

PERSPECTIVE

Mycorrhizal-mediated plant–herbivore interactions in a high CO₂ worldAdam Frew^{1,2,3}  | Jodi N. Price³¹School of Agricultural and Wine Sciences, Charles Sturt University, Wagga Wagga, New South Wales, Australia²Graham Centre for Agricultural Innovation, Charles Sturt University, Wagga Wagga, New South Wales, Australia³Institute for Land, Water and Society, Charles Sturt University, Albury, New South Wales, Australia

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Abstract

1. The symbiotic relationship between terrestrial plants and arbuscular mycorrhizal (AM) fungi is a key driver of plant nutritional and defence traits influencing insect herbivory. These tripartite interactions have been fundamental to shaping the evolution of land plants and the diversity of insect herbivores. Surprisingly, we have little understanding of how these interactions will function under elevated atmospheric CO₂ concentrations (eCO₂), despite the considerable implications for both natural and managed ecosystems.
2. Although substantial research has revealed how eCO₂ alters mycorrhizal–plant interactions, or plant–herbivore interactions, there is a stark scarcity of studies which investigate how eCO₂ impacts mycorrhizal-mediated plant–insect herbivore relationships.
3. Here, we synthesise some of the main effects of eCO₂ on the mycorrhizal symbiosis, the concomitant impacts on plant nutrient dynamics and secondary metabolism, and how eCO₂-driven changes in plant growth, biochemistry and communities impact insect herbivores.
4. We point out that potential mechanistic drivers of AM fungal–plant–insect herbivore relationships under eCO₂ can function antagonistically and are highly context-dependent, which poses a particular challenge. Still, we hypothesise as to the potential outcomes for AM fungal–plant–herbivore dynamics under eCO₂.
5. We identify key research priorities to tackle the substantial gap in our understanding. If ecological theory is to effectively inform agricultural and natural management practices in the future, research needs to directly investigate how changes in global atmospheric CO₂ concentrations impact the tripartite relationship between AM fungi, plants and insect herbivores.

KEYWORDS

arbuscular mycorrhizal fungi, climate change, elevated atmospheric CO₂ concentrations, herbivory, insect

1 | INTRODUCTION

The symbiotic relationship between arbuscular mycorrhizal (AM) fungi and terrestrial plants is an ancient interaction that played

an important role in the evolution of land plants (van der Heijden, Martin, Selosse, & Sanders, 2015). This relationship is principally based on the transfer of nutrients where the fungi provide access to phosphorus (P), nitrogen (N) and other nutrients, while the host

plant(s) provides the fungi with carbon, in the form of hexose sugars and lipids (Rich, Nouri, Courty, & Reinhardt, 2017).

The influence of the AM symbiosis reaches far beyond the host plants. More than half of the world's described insects feed on living plant material (Price, Denno, Eubanks, Finke, & Kaplan, 2011). Their growth, survival and fitness are largely determined by the quality of their hosts, most of which form associations with AM fungi. These fungi not only affect the nutrient status of their host plant, but also impact their physiology and secondary chemistry, which are major components of plant resistance to herbivory (Agrawal & Weber, 2015). Hence, AM fungi can significantly affect insect herbivore performance and ultimately insect population densities and herbivore damage. This relationship is integral to many ecological and agricultural processes including carbon sequestration, nutrient cycling, plant growth, plant resistance to pests and disease, crop yield and plant community structure.

Global atmospheric concentrations of CO₂ are expected to continue to rise between 478 and 1,099 ppm by the end of this century, according to different climate scenarios (IPCC, 2014). These changes in our atmosphere will affect plant growth, physiology, chemistry, the mycorrhizal symbiosis and the relationship that plants have with herbivorous insects. Considerable research has focussed on elucidating how eCO₂ is likely to affect the mycorrhizal symbiosis (Dong, Wang, Sun, Yang, & Xu, 2018; Terrer, Vicca, Hungate, Phillips, & Prentice, 2016; Treseder, 2004). Yet when an insect feeds on its host plant, it is more than likely associated with an AM fungal community (Brundrett, 2009); similarly, every mycorrhizal plant in the world is likely to have at least one species of insect herbivore which attacks it (Agrawal, Hastings, Johnson, Maron, & Salminen, 2012; Futuyama & Agrawal, 2009). Mycorrhizal–plant–insect herbivore interactions are ubiquitous, yet our understanding of how this tripartite relationship will function under eCO₂ is ambiguous at best.

