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Letter

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

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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; Frąc *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 *Acyrthosiphon 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

Claroideoglomus 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., CRSPR/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 fugal 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.

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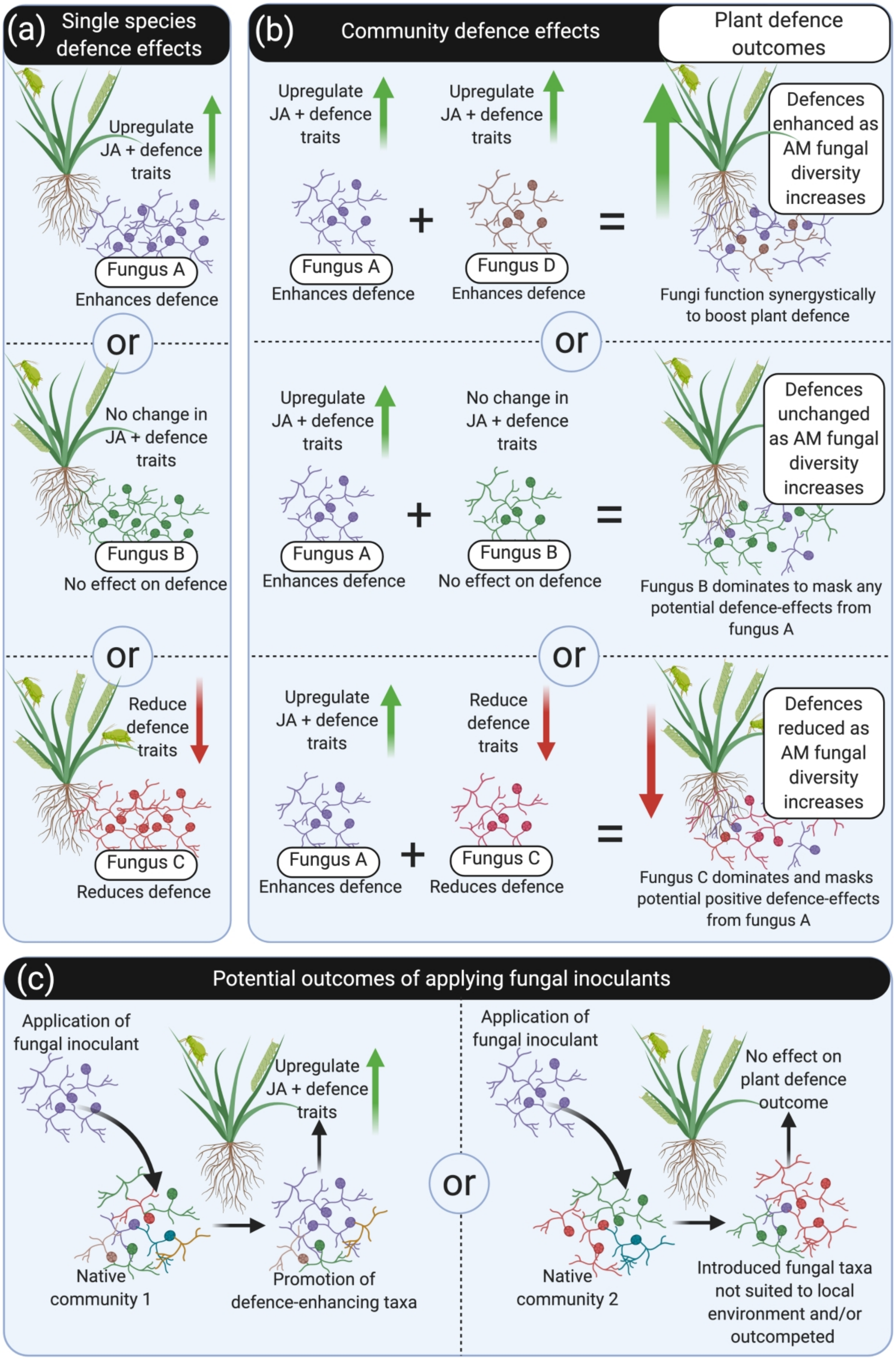
Key words: arbuscular mycorrhizal fungal diversity, insect herbivores, microbial communities, plant defence, resistance, tolerance

Figure legends

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. Maarj*AM*) 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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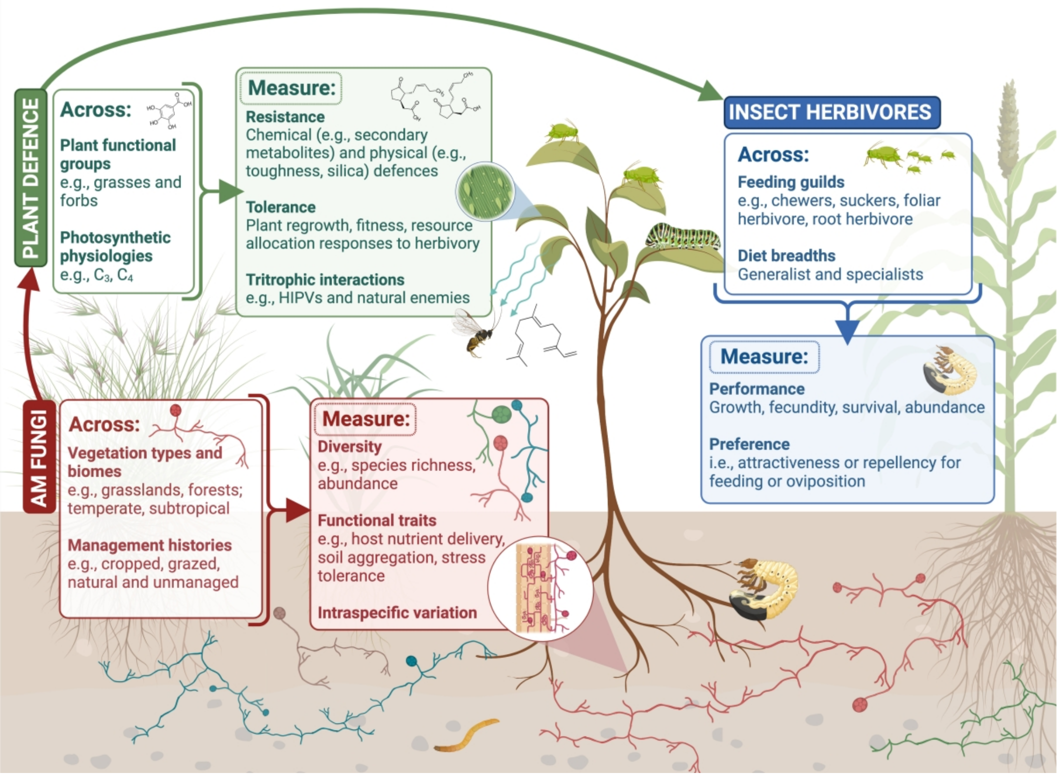

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