynthetic radiation (Fig 2.a). The optimal
118 model had an intercept of -0.5 ($F=9.7$, $P<0.001$) and a slope per $\text{MJ}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ radiation of 0.23
119 ($F=6.1$, $P=0.019$). Fitted intercepts for the different plant species shared a standard deviation
120 of 0.048 (Fig. 2a). Analysis of maize lines demonstrated that eco-evolutionary processes also
121 drive latitude-dependencies on mycorrhizal responsiveness. The Mann-Whitney test between
122 temperate- (i.e. middle two quartiles) and tropical-climate adapted lines of maize revealed
123 higher responsiveness for temperate lines ($U = 24.5$, $P=0.034$). When we repeated this
124 analysis for tropical lines through maintaining the two middle quartiles, the differences
125 became even more apparent ($U = 4$, $P<0.001$, Fig. 2b). Mycorrhizal responsiveness of species
126 in Wilson and Hartnett (1998) could be predicted by latitude of their distribution, which
127 suggests that mycorrhizal responsiveness might induce an environmental filtering. We raised
128 latitude to the fourth power to address fitting issues and obtained an intercept of 0.65; latitude
129 slope of $-2.44 \cdot 10^{-8}$ ($F_{\text{lat}}=23.32$; $P<0.001$; $R^2_{\text{adj}}=0.19$; Fig. 2c). We subsequently fitted an
130 additional parameter that differentiated between annual and perennial plants. Inclusion of the
131 categorical variable perennial was significant ($F=23.36$, $P<0.001$) and there was a significant
132 interaction between this parameter and latitude ($F=9.47$, $P=0.003$) suggesting that slopes also
133 differed. When we analyzed annual and perennial plants separately, we found a significant
134 relationship only for perennials (Kendall Tau was -0.32 - $P=0.004$, whereas for annuals the
135 Kendall Tau was 0.03 - $P=0.87$).

136 The sun-worshipper hypothesis predicts that latitude impacts mycorrhizal
137 responsiveness in plants via three complementary mechanisms, namely phenotypic responses,
138 eco-evolutionary processes and environmental filtering (Fig. 1). Even though the analyses we
139 report have limited resolution, they were supportive of the sun worshipper hypothesis. We
140 found evidence that phenotypic plasticity (Fig. 2a), eco-evolutionary processes (Fig. 2b) and
141 environmental filtering (Fig. 2c) might be operational for all three different types of latitude
142 related differences in mycorrhizal responsiveness (Thuiller *et al.*, 2013). Despite the findings
143 from our analyses, it is important to highlight additional factors that may also influence
144 mycorrhizal responsiveness, and which have the potential to confound our findings. For
145 example, our observations may correlate with systematic differences in soil fertility; high
146 weathering rates generally lead to poorer fertility, as occurs in many parts of the tropics (Read
147 and Perez-Moreno, 2003). Therefore, disentangling the specific role of light versus other
148 edaphic and environmental factors in driving mycorrhizal responsiveness likely requires
149 additional experimentation. Testing competing hypotheses could be done with carefully
150 designed common garden experiments or synthesizing evidence from altitudinal experiments.
151 Nevertheless, our analysis and associated hypothesis prompts further mechanistic analyses to
152 test how resource stoichiometry and other critical functions undertaken by mycorrhizal fungi
153 are influenced by latitudinal gradients.

154

155

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161

162 **Contributions**

163 SDV: Conceived the project and carried out the analyses; SDV TH, APM, MCR, AR, DJ:
164 Discussed and further developed the idea; SDV, DJ: Wrote the manuscript; All authors
165 commented to the manuscript and approved the final version of it.

166

167 **Supplementary Information**

168 Appendix 1: Mycorrhizal dependency as proxy of investment

169 Appendix 2: Meta-analysis on phenotypic plasticity

170 Appendix 3: Eco-evolutionary processes on LGMR

171 Appendix 4: Environmental filtering on LGMR

172 Fig. S1: Locations of the 40 studies included in the meta-analysis

173 Table S1. Primary data on the 42 studies which we considered in our meta-analysis.

174

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250 colonization in tallgrass prairie. *American Journal of Botany* **85**, 1732-1738.
- 251

253 **Legends to Figures**

254

255 Fig. 1. The ‘sun-worshipper’ hypothesis: Light availability declines with latitude (x -axis) to
256 which plant species that associate with AM fungi respond via reducing their mycorrhizal
257 responsiveness (LGMR – y -axis right). This is depicted in the figure with the black
258 continuous line describing phenotypic plasticity (Mechanism 1). Eco-evolutionary responses
259 partially offset the decline in LGMR with latitude (the resulting black discontinuous line has a
260 lower slope - Mechanism 2). Reduced mycorrhizal responsiveness further induces a decline in
261 species that associate with AM fungi (red line) with species that either associate with
262 ectomycorrhizal (ECM) or ericoid (ERM) mycorrhizal fungi (green continuous line – y -axis
263 left). This represents Mechanism 3. As a result, latitude is a key factor that determining plant
264 responsiveness to mycorrhizal fungi

265

266

267 Fig. 2 (a) Scatterplot of mycorrhizal responsiveness plotted against photosynthetic radiation
268 during the growth period for the annual crops that we included in our crop dataset. The
269 relationship is positive; (b) beehive plot of mycorrhizal responsiveness of maize lines adapted
270 to growth under temperate vs tropical conditions. In the plot, we only used the two central
271 quartiles of the two groups of data. The differences are significant ($U = 4$, $P < 0.001$); (c)
272 maximum latitude of the distribution of North American herbaceous plants plotted against the
273 mycorrhizal responsiveness as assayed in a common garden experiment. Each cross describes
274 the maximum latitude of a single species and the red line is the best fit line for the relationship
275 with mycorrhizal responsiveness. We found few plants having a high mycorrhizal
276 responsiveness occurring at high latitudes.