Predicting the outcome of interactions with more than two players is fundamentally challenging, presenting a classic “three-body problem” (Nielsen, Fedorov, Jensen, & Garrido, 2001). The innate difficulties in working with tripartite interactions in ecology are made more complicated by the often individualistic responses of mycorrhizal, plant and insect species. Interactions among multiple abiotic factors can affect AM fungi, plants and invertebrates in ways which are not easily predictable from measuring a single factor. Interactive effects can impair the predictability of impacts on mycorrhizal–plant–insect interactions.

There is a substantial body of literature which explores how AM fungi can impact insect herbivores via their shared host plant (Biere & Bennett, 2013; Hartley & Gange, 2009; Jung, Martinez-Medina, Lopez-Raez, & Pozo, 2012; Koricheva, Gange, & Jones, 2009; Pineda, Kaplan, & Bezemer, 2017). Likewise, there is an evolving knowledge of how eCO₂ impacts mycorrhizal–plant relations (Dong et al., 2018; Terrer et al., 2016; Treseder, 2004) and plant–insect relations (Gherlenda, Haigh, Moore, Johnson, & Riegler, 2016; Johnson & Jones, 2017; Lincoln, Fajer, & Johnson, 1993). Here, we do not provide a comprehensive review of these bipartite interactions, rather we raise the issue of our lack of knowledge—or even attempts

to directly test—how eCO₂ will alter the nature and strength of tripartite mycorrhizal-mediated plant–insect herbivore interactions. We focus on the AM symbiosis as the most common, and most ancient, of the mycorrhizal symbioses, present in nearly all seed plants (Brundrett, 2009; Taylor, Remy, Hass, & Kerp, 1995). As such, plant–herbivore interactions mediated by AM fungi are the most pervasive of mycorrhizal–plant–insect relationships.

To motivate researchers to address this gap, we synthesise some general impacts of eCO₂ on the bipartite interactions between AM fungi and plants, and between plants and herbivorous insects (Figures 1 and 2). We highlight that potential driving mechanisms (focussing on plant nutritional quality and defences) of mycorrhizal–plant–insect herbivore interactions under eCO₂ are often context-specific and can act antagonistically, making it difficult to predict the outcomes. We also point out that studies tend to focus on a small targeted selection of well-known secondary defence compounds or indicators of nutritional quality, highlighting the necessity to utilise available comprehensive analytical techniques. We urge researchers to realise the pressing need for empirical evidence to begin to disentangle how the nature of this globally pervasive tripartite relationship might be altered under eCO₂.

2 | IMPACTS OF eCO₂ ON BIPARTITE INTERACTIONS

2.1 | Impacts of eCO₂ on the arbuscular mycorrhizal symbiosis

As eCO₂ augments photosynthesis, thereby increasing nutrient limitation in plants, the classic prediction is that plant nutrient demand increases to meet growth requirements (Dong et al., 2018; Treseder, 2004). Plants increase C allocation towards AM fungal symbionts below-ground to facilitate their own increase in nutrient acquisition (Gavito, Schweiger, & Jakobsen, 2003); thus, meta-analyses suggest AM fungi generally increase in abundance and colonisation under CO₂ enrichment (Figure 1; Alberton, Kuyper, & Gorissen, 2005; Treseder, 2004).

This response can vary as plant responses to eCO₂ depend on their photosynthetic physiology (Johnson, Angelard, Sanders, & Kiers, 2015; Johnson, Wolf, & Koch, 2003). C₃ plant species, for example, often benefit more from eCO₂ than C₄ plants, for whom photosynthesis is already saturated at ambient CO₂ concentrations (although the opposite effect has been observed; Reich, Hobbie, Lee, & Pastore, 2018). Therefore, it could be argued that under eCO₂ we are likely to see a stronger increase in AM fungal dependence in C₃ plants compared with C₄ plants. However, AM fungal colonisation of C₄ plants may increase under eCO₂ more than C₃, which may utilise their augmented C reserves under eCO₂ primarily for their own growth, while C₄ plants invest more in their mycorrhizal partners (Compant, Van Der Heijden, & Sessitsch, 2010; Monz, Hunt, Reeves, & Elliott, 1994; Tang, Xu, Chen, & Hu, 2009). Outcomes will also depend on soil physical characteristics (Polley et al., 2018) and nutrient status. For example, plants often invest more in their mycorrhizal counterparts where P or N is limiting to growth (Becklin, Walker, Way, & Ward, 2017; Jiang

