Mycorrhizal response in crop versus wild plants

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We proposed a theoretical framework predicting mutualistic outcomes for the arbuscular mycorrhizal (AM) symbiosis based on host identity (crop versus wild).

To test the framework, we grew two isolates of R*hizoglomus irregulare* (commercial versus an isolate locally sourced from a site in Saskatchewan), with five crop plants and five wild plants that are endemic to the region and co-occur with the locally sourced fungus.

While inoculation had no effect on plant biomass, it decreased leaf P content, particularly for wild plants. All plants associating with the commercial fungus had lower leaf P. Overall, our data shows that wild plants may be more sensitive to differences in mutualistic quality among commercial biofertilizers.

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Abstract

We proposed a theoretical framework predicting mutualistic outcomes for the arbuscular mycorrhizal (AM) symbiosis based on host identity (crop versus wild).
To test the framework, we grew two isolates of *Rhizoglomus irregulare* (commercial versus an isolate locally sourced from a site in Saskatchewan), with five crop plants and five wild plants that are endemic to the region and co-occur with the locally sourced fungus.
While inoculation had no effect on plant biomass, it decreased leaf P content, particularly for wild plants. All plants associating with the commercial fungus had lower leaf P. Overall, our data shows that wild plants may be more sensitive to differences in mutualistic quality among commercial biofertilizers.

Introduction

Arbuscular mycorrhizal (AM) fungi are obligate root symbionts that provide a wide spectrum of benefits to their hosts, such as improved nutrient relations and stress tolerance (Delavaux, Smith-Ramesh & Kuebbing, 2017). These benefits have led to their use as bio-fertilizers in agriculture and horticulture over the past 30+ years (Hamel, 1996). Consumer demand for AM fungal biofertilizers is growing; the number of companies producing inoculum have more than doubled in in the past decade (Gianinazzi & Vosátka, 2004; Vosatka et al., 2012).

Despite early promise (Menge, 1983), inoculation by AM fungi does not always lead to improved plant performance. Even under controlled greenhouse conditions, failure to colonize is common (Rowe, Brown & Claassen, 2007; Tarbell & Koske, 2007) and in cases of successful colonization, effects range from negative (Poulsen et al., 2005; Christophersen, Smith & Smith, 2009; Grace et al., 2009; Facelli et al., 2010), no detectable effect (Perner et al., 2007; Emam, 2016) to significant yield increase (Buysens et al., 2016). Inoculation with AM fungi in the field is likewise inconsistent, ranging from yield increases (Baltruschat, 1987; Al-Karaki, McMichael & Zak, 2004; Ceballos et al., 2013; Hijri, 2016) to no significant effect (Hamel & Smith, 1991; Ryan & Graham, 2002).

What consequences could result from such differences in mutualistic outcomes? Most of our knowledge about host responses to inoculation by AM fungi is based on domesticated cultivars (Ceballos et al., 2013; Pellegrino et al., 2015; Cely et al., 2016; Hijri, 2016), meaning we have a poor understanding of how inoculants may affect local plant populations and communities if they disperse beyond the target plant community (Hart et al., 2018).

Although it has been argued that AM fungal inoculants pose little threat to natural plant communities because most commercial inoculants comprise cosmopolitan species with worldwide distribution (Rodriguez & Sanders, 2015), the large intraspecific variation reported in the literature among conspecifics, in life history traits, (Stahl & Christensen, 1991; Hart & Reader, 2002a; Koch et al., 2004; Munkvold et al., 2004), mutualistic quality (Koch et al., 2017) and genetics (Koch et al., 2004; Börstler et al., 2008; Croll et al., 2008), expose possible different mutualistic outcomes, even if conspecifics naturally occur.

Mutualistic outcomes for native plants may differ from domesticated cultivars, leading to differential responses to inoculation (Fig. 1). Because wild plants are generally more mycorrhizal dependent than cultivars (Hetrick, Wilson & Cox, 1993; Zhu et al., 2001; Wright et al., 2005; Xing et al., 2012), mutualistic outcomes may be more pronounced (positive or negative) for wild plants compared to cultivars. This effect may be exacerbated by local adaptation between wild plants and soil biota as native plants respond more positively to local, versus exotic AM fungi (Antunes et al., 2011; Rua et al., 2016). Not only are local fungi adapted to local conditions (Johnson et al., 2010; Middleton et al., 2015), but there is evidence that mutualism is more beneficial when partners share evolutionary history (Klironomos, 2003a). Taken together, such differential responses to commercial fungal inoculum may result in less beneficial mutualisms for local plants if commercial inoculants become naturalized.

We evaluated the mycorrhizal response of five wild plants and five crop plant species, representing multiple functional groups, when grown with a commercial AM fungal isolate and a locally sourced conspecific, to test the questions: *Does plant provenance affect mycorrhizal response? And does plant provenance affect fungal response?*

Materials & Methods

Experimental treatments

We tested the effect of host plant identity (five cultivars and five local plant species) and AM fungal identity (commercial, locally sourced, non-mycorrhizal control) in a completely randomized block design (n=8, total 240 experimental units). This experiment was conducted in greenhouse at UBC Okanagan from September 2015 to February 2016.

Plant identity

We tested the effect of host identity using "crop" and "wild" plants representing different functional groups (C4, forb, C3, N_2-fixer) with known ability to interact with AM fungi (Table 1). These plants were selected to represent both common agricultural crops in the local area, and naturally occurring wild plants. Native plant seeds were collected from wild populations near the source of the local inoculant. (Table 1). All native plant seeds as well as the flax (*Linum usitatissimum)*, lentils (*Lens culinaris)* and wheat (*Triticum aestivum)* seeds were provided by Dr. M. Schellenberg from Semiarid Prairie Agricultural Research Centre, Agriculture and Agri-Food Canada in Swift Current, Saskatchewan. Corn (*Zea mays*) and soybean (*Glycine max)* seeds were obtained from West Coast Seeds Ltd.

Inoculant identity

Rhizophagus irregularis Schenck & Smith (DAOM 197198) (synonym *Glomus intraradices, G. irregulare* (Stockinger, Walker & Schüßler, 2009) and recently *Rhizoglomus irregulare* (Sieverding et al., 2014) was provided by BioSynettera, Inc. This isolate has been cultivated in-vitro for more than 30 years (Stockinger, Walker & Schüßler, 2009) and is sold globally as a commercial inoculant. We also tested a locally sourced *Rhizophagus irregularis*

(GD50) (isolated in 2007 from SK (50° 34' 56.94" N/105° 29' 17.41" W)) (Agriculture and Agri-Food Canada, Swift Current Research and Development Centre). For the experiment, we used whole inoculum for both isolates (infected root fragments and spores), standardized based on propagule density per gram quantity. The propagule density for the locally sourced isolate inoculum was determined using the infection unit method by (Franson & Bethlenfalvay, 1989) (data not shown) Propagule density of the commercial isolate, as defined by the provider.

Growing conditions

2-l pots were filled with a sterile by autoclaving growing medium (75 % medium-fine sand/25 % Turface (Turface athletics MVP)). The medium was low in resources, as specified by the manufacturer's information, so we could control the nutrient status with fertilization, and had high drainage abilities in order for a common irrigation system to be used regardless plant identity. In each pot, we placed 26 propagules (8.7 g of inoculum containing infected root fragments and spores of the locally sourced isolate and 7 g similar inoculum of the commercial isolate). Three seeds were placed on top of the inoculum and covered with ~200 mL of growing medium, then thinned to one seedling per pot. Plants were watered with emitters supplying 2 l hr^{-1} to each pot, ~35 ml every day (1 minute per day) through the irrigation system and after 45 days the same amount of water as delivered every 2 days.

A microbial wash from both the inoculants was applied at the beginning of the experiment to ensure that microbial community was same in all treatments and that any effect would be due to AM fungal isolate differences. This was made by adding 100 g of each inoculant to 4 l of water and mixing. The resulting solution was filtered through a 5µm mesh to exclude mycorrhizal fungal spores and infected roots.

Location of plants was randomized on greenhouse benches with each bench representing a ‘block’. The pots were subjected to 16 h light per day, with daily light integral (DLI) 71 µmol s^{-1} m^{-2} per µA measured with LI-250A light meter, Biosciences. Low P fertilizer (Miracle-gro® 24-8-16) was added at half the manufacturer recemented dosage. Plants were grown for 16 weeks.

Plant responses

Root and shoot biomass

At harvest the shoot of each plant was separated from the root system. Fresh weight was measured then, seeds and leaves were dried at 60 °C for 48 h for subsequent analyses. Roots were washed carefully before weighing. A subsample of the root system was obtained for subsequent colonization measurements This subsample was included in the total root biomass value. After 48h at 60 °C, dry weight of the roots was obtained. In addition to raw values, we calculated changes in biomass as Root: Shoot ratio.

Seed number and weight

Only cultivars developed seeds during the experiment. Seeds were counted, then dried at 60 °C for 48h for dry weight.

% Leaf P

Dried leaves were collected, pulverized and homogenized. % P in the leaves was calculated using a color development method, (using an acidified solution of ammonium molybdate, ascorbic acid and antimony) after acid digestion (Murphy & Riley, 1962).

Mycorrhizal response (MR)

All plant responses were evaluated as mycorrhizal responsiveness. Mycorrhizal response (MR) represents the amount of benefit a plant gains from an AM fungal associate versus a nonmycorrhizal control (Baon, Smith & Alston, 1993). For this study, we measured a) root: shoot ratio and b) % leaf P content. MR for root: shoot ratio was calculated for every plant species by the following formula:

$$MR = ln\ (a/b)$$

where a = root: shoot ratio of mycorrhizal plants and b = mean root: shoot ratio of non-mycorrhizal plants (Baon et al., 1993). MR for % leaf P content was calculated using the same formula but with % leaf P in lieu of root: shoot. To test for variability in response between cultivars and native plants we used Leven's test.

Fungal responses

Root colonization

Roots were stained based on the protocol of (Koske & Gemma, 1989). Briefly, fresh roots were cut into 2-cm fragments and stained with Trypan blue. Ten root pieces were randomly collected and placed on a glass slide. The percentage of fungal organs (hyphae, vesicles and arbuscules) and the total root colonization were determined microscopically using the gridline intersect method of (McGonigle et al., 1990).

External mycelium

The entire soil from each pot was homogenized. From each pot, 100 g (wet) soil was used to determine external mycelia length as in (Miller, Jastrow & Reinhardt, 1995).

Spores

A second 100 g (wet) soil sample was collected and dried. That sample was used to quantify spore density based on the protocol of (Gerdemann & Nicolson, 1963). Briefly, after recording the dry weight, each sample was placed into a blender and mixed in high speed for 5 seconds. The blended material was filtered through a series of sieves the final of which had an opening of

38 µm. After spores were transferred to 50 ml falcon tubes, centrifuged twice (at 1200 x g and 960 x g), and AM fungal spores were collected from the final supernatant in 50 ml falcon tubes. The number of spores was counted in each part of the grid.

Statistical analysis

Does plant provenance affect mycorrhizal response?

We used a mixed effects linear model ("lme4" version 1.1 – 12, Fitting Linear Mixed-Effects Models) (Bates et al., 2015) to examine the differences in mycorrhizal response of plant provenance (cultivars-native, fixed), to different inoculation treatments (commercial inoculum (com), locally sourced inoculum (local), non-mycorrhizal control) with plant identity (10 species, random) and block (random). Data were logarithmically transformed, when necessary, to allow for normal distribution of residuals of the model. We examined biomass, P in the leaves, MR total biomass, MR root: shoot ratio and MR % P in the leaves. To test for equality of variances between cultivars and native plant we used Levene's test ("Rcmdr" version 2.4-4).

Does plant provenance affect fungal response?

Fungal traits

Similar to above, we used a mixed effect linear model lme4" version 1.1 – 12 to test for differences between plant treatments and AM fungal treatments on the fungal responses. Factors were, AM fungal isolate (fixed), plant provenance (cultivar-native plants, fixed) with plant identity (random) and block (random). Data were logarithmically transformed, when necessary, to allow for normal distribution of residuals of the model. When normalization of the residuals of the model was not possible, we used a generalized mixed model, which does not assume normality, with fixed and random factors as described above.

Allometry: proportional representation of fungal traits (Intraradical: extraradical investment)

To proportionally represent the fungal traits (intra: extraradical) of each isolate the data were standardized using the "vegan version 2.3-5" package (Community Ecology Package) (Oksanen et al., 2016). Normalized trait values per isolate were summed and scaled to 100 %. The ratio of intraradical to extraradical traits after normalization was calculated and we used a mixed effects linear model (lme4" version 1.1 – 12, Fitting Linear Mixed-Effects Models) (Bates et al., 2015) to examine the differences in trait investment strategies between the two isolates (commercial, locally sourced) among plant provenance (cultivars-native, fixed), plant identity (10 species, random) and block (random).

R studio (Version 1.0.136 – © 2009-2016 RStudio, Inc.) was used for all analyses.

Results

Does plant provenance affect mycorrhizal response?

Total biomass

As expected, native plants had significantly lower total biomass compared to cultivars ($p<0.001$). AM fungal identity did not affect total plant biomass compared to nonmycorrhizal controls for cultivars or native plants ($p=0.51$) (Fig. 2a). Contrary to our prediction, native plants were not more responsive to AM fungi in terms of biomass compared to cultivars overall ($p=0.89$) (Fig. 3a), but while examining individual responses, wild plants had significantly higher variation in their response to AM fungi in terms of biomass (Levene's test, $p<0.001$) (Fig 4a). Individual plant responses are presented in Supplementary Table S1.

Root: Shoot ratio

There was no difference among plants in root: shoot ratio ($p=0.63$). Fungal identity had a significant effect on root: shoot ratio ($p<0.01$), that is the commercial AM isolate leading to larger root: shoot ratio compared to locally sourced AM isolate. There was a significant interaction between fungal identity and plant provenance ($p<0.001$) with locally sourced inoculum leading to increased root: shoot ratio for cultivars and decreased root: shoot ratio for native plants (Fig. 3b).

