Relationships between mycorrhizal type and leaf flammability in the Australian flora

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Highlights

- Variation in morphological and chemical leaf traits is an important driver of fire regimes.
- Many leaf and root traits are likely to evolve in a coordinated fashion.
- Mycorrhizal type is a root trait that is also associated with variation in leaf traits.
- Arbuscular mycorrhizal plants, on average, express leaf traits that support rapid leaf ignition.
- Non-mycorrhizal and dual ecto- and arbuscular-mycorrhizal plants express leaf traits associated with longer burn duration.

Abstract

Mycorrhizal fungi have been linked to fire processes in natural ecosystems via their effects on litter decomposability but, to our knowledge, relationships between mycorrhizal fungi and leaf traits directly associated with aspects of flammability have not been studied. Here, we assessed the relationships among leaf traits and host mycorrhizal type for 77 species of Australian trees and shrubs to determine whether mycorrhizal type can explain variation in three aspects of leaf flammability (ignitability, fire duration, and smoulder duration). Several associations were observed between mycorrhizal type and leaf traits directly linked to flammability measures, including specific leaf area, leaf mass, leaf moisture content, and leaf chemistry. The observed patterns suggest that interactions between mycorrhizal fungi and their host plants during the growth and senescence of leaves may have subsequent effects on fire processes. However, further work is necessary to evaluate the importance of these effects in real ecosystems, including whether plants or fungi are responsible for these patterns, and we propose four questions that will further progress in this area.

Main text

Substantial functional variation exists among groups of mycorrhizal fungi, particularly in the ability to directly access nutrients from organic matter. Some, such as ectomycorrhizal (ECM) and ericoid mycorrhizal (ERM) fungi, express enzymes that allow access to organic nitrogen (N; Chalot and Brun, 1998) and phosphorus (P; Cairney, 2011), and possibly even carbon (C; Talbot et al., 2008). Arbuscular mycorrhizal (AM) fungi facilitate increased access to inorganic forms of N and P but generally do not express enzymes that allow access to organic forms (although some have proposed that acid phosphatase is potentially expressed by some AM fungi; reviewed by Joner et al., 2000). Nonmycorrhizal (NM) plant species have alternative strategies for obtaining nutrients such as proteoid cluster roots (Shane and Lambers, 2005) and symbiosis with N-fixing organisms (Peoples et al., 2009). This variation and observed stoichiometric relationships between carbon and nutrients in soil have led to hypotheses that ecosystems vary substantially in their capacities to store carbon in soil based on the dominant mycorrhizal type and its effects on soil nutrient pools (Averill et al., 2014; Phillips et al., 2013).

Fire is another important driver of the capacity of an ecosystem to store carbon and much work has been done in attempts to understand the important drivers of fire frequencies, intensities, and durations (Cornwell et al., 2009; Grootemaat et al., 2015a). Mycorrhizal fungi may directly influence on the likelihood of fire within an ecosystem due to their effects on standing litter (Gadgil and Gadgil, 1971), either via its quantity (through changes in decomposability, due to increasing C:N and C:P ratios during nutrient uptake; Bending and Read, 1995) or its flammability (through reductions in litter moisture content; Koide and Wu, 2003). Thus, functional variation among mycorrhizal types in their nutrient uptake capacities from litter leads to predictions that fire-related processes are related to the dominant mycorrhizal association.

Even more interesting is the extent to which the activity of mycorrhizal fungi influences the decomposition rate via their effect on the traits of their plant partner. Mycorrhizal fungi form an important part of many species' mineral nutrient uptake strategy, and this is linked to the species economic strategy with special implications for the both leaf and root traits (Reich et al. 1999, Hobbie etc.). The traits of the plant while alive have important implications for the characteristics of the dead and dying organic matter produced: many living traits have subsequent effects following leaf abscission, affecting important processes in the litter layer (Cornwell et al. 2008). For instance, Cornellissen et al. (2001) linked variation in ecosystem carbon cycling to differences among plants of differing mycorrhizal types, largely via effects on plant growth rates and leaf nutrient contents. In addition, leaf traits have been hypothesised to have co-evolved in a coordinated fashion with root traits according to the plant economic spectrum (Tjoelker et al., 2005) suggesting a further link between mycorrhizal type and leaf traits linked to flammability.