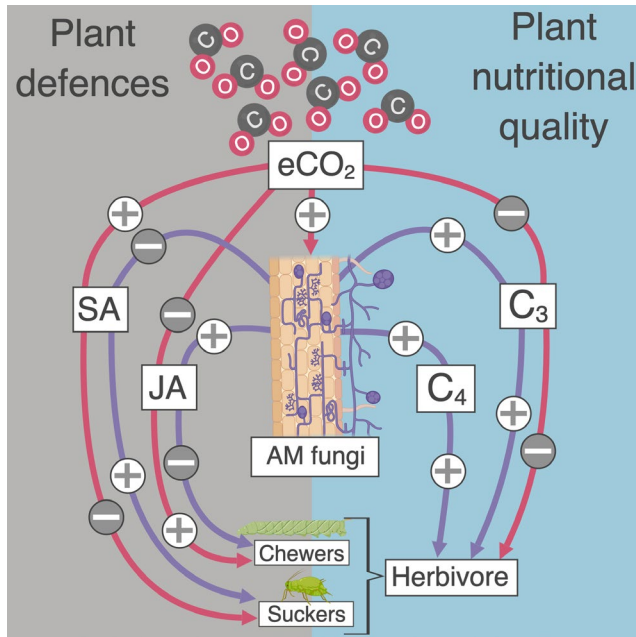


FIGURE 1 Some potential effects of elevated atmospheric CO_2 ($e\text{CO}_2$) concentrations on tripartite interactions between arbuscular mycorrhizal (AM) fungi, plants and insect herbivores. Interactions on the left highlight effects mediated by host-plant defences (secondary chemistry), and interactions on the right highlight effects mediated by host-plant nutritional quality; red arrows indicate effects driven by $e\text{CO}_2$, and purple arrows indicate effects mediated by AM fungi; arrows with “+” indicate positive effect, and arrows with “-” indicate negative effects. Overall, $e\text{CO}_2$ increases AM fungal abundance and colonisation. $e\text{CO}_2$ can reduce the nutritional quality of C_3 plants, potentially negatively impacting insect herbivores overall. However, AM fungi can promote plant nutritional quality in both C_3 and C_4 plants under $e\text{CO}_2$, which could benefit insect herbivores, potentially conflicting with the effects of $e\text{CO}_2$. $e\text{CO}_2$ can suppress the jasmonic acid (JA) pathway and promote the salicylic acid (SA) pathway, which could benefit chewing insects but negatively impact sucking insects. Conversely, however, AM fungi can enhance the JA pathway and suppress the SA pathway, potentially conflicting with the impacts of $e\text{CO}_2$

et al., 2018), while in N-limited soil $e\text{CO}_2$ does not increase growth in plants which associate with AM fungi (Terrer et al., 2016).

Changes in atmospheric CO_2 concentrations not only alter mycorrhizal-plant interactions but also impact mycorrhizal community structure as well. $e\text{CO}_2$ often reduces the abundance of the Gigasporaceae, while the Glomeraceae are promoted (Cotton, Fitter, Miller, Dumbrell, & Helgason, 2015; Klironomos, Ursic, Rillig, & Allen, 1998; Wolf, Johnson, Rowland, & Reich, 2003). This may have negative implications for insect herbivores, as fungi in the Glomeraceae are often associated with increased plant resistance to herbivory (Maherali & Klironomos, 2007).

Indeed, AM fungi not only alter the growth and nutrient status of their host plant, but also affect the production of secondary compounds (Frew, Powell, Glauser, Bennett, & Johnson, 2018; Hill et al., 2018), and other plant traits which drive herbivory (Frew, Powell, Allsopp, Sallam, & Johnson, 2017). Interestingly, there are significantly

