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

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Keywords
Arbuscular mycorrhiza; eco-evolutionary processes; environmental filtering; Glomeromycotina; mycorrhizal responsiveness; phenotypic adaptation; plant biogeography; the sun-worshipper hypothesis

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

There is compelling evidence that the alpha-diversity of Glomeromycotan fungi, which form AM symbioses, decreases with latitude (Davison *et al.,* 2015). This finding can be partially explained by the transition from ecosystems dominated by AM host plants in the tropics, to ectomycorrhizal and ericoid mycorrhizal dominated ecosystems at higher latitudes (Smith &Read, 2008). We know less about the extent to which latitude impacts the functioning of AM symbioses, which could occur either through latitudinal differences in solar radiation or resulting changes in temperature (Clarke & Gaston, 2006; Schluter, 2016). Here, we propose the 'sun-worshipper' hypothesis that discriminates three different types of underlying responses of latitudinal gradient-induced changes in plant host mycorrhizal responsiveness (Fig. 1). Changes in abiotic conditions may allow plants to derive more benefits from the symbiosis at lower latitudes through phenotypic plasticity (mechanism one – Fig.1). A likely example of phenotypic plasticity might involve changes in the expression of genes that allow crosstalk with AM fungi when light availability is low as has been shown for drought (Li *et al.,* 2016). Abiotic conditions more favourable for the symbiosis close to the tropics could further exclude, via competition, species less dependent on AM fungi, resulting in distinct plant communities from a perspective of AM fungal-associating behaviour; such a process can be described as environmental filtering (mechanism two – Fig. 1). Finally, we know that AM plants at high latitudes encounter a less diverse pool of potential symbiotic partners (e.g. because of the observed latitudinal gradient in Glomeromycotan diversity; Davison *et al*., 2015) and at the same time communities at high latitudes are in general dominated by plants that associate with ectomycorrhizal and ericoid mycorrhizal fungi. Plants distant from the tropics could thus form less profitable AM symbioses (but also support fewer AM partners) because of a more limited pool of suitable AM fungal partners, and this mechanism is analogous to the indirect eco-evolutionary causes (Pärtel, 2002) (mechanism three - Fig. 1). Here, we use the term eco-evolutionary processes to describe combined effects of latitude on phenotypic plasticity, environmental filtering and eco-evolutionary adaptation of the host plant trait mycorrhizal dependency (e.g. Thuiller *et al.,* 2013). Even though these different mechanisms are not mutually exclusive, it is important to disentangle how each of them influences how host plants respond to mycorrhizal symbioses along gradients of latitude and solar radiation.

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

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

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

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

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Contributions

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

Supplementary Information

Appendix 1: Mycorrhizal dependency as proxy of investment

Appendix 2: Meta-analysis on phenotypic plasticity

Appendix 3: Eco-evolutionary processes on LGMR

Appendix 4: Environmental filtering on LGMR

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

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

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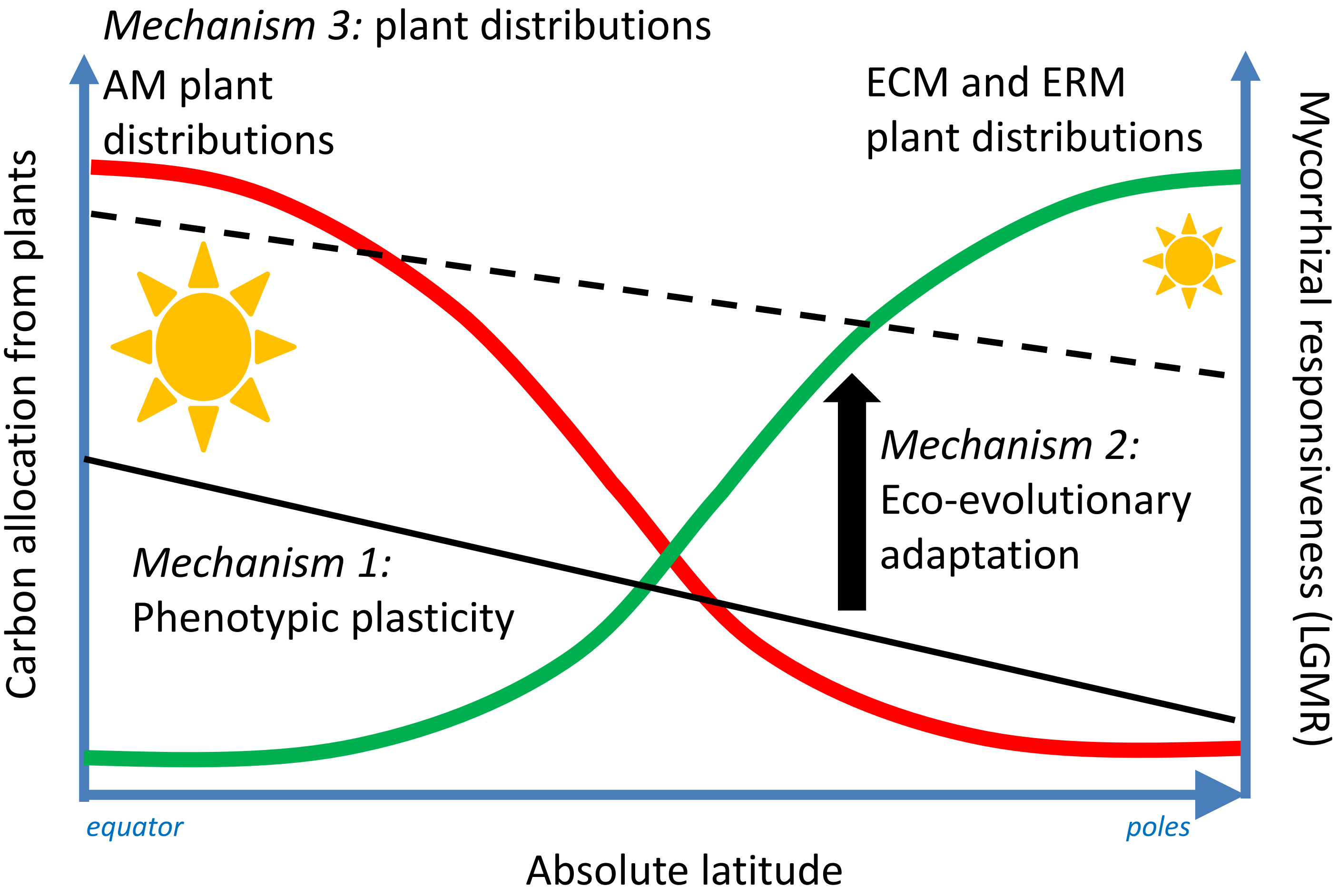
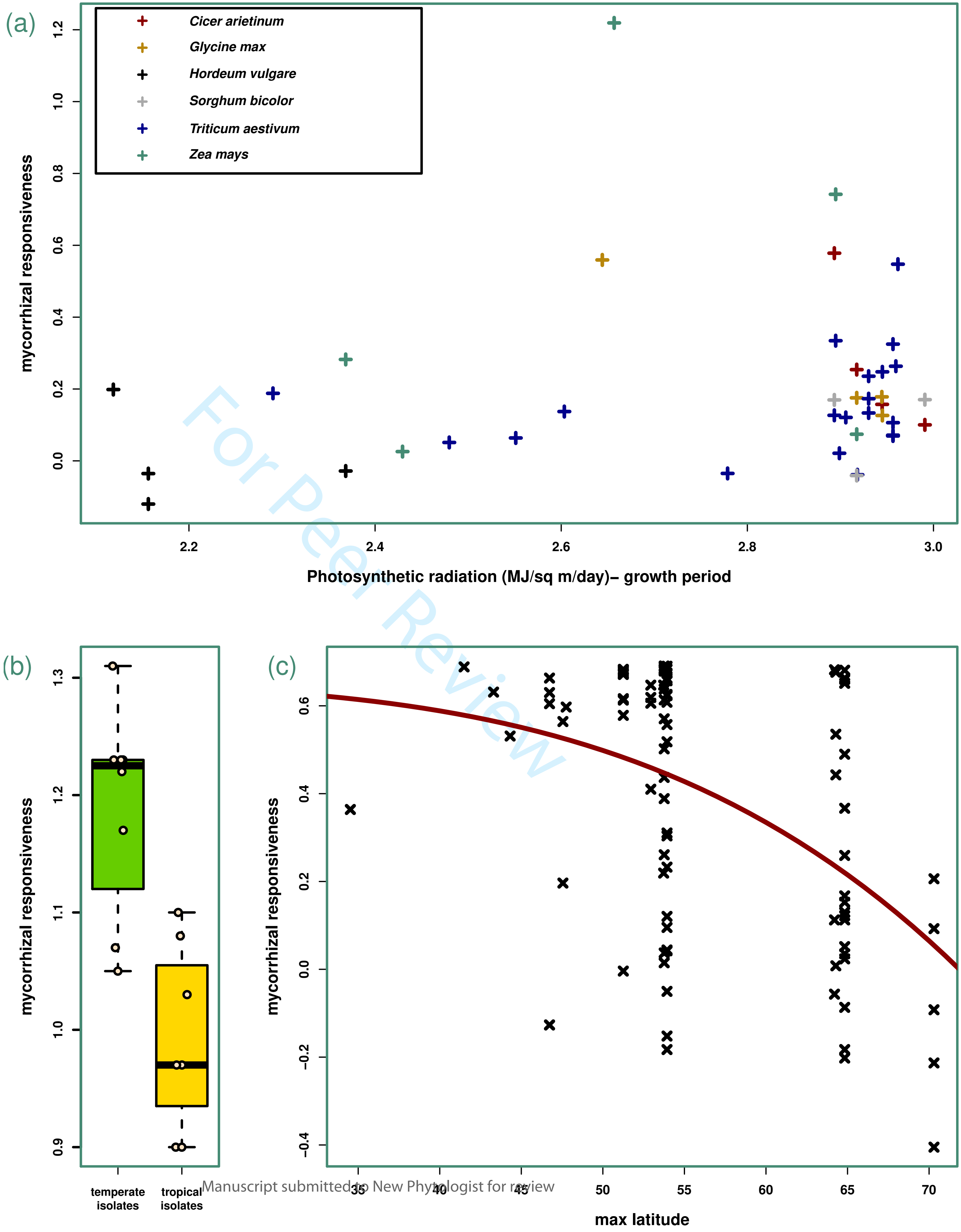
Legends to Figures

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

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


Mechanism 3: plant distributions
AM plant distributions
ECM and ERM plant distributions
Carbon allocation from plants
Mycorrhizal responsiveness (LGMR)
Mechanism 1: Phenotypic plasticity
Mechanism 2: Eco-evolutionary adaptation
equator
poles
Absolute latitude


(a)
Cicer arietinum
Glycine max
Hordeum vulgare
Sorghum bicolor
Triticum aestivum
Zea mays
mycorrhizal responsiveness
0.0
0.2
0.4
0.6
0.8
1.0
1.2
2.2
2.4
2.6
2.8
3.0
Photosynthetic radiation (MJ/sq m/day)– growth period
(b)
mycorrhizal responsiveness
0.9
1.0
1.1
1.2
1.3
temperate isolates
tropical isolates
(c)
mycorrhizal responsiveness
−0.4
−0.2
0.0
0.2
0.4
0.6
35
40
45
50
55
60
65
70
max latitude