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Frew, A., Antunes, P.M., Cameron, D.D. [orcid.org/0000-0002-5439-6544](https://orcid.org/0000-0002-5439-6544) et al. (4 more authors) (2022) *Plant herbivore protection by arbuscular mycorrhizas : a role for fungal diversity?* *New Phytologist*, 233 (3). pp. 1022-1031. ISSN 0028-646X

<https://doi.org/10.1111/nph.17781>

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This is the peer reviewed version of the following article: Frew, A., Antunes, P.M., Cameron, D.D., Hartley, S.E., Johnson, S.N., Rillig, M.C. and Bennett, A.E. (2021), *Plant herbivore protection by arbuscular mycorrhizas: A role for fungal diversity?*. *New Phytologist*. Accepted Author Manuscript., which has been published in final form at <https://doi.org/10.1111/nph.17781>. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Use of Self-Archived Versions. This article may not be enhanced, enriched or otherwise transformed into a derivative work, without express permission from Wiley or by statutory rights under applicable legislation. Copyright notices must not be removed, obscured or modified. The article must be linked to Wiley's version of record on Wiley Online Library and any embedding, framing or otherwise making available the article or pages thereof by third parties from platforms, services and websites other than Wiley Online Library must be prohibited.

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Article type : Letter

**Letter**

**Plant herbivore protection by arbuscular mycorrhizas: A role for fungal diversity?**

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This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/NPH.17781](https://doi.org/10.1111/NPH.17781)

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Received, 2 July 2021; accepted, 3 October 2021.

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The symbiosis between arbuscular mycorrhizal (AM) fungi, subphylum Glomeromycotina, and terrestrial plants is one of the most widespread and arguably most successful plant symbioses on Earth. This ancient relationship, going back 475 MY (Remy *et al.*, 1994; Redecker & Raab, 2006; Field *et al.*, 2015; Rich *et al.*, 2021) is beneficial for the fungi and normally benefits their plant partners. Through colonisation of plant roots, the fungi provide their host plants with access to soil elements including phosphorus (P) and nitrogen (N) while the fungi are provided with carbon (Hodge *et al.*, 2001; Smith & Read, 2008; Keymer & Gutjahr, 2018). The contribution of AM fungi to ecosystems goes beyond nutrient delivery to plants. They are active players that influence key ecosystem functions such as nutrient cycling, decomposition, soil aggregation, belowground biodiversity, and plant community ecology (Powell & Rillig, 2018; Tedersoo *et al.*, 2020). There is widespread recognition that the morphological and functional diversity of AM fungi affects their impact on these functions (Van Der Heijden & Scheublin, 2007), and on host plant growth promotion and nutrient uptake (Chagnon *et al.*, 2013).

In addition to these functions, AM fungi can enhance host defence against pathogens and insect herbivory, to which much research has been dedicated (e.g., Bennett *et al.*, 2006; Cameron *et al.*, 2013; Tao *et al.*, 2016; Rivero *et al.*, 2021). Despite this, the role of AM fungal diversity (comprising species richness and relative abundance) in these interactions continues to be largely overlooked by researchers. This is problematic considering plants typically associate with multiple AM fungi in both natural and

agriculturally managed environments (Öpik *et al.*, 2006, 2013; Bainard *et al.*, 2014). Wehner *et al.* (2010) previously highlighted this blind-spot with regard to plant protection from pathogens. Here, we contend that research on AM fungal effects on plant protection from insect herbivory suffers from a similar weakness. The importance of mycorrhizal fungal diversity is being increasingly recognised and incorporated into research efforts across various facets of ecology (Anderson & Cairney, 2004; Frac *et al.*, 2018; Powell & Rillig, 2018). Meanwhile progress on how AM fungal diversity mediates mycorrhiza-enhanced protection from herbivory is fragmented and piecemeal.

Our purpose here is to (i) briefly outline key mechanisms by which the AM symbiosis enhances plant defences to insect herbivores, (ii) summarise where research has made progress in understanding the role of fungal diversity in plant defences against insect herbivory, (iii) emphasise why it is important to understand how AM fungal diversity determines plant defence outcomes while highlighting the key knowledge gaps to be addressed.

### **How can AM fungi protect plants from herbivory?**

To enhance their fitness and survival when challenged with herbivore attack, plants rely on different defence strategies. These strategies can be categorised as tolerance-based, reflecting the ability of a plant to regrow and reproduce after damage from herbivores (compensatory growth), or resistance-based defences that reduce the performance or host preference of the insect (Strauss & Agrawal, 1999; Agrawal & Weber, 2015). AM fungi can improve access for plants to nutrients, and as such, it then follows that plants engaged in the AM symbiosis can be better equipped to defend themselves from biotic attackers, particularly in nutrient deficient environments. That said, better access to nutrients may also drive shifts in plant defence strategies, which can include decreased allocation to active defences and increased investment to improve regrowth and tolerance to herbivory (Coley *et al.*, 1985). Furthermore, in addition to improving access to P and N, AM fungi are able to enhance uptake of other elements important for plant defence. For example, when soil silicon availability is limiting plant uptake, AM fungi can increase plant tissue silicon concentrations, and so augment silicon-based herbivore resistance (Frew *et al.*, 2017). It is also worth acknowledging that improved nutrient access can also directly benefit insect herbivores, which are able to acquire fungal-delivered nutrients (Wilkinson *et al.*, 2019a).

Commonly accepted theory predicts that there are investment trade-offs between tolerance and resistance-based defence mechanisms (van der Meijden *et al.*, 1988; Simms & Triplett, 1994), although evidence also suggests plants can simultaneously invest resources in both (Leimu & Koricheva, 2006). Still,

for many plants their ability to regrow following herbivory will rely heavily on their mycorrhizal associations as tolerance is determined, in part, by the availability of resources (Wise & Abrahamson, 2005). Thus, plant tolerance should be higher in plants associated with AM fungi. However, research has found the AM symbiosis can increase, decrease, or have no effect on tolerance-associated mechanisms (Borowicz, 2013). Such variation is not related to plant functional group, and we have limited data on the influence of herbivore feeding guilds (i.e., chewing or piercing insect, foliar or root herbivory; Borowicz, 2013). Indeed, the role and effects of AM fungi on plant tolerance to herbivory are arguably less well-characterised compared to their effects on resistance. This may be partly due to a lagging understanding of the ecology of tolerance more broadly (Fornoni, 2011), and that tolerance is infrequently observed or reported in cultivated plants (Stoner, 1992).

In addition to tolerating attack, plants rely on a suite of resistance-based defence mechanisms that reduce herbivore performance (e.g., reduced growth, survival, fecundity) or preference (e.g., reduced consumption, avoidance). There is an abundance of research showing the variety of resistance mechanisms AM fungi can affect, both positively and negatively, which have been covered in several reviews (Hartley & Gange, 2009; Johnson & Rasmann, 2015; Schweiger & Müller, 2015; Bennett *et al.*, 2018). Examples include the regulation of secondary metabolites such as cardenolides (Vannette *et al.*, 2013), benzoxazinoids (Song *et al.*, 2011; Frew *et al.*, 2018), flavonoids and tannins (Pedone-Bonfim *et al.*, 2013), silicon-based resistance mechanisms (Frew *et al.*, 2017), and many others.