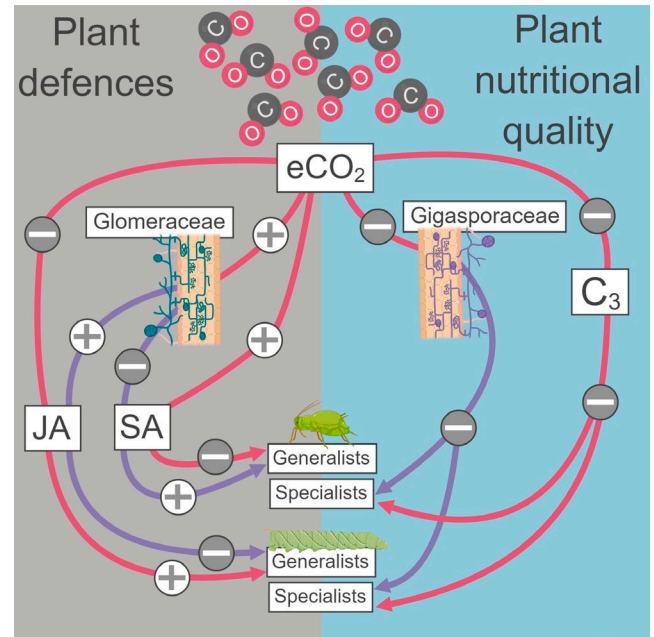


FIGURE 2 Potential effects of elevated atmospheric CO_2 ($e\text{CO}_2$) concentrations on tripartite interactions between arbuscular mycorrhizal (AM) fungi, plants and insect herbivores. Interactions on the left highlight effects mediated by host-plant defences (secondary chemistry), and interactions on the right highlight effects mediated by host-plant nutritional quality; red arrows indicate effects driven by $e\text{CO}_2$, and purple arrows indicate effects mediated by AM fungi; arrows with “+” indicate positive effects, and arrows with “-” indicate negative effects. $e\text{CO}_2$ can reduce the nutritional quality of C_3 plants, potentially negatively impacting specialist herbivores in particular, which may be more sensitive to nutritional changes than generalists. Additionally, $e\text{CO}_2$ may reduce relative abundance of AM fungal species in the Gigasporaceae (particularly associated with enhanced plant nutrition), reducing host-plant nutritional quality, negatively impacting specialist herbivores. From a defence perspective, $e\text{CO}_2$ may promote AM fungal species within the Glomeraceae (particularly associated with enhanced plant defence) enhancing the jasmonic acid (JA) pathway and suppress the salicylic acid (SA) pathway. This could benefit generalist sucking insects but negatively impact generalist chewing insects. Conversely, $e\text{CO}_2$ directly can suppress the JA pathway and promote the SA pathway, potentially conflicting with the impacts of AM fungi

fewer studies which assess mycorrhizal-driven changes in plant secondary metabolites and defence traits under CO_2 enrichment (Dong et al., 2018). Addressing this particular paucity is a critical step towards our ability to predict how mycorrhizal-plant-herbivore dynamics will function in high atmospheric CO_2 environments (Agrawal & Weber, 2015; Carmona, Lajeunesse, & Johnson, 2010).

2.2 | Impacts of $e\text{CO}_2$ on insect herbivores

How plant performance and biochemistry respond to CO_2 enrichment, and the impact of these changes on herbivorous insects has been a topic of extensive research (Bidart-Bouzat & Imeh-Nathaniel,

2008; Ellsworth et al., 2017; Hunter, 2001; Johnson, Ryalls, & Staley, 2016; Johnson & Züst, 2018; Lindroth, 2010; Robinson, Ryan, & Newman, 2012; Zavala, Nabity, & DeLucia, 2013). Overall, insect growth rates typically decrease in response to eCO_2 , consumption rates increase (Robinson et al., 2012), and for many insects, their development time is extended (Goverde & Erhardt, 2003), although there are some variable responses, particularly when it comes to insect diet breadth and feeding guild-specific responses to eCO_2 .

Plant nutritional quality and defence chemistry are key drivers of insect herbivore performance and thus underpin insect responses to eCO_2 (Figure 1). Under higher atmospheric CO_2 concentrations, many plants increase in carbohydrates, starch and sugars, while proteins and amino acids tend to decrease (Stiling & Cornelissen, 2007). This general increase in the C:N ratio, which implies a reduction in protein, can have significant negative consequences for insects as they are typically limited by protein in their diet (Robinson et al., 2012; Zvereva & Kozlov, 2006). However, sucking insects which feed on phloem are sometimes able to compensate for this reduction in sap quality, or even benefit from changes in the phloem amino acid profile (Ryalls et al., 2017; Sun, Jing, & Ge, 2009). Still, an increase in the C:N ratio typically translates to a reduction in the nutritional quality of the host plant. This can often reduce the ability of insects to convert plant tissue into their own biomass reducing their growth rates (Coviella & Trumble, 1999; Mattson, 1980; Stiling & Cornelissen, 2007). Though, insects can also behaviourally compensate for this reduced quality by increasing their consumption, offsetting the negative effects of higher C:N ratios (Slansky & Wheeler, 1989; Stiling & Cornelissen, 2007).

Elevated atmospheric CO_2 concentrations can also alter plant secondary chemistry and interact with plant hormonal signalling which modulates their defence responses to insect herbivory. These changes in secondary compounds are arguably much more difficult to predict than changes in plant N, sugar and starch content (which tend to be more consistent) as they are more variable between species (Zavala et al., 2013). This difficulty is compounded by the fact that relatively less focus has been given to how eCO_2 alters plant secondary metabolism. Our general understanding in terms of plant defence signalling is that eCO_2 can suppress ethylene and the jasmonic acid (JA) pathway (Sun, Guo, Zhu-Salzman, & Ge, 2013; Sun et al., 2011; Zavala et al., 2013), key hormones in plant defence responses to chewing insect herbivores (Erb, Meldau, & Howe, 2012). These pathways often operate antagonistically with the salicylic acid (SA) pathway, which is commonly considered to be activated by attack from sucking/piercing insects (Erb et al., 2012). Therefore eCO_2 may increase plant susceptibility to attack from some herbivores such as chewing insects, but elevate resistance towards others, through promotion or suppression of different plant defences (Figure 1).

3 | MYCORRHIZAL-MEDIATED PLANT-INSECT HERBIVORE INTERACTIONS

The impacts of AM fungi on insect herbivores are highly variable even under ambient atmospheric CO_2 concentrations. Mycorrhizae have

been observed to increase plant resistance, have no effect or even increase plant susceptibility to herbivory (Bennett, Alers-Garcia, & Bever, 2006; Biere & Bennett, 2013; Frew et al., 2018; Pineda et al., 2017). The AM symbiosis often benefits the host plant in terms of nutrient acquisition and nutritional quality, this can benefit the insects which feed on it (Koricheva et al., 2009), but an increase in nutrient acquisition can also mean greater investment in defences (Pozo & Azcón-Aguilar, 2007). Indeed, to successfully establish a mutualistic interaction, AM fungi suppress the SA pathway and enhance JA-regulated defence responses (García-Garrido & Ocampo, 2002; Hause, Maier, Miersch, Kramell, & Strack, 2002). This could partially explain how AM fungi often decrease the performance of generalist, chewing insects, but increase the performance of specialists and sucking insects (Kempel, Schmidt, Brandl, & Schädler, 2010; Koricheva et al., 2009). Specialist (monophagous and oligophagous) insects can often tolerate—or sequester—defence-associated compounds of their hosts, while generalist (polyphagous) insects cannot. Thus, it may be the case that specialists are able to benefit from mycorrhizal-driven increases in host-plant nutritional quality, and due to the specialisation of their diet breadth they may not suffer from mycorrhizal-driven increases in defence chemistry, in the same way that generalists would. Outcomes can also depend on mycorrhizal identity, for example AM fungi from the Family Glomeraceae have been strongly associated with host-plant defence, while fungi from the Family Gigasporaceae are more associated with enhanced plant nutrient acquisition (Maherali & Klironomos, 2007; Sikes, Cottenie, & Klironomos, 2009).

4 | MYCORRHIZAL-MEDIATED PLANT-INSECT HERBIVORE INTERACTIONS UNDER eCO_2

From the perspective of host-plant quality, eCO_2 can decrease nutritional quality by increasing carbohydrates and diluting nutrients, reducing herbivore performance (Figure 1). Under this scenario, however, if AM fungi increase in abundance and host colonisation under eCO_2 and are able to meet the increased nutrient demands of their host, this could correct the eCO_2 -driven reduction in nutritional quality (Johnson et al., 2015). This is likely to differ between C_3 and C_4 hosts. If C_3 plants invest in AM fungi, which satisfy their nutrient deficits, insect herbivores may not be affected one way or the other, or even benefit. Alternatively, C_3 plants may invest their augmented photosynthate reserves towards their own growth, rather than towards their AM fungal symbionts, thereby reducing nutrient uptake, negatively impacting herbivores (Compant et al., 2010), while C_4 plants invest their photosynthate in AM fungi, increasing nutritional quality and benefiting insect herbivores.