% Leaf P

Wild plants were no different from crop plants in terms of relative leaf P ($p=0.056$) but when accounting for total plant biomass wild plants had significant lower leaf P than cultivars ($p<0.001$). There was a significant interaction between fungal identity and plant provenance, with wild plants having a significant less % P than crop for the commercial AM fungus ($p<0.05$) (Fig. 3c). AM fungal identity significantly affected plant % leaf P ($p<0.001$).

The commercial isolate reduced plant % leaf P levels ($p<0.001$) across all plants and plant provenance compared to control and locally sourced inoculum (Fig. 2b). The locally sourced isolate increased cultivar % leaf P compared to control ($p<0.05$) but did not affect % leaf P of native plants compare to control ($p=0.71$) (Fig. 2b). For more detailed results please see Supplementary Fig. S1 and Fig. S2). Individual plant responses are presented in Supplementary Table S1.

Wild plants had significantly higher variation in their response to AM fungi in terms of % leaf P (Levene's test $p<0.01$) (Fig 4b).

Does plant provenance affect fungal response?

Root colonization

Native plants had lower colonization compared to the cultivars for both isolates ($p<0.01$) (Fig. 5a). No AM colonization was observed in non-mycorrhizal controls. The commercial isolate had lower root colonization compared to the locally sourced isolate ($p<0.001$) (Fig 5a).

Arbuscules

In general, native plants had fewer arbuscules for compared to cultivars ($p<0.01$) (Fig. 5b). The commercial isolate formed fewer arbuscules compared to the locally sourced isolate ($p<0.001$) The number of arbuscules differed significantly among the two AM fungal isolates (Fig 5b).

Vesicles

Fewer vesicles were observed for the native plants compared to the cultivars for both isolates ($p<0.05$) (Fig. 5c). The number of vesicles differed significantly among the two AM fungal isolates in all hosts ($p<0.05$) (Fig. 5c). The commercial isolate formed fewer vesicles compared to the locally sourced isolate

Spores

Sporulation was not influenced by the plant provenance ($p=0.33$) (Fig. 5e). However, spore density differed significantly between fungal isolates. The commercial isolate produced more spores compared to the locally sourced isolate ($p<0.001$) (Fig. 5d).

Extraradical mycelium (ERM) length

There was no difference in extraradical mycelium length between native plants and cultivars ($p=0.34$). nor the fungal isolates ($p=0.58$).

Proportional fungal trait distribution (Intraradical traits/extraradical traits)

Native plants had a lower intraradical: extraradical ratio compared to cultivars ($p<0.01$) (Fig. 6). There was a significant difference at the ratio of intraradical to extraradical traits between the two AM fungi ($p<0.001$). The commercial isolate invested more extraradically compared to the locally sourced isolate.

Discussion

Wild plants had pronounced variation in their response to fungi compared to cultivars. Responses ranged from positive to strongly negative revealing the strong sensitivity of wild plants to fungal identity, even to isolates within the same fungal species.

Plant performance

Plant Biomass

While native plants have been reported to be more responsive to AM fungi (Hetrick, Wilson & Cox, 1993; Zhu et al., 2001; Wright et al., 2005; Xing et al., 2012), we did not find support for this in terms of biomass when looking at plants as either ‘cultivars’ or ‘wild’ plants.. Because our wild plants were perennials, it is possible that our study did not allow enough time for full biomass differences to manifest, as the study ended when cultivars, but not natives, had senesced. Thus our inability to detect a difference among cultivars may have been due to time constraints. (Emam, 2016).

When we looked at responses of individual plant species, wild plants had significantly higher variation in their response to inoculation with AM fungi, from highly negative to highly positive. Variation in biomass has been documented for wild plants in the literature, particularly, for perennials versus annuals (Wilson & Hartnett, 1998), and natives versus exotics (Klironomos, 2003b).

Root: Shoot ratio

Inoculation with the commercial isolate led to increased shoot: root for cultivars but not for native plants. It is not uncommon to observe alteration in root: shoot ratio with inoculation by AM fungi (Ravnskov and Jakobsen 1995; Koch et al. 2006; Lee and Eom 2015). The "functional equilibrium" theory (Brouwer, 1983) suggests that plants allocate biomass preferentially to maximize resource acquisition, a plant should favor above ground growth when carbon is limited. Because carbon allocation from plant to fungus can lead to carbon limitation (Fitter, 1991), our results indicate that the commercial isolate may have posed more of a carbon demand than the local isolate, leading to increased shoot allocation. Such changes may lead to reduced nutrient acquisition for plants associated with the commercial fungus in some condition.

% leaf P

We found support to our prediction that plant provenance would affect mycorrhizal response in terms of % leaf P. Native plants, surprisingly, experienced a decrease in percent % leaf P when inoculated with AM fungi. While there is a lot of evidence showing that wild plants are more mycorrhizal depended compared to cultivars (Hetrick, Wilson & Cox, 1993; Zhu et al., 2001; Wright et al., 2005; Xing et al., 2012), it is important to consider that, their increased sensitivity to AM fungi can lead to magnified negative effects as well (Klironomos 2003), particularly when fungi and plants are competing for limited resources.

In our study, the commercial isolate was less mutualistic in terms of leaf P and this was magnified in wild plants. Other studies have shown of AM fungal inoculation leading to reduced host P (Poulsen et al., 2005; Christophersen, Smith & Smith, 2009; Grace et al., 2009; Facelli et al., 2010). While such reductions may be related to greenhouse growing conditions, reduced P following inoculation may also indicate a less mutualistic AM association in some cases (Li et al., 2008; Grace et al., 2009; Smith, Grace & Smith, 2009). In our study, plants inoculated with the commercial isolate had lower P compared to non-mycorrhizal controls which could indicate either direct competition between plant and fungus for P, or P hoarding by the fungus (Kiers et al., 2011). It may also mean that the commercial isolate does not have enhanced P uptake ability over plant-direct uptake routes, perhaps through loss of traits during domestication. Further studies comparing more isolates with isotope labelling and genomic studies could elucidate the mechanism involved.

Fungal performance

Root colonization

In general, we observed low values of colonization for both isolates and all plants compared to the literature. Low colonization values have been observed in the past in cultivars (Jackson, Miller & Smith, 2002) and wild plants (Wang et al., 2004), with lower colonization for wild plants compared to cultivars (Khalil, Loynachan & Tabatabai, 1994; Jackson, Miller & Smith, 2002). Differences in intraradical investment between species ((Hart & Reader, 2002a) or even isolates (Koch et al., 2004) can reflect differences in life history strategies (LHS). Variation in LHS could explain part of the AM fungal functional diversity (Hart & Reader, 2002b; Parrent et al., 2010; Chagnon et al., 2013). But root colonization is not a good predictor of the quality of the symbiosis (Mcgonigle, 1988; Lekberg & Koide, 2005). On the contrary, specific traits and fungal allometric relationships may be more meaningful metrics (Johnson et al., 2003; Engelmoer, Behm & Kiers, 2014).

Internal fungal structures

The commercial isolate in our study had very few arbuscules at the harvest. This is unusual, as arbuscules (or coils) are considered fundamental to the mutualism under natural conditions (Smith & Read, 2008). Reduction of arbuscules has been reported for a variety of AM fungal species (including Rhizophagus sp.) under stressful environments (Druille et al., 2013; Alejandro-Córdova et al., 2017), and due to differences in harvest time and level of fertilization (Jackson, Miller & Smith, 2002; Shukla et al., 2012). Specifically, suppression of arbuscules can occur with increasing P or N (Jackson, Miller & Smith, 2002) and changes in arbuscule formation due to time of harvest can be regulated by the species identity (Shukla et al., 2012). In our experiment, differences are likely do to fungal strategies since there was no suppression of arbuscules in the locally sourced isolate.

Low levels of arbuscules in the commercial isolate may be explained by considering the conditions under which the commercial isolate was propagated. Large-scale inoculum production occurs mostly on transformed roots, which are able to directly uptake most of their resources from the nutrient medium (Fortin et al., 2002) and have very low nutrient requirements (Chabot, Becard & Piche, 1992). Such an unnatural environment may have reduced the need for arbuscules, or enhance the resource sink abilities of the isolate, but this remains to be seen. Given that there is still considerable debate over the function of arbuscules (Keymer et al., 2017; Luginbuehl et al., 2017), it is difficult to identify factors that promote or suppress their production.

External fungal structures

While there was no difference in the extent of ERM among fungal isolates, the commercial isolate invested heavily in spore production compared to the local isolate. Large differences in spore production among isolates is not unusual, as there have been many reports of inter and intraspecific variation in fungal traits, over several orders of magnitude in some cases

(Koch et al., 2004; Munkvold et al., 2004; Ehinger, Koch & Sanders, 2009; Campagnac & Khasa, 2014; Lee & Eom, 2015). Nevertheless, the difference in sporulation rate observed in this study, is unusually large (50x) and represents a significant carbon drain for hosts associating with this fungus.

Allometry (Intraradical: extraradical investment)

The commercial isolate had a significantly different growth pattern compared to the locally sourced isolate that was consistent among hosts and plant provenance, revealing important LHS variations between the two isolates. The commercial isolate had a high soil biomass, which could enhance soil exploration potential and subsequently, host benefit (Jakobsen, Abbott & Robson, 1992). Although, considering the differences in spore number between the two isolates, deriving from the same quantity of ERM, means that the commercial isolate represented a nutrient sink rather than a source (including C and P).

Conclusions

Wild plants had highly variable responses to inoculation by AM fungi compared to crop plants which had a uniform response to fungal inoculation, regardless of the identity of the fungus. This raises concerns about how inoculation practices may affect wild plant/soil communities. Our study provides evidence that the commercial isolate used in this study may be less mutualistic under some conditions. The commercial isolate invested in spore production at the expense of intraradical structures, suggesting a more “selfish” strategy. Correspondingly, plants experienced decreased P with the commercial isolate. It is important for future studies to consider fitness consequences associated with inoculation studies, as poor mutualists may not be apparent over one generation. Considering the number of propagules produced by the commercial isolate, there is a high likelihood of spread beyond the agricultural fields displacing native AM fungi. Future studies need focus on the viability and establishment of these propagules beyond agricultural systems.

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Table 1(on next page)

Crop and wild plants used.

Crop plants	Wild plants
Zea mays (Corn, var. Early Sunglow C4 grass)	*Schizachyrium scoparium* (Little blue stem- C4)
Linum usitatissimum (Flax, var. Bethune, forb)	*Dalea candida* (White prairie clover, N_2-fixer)
*Triticum aestivum (*Lillian spring wheat, C3)	*Hedysarum alpinum* (Alpine Sweetvetch, N_2-fixer)
Glycine max (Soybean, var. Kuroshinja Edamame, N_2-fixer)	*Calamovilfa longifolia* (Prairie sandreed, C4)
Lens culinaris (Lentils, N_2-fixer)	*Agropyron dasystachyum* (Northern wheatgrass, C3)

1

Figure 1(on next page)

Theoretical framework of differential response of wild and crop plants to AM fungi.

Red arrows represent negative responses, while green arrows represent positive responses. The thickness of the arrows corresponds to the magnitude of the response. **Inoculation effects on cultivars and wild plants:** We expect inoculation with AM fungi to have little or negative effect on crop hosts due to lack of coadaptation (Antunes et al., 2011; Rua et al., 2016) and reduced mycorrhizal responsiveness of domesticated plants (Hetrick, Wilson & Cox, 1993; Zhu et al., 2001; Wright et al., 2005; Xing et al., 2012). For wild plants, we expect that inoculation effects will be magnified due to strong mycorrhizal dependence of wild plants on AM fungi (Hetrick, Wilson & Cox, 1993; Zhu et al., 2001; Wright et al., 2005; Xing et al., 2012). **Effects of plant provenance on AM fungi:** We expect wild plants to have positive effect on AM fungal growth due to increased dependency while crop plants will have little to negative effect to AM fungi due to lack of coadaptation and reduced mycorrhizal responsiveness (Antunes et al., 2011; Rua et al., 2016).

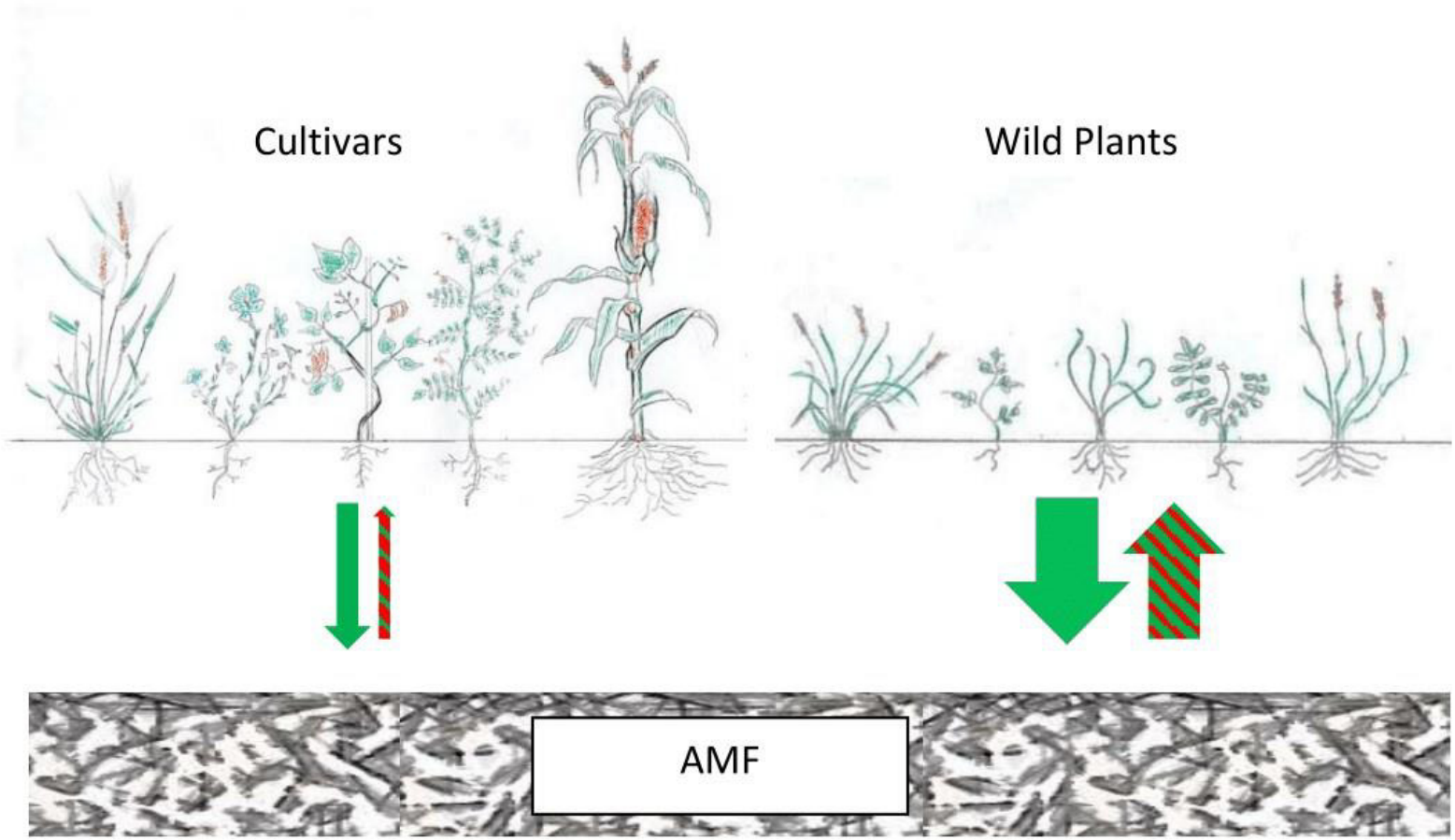

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Figure 2(on next page)

Fungal inoculation effects on crop plants and wild plants.

(a) Total plant biomass (g) (**b**) % leaf P. Com: plants interacting with the commercial isolate, Local: plants interacting with the locally sourced isolate. Control: plants without AM fungi. Box-plots show the third quartile and first quartile (box edges), median (middle line), range of the data (whiskers) and data outliers (circles). *** $p<0.001$.

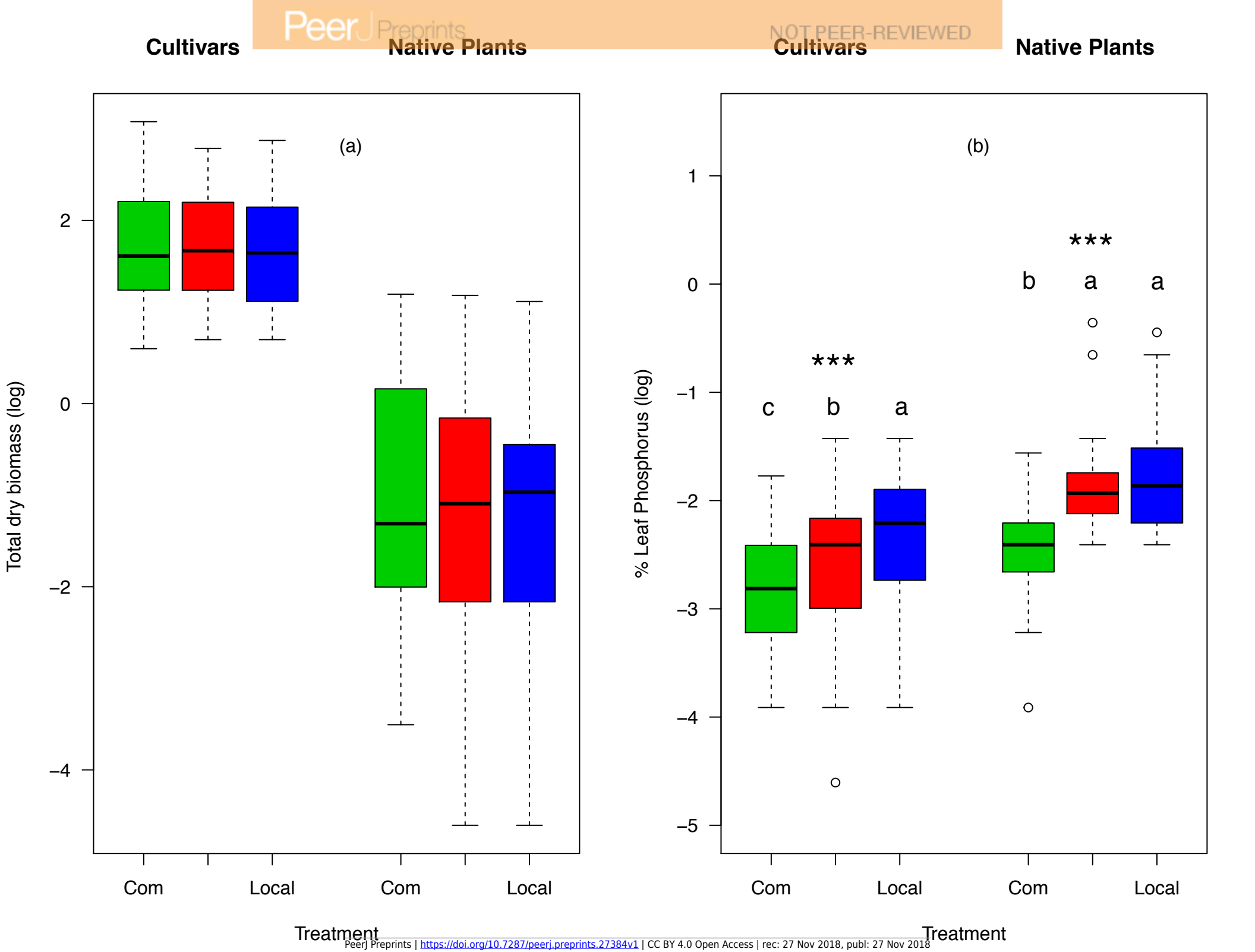

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Figure 3(on next page)

Mycorrhizal response in crop plants versus wild plants.

(a) MR of total biomass of crop plants and wild plants when interacting with the commercial isolate (com) and the locally sourced isolate (local) \. Red line indicates the mean value of non-mycorrhizal plants. **(b)** MR of root: shoot ratio of crop and wild plants when interacting with the commercial isolate and the locally sourced isolate (local). Red line indicates the mean value of the non-mycorrhizal plants. **(c)** MR of % leaf P of crop and wild plants when interacting with the commercial isolate (com) and the locally sourced isolate (local). Red line indicates the mean value of the non-mycorrhizal plants. Box-plots show the third quartile and first quartile (box edges), median (middle line), range of the data (whiskers) and data outliers (circles). * $p<0.05$. Mycorrhizal response (MR) represents the amount of benefit a plant gains from an AM fungal associate versus a nonmycorrhizal control (Baon et al. 1993).

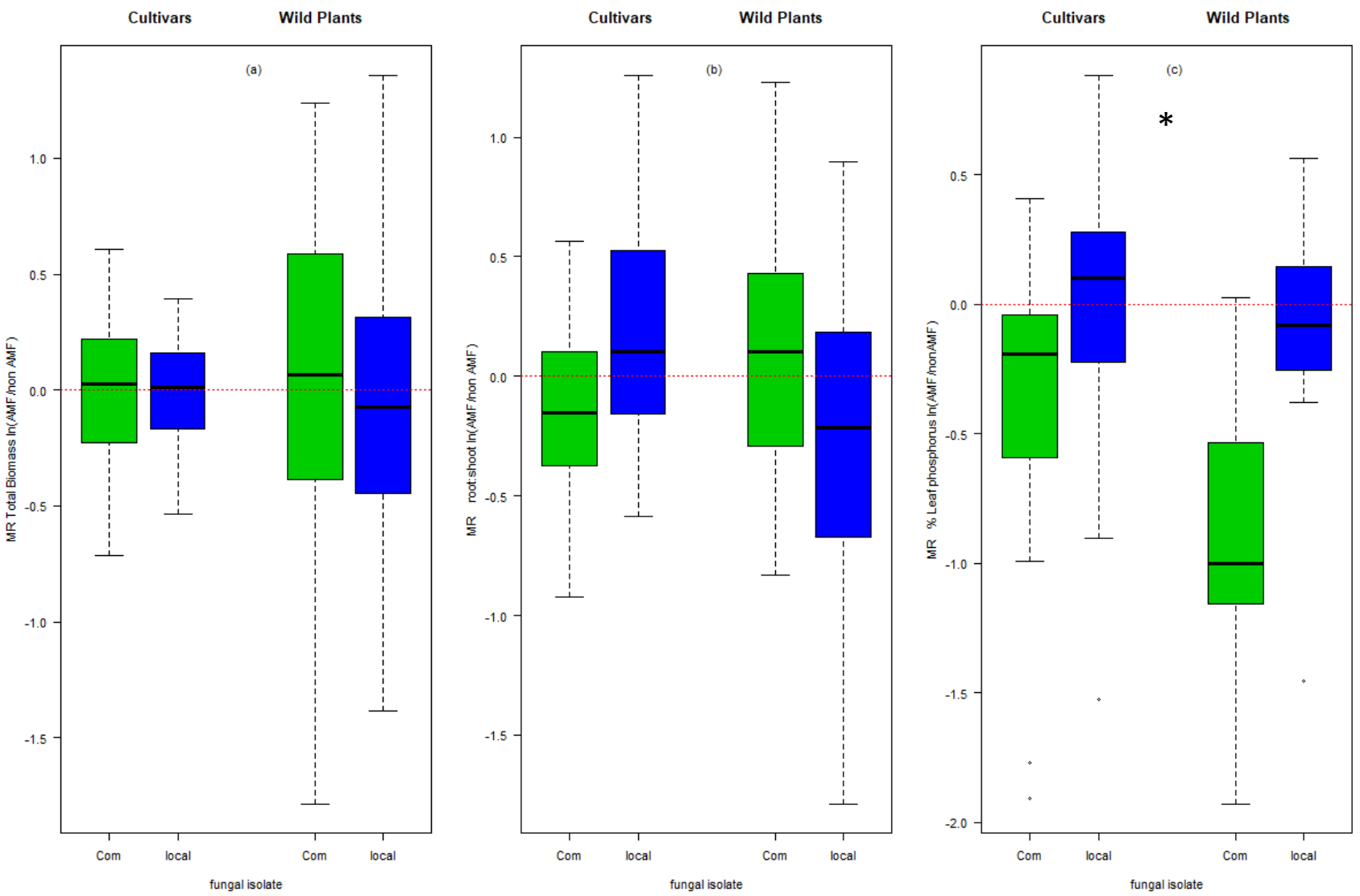

Figure 4(on next page)

Mycorrhizal response variation in crop plants vs wild plants.

(a) Biomass and **(b)** % leaf P. Red line indicates the mean value of the non-mycorrhizal plants. Crop plants are represented with green [ZM (Zea mays), LI (Linum usitatissimum), TA (Triticum aestivum), GM (Glycine max), LC (Lens culinaris)] and wild plants with blue colour [(SC (Schizachyrium scoparium), DC (Dalea candida), HA (Hedysarum alpinum), CL (Calamovilfa longifolia), AD (Agropyron dasystachyum)]. Red line indicates the mean biomass of non-mycorrhizal plants. The third quartile and first quartile (box edges), median (middle line), and range of the data (whiskers) are shown. To test for equality of variance between crop and wild plant we used Levene's test. Wild plants had significantly more variation compared to cultivars in terms of biomass $p<0.001$ and % P, $p<0.01$). Box-plots show the third quartile and first quartile (box edges), median (middle line), range of the data (whiskers) and data outliers (circles). ** $p<0.01$. *** $p<0.001$. Mycorrhizal response (MR) represents the amount of benefit a plant gains from an AM fungal associate versus a nonmycorrhizal control (Baon et al. 1993).

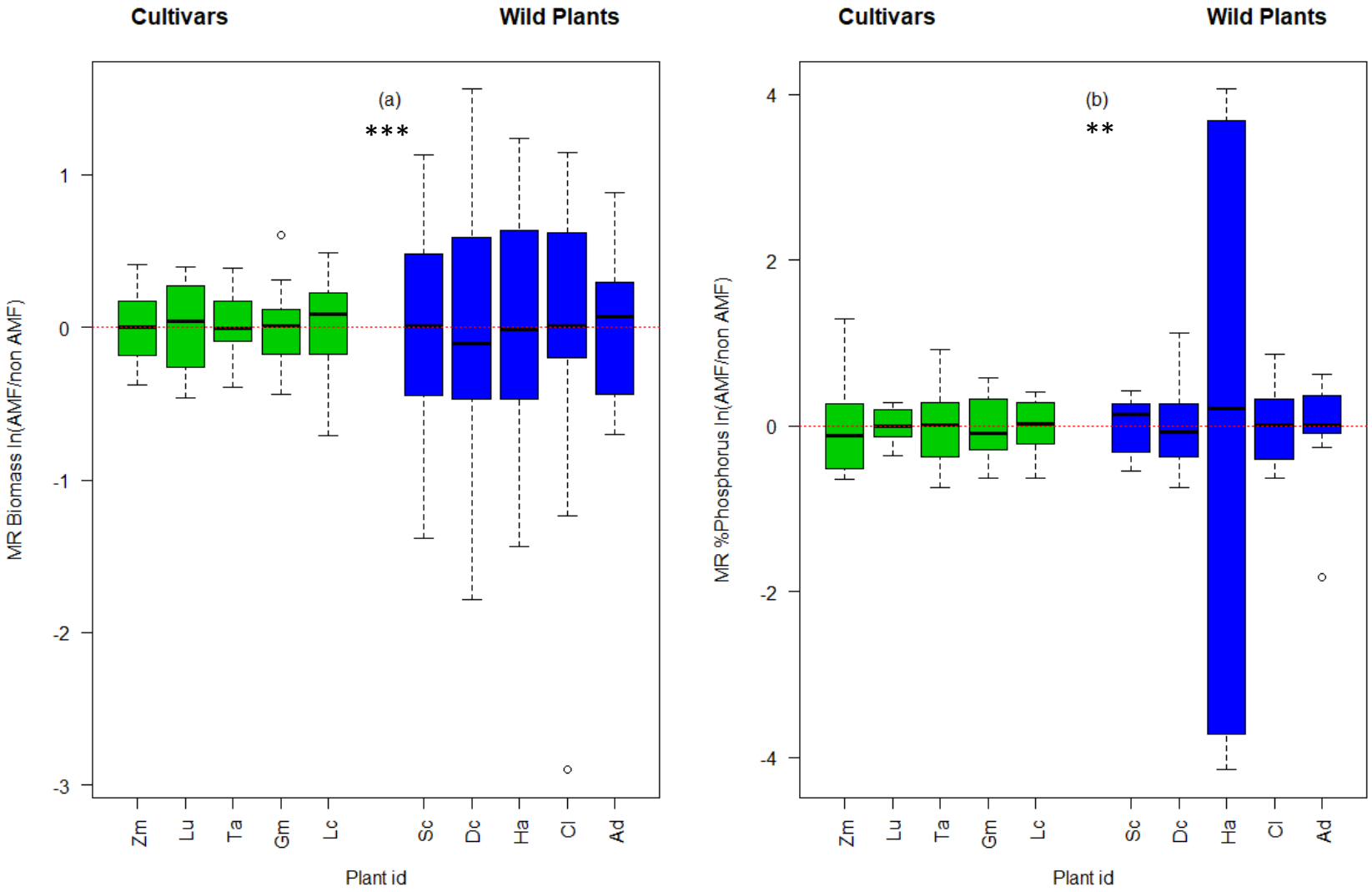

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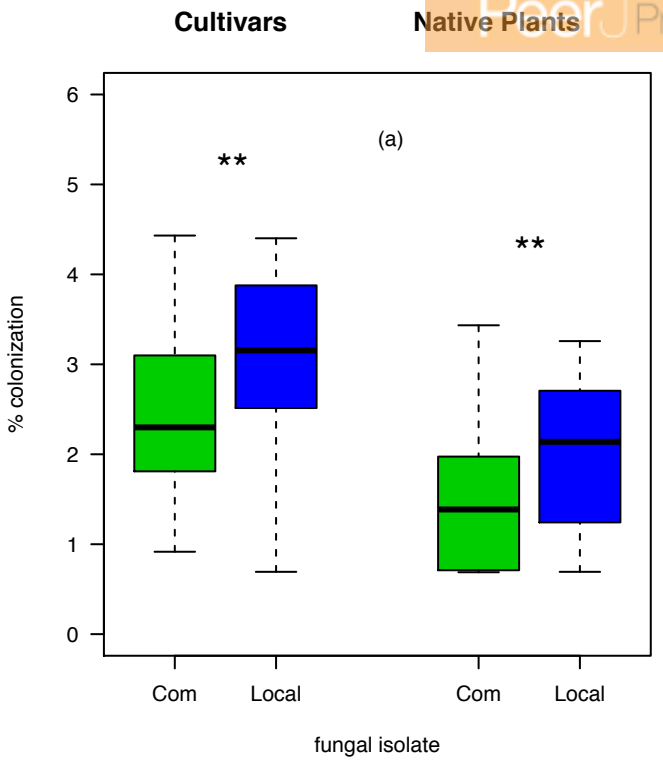
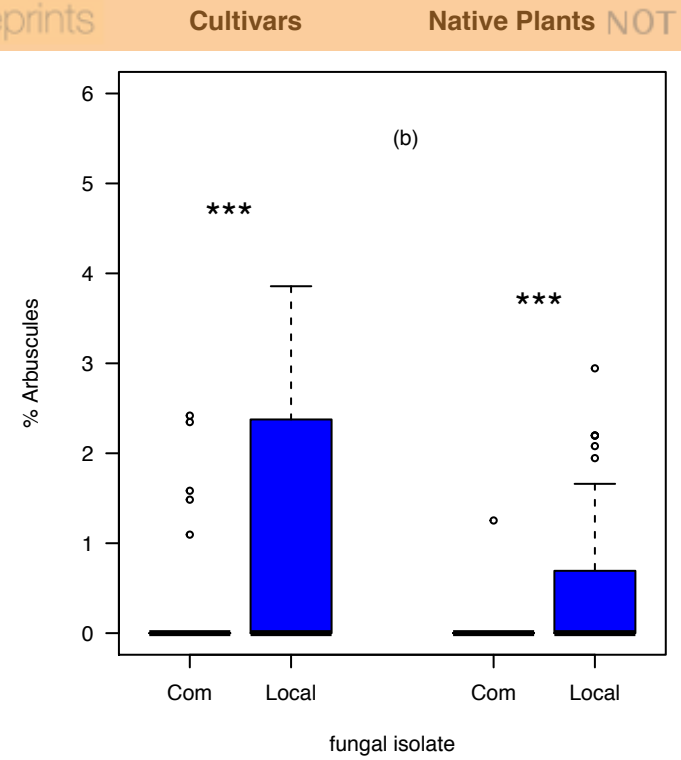
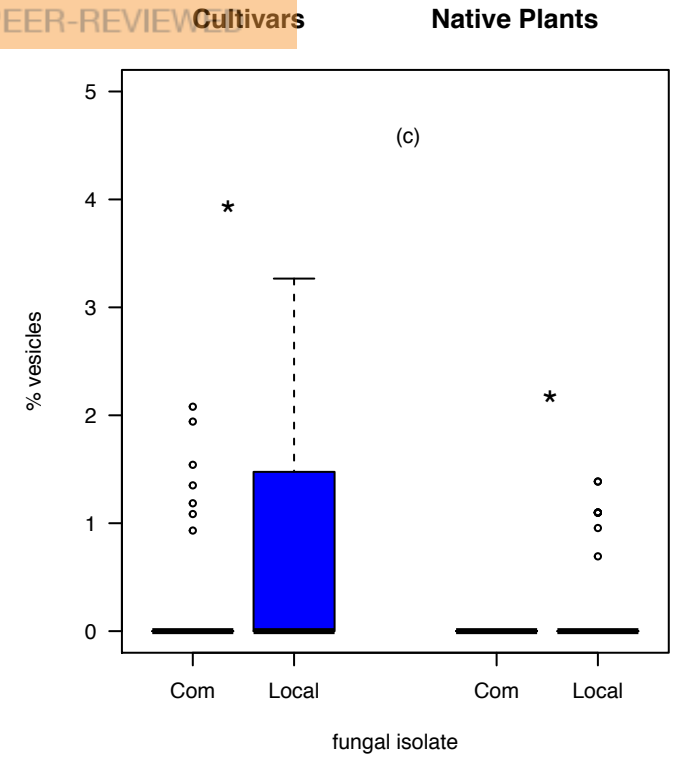
Figure 5(on next page)

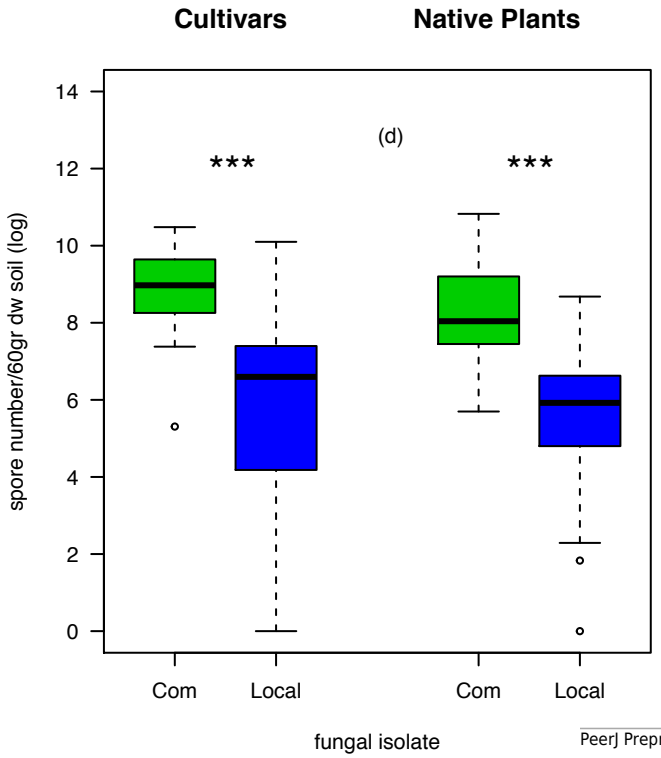
Fungal response when associating crop plants or wild plants (Commercial isolate, local isolate).

(a) per cent colonization, **(b)** per cent arbuscules, **(c)** per cent vesicles, **(d)** spore number per 60 gr of substrate (dry) logarithmically transformed, **(e)** extraradical mycelium (ERM) per gram of substrate. Box-plots show the third quartile and first quartile (box edges), median (middle line), range of the data (whiskers) and data outliers (circles). * $p<0.05$, ** $p<0.01$ *** $p<0.001$.









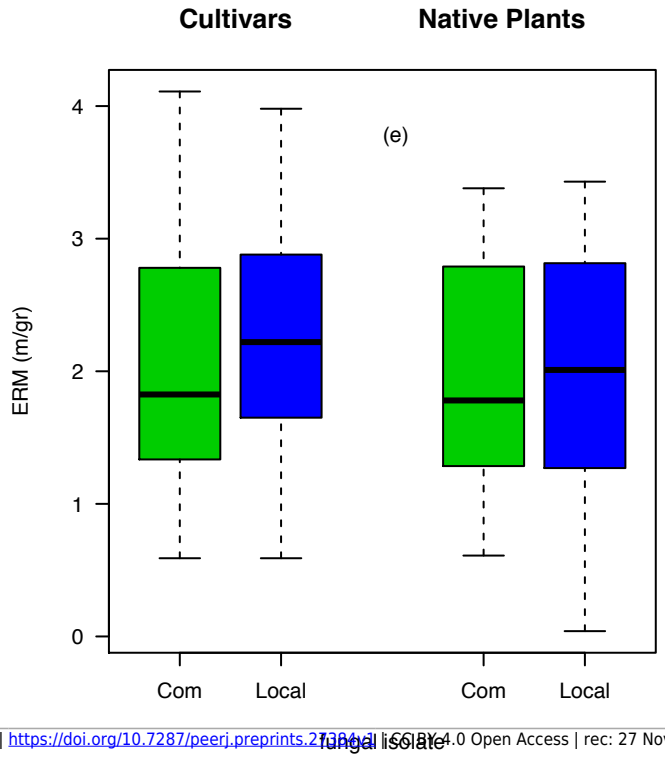
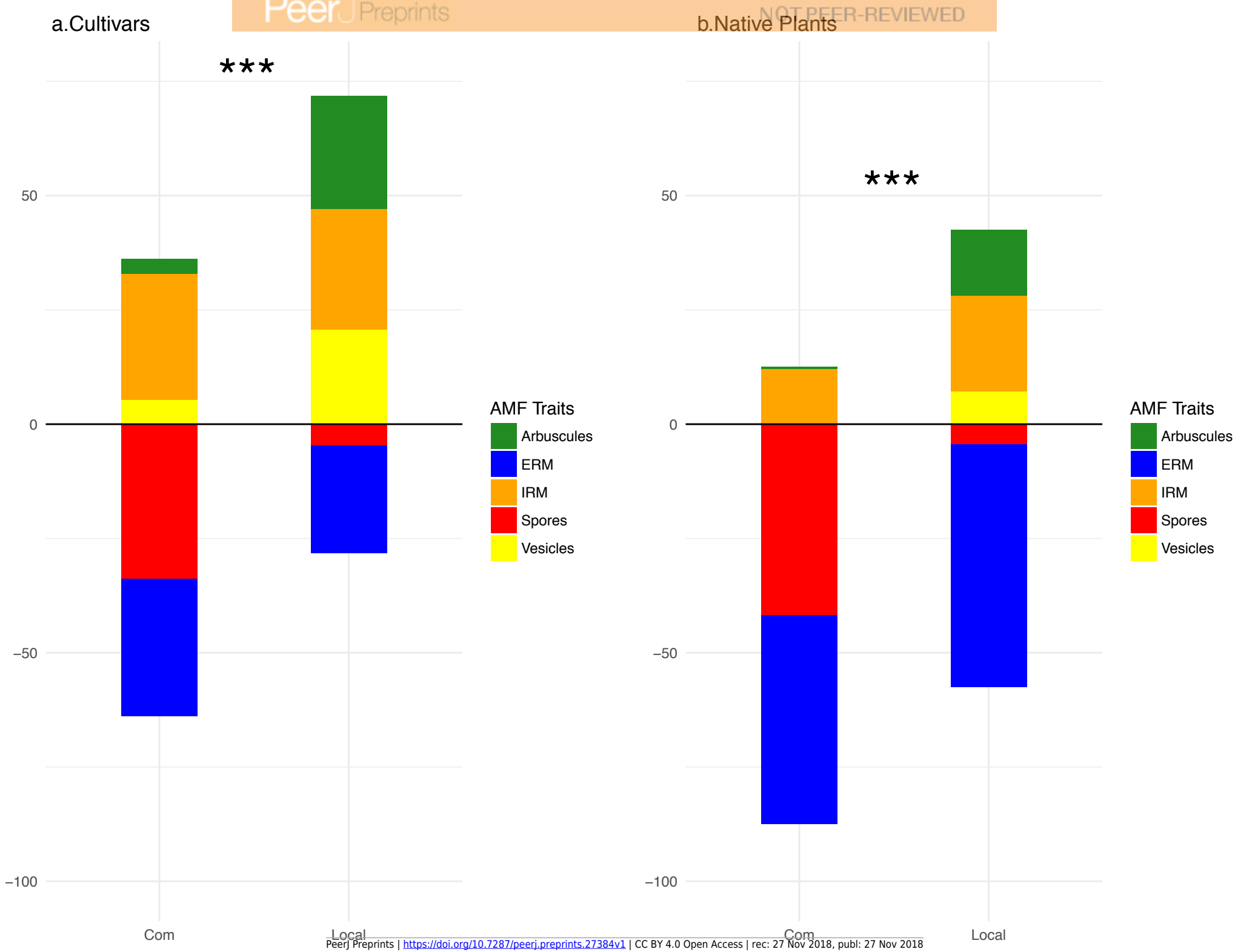


Figure 6(on next page)

Proportional representation of fungal structures in crop and wild plants.

Arbuscules (green), extraradical mycelium (blue), intraradical mycelium (orange), spores (red) and vesicles (yellow) of the commercial (Com) and local isolates (Local) when associated with **(a)** crop and **(b)** wild plants. Positive values represent intraradical traits and negative values represent extraradical traits for purpose of visualization. *** $p<0.001$.



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