Nonetheless, beyond the elucidation of specific resistance-associated traits, the ability of AM fungi to induce systemic resistance to insect herbivores and pathogens is increasingly recognised as defence priming, or AM fungal-induced resistance (Pineda *et al.*, 2010; Jung *et al.*, 2012; Cameron *et al.*, 2013; Martinez-Medina *et al.*, 2016; Bennett *et al.*, 2018; Rivero *et al.*, 2021). Here, there is regulation of plant defence-associated phytohormones where the development of mycorrhiza-induced resistance occurs over four-phases as the fungi colonise their host plant and an arbuscular mycorrhiza is formed (see model proposed in Cameron *et al.*, 2013). Once established, evidence suggests the jasmonic acid (JA) and ethylene defence pathway is upregulated, while the salicylic acid (SA) pathway is suppressed (Pozo & Azcón-Aguilar, 2007; Nair *et al.*, 2015; Song *et al.*, 2015; Schoenherr *et al.*, 2019). This defence priming itself does not necessarily lead to the expression of defences, but when subsequently challenged by a herbivore (or other biotic stressor) JA-associated defences are typically expressed more rapidly and with greater efficacy (Jung *et al.*, 2012; Rivero *et al.*, 2021). This understanding corresponds with the general patterns of how different insect herbivores are affected by the AM symbiosis. Specifically, chewing insects who are sensitive to JA-associated defences tend to be negatively affected, while piercing insects,

sensitive to SA-associated defences, are less negatively affected or even benefit from the AM symbiosis (Hartley & Gange, 2009; Koricheva *et al.*, 2009; Yang *et al.*, 2014; Johnson & Rasmann, 2015). This defence induction can even be elicited via the common mycelial network that connects the roots of different individual plants. For example, Song *et al.* (2014) showed that a herbivore-free plant connected to a conspecific neighbour, solely via mycorrhizal fungal mycelia, upregulated JA-associated genes and defence enzymes when the neighbouring plant was attacked by the chewing herbivore *Spodoptera litura*. Similarly, Babikova *et al.* (2013) demonstrated that a herbivore-free plant connected (via fungal mycelia) to a conspecific neighbour, exhibited changes in herbivore-induced plant volatile production when the neighbouring plant was subjected to the sucking herbivore *Acyrtosiphon pisum*.

### **Influence of fungal species identity and diversity on defence**

The outcomes of the AM symbiosis for plant growth and nutrient uptake can be highly context-specific, dependent on factors such as soil nutrient availability, plant and AM fungal identities, and diversity (Fig. 1a; Bever, 2002; Hoeksema *et al.*, 2010; Veresoglou *et al.*, 2012). Plant performance responses are often stronger when inoculated with multiple AM fungal taxa compared with single-species inoculation (Veresoglou *et al.*, 2012; Zhang *et al.*, 2019). Yet, it is worth noting the vast majority of experimental studies of plant responses to AM fungi, including plant responses under stress, use single-species inocula, a point that has been raised across multiple meta-analyses and reviews over the years (Hoeksema *et al.*, 2010; Chandrasekaran *et al.*, 2014; Jayne & Quigley, 2014; Augé *et al.*, 2015; Pellegrino *et al.*, 2015).

### **Tolerance**

Given the functional diversity of AM fungi with regard to plant growth and nutrient uptake, it follows that plant tolerance to herbivory can also depend on fungal partner identity. In one of the few studies to experimentally manipulate AM fungal diversity and directly examine tolerance, Bennett and Bever (2007) demonstrated AM fungal taxon-specific tolerance outcomes, and found that the combined effects of a fungal community were driven by a single 'dominant' fungal species within the community. Other studies have also shown species-specific associations with AM fungi can drive plant tolerance to herbivory (Kula *et al.*, 2005), and that AM fungal abundance can increase tolerance capacity (Tao *et al.*, 2016).

When considering only single AM fungal species studies, the meta-analysis by Borowicz (2013) found plant growth responses to herbivory strongly depended on fungal identity, highlighting that the model AM fungus *Rhizophagus irregularis* typically reduces tolerance, while *Funnelformis mosseae* improves it.

The authors also highlighted that single-species inoculants tended to enhance tolerance while, perhaps unexpectedly, multi-species inoculants actually augmented the effects of herbivory on plant growth.

### **Resistance**

Taxon-specific effects of AM fungi also extend to plant resistance-based defences (Fig. 1a). In one study, Goverde *et al.* (2000) found three AM fungal species differentially affected insect herbivore performance, although neither the AM fungi nor resistance-conferring mechanisms were identified. Building on this, and earlier pioneering work (Gange, 1996), research has continued to establish more broadly how different fungal species, or combinations of species, can deliver different resistance outcomes for plants (Gange, 2001; Wooley & Paine, 2007; Bennett *et al.*, 2009; Currie *et al.*, 2011; Roger *et al.*, 2013; Vannette *et al.*, 2013; Barber *et al.*, 2013; He *et al.*, 2017; Malik *et al.*, 2018). Furthermore, research has shown that different isolates of the same AM fungal species can have distinct impacts on plant-herbivore interactions, highlighting a potential role for within-species genetic variation of AM fungi (See Box 1).

As we garner greater appreciation for the differential effects of AM fungal taxa on herbivore performance, we are acquiring clarity as to how specific resistance-based defence mechanisms might underpin these effects. Bennett *et al.* (2009) investigated how resistance-associated chemistry in response to herbivory varies with different AM fungal species and diversity. The authors found that constitutive and induced defences were increased by specific AM fungal species (*Scutellospora calospora* and *A. trappei*, respectively), but their effects were lost if the fungi were applied as a mixed community, rather than single-species inoculation. Furthermore, several other studies have reported mixed communities of AM fungi can confer inferior plant resistance compared to single-species inoculation (Fig. 1b; Currie *et al.*, 2011; Gange, 2001).

A number of additional experiments have now shown how different species, or levels of species richness, affect different herbivore-associated defence compounds (Nishida *et al.*, 2010; Ceccarelli *et al.*, 2010; Jung *et al.*, 2012; Zubek *et al.*, 2015; Malik *et al.*, 2018; Frew & Wilson, 2021). We also have a better understanding of the AM fungal species-specific impacts on phytohormonal signalling that underpin mycorrhiza-induced resistance (Jung *et al.*, 2012; Cameron *et al.*, 2013). Specifically, studies have found *F. mosseae* induces greater expression of JA marker genes and JA-associated defence compounds when compared to *R. irregularis* (López-Ráez *et al.*, 2010; Fernández *et al.*, 2014). This reflects the aforementioned superior ability of *F. mosseae* to also confer greater tolerance to herbivory, compared to *R. irregularis* (Borowicz, 2013), suggesting *F. mosseae* can promote both tolerance and resistance-based defence. Indeed, as plant secondary metabolism is a strong driver of host plant choice for insect herbivores (Hopkins *et al.*, 2017), any species-specific impacts of AM fungi on different components of

plant secondary chemistry will not only alter defence outcomes but have significant ecologically cascading effects (Babikova *et al.*, 2014). Yet there seems to be surprisingly few empirical studies that directly demonstrate how any AM fungal species-specific changes in defence chemistry affect herbivore performance. Many demonstrate changes in plant secondary chemistry without measuring effects on herbivores, or show effects on herbivores without identifying the mediating defence mechanisms. As such, the vast majority of studies on how AM fungal taxa alter plant defence traits actually infer resistance to herbivory, rather than demonstrate it.

In addition to using 'mock' communities, either from commercial inocula or from maintained cultures, studies have employed naturally occurring (or native) AM fungal communities in plant-herbivore experiments (Bennett *et al.*, 2009, 2016; Karley *et al.*, 2017; Real-Santillán *et al.*, 2019; Damin *et al.*, 2020; Frew & Wilson, 2021). Still, very few directly assess how the diversity of native AM fungal communities can differentially impact resistance mechanisms to herbivory. This is particularly surprising considering the widespread recognition of the importance of AM fungal functional diversity for host plant outcomes, and broader ecosystem functions. In one study, Barber *et al.* (2013) compared two native field-sourced communities with a commercial AM fungal inoculum (*R. irregularis*) and found the native communities induced greater concentrations of root secondary metabolites (cucurbitacin C) compared to the single-species inoculum. Although the authors did not identify the fungal taxa within the native communities, or measure herbivore responses, the study highlights that drawing conclusions on AM fungal effects on plant defence from research on a small selection of AM fungal species (or communities) can misrepresent plant defence outcomes conferred by fungal communities in the field. The paucity of field studies, compared to laboratory, growth-chamber, or glasshouse studies, remains a key barrier to incorporating fungal diversity into our understanding of AM fungal effects on plant defence.

**Box. 1 Importance of within-species genetic variation in AM fungi**

In addition to between species genetic variation, within species genetic variation may also play a role in the outcome of AM fungal-plant-herbivore interactions. There are a number of examples demonstrating that both plant and herbivore diversity can alter the outcome of this multi-species interaction (e.g., Bennett *et al.*, 2016; Rasmussen *et al.*, 2017), but within AM fungal species variation has been assessed significantly less often. The lowest level of genetic diversity in AM fungi is an 'isolate' or a 'line' but as AM fungi are multi-nucleate and some isolates are dikaryons, with two distinct nuclear genotypes (Kokkoris *et al.*, 2020), defining an 'individual' for AM fungi is challenging. We know of only three studies which have examined the impact of within AM fungal species variation on plant herbivore interactions. The first two studies tested the impact of two isolates of



*Claroideoglossum etunicatum* on the piercing herbivores mirids (Wooley & Paine, 2007) and silver leaf whitefly (Wooley & Paine, 2011) feeding on tobacco. Isolates promoted different mirid nymph population sizes (depending on nymphal stage), but no difference in silver leaf whitefly abundance. However, in the latter study, whitefly experienced different parasitism rates by *Eretmocerus eremicus* depending on the isolate. The third study tested the impact of four isolates of *R. irregularis* alone and in combination on herbivory by the chewing herbivore *Spodoptera littoralis* feeding on strawberry (Roger *et al.*, 2013). Most isolates tended to suppress insect mass and survival, but this was not consistent across all isolates or combinations of isolates. Thus, the direction of responses (positive for piercing herbivores, negative for chewing herbivores) appears to be relatively consistent across isolates, but the degree of impact (from neutral to significantly positive or negative) varies by isolate. Our ability to identify and manipulate AM fungal genetic variation has significantly advanced since the first two tests, and the most recent study built on these advancements. The two isolates used in the two studies above were chosen based on geographical distance (Arizona and Georgia) in an effort to maximize genetic variation between them. However, we now know that there can be great genetic variation within individual AM fungal isolates (e.g., Mateus *et al.*, 2019; Masclaux *et al.*, 2019; Reinhardt *et al.*, 2021), and there are approaches for creating isolates that vary genotypically and phenotypically. For example, the isolates used in the third study were developed from a cross of two clonal lines that have been shown to vary widely in host growth promotion (Angelard *et al.*, 2010) and drought stress tolerance (Peña *et al.*, 2020) capacity. While the use of some genetic tools (e.g., CRISPR/CAS9) in AM fungi are still a long way off, the advance of sequencing and other approaches may allow us to select for AM fungi with specific traits in the not so distant future. Thus, using these tools we could more explicitly test for the impact of within species genetic variation, and even test the importance of particular AM fungal traits on plant-herbivore interactions.

### **Why consider diversity?**

AM fungal diversity has a strong influence on plant communities and plant productivity (Bever *et al.*, 2013; Manoharan *et al.*, 2017; Powell & Rillig, 2018; Tedersoo *et al.*, 2020). We argue that the role of AM fungal diversity in plant defence against insect herbivory continues to be overlooked, something we cannot afford if we are to be effective in managing AM fungi across a variety of contexts (i.e., agriculture, invasive species management, ecosystem restoration).

When it comes to demonstrating the functional diversity of AM fungi in the context of their effects on plant tolerance and resistance to herbivory, there has been progress, which we have briefly touched on. Yet experimental research has continued to focus only on a very limited number of commonly used AM fungal taxa. Indeed, a survey of studies on AM fungal-induced plant defence published between 2014-2017 found that 75% of studies used a single AM fungal taxon, while 72% used *R. irregularis* and *F. mosseae* (Malik, 2018). With around 288 described species of AM fungi, or c. 1,700 putative species (Öpik & Davison, 2016) it is clear that we are likely to have barely scratched the surface of defence functional diversity of AM fungi (Heinen *et al.*, 2018). To properly understand the mechanistic basis of mycorrhiza-induced resistance, it is imperative to consider the role of fungal diversity in these interactions. In both natural and agricultural field environments plants interact with many different AM fungal taxa in a manner that can vary temporally and spatially (Öpik *et al.*, 2013; Helgason *et al.*, 2014; Bainard *et al.*, 2014). Yet currently there is no information on the relative importance of different aspects of diversity (i.e. species richness, relative abundance) to plant defence (Fig. 2), or the consequences of temporal changes (e.g., seasonality) in fungal diversity. Indeed, from a long-term perspective, shifts in plant nutrient acquisition strategies as ecosystems develop are also likely to have implications for plant defence strategies. For example, some systems may exhibit a reduction in the relative cover of AM plants in favour of other strategies i.e., cluster roots (Zemunik *et al.*, 2015). Alternatively, AM plants may also persist and dominate as ecosystems progress (Holdaway *et al.*, 2011). Although different mycorrhizal types (i.e., AM, ectomycorrhizal, ericoid mycorrhizal) can dominate any stage of ecosystem development (Dickie *et al.*, 2013), any shifts that do occur are likely to alter the relative influence of AM fungal diversity on defence (Tombeur *et al.*, 2021), an area which requires further examination.

In addressing how AM fungal diversity determines plant defence outcomes, a trait-based approach could be employed (Zanne *et al.*, 2020). This has been successful in other contexts in plant ecology, where traits have been valuable across a range of ecological inquiries such as identifying how plants invest resources to certain functions and components of fitness (Westoby *et al.*, 2002; Wright *et al.*, 2004), or in linking plant functional diversity to certain ecosystem processes (e.g., productivity) (Petchey & Gaston, 2006). As the identification of fungal traits develops and becomes more clearly defined (Chagnon *et al.*, 2013; Rillig *et al.*, 2015; Aguilar-Trigueros *et al.*, 2015; Soudzilovskaia *et al.*, 2020), AM fungal traits may underpin their function in the context of plant defence against herbivory. Indeed, in this context, fungal traits should be considered alongside the traits and life history strategies of the plant hosts. These may be considered within a life history strategy framework, for example the C-S-R (competitor, stress tolerator, ruderal) framework (Grime, 1979). Here, 'ruderal' AM fungi, with high growth rates and hyphal turnover,

would provide better herbivore protection, as their ruderal plant hosts are less likely to be nutrient limited and more likely to be susceptible to pathogen and herbivore attack (Chagnon *et al.*, 2013). There may also be potential trade-offs between fungal functional traits (Fig. 2), for example, do traits which enhance the ability of AM fungi to provide resistance to herbivory impact on other functions such as soil aggregation or nutrient uptake? Resistance-associated traits may also inherently affect the competitiveness of a fungal species, or its role in ecosystem functions.

### **AM fungal inoculants and diversity**

Interest in the application of AM fungi as inoculants to serve certain ecological outcomes (e.g., accelerate ecosystem restoration, promote plant growth) has been around for some time. However, with mounting global efforts to improve food security and sustainability, there has been particular attention given towards their use to sustainably enhance crop productivity and a concomitant interest in commercially available 'biofertilisers' (Hart *et al.*, 2018). Although some work has shown the application of cosmopolitan AM fungal species (such as *R. irregularis*) in the field can increase crop yields (Pellegrino *et al.*, 2012; Ceballos *et al.*, 2013; Zhang *et al.*, 2019), strong and consistent evidence is still lacking (Thirkell *et al.*, 2017; Hart *et al.*, 2018). This is likely to be partly due to the fact that the AM fungal communities that colonise plant roots in response to inoculation are strongly influenced by the identities of the resident root-colonising fungi prior to inoculation, coupled with strong environmental drivers such as soil pH (Mummey *et al.*, 2009; Dumbrell *et al.*, 2010; Davison *et al.*, 2021). Variation in suitability and competitiveness of certain fungal taxa for certain environments can mean that AM fungi with desired functions, such as crop growth promotion or herbivore resistance, may establish, but equally, they may be filtered out while other fungal species that are less 'effective' may dominate (Fig. 1c). Additionally, fungal species richness can have positive and negative effects on plant defence (Bennett *et al.*, 2009; Currie *et al.*, 2011; Roger *et al.*, 2013; Vannette & Hunter, 2013), meaning it is difficult to predict if plants will receive any defence benefit from inoculation without knowing the composition of the resident soil fungal community, and how the application of foreign AM fungi might interact with the resident community. Thus, in agricultural systems, identifying land management approaches that favour particular AM fungal communities with a desired set of plant defence-associated traits is likely to be a more effective and pragmatic option over fungal inoculation. Regarding crop productivity, Rodriguez and Sanders (2015) pointed out the lack of field studies that assess if or how inoculation affects the soil or root-colonising AM fungal communities over time, a point later echoed by others (Hart *et al.*, 2018). The same can be said for

plant herbivore defence where no studies, to our knowledge, have attempted to monitor AM fungal communities post-inoculation over time, and assess impacts on plant defences.

## **Conclusions**

The vast majority of plants in nature have mycorrhizas (Brundrett & Tedersoo, 2018), so any understanding of how plants defend themselves from insect herbivores is incomplete without considering their AM fungi. Our brief discussion here has touched on how AM fungi can affect plant defences, and that these effects differ between AM fungal taxa. As most research continues to focus on a handful of fungal species, the conclusions are far from representative of the range of interactions between AM fungi, plants and insect herbivores. Furthermore, even fewer studies have attempted to tackle the formidable challenge of determining how AM fungal diversity in the field can shape plant defence. Metabolomic and metagenomic-based approaches (e.g., DNA metabarcoding; Öpik *et al.*, 2010) are valuable tools in addressing these knowledge gaps, where the inclusion of AM fungal community interactions into plant-herbivore research is likely to pave the way towards effectively managing AM fungi to enhance plant protection (Hill *et al.*, 2018; Wilkinson *et al.*, 2019b). Over a decade ago Wehner *et al.* (2010) highlighted how the functional diversity of AM fungi necessitates that fungal diversity take a prominent role in research into plant pathogen protection. We echo this message and urge researchers to acknowledge the importance of AM fungal diversity, and to incorporate the community ecology of AM fungi in efforts to understand how the AM symbiosis governs plant defence against herbivory.

## **Author contributions**

The rationale behind the manuscript was led by AF and developed in collaboration with all authors. AF wrote the first draft of the article and all authors contributed ideas and helped write the final version. AF and PMA led the creation of the figures with contributions from all authors.

## **Acknowledgements**

The authors would like to thank the handling editor and three anonymous reviewers for their helpful comments on previous versions of the manuscript.

## References

- Agrawal AA, Weber MG. 2015.** On the study of plant defence and herbivory using comparative approaches: how important are secondary plant compounds. *Ecology Letters* **18**: 985–991.
- Aguilar-Trigueros CA, Hempel S, Powell JR, Anderson IC, Antonovics J, Bergmann J, Cavagnaro TR, Chen B, Hart MM, Klironomos J, et al. 2015.** Branching out: Towards a trait-based understanding of fungal ecology. *Fungal Biology Reviews* **29**: 34–41.
- Anderson IC, Cairney JWG. 2004.** Diversity and ecology of soil fungal communities: increased understanding through the application of molecular techniques. *Environmental Microbiology* **6**: 769–779.
- Angelard C, Colard A, Niculita-Hirzel H, Croll D, Sanders IR. 2010.** Segregation in a mycorrhizal fungus alters rice growth and symbiosis-specific gene transcription. *Current Biology* **20**: 1216–1221.
- Augé RM, Toler HD, Saxton AM. 2015.** Arbuscular mycorrhizal symbiosis alters stomatal conductance of host plants more under drought than under amply watered conditions: a meta-analysis. *Mycorrhiza* **25**: 13–24.
- Babikova Z, Gilbert L, Bruce TJA, Birkett M, Caulfield JC, Woodcock C, Pickett JA, Johnson D. 2013.** Underground signals carried through common mycelial networks warn neighbouring plants of aphid attack. *Ecology Letters* **16**: 835–843.
- Babikova Z, Gilbert L, Bruce T, Dewhurst SY, Pickett JA, Johnson D. 2014.** Arbuscular mycorrhizal fungi and aphids interact by changing host plant quality and volatile emission. *Functional Ecology* **28**: 375–385.
- Bainard LD, Bainard JD, Hamel C, Gan Y. 2014.** Spatial and temporal structuring of arbuscular mycorrhizal communities is differentially influenced by abiotic factors and host crop in a semi-arid prairie agroecosystem. *FEMS Microbiology Ecology* **88**: 333–344.
- Barber NA, Kiers ET, Theis N, Hazzard RV, Adler LS. 2013.** Linking agricultural practices, mycorrhizal fungi, and traits mediating plant–insect interactions. *Ecological Applications* **23**: 1519–1530.
- Bennett AE, Alers-Garcia J, Bever JD. 2006.** Three-way interactions among mutualistic mycorrhizal fungi, plants, and plant enemies: hypotheses and synthesis. *The American Naturalist* **167**: 141–152.

**Bennett AE, Bever JD. 2007.** Mycorrhizal species differentially alter plant growth and response to herbivory. *Ecology* **88**: 210–218.

**Bennett AE, Bever JD, Bowers MD. 2009.** Arbuscular mycorrhizal fungal species suppress inducible plant responses and alter defensive strategies following herbivory. *Oecologia* **160**: 771–779.

**Bennett AE, Millar NS, Gedrovics E, Karley AJ. 2016.** Plant and insect microbial symbionts alter the outcome of plant–herbivore–parasitoid interactions: implications for invaded, agricultural and natural systems. *Journal of Ecology* **104**: 1734–1744.

**Bennett AE, Orrell P, Malacrino A, Pozo MJ. 2018.** Fungal-mediated above–belowground interactions: The community approach, stability, evolution, mechanisms, and applications. In: Ohgushi T, Wurst S, Johnson SN, eds. *Ecological Studies. Aboveground–Belowground Community Ecology*. Cham: Springer International Publishing, 85–116.

**Bever JD. 2002.** Negative feedback within a mutualism: host–specific growth of mycorrhizal fungi reduces plant benefit. *Proceedings of the Royal Society of London B: Biological Sciences* **269**: 2595–2601.

**Bever JD, Broadhurst LM, Thrall PH. 2013.** Microbial phylotype composition and diversity predicts plant productivity and plant–soil feedbacks. *Ecology Letters* **16**: 167–174.

**Borowicz VA. 2013.** The impact of arbuscular mycorrhizal fungi on plant growth following herbivory: A search for pattern. *Acta Oecologica* **52**: 1–9.

**Brundrett MC, Tedersoo L. 2018.** Evolutionary history of mycorrhizal symbioses and global host plant diversity. *New Phytologist* **220**: 1108–1115.

**Cameron DD, Neal AL, van Wees SCM, Ton J. 2013.** Mycorrhiza-induced resistance: more than the sum of its parts? *Trends in Plant Science* **18**: 539–545.

**Ceballos I, Ruiz M, Fernández C, Peña R, Rodríguez A, Sanders IR. 2013.** The in vitro mass-produced model mycorrhizal fungus, *Rhizophagus irregularis*, significantly increases yields of the globally important food security crop cassava. *PLOS ONE* **8**: e70633.

**Ceccarelli N, Curadi M, Martelloni L, Sbrana C, Picciarelli P, Giovannetti M. 2010.** Mycorrhizal colonization impacts on phenolic content and antioxidant properties of artichoke leaves and flower heads two years after field transplant. *Plant and Soil* **335**: 311–323.

**Chagnon P-L, Bradley RL, Maherali H, Klironomos JN. 2013.** A trait-based framework to understand life history of mycorrhizal fungi. *Trends in Plant Science* **18**: 484–491.

**Chandrasekaran M, Boughattas S, Hu S, Oh S-H, Sa T. 2014.** A meta-analysis of arbuscular mycorrhizal effects on plants grown under salt stress. *Mycorrhiza* **24**: 611–625.

**Coley PD, Bryant JP, Chapin FS. 1985.** Resource availability and plant antiherbivore defense. *Science* **230**: 895–899.

**Currie AF, Murray PJ, Gange AC. 2011.** Is a specialist root-feeding insect affected by arbuscular mycorrhizal fungi? *Applied Soil Ecology* **47**: 77–83.

**Damin S, Carrenho R, Martins S. 2020.** The influence of mycorrhization on the growth of *Zea mays* L. and the sclerification of foliar tissues susceptible to chewing insect attacks. *Brazilian Journal of Botany* **43**: 493–502.

**Davison J, Moora M, Semchenko M, Adenan SB, Ahmed T, Akhmetzhanova AA, Alatalo JM, Al-Quraishy S, Andriyanova E, Anslan S, et al. 2021.** Temperature and pH define the realized niche space of arbuscular mycorrhizal fungi. *New Phytologist* **231**: 763–776.

**Dickie IA, Martínez-García LB, Koele N, Grelet G-A, Tylianakis JM, Peltzer DA, Richardson SJ. 2013.** Mycorrhizas and mycorrhizal fungal communities throughout ecosystem development. *Plant and Soil* **367**: 11–39.

**Dumbrell AJ, Nelson M, Helgason T, Dytham C, Fitter AH. 2010.** Relative roles of niche and neutral processes in structuring a soil microbial community. *The ISME Journal* **4**: 337–345.

**Fernández I, Merlos M, López-Ráez JA, Martínez-Medina A, Ferrol N, Azcón C, Bonfante P, Flors V, Pozo MJ. 2014.** Defense related phytohormones regulation in arbuscular mycorrhizal symbioses depends on the partner genotypes. *Journal of Chemical Ecology* **40**: 791–803.

**Field KJ, Rimington WR, Bidartondo MI, Allinson KE, Beerling DJ, Cameron DD, Duckett JG, Leake JR, Pressel S. 2015.** First evidence of mutualism between ancient plant lineages (Haplomitriopsida liverworts) and Mucoromycotina fungi and its response to simulated Palaeozoic changes in atmospheric CO<sub>2</sub>. *New Phytologist* **205**: 743–756.

**Fornoni J. 2011.** Ecological and evolutionary implications of plant tolerance to herbivory. *Functional Ecology* **25**: 399–407.

**Fraç M, Hannula SE, Bełka M, Jędryczka M. 2018.** Fungal biodiversity and their role in soil health. *Frontiers in Microbiology* **9**: 707.

**Frew A, Powell JR, Allsopp PG, Sallam N, Johnson SN. 2017.** Arbuscular mycorrhizal fungi promote silicon accumulation in plant roots, reducing the impacts of root herbivory. *Plant and Soil* **419**: 423–433.

**Frew A, Powell JR, Glauser G, Bennett AE, Johnson SN. 2018.** Mycorrhizal fungi enhance nutrient uptake but disarm defences in plant roots, promoting plant-parasitic nematode populations. *Soil Biology and Biochemistry* **126**: 123–132.

**Frew A, Wilson BAL. 2021.** Different mycorrhizal fungal communities differentially affect plant phenolic-based resistance to insect herbivory. *Rhizosphere* **19**: 100365.

**Gange AC. 1996.** Reduction in vine weevil larval growth by mycorrhizal fungi. *Mitteilungen-Biologischen Bundesanstalt für Land und Forstwirtschaft* **316**: 56–60.

**Gange AC. 2001.** Species-specific responses of a root-and shoot-feeding insect to arbuscular mycorrhizal colonization of its host plant. *New Phytologist* **150**: 611–618.

**Goverde M, van der Heijden M, Wiemken A, Sanders I, Erhardt A. 2000.** Arbuscular mycorrhizal fungi influence life history traits of a lepidopteran herbivore. *Oecologia* **125**: 362–369.

**Grime JP. 1979.** *Plant Strategies and Vegetation Processes*. Oxford, UK: John Wiley & Sons.

**Hart MM, Antunes PM, Chaudhary VB, Abbott LK. 2018.** Fungal inoculants in the field: Is the reward greater than the risk? *Functional Ecology* **32**: 126–135.

**Hartley SE, Gange AC. 2009.** Impacts of plant symbiotic fungi on insect herbivores: mutualism in a multitrophic context. *Annual Review of Entomology* **54**: 323–342.

**He L, Li C, Liu R. 2017.** Indirect interactions between arbuscular mycorrhizal fungi and *Spodoptera exigua* alter photosynthesis and plant endogenous hormones. *Mycorrhiza* **27**: 525–535.



**Heinen R, Biere A, Harvey JA, Bezemer TM. 2018.** Effects of soil organisms on aboveground plant-insect interactions in the field: patterns, mechanisms and the role of methodology. *Frontiers in Ecology and Evolution* **6**: 106.

**Helgason T, Feng H, Sherlock DJ, Young JPW, Fitter AH. 2014.** Arbuscular mycorrhizal communities associated with maples (*Acer* spp.) in a common garden are influenced by season and host plant. *Botany* **92**: 321–326.

**Hill EM, Robinson LA, Abdul-Sada A, Vanbergen AJ, Hodge A, Hartley SE. 2018.** Arbuscular mycorrhizal fungi and plant chemical defence: effects of colonisation on aboveground and belowground metabolomes. *Journal of Chemical Ecology* **44**: 198–208.

**Hodge A, Campbell CD, Fitter AH. 2001.** An arbuscular mycorrhizal fungus accelerates decomposition and acquires nitrogen directly from organic material. *Nature* **413**: 297–299.

**Hoeksema JD, Chaudhary VB, Gehring CA, Johnson NC, Karst J, Koide RT, Pringle A, Zabinski C, Bever JD, Moore JC, et al. 2010.** A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecology Letters* **13**: 394–407.

**Holdaway RJ, Richardson SJ, Dickie IA, Peltzer DA, Coomes DA. 2011.** Species- and community-level patterns in fine root traits along a 120 000-year soil chronosequence in temperate rain forest. *Journal of Ecology* **99**: 954–963.

**Hopkins DP, Cameron DD, Butlin RK. 2017.** The chemical signatures underlying host plant discrimination by aphids. *Scientific Reports* **7**: 8498.

**Jayne B, Quigley M. 2014.** Influence of arbuscular mycorrhiza on growth and reproductive response of plants under water deficit: a meta-analysis. *Mycorrhiza* **24**: 109–119.

**Johnson SN, Rasmann S. 2015.** Root-feeding insects and their interactions with organisms in the rhizosphere. *Annual Review of Entomology* **60**: 517–535.

**Jung SC, Martinez-Medina A, Lopez-Raez JA, Pozo MJ. 2012.** Mycorrhiza-induced resistance and priming of plant defenses. *Journal of Chemical Ecology* **38**: 651–664.

**Karley AJ, Emslie-Smith M, Bennett AE. 2017.** Potato aphid *Macrosiphum euphorbiae* performance is determined by aphid genotype and not mycorrhizal fungi or water availability. *Insect Science* **24**: 1015–1024.

**Keymer A, Gutjahr C. 2018.** Cross-kingdom lipid transfer in arbuscular mycorrhiza symbiosis and beyond. *Current Opinion in Plant Biology* **44**: 137–144.

**Kokkoris V, Stefani F, Dalpé Y, Dettman J, Corradi N. 2020.** Nuclear dynamics in the arbuscular mycorrhizal fungi. *Trends in Plant Science* **25**: 765–778.

**Koricheva J, Gange AC, Jones T. 2009.** Effects of mycorrhizal fungi on insect herbivores: a meta-analysis. *Ecology* **90**: 2088–2097.

**Kula AAR, Hartnett DC, Wilson GWT. 2005.** Effects of mycorrhizal symbiosis on tallgrass prairie plant–herbivore interactions. *Ecology Letters* **8**: 61–69.

**Leimu R, Koricheva J. 2006.** A meta-analysis of tradeoffs between plant tolerance and resistance to herbivores: combining the evidence from ecological and agricultural studies. *Oikos* **112**: 1–9.

**López-Ráez JA, Verhage A, Fernández I, García JM, Azcón-Aguilar C, Flors V, Pozo MJ. 2010.** Hormonal and transcriptional profiles highlight common and differential host responses to arbuscular mycorrhizal fungi and the regulation of the oxylipin pathway. *Journal of Experimental Botany* **61**: 2589–2601.

**Malik RJ. 2018.** Recent trend: Is the role of arbuscular mycorrhizal fungi in plant-enemies performance biased by taxon usage? *The American Midland Naturalist* **180**: 306–311.

**Malik RJ, Ali JG, Bever JD. 2018.** Mycorrhizal composition influences plant anatomical defense and impacts herbivore growth and survival in a life-stage dependent manner. *Pedobiologia* **66**: 29–35.

**Manoharan L, Rosenstock NP, Williams A, Hedlund K. 2017.** Agricultural management practices influence AMF diversity and community composition with cascading effects on plant productivity. *Applied Soil Ecology* **115**: 53–59.

**Martinez-Medina A, Flors V, Heil M, Mauch-Mani B, Pieterse CMJ, Pozo MJ, Ton J, van Dam NM, Conrath U. 2016.** Recognizing plant defense priming. *Trends in Plant Science* **21**: 818–822.

**Masclaux FG, Wyss T, Pagni M, Rosikiewicz P, Sanders IR. 2019.** Investigating unexplained genetic variation and its expression in the arbuscular mycorrhizal fungus *Rhizophagus irregularis*: A comparison of whole genome and RAD sequencing data. *PLOS ONE* **14**: e0226497.

**Mateus ID, Masclaux FG, Aletti C, Rojas EC, Savary R, Dupuis C, Sanders IR. 2019.** Dual RNA-seq reveals large-scale non-conserved genotype × genotype-specific genetic reprogramming and molecular crosstalk in the mycorrhizal symbiosis. *The ISME Journal* **13**: 1226–1238.

**van der Meijden E, Wijn M, Verkaar HJ. 1988.** Defence and regrowth, alternative plant strategies in the struggle against herbivores. *Oikos*: 355–363.

**Mummey DL, Antunes PM, Rillig MC. 2009.** Arbuscular mycorrhizal fungi pre-inoculant identity determines community composition in roots. *Soil Biology and Biochemistry* **41**: 1173–1179.

**Nair A, Kolet SP, Thulasiram HV, Bhargava S. 2015.** Systemic jasmonic acid modulation in mycorrhizal tomato plants and its role in induced resistance against *Alternaria alternata*. *Plant Biology* **17**: 625–631.

**Nishida T, Katayama N, Izumi N, Ohgushi T. 2010.** Arbuscular mycorrhizal fungi species-specifically affect induced plant responses to a spider mite. *Population Ecology* **52**: 507–515.

**Öpik M, Davison J. 2016.** Uniting species- and community-oriented approaches to understand arbuscular mycorrhizal fungal diversity. *Fungal Ecology* **24**: 106–113.

**Öpik M, Moora M, Liira J, Zobel M. 2006.** Composition of root-colonizing arbuscular mycorrhizal fungal communities in different ecosystems around the globe. *Journal of Ecology* **94**: 778–790.

**Öpik M, Vanatoa A, Vanatoa E, Moora M, Davison J, Kalwij JM, Reier Ü, Zobel M. 2010.** The online database MaarjAM reveals global and ecosystemic distribution patterns in arbuscular mycorrhizal fungi (Glomeromycota). *New Phytologist* **188**: 223–241.

**Öpik M, Zobel M, Cantero JJ, Davison J, Facelli JM, Hiiesalu I, Jairus T, Kalwij JM, Koorem K, Leal ME, et al. 2013.** Global sampling of plant roots expands the described molecular diversity of arbuscular mycorrhizal fungi. *Mycorrhiza* **23**: 411–430.

**Pedone-Bonfim MV, Lins MA, Coelho IR, Santana AS, Silva FS, Maia LC. 2013.** Mycorrhizal technology and phosphorus in the production of primary and secondary metabolites in cebil (*Anadenanthera colubrina* (Vell.) Brenan) seedlings. *Journal of the Science of Food and Agriculture* **93**: 1479–1484.

**Pellegrino E, Öpik M, Bonari E, Ercoli L. 2015.** Responses of wheat to arbuscular mycorrhizal fungi: A meta-analysis of field studies from 1975 to 2013. *Soil Biology and Biochemistry* **84**: 210–217.

**Pellegrino E, Turrini A, Gamper HA, Cafà G, Bonari E, Young JPW, Giovannetti M. 2012.** Establishment, persistence and effectiveness of arbuscular mycorrhizal fungal inoculants in the field revealed using molecular genetic tracing and measurement of yield components. *New Phytologist* **194**: 810–822.

**Peña R, Robbins C, Corella JC, Thuita M, Masso C, Vanlauwe B, Signarbieux C, Rodriguez A, Sanders IR. 2020.** Genetically different isolates of the arbuscular mycorrhizal fungus *Rhizophagus irregularis* induce differential responses to stress in cassava. *Frontiers in Plant Science* **11**: 596929.

**Petchey OL, Gaston KJ. 2006.** Functional diversity: back to basics and looking forward. *Ecology Letters* **9**: 741–758.

**Pineda A, Zheng S-J, van Loon JJA, Pieterse CMJ, Dicke M. 2010.** Helping plants to deal with insects: the role of beneficial soil-borne microbes. *Trends in Plant Science* **15**: 507–514.

**Powell JR, Rillig MC. 2018.** Biodiversity of arbuscular mycorrhizal fungi and ecosystem function. *New Phytologist* **220**: 1059–1075.

**Pozo MJ, Azcón-Aguilar C. 2007.** Unraveling mycorrhiza-induced resistance. *Current Opinion in Plant Biology* **10**: 393–398.

**Rasmussen PU, Amin T, Bennett AE, Green KK, Timonen S, Nouhuys SV, Tack AJM. 2017.** Plant and insect genetic variation mediate the impact of arbuscular mycorrhizal fungi on a natural plant–herbivore interaction. *Ecological Entomology* **42**: 793–802.

**Real-Santillán RO, del-Val E, Cruz-Ortega R, Contreras-Cornejo HÁ, González-Esquivel CE, Larsen J. 2019.** Increased maize growth and P uptake promoted by arbuscular mycorrhizal fungi coincide with higher foliar herbivory and larval biomass of the Fall Armyworm *Spodoptera frugiperda*. *Mycorrhiza* **29**: 615–622.

**Redecker D, Raab P. 2006.** Phylogeny of the Glomeromycota (arbuscular mycorrhizal fungi): recent developments and new gene markers. *Mycologia* **98**: 885–895.

**Reinhardt D, Roux C, Corradi N, Di Pietro A. 2021.** Lineage-specific genes and cryptic sex: Parallels and differences between arbuscular mycorrhizal fungi and fungal pathogens. *Trends in Plant Science* **26**: 111–123.

**Remy W, Taylor TN, Hass H, Kerp H. 1994.** Four hundred-million-year-old vesicular arbuscular mycorrhizae. *Proceedings of the National Academy of Sciences* **91**: 11841–11843.

**Rich MK, Vigneron N, Libourel C, Keller J, Xue L, Hajheidari M, Radhakrishnan GV, Ru AL, Diop SI, Potente G, et al. 2021.** Lipid exchanges drove the evolution of mutualism during plant terrestrialization. *Science* **372**: 864–868.

**Rillig MC, Aguilar-Trigueros CA, Bergmann J, Verbruggen E, Veresoglou SD, Lehmann A. 2015.** Plant root and mycorrhizal fungal traits for understanding soil aggregation. *New Phytologist* **205**: 1385–1388.

**Rivero J, Lidoy J, Llopis-Giménez Á, Herrero S, Flors V, Pozo MJ. 2021.** Mycorrhizal symbiosis primes the accumulation of antiherbivore compounds and enhances herbivore mortality in tomato. *Journal of Experimental Botany* **72**: 5038–5050.

**Rodriguez A, Sanders IR. 2015.** The role of community and population ecology in applying mycorrhizal fungi for improved food security. *The ISME Journal* **9**: 1053–1061.

**Roger A, Gétaz M, Rasmann S, Sanders IR. 2013.** Identity and combinations of arbuscular mycorrhizal fungal isolates influence plant resistance and insect preference. *Ecological Entomology* **38**: 330–338.

**Schoenherr AP, Rizzo E, Jackson N, Manosalva P, Gomez SK. 2019.** Mycorrhiza-induced resistance in potato involves priming of defense responses against cabbage looper (Noctuidae: Lepidoptera). *Environmental Entomology* **48**: 370–381.

**Schweiger R, Müller C. 2015.** Leaf metabolome in arbuscular mycorrhizal symbiosis. *Current Opinion in Plant Biology* **26**: 120–126.

**Simms EL, Triplett J. 1994.** Costs and benefits of plant responses to disease: resistance and tolerance. *Evolution* **48**: 1973–1985.

**Smith SE, Read DJ. 2008.** *Mycorrhizal Symbiosis*. Amsterdam, the Netherlands & Boston, MA: Academic Press.

**Song YY, Cao M, Xie LJ, Liang XT, Zeng RS, Su YJ, Huang JH, Wang RL, Luo SM. 2011.** Induction of DIMBOA accumulation and systemic defense responses as a mechanism of enhanced resistance of mycorrhizal corn (*Zea mays* L.) to sheath blight. *Mycorrhiza* **21**: 721–731.

**Song Y, Chen D, Lu K, Sun Z, Zeng R. 2015.** Enhanced tomato disease resistance primed by arbuscular mycorrhizal fungus. *Frontiers in Plant Science* **6**: 786.

**Song YY, Ye M, Li C, He X, Zhu-Salzman K, Wang RL, Su YJ, Luo SM, Zeng RS. 2014.** Hijacking common mycorrhizal networks for herbivore-induced defence signal transfer between tomato plants. *Scientific Reports* **4**: 3915.

**Soudzilovskaia NA, Vaessen S, Barcelo M, He J, Rahimlou S, Abarenkov K, Brundrett MC, Gomes SIF, Merckx V, Tedersoo L. 2020.** FungalRoot: global online database of plant mycorrhizal associations. *New Phytologist* **227**: 955–966.

**Stoner KA. 1992.** Bibliography of plant resistance to arthropods in vegetables, 1977–1991. *Phytoparasitica* **20**: 125–180.

**Strauss SY, Agrawal AA. 1999.** The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology & Evolution* **14**: 179–185.

**Tao L, Ahmad A, Roode JC de, Hunter MD. 2016.** Arbuscular mycorrhizal fungi affect plant tolerance and chemical defences to herbivory through different mechanisms. *Journal of Ecology* **104**: 561–571.

**Tedersoo L, Bahram M, Zobel M. 2020.** How mycorrhizal associations drive plant population and community biology. *Science* **367**: eaba1223.

**Thirkell TJ, Charters MD, Elliott AJ, Sait SM, Field KJ. 2017.** Are mycorrhizal fungi our sustainable saviours? Considerations for achieving food security. *Journal of Ecology* **105**: 921–929.

**Tombeur F de, Laliberté E, Lambers H, Faucon M-P, Zemunik G, Turner BL, Cornelis J-T, Mahy G. 2021.** A shift from phenol to silica-based leaf defences during long-term soil and ecosystem development. *Ecology Letters* **24**: 984–995.

**Van Der Heijden MG, Scheublin TR. 2007.** Functional traits in mycorrhizal ecology: their use for predicting the impact of arbuscular mycorrhizal fungal communities on plant growth and ecosystem functioning. *New Phytologist* **174**: 244–250.

**Vannette RL, Hunter MD. 2013.** Mycorrhizal abundance affects the expression of plant resistance traits and herbivore performance. *Journal of Ecology* **101**: 1019–1029.

**Vannette RL, Hunter MD, Rasmann S. 2013.** Arbuscular mycorrhizal fungi alter above- and below-ground chemical defense expression differentially among *Asclepias* species. *Frontiers in Plant Science* **4**: 361.

**Veresoglou SD, Menexes G, Rillig MC. 2012.** Do arbuscular mycorrhizal fungi affect the allometric partition of host plant biomass to shoots and roots? A meta-analysis of studies from 1990 to 2010. *Mycorrhiza* **22**: 227–235.

**Wehner J, Antunes PM, Powell JR, Mazukatow J, Rillig MC. 2010.** Plant pathogen protection by arbuscular mycorrhizas: A role for fungal diversity? *Pedobiologia* **53**: 197–201.

**Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ. 2002.** Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* **33**: 125–159.

**Wilkinson TDJ, Ferrari J, Hartley SE, Hodge A. 2019a.** Aphids can acquire the nitrogen delivered to plants by arbuscular mycorrhizal fungi. *Functional Ecology* **33**: 576–586.

**Wilkinson TDJ, Miranda J-P, Ferrari J, Hartley SE, Hodge A. 2019b.** Aphids influence soil fungal communities in conventional agricultural systems. *Frontiers in Plant Science* **10**: 895.

**Wise MJ, Abrahamson WG. 2005.** Beyond the compensatory continuum: environmental resource levels and plant tolerance of herbivory. *Oikos* **109**: 417–428.

**Wooley SC, Paine TD. 2007.** Can intra-specific genetic variation in arbuscular mycorrhizal fungi (*Glomus etunicatum*) affect a mesophyll-feeding herbivore (*Tupiocoris notatus* Distant)? *Ecological Entomology* **32**: 428–434.

**Wooley SC, Paine TD. 2011.** Infection by mycorrhizal fungi increases natural enemy abundance on tobacco (*Nicotiana rustica*). *Environmental Entomology* **40**: 36–41.

**Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, et al. 2004.** The worldwide leaf economics spectrum. *Nature* **428**: 821–827.

**Yang H, Dai Y, Wang X, Zhang Q, Zhu L, Bian X. 2014.** Meta-analysis of interactions between arbuscular mycorrhizal fungi and biotic stressors of plants. *The Scientific World Journal* **2014**: 746506.

Zanne AE, Abarenkov K, Afkhami ME, Aguilar-Trigueros CA, Bates S, Bhatnagar JM, Busby PE, Christian N, Cornwell WK, Crowther TW, *et al.* 2020. Fungal functional ecology: bringing a trait-based approach to plant-associated fungi. *Biological Reviews* **95**: 409–433.

Zemunik G, Turner BL, Lambers H, Laliberté E. 2015. Diversity of plant nutrient-acquisition strategies increases during long-term ecosystem development. *Nature Plants* **1**: 1–4.

Zhang S, Lehmann A, Zheng W, You Z, Rillig MC. 2019. Arbuscular mycorrhizal fungi increase grain yields: a meta-analysis. *New Phytologist* **222**: 543–555.

Zubek S, Rola K, Szewczyk A, Majewska ML, Turnau K. 2015. Enhanced concentrations of elements and secondary metabolites in *Viola tricolor* L. induced by arbuscular mycorrhizal fungi. *Plant and Soil* **390**: 129–142.

**Key words:** arbuscular mycorrhizal fungal diversity, insect herbivores, microbial communities, plant defence, resistance, tolerance

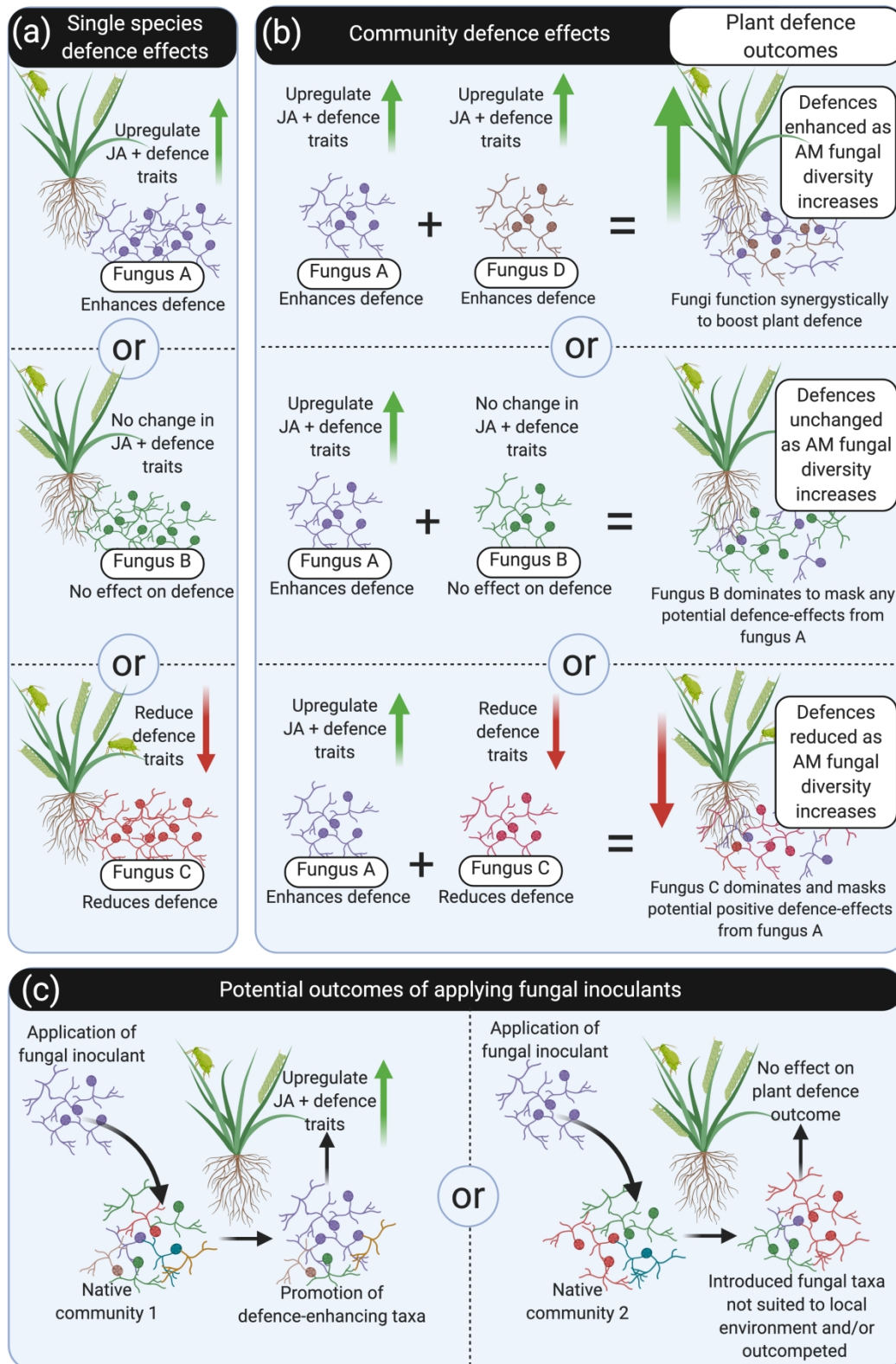
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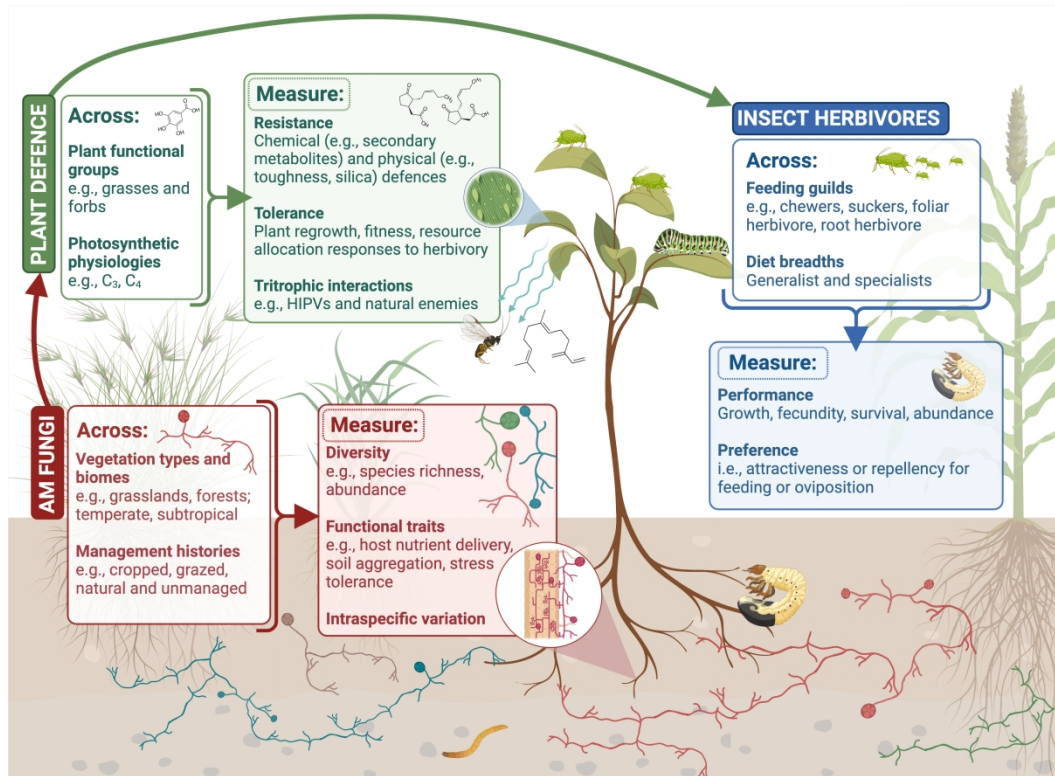
**Figure 1.** Hypothetical effects of arbuscular mycorrhizal (AM) fungi on plant defences against insect herbivores. **(a)** Potential differential effects of AM fungi on plant defences where different taxa confer distinct effects on plant defences, potentially upregulating defence, having no impact, or reducing plant defence. **(b)** Different outcomes of multi-species fungal associations on plant defence. Dual-species colonisation may confer greater defence benefits than single species colonisation, alternatively the defence phenotype of one fungal species may dominate which may provide little/no defence or nutrient benefit, consequently greater fungal diversity may not confer greater defence benefits, or even reduce



defence. **(c)** Two potential effects of inoculation with an AM fungus on native AM fungal communities and outcomes for plant defence. Inoculation could result in a change in fungal communities to promote plant defence, or the introduced AM fungus may not persist in the environment and thus have no impacts on plant defence. Figure created with BioRender.com. JA, jasmonic acid.

**Figure 2.** Priority areas to be incorporated into research investigating arbuscular mycorrhizal (AM) fungal effects on plant defence and insect herbivores. Research should assess how 'native' AM fungal communities across environmental contexts (i.e., different vegetation types and biomes) and management histories (e.g., organic agricultural management, unmanaged natural ecosystems) affect plant herbivore defences. Exploring how different components of fungal diversity (e.g., species richness, relative abundance), within-species genetic variation, and fungal traits relate to defence outcomes is a particularly important knowledge gap. A DNA metabarcoding approach referencing appropriate databases (e.g. MaarjAM) will be a valuable tool in addressing such gaps. Researchers should look at how defence outcomes vary across a range of host plant species (e.g. different plant functional groups), measuring resistance and tolerance defence mechanisms, including other trophic level interactions (i.e. natural enemy attraction via changes in herbivore-induced plant volatiles [HIPVs]). Measurement of herbivore responses (e.g., growth, survival, preference) is important to demonstrate defence outcomes, these should be assessed across herbivores of various feeding guilds and diet breadths. Figure created with BioRender.com.





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