These outcomes will depend on the AM fungal community composition. For example, fungi from the Gigasporaceae are often seen to decrease (Cotton et al., 2015; Maherali & Klironomos, 2007), which suggests that, coupled with the direct effects of eCO_2 , overall

plant nutritional quality could see a marked decrease. This could potentially have a pronounced impact on specialist insect herbivores in particular, whose performance is often less sensitive to changes in host-plant defences, and therefore could be driven by changes in nutritional quality (Figure 2; Agrawal & Weber, 2015). This will also depend on environmental context, soil nutrient availability, moisture and light which will influence the outcomes for the host plant and, therefore, insect herbivores.

Predicting how AM fungal effects on plant secondary metabolism will be altered under eCO₂ is arguably more complex than the nutritional drivers of these interactions (Jung et al., 2012). AM fungi tend to suppress the SA-associated defences and enhance JA-regulated defence responses (García-Garrido & Ocampo, 2002; Hause et al., 2002). Conversely, however, eCO₂ tends to promote the SA pathway and suppress the JA pathway (Robinson et al., 2012). Consequently, from a phytohormonal plant defence standpoint, eCO₂ and AM fungi may act antagonistically (Figures 1 and 2). Just as AM fungal associations may mitigate an eCO₂-driven reduction in plant nutritional quality, they may also mitigate the eCO₂-driven promotion of SA-associated defences and suppression of JA defences. The efficacy of the AM fungal community to make such “corrections” will again depend on plant photosynthetic physiology as well as AM fungal community structure. Thus, if an eCO₂-driven increase in AM fungi (Glomeraceae) caused an overall upregulation of JA-associated defences, this could have negative consequences for generalist chewing insect herbivores in particular (Figure 2; Ali & Agrawal, 2012). This could increase evolutionary pressure towards host-plant dietary specialisation and a monophagous/oligophagous diet breadth (also see Section 5.14feature).

As discussed, the potential mechanistic drivers of mycorrhizal-mediated plant–insect herbivore interactions under eCO₂ can ostensibly act antagonistically. We can speculate on the outcomes based on what information is available; however, this presents a significant challenge when making predictions. For example, eCO₂ can reduce nutritional quality of C₃ plants, but AM fungi can increase nutritional quality, yet at the same time eCO₂ can reduce JA-associated plant defences, but AM fungi can promote them (Figures 1 and 2). Predicting how an insect herbivore will respond to this will depend not only on the strength of these potentially interacting effects, but also on if they are truly accurate predictors of herbivory. The relative importance of plant nutritional quality and secondary defences as drivers of herbivore performance is actively debated (Agrawal & Weber, 2015). At present, we have little to go on when it comes to predicting how changes in atmospheric CO₂ concentrations might alter mycorrhizal-mediated plant–herbivore interactions (Pineda, Dicke, Pieterse, & Pozo, 2013). By considering what is known of how eCO₂ affects the relationship between plants and AM fungi, and how it can alter interactions between plants and insect herbivores, we can speculate on how the nutritional and defence mechanisms driving these bipartite interactions may interact when considered together (Box , Figures 1 and 2).

5 | WHERE TO NEXT?

Increasing atmospheric CO₂ concentrations are a key driver of global climate change, which is associated with many other factors including changing rainfall patterns and temperature. It would be naïve not to consider how the effects of eCO₂ on mycorrhizal-mediated

BOX 1 Predicted scenarios

We identify potential outcomes for mycorrhizal-mediated plant–herbivore interactions under eCO₂ based on changes in plant nutritional quality and defences.

1. eCO₂ will significantly increase photosynthate production in C₃ plants which allocate most of their excess C to towards their own growth, rather than to AM fungi. This leads to a reduction in nutritional quality, which negatively impacts insect herbivores. C₄ plants invest their excess photosynthates towards their AM fungal partners, increasing their nutrient acquisition. Therefore, insects feeding on C₄ plants have an improved performance overall, while those feeding on C₃ may be negatively impacted.
2. eCO₂ will enhance photosynthesis and reduce plant nutritional quality. The greater plant nutrient demand is not entirely satisfied by the AM symbiosis due to an eCO₂-driven reduction in AM fungal taxa particularly associated with enhancing nutrition (Gigasporaceae). Thus, both C₃ and C₄ plants exhibit an overall reduction in nutritional quality, reducing insect herbivore performance, but increasing insect plant consumption as they attempt to meet their own nutritional needs.
3. eCO₂ will enhance SA-associated defences and suppress JA-associated defences; however, eCO₂ will also cause an increase in the abundance of AM fungal taxa particularly associated with enhanced plant defences (Glomeraceae). These AM fungi effectively suppress SA-associated defences and enhance JA-associated defences, countering the effects of eCO₂ on defence pathways. The effects of eCO₂ and AM fungi act antagonistically on plant defence with no significant impacts on insect herbivore performance overall.
4. eCO₂ will promote AM fungi and host-plant colonisation, in particular AM fungal taxa associated with plant defence (Glomeraceae). These fungi suppress SA-associated defences and increase JA-associated defences (sufficiently to overcome the opposing direct effects of eCO₂ on plant defences). This reduces the performance of chewing insect herbivores, negatively impacting generalist chewing insects in particular.

plant–herbivore interactions would interact with these additional factors. Thus, it is pertinent for future research to investigate the impacts of all facets of climate change to better understand how they will function in the future, but we need to get the ball rolling.

Considering the general trends, we recommend specific priorities for research investigating these interactions: (a) elucidation of how eCO₂ and AM fungi, singly and in combination, alter plant traits (i.e., nutritional quality and defence chemistry) driving insect herbivore performance; (b) investigate how the effects of eCO₂ and AM fungi on these plant traits (nutrition and defences) differ between plant functional groups (e.g., C₃ and C₄) and insect functional groups (e.g., chewers, suckers, generalists and specialists); (c) identify how edaphic variables (e.g., soil N and P availability, pH and moisture) alter the outcomes of these interactions under eCO₂; and (d) assess the variability in outcomes from different mycorrhizal fungal communities and shifts in community composition.

In investigating questions relating to our suggested priorities, researchers should use controlled-environment experiments in combination with field-based work, which will strengthen findings and ensure observed outcomes are not simply artefacts of an experimental set-up. Field-based CO₂ manipulative experiments within forest, grassland and tundra biomes across the globe are necessary to determine response variability of mycorrhizal–plant–herbivore interactions to eCO₂ across ecosystems. Furthermore, agricultural vulnerability to climate change also necessitates the prioritisation of crop species important to global food security such as wheat (*Triticum* spp. L), rice (*Oryza sativa* L. and *Oryza glaberrima* Steud.) and maize (*Zea mays* L.). The increasing frequency of heat waves, drought and deluge events (Frich et al., 2002) will also alter the outcomes of these interactions for mycorrhizal, plant and insect communities, and should be explored in the future. In addressing these research priorities, a significant logistical challenge will be successfully identifying mediating mechanisms. Measuring all of the numerous plant traits and metabolites which can be altered by AM fungi and impact herbivory, and successfully identifying the key mechanisms is a formidable task. However, non-targeted metabolomics offers the ability to identify contributing mechanisms driving

such interactions (see Box) by assessing changes in the host-plant metabolism.

An important caveat in all of this is that these kinds of manipulative experiments can only tell us so much. In particular, as highlighted by Klironomos et al. (2005), a single-step increase in atmospheric CO₂ concentrations can yield quite different responses from the AM symbiosis and from AM fungal communities, compared to a gradual increase (as in nature). Therefore, the outcome for the mycorrhizae, the host plants or the insect herbivores may simply be an artefact of a sudden increase in CO₂, rather than a realistic representation of how the interactions will function in the future. Furthermore, it remains unclear what role transgenerational plasticity and adaption will play in the response of mycorrhizal–plant–insect relationships to gradually rising CO₂ concentrations. Plant photosynthetic responses to rising CO₂ reach their limit around 740 ppm for angiosperms and 1,250 ppm for conifers (de Boer et al., 2011). Thus, conifers may continue to optimise their photosynthesis to rising CO₂ levels when angiosperms have already reached their limit. Longer-term studies where gradual increases in atmospheric CO₂ are applied may be able to provide valuable insight into the mechanistic basis of responses to eCO₂. Free-air CO₂ enrichment (FACE) facilities offer opportunities to investigate these longer-term outcomes of eCO₂ on mycorrhizal–plant–herbivore interactions (Norby et al., 2016; Saban, Chapman, & Taylor, 2019).

5.1 | Evolutionary consequences

Recently, Bennett, Orrell, Malacrino, and Pozo (2018) highlighted the potential ways in which selection might act in mycorrhizal-mediated plant–insect interactions, such as simple “one-way” responses driven by AM fungi, evolutionary feedbacks and co-evolutionary arms races. This provides a useful framework to predict the evolutionary consequences of eCO₂ for these interactions. For example, eCO₂ may promote AM fungal taxa associated with plant defence, which could promote selection for tolerance by herbivores, or promote particular herbivore feeding guilds (i.e., phloem feeders). This

BOX 2 A metabolomics approach

Targeting a comparatively small selection of plant traits (e.g., leaf toughness, N and P concentrations and cardenolides) which mediate mycorrhizal–plant–insect interactions can lead to ambiguous or even erroneous conclusions as to potential mediating mechanisms. Unmeasured traits could be driving outcomes, but are missed entirely, largely due to the unsurmountable logistics of measuring every relevant variable. The use of a non-targeted metabolomics approach allows the simultaneous analysis of all primary compounds (such as nitrogen, amino acids and sugars which are of nutritional importance to insect herbivores) and secondary compounds (defence-related compounds such as benzoxazinoids or terpenoids) within plant (fungal or insect) tissues (Maag, Erb, & Glauser, 2015). This approach is extensively utilised across many fields, including plant and mycorrhizal ecology (Frew et al., 2018; Hill et al., 2018; Jones et al., 2013). Although this produces vast quantities of data, and plant metabolisms are extensive and complex, it provides an in-depth picture of an organism's phenotype and can be a critical tool for ecologists, particularly when dealing with highly variable biotic interactions with multiple potential mediating mechanisms. Therefore, in disentangling the mechanistic drivers of mycorrhizal–plant–insect herbivore interactions under eCO₂, this tool is likely to prove to be immensely valuable.

will shape the plant communities in response to altered herbivore pressure (Agrawal et al., 2012). Alternatively, it may also promote enhanced plant resistance rapid enough to overcome insect tolerance, such that the rate of insect adaptation may be inadequate to ensure persistence. That said, there is considerable research on the impacts of climate change on plant–insect interactions (Johnson & Jones, 2017), but there is a need for more studies to be done within an evolutionary context (DeLucia, Nability, Zavala, & Berenbaum, 2012). Moreover, there is little research on the evolutionary dynamics of mycorrhizal-mediated plant–insect herbivore interactions (Bennett et al., 2006, 2018), an area ripe for investigation.

Predicting the evolutionary consequences for AM fungi is arguably more challenging as we are only beginning to understand the global distribution and evolutionary biology of the Glomeromycota (Öpik et al., 2010). Increasing atmospheric CO₂ may promote selection for species in the Glomeraceae, as discussed, resulting in stronger selection against other taxa. However, as eCO₂ augments plant nutrient requirements, there will be selection pressure to associate with fungal species that provide adequate nutritional benefits. The AM symbiosis is considered to be the ancestral condition for land plants, yet a considerable number of plant species have now lost the ability to associate with AM fungi (Maherali, Oberle, Stevens, Cornwell, & McGlenn, 2016). Thus, if a high CO₂ world is an environment where the AM symbiosis has a neutral or negative net effect on plants, there will be stronger selection pressure for them to lose the AM symbiosis altogether (Maherali et al., 2016).

6 | CONCLUDING REMARKS

Arbuscular mycorrhizal fungi associate with most land plants, and all land plants are consumed by at least one, if not many, species of insect herbivore. The importance of each player in this relationship to ecosystems globally needs no argument. Mycorrhizal–plant–insect herbivore dynamics are arguably fundamental to almost all natural and managed ecosystems, including agro-ecosystems. From the viewpoint of food security, we face an increasing global population, an increasing demand for food, water and energy, all while tackling the challenges posed by climate change. Therefore, agriculture needs to be informed and equipped to continue to produce food sustainably (Beddington, 2009). If ecological theory is to reliably inform management practices in the future, then urgent attention needs to be given to disentangling how global atmospheric change will alter mycorrhizal–plant–insect dynamics. The context dependency and variability of these interactions are key challenges. Nonetheless, we are optimistic. These gaps in our knowledge can be addressed with appropriately designed experimental studies coupled with observational fieldwork built around our suggested key priorities. As studies begin to inform our understanding of the functioning of this tripartite relationship, we will gradually become better equipped to anticipate the challenges that a high CO₂ world will present.

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AUTHORS' CONTRIBUTIONS

A.F. and J.N.P. conceived the rationale and ideas behind the article. A.F. led the writing of the manuscript with significant input from J.N.P.

DATA ACCESSIBILITY

This paper does not include any data.

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SUPPORTING INFORMATION

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