Here, we assess the relationships among leaf traits and host mycorrhizal type for 77 species of Australian trees and shrubs to determine whether mycorrhizal type is associated with variation in three aspects of leaf flammability (ignitability, fire duration, and smoulder duration). Leaf trait and flammability data were obtained from two studies: a survey of tree and shrub species growing in gardens in the Australian Capital Territory (Gill and Moore, 1996), and a survey of tree and shrub species from four vegetation types in two rainfall zones in New South Wales (Grootemaat et al., 2015a, 2015b); data represent means for each species in each study, calculated from at least ten leaves per sample type. Grootemaat et al. measured time to ignition (seconds), flame duration (seconds), and smoulder duration (seconds) on fresh green leaves ('fresh'), and on green ('dried') and senesced ('senesced') leaves dried at 37 ^{o}C for 72 h. Gill and Moore measured time to ignition (seconds) on 'fresh' and 'dried' (at 95 ^{o}C for at least 22 h). Mycorrhizal type was assigned to each species based on classifications at the genus level in Brundrett (2009), as depicted at http://mycorrhizas.info/ozplants.html (accessed 5 April 2016) and additional sources (Supplementary Table 1). All but one species in these data were classified as either 'AM', 'ECM-AM' or 'NM'; for this analysis, *Dodonaea viscosa* was reclassified from 'AM(NM)' to 'AM'.

Trait and flammability variables were log-transformed as performed by Grootemaat et al. (2015a), where appropriate. Structural equation models (SEMs) where used to assess whether mycorrhizal type was associated with leaf flammability measures via leaf trait associations or via direct paths (indicating associations mediated via unmeasured variables). Four models (Supplementary Figure 1) were compared for each combination of sample type and leaf flammability measure, each differing in the direct effects on flammability that were included: (i) leaf traits and both the ECM-AM and NM types; (ii) leaf traits and the ECM-AM (but not NM) type; (iii) leaf traits and the NM (but not ECM-AM) type, and; (iv) only leaf traits. All models included indirect effects (via leaf traits) of mycorrhizal type on flammability; we used a binary variable to represent each of the ECM-AM and NM types in the models, including an independent path from each binary variable to each leaf trait and (where appropriate) flammability measure. A variable representing the AM type was omitted from each model, thus NM and ECM-AM paths are expressed relative to this missing class. We chose this approach due to the ancestral status of the AM type (Wang and Qiu, 2006) and evidence that the ECM/ECM-AM type and NM type likely represent independent evolutionary events (Maherali et al., 2016). SEMs were fit and evaluated in 'R' version 3.3.0 (R Core Team, 2016) using the 'lavaan' package (Rosseel, 2012). For each combination of sample type and leaf flammability measure, the model with the lowest Bayesian Information Criterion (BIC) was selected for estimation of mycorrhizal type effects, presented below. Further details of the methods used during model selection and model evaluation are given in the supplemental online materials, with model fit statistics presented in Table 1 and Supplementary Table 2.

Several significant relationships were observed among leaf traits and mycorrhizal type. These were weak for the leaf traits most strongly associated with flammability ($R^2_{\text{SLA*[fresh]}} = 0.10$, $R^2_{\text{SLA*[dried]}} = 0.11$, $R^2_{\text{moisture[fresh]}} = 0.06$, $R^2_{\text{mass[dried]}} = 0.06$; Figure 1, Supplementary Table 3). SLA*, which is negatively correlated with all three measures of leaf flammability, was generally 32% lower for NM species than for AM species. However, this was only significant in models using data from both studies, where sample sizes were much larger [n > 70]; in these studies, standardised partial regression coefficients (± standard error) for the NM type were -0.35 ± 0.11 (fresh leaves; $P = 0.002$) and -0.38 ± 0.12 (fresh dried leaves; $P = 0.001$) for the NM type. SLA* was 19% lower for the ECM-AM type relative to the AM type in these same models, but these relationships were marginally nonsignificant: -0.23 ± 0.13 (fresh leaves; $P = 0.059$) and -0.22 ± 0.12 (fresh dried leaves; $P = 0.081$). Leaf moisture content, which is positively correlated with time to ignition, was 25% lower in fresh leaves for ECM-AM species than for AM species (-0.29 ± 0.12, $P = 0.014$). Leaf mass, which is positively associated with time to ignition but is negatively associated with both flame duration and smoulder duration, was 82% higher for ECM-AM species than AM species (0.25 ± 0.13). However, this latter relationship was of marginal statistical significance ($P = 0.049$), highly variable (Figure 1d-f), and only observed when data from both studies were included in the model.

Significant associations between mycorrhizal type and tissue chemistry were also observed and were generally stronger in the amount of variation explained relative to the other leaf traits ($R^2_{\text{N[dried]}} = 0.64$, $R^2_{\text{P[senesced]}} = 0.54$, $R^2_{\text{lignin[senesced]}} = 0.18$; Figure 2, Supplementary Table 3). Flame duration is negatively associated with concentrations of both P and N within leaves (Scarff et al., 2012; Grootemaat et al., 2015a). Leaves from NM species were reduced in N (by 50%) and P (by 67%) compared with AM species (N: -0.90 ± 0.07, $P < 0.001$; P: -0.83 ± 0.09, $P < 0.001$); note that all NM species in the subset for this analysis were from the Proteaceae. ECM-AM species were 16% lower in N compared with AM species (-0.36 ± 0.12, $P = 0.003$) and also 27% lower in P (-0.25 ± 0.14), but this latter effect was marginally nonsignificant ($P = 0.079$). Lignin concentrations are positively associated with smoulder duration (Grootemaat et al. 2015a) and were higher in senesced leaves of ECM-AM (by 36%; 0.44 ± 0.16, $P = 0.007$) and

NM (by 35%; 0.39 ± 0.17, $P = 0.019$) species than in AM species. Effects of mycorrhizal type on tannin concentrations were not observed.

These analyses do not exclude the possibility that relationships between leaf traits and mycorrhizal types are simply due to the shared influence of evolutionary history on each character, and not due to any causal relationship (regardless of the direction). To address this, we assessed the extent to which mycorrhizal type explained variation in leaf traits after accounting for the effect of shared evolutionary history in four partial Mantel tests, one for each combination of trait type (associated with leaf ignitability or burn duration) and shift in mycorrhizal type (AM to ECM-AM or AM to NM). Pairwise phylogenetic distances were obtained from the plant phylogeny published in Zanne et al. (2014), using Phylomatic Version 3 (http://phylodiversity.net/phylomatic/, accessed 20 June 2017). Analyses were performed in R using functions from 'ape' (Paradis et al., 2004) and 'vegan' (Oksanen et al., 2016) libraries; more details of the analysis are provided in the supplemental online materials. We found evidence for the relationship between mycorrhizal type and leaf traits associated with ignitability to be at least partially unrelated to shared evolutionary history for both the ECM-AM type ($r = 0.06$, $P = 0.008$) and the NM type ($r = 0.10$, $P = 0.004$). The same was the case for leaf traits associated with burn duration for the NM type ($r = 0.39$, $P = 0.001$) but not for the ECM-AM type ($r = 0.06$, $P = 0.13$). Thus, in most cases, there does appear to be a direct relationship between mycorrhizal type and leaf traits associated with flammability.

It is unlikely that measurement of other leaf traits would improve predictions of the relationship between leaf flammability and mycorrhizal type. This is because the SEMs were generally not improved by including paths directly linking mycorrhizal type to any of the leaf flammability measures, with the exception of flame duration for dried leaves (see outcomes of model comparisons in Table 1). In this latter case, nonmycorrhizal plants produced leaves that burned more rapidly independently of other leaf traits (leaf mass, leaf [P], SLA; -0.26 ± 0.10, $P = 0.009$). However, all of the nonmycorrhizal hosts in this subset of the data belonged to the Proteaceae, raising the question of whether this is an effect of mycorrhizal type or plant taxon. Taken together, these results suggest that mycorrhizal type does not influence leaf flammability, during growth and senescence, independently of the leaf traits analysed here.

These observations suggest the possibility that mycorrhizal associations, during leaf growth and senescence, may influence leaf flammability as a result of their link with leaf traits that have been identified as determinants of leaf flammability (Figure 3). If so, their effects may mediate or exacerbate fire likelihoods if not accounted for, affecting our ability to predict ecosystem carbon balances. The patterns observed here also suggest that mycorrhizal type may play a larger role in influencing fire-related processes via litter decomposability and burn duration than via ignitability (Figure 3). However, this study is only a first step towards the development of a comprehensive understanding of mycorrhizal fungal contributions to fire-related processes in ecosystems. Below, we propose four questions that will further progress toward this understanding.

(1) How reproducible are these patterns for non-Australian plant species? – The observations here are limited to a set of tree and shrub species sampled from eastern Australia. Fire-related processes are understandably at the forefront of ecosystem management and monitoring issues in Australia, resulting in a relatively rich availability of data to address these questions. However, these patterns may not be generalisable. For instance, dual ECM and AM associations are relatively common in Australia but occur less frequently on other continents (Brundrett, 2009), and it remains to be seen whether solely ECM trees exhibit flammability-associated leaf traits that are similar to ECM-AM trees. There were also few ERM plant species and no representatives from other mycorrhizal types represented in the data, preventing us from estimating the contribution of other mycorrhizal types to leaf flammability, even though they are frequently observed in some fire-prone ecosystems (e.g., South African fynbos, van de Venter and Esterhuizen, 1988; California chapparal, Keeley, 1987). In addition, the mechanisms that affect evolution of plant traits that affect flammability are still an area of controversy (e.g., Bond and Keeley, 2005; Schwilk and Ackerly, 2001). However, the occurrence of relationships between mycorrhizal type and traits associated with flammability does not require leaf flammability to be directly under selection. Instead, this variation might arise as a result leaf traits evolving in response to other agents of selection, with indirect effects on fire regimes.

(2) Does fire frequency and intensity determine the predominant mycorrhizal association within an ecosystem? – The primary assumption behind the analyses described above is that the mycorrhizal type of the host plant is contributing toward the suite of leaf traits observed for that tree or shrub species. However, an argument could be made that the direction of causality is actually reversed: that leaf traits associated with variation in fire frequency and intensity have selected for stronger associations with one type of mycorrhizal fungus, leading to that strategy being more successful in particular ecosystems. Studies of mycorrhizal fungal recolonisation of ecosystems following fire events suggest that AM fungal communities may have some level of resistance or may recover rapidly following fire (e.g., Bellgard et al., 1994; Treseder et al., 2004), although fires that raise soil temperatures substantially and/or for prolonged periods of time are likely to negatively affect AM fungi (Pattinson et al., 1999). Studies of ECM systems reveal relatively slow recoveries of ECM fungal communities post-fire (Stendell et al., 1999; Treseder et al., 2004; but see Baar et al., 1999 and Peay et al., 2009). In ecosystems where fire frequency is high, the AM symbiosis may be a successful strategy for mycorrhizal-mediated nutrient uptake in the post-fire soil environment, particularly for resprouting trees and shrubs that might benefit from interactions with intact networks of mycorrhizal fungal hyphae, but much more work is needed to evaluate this hypothesis.

(3) To what degree does the prevalence of crown-fire and surface-fire within ecosystems affect the importance of mycorrhizal type in explaining fire-related processes? – Fire behaviours are likely linked to a complex interaction of the environment and leaf traits. Simply looking at leaf traits associated with species classified into different mycorrhizal types might not provide the best insight into how mycorrhizal fungi mediate fire behaviour or plant nutrition in a post-fire environment. For instance, leaves that produce litter with low decomposability,

low packing ratios, and high fire sustainability may be the most important components of surface fires (Cornwell et al., 2009; Grootemaat et al., 2017), while transitions to crown fires may be more strongly associated with high leaf ignitability, linked with leaf moisture content and leaf mass (Grootemaat et al., 2015a; Belcher and Hudspith, 2017). In the analyses reported here, associations between mycorrhizal type and different leaf traits (specific leaf area and leaf moisture content) sometimes had conflicting effects that largely negated the overall indirect effect on leaf flammability (Figure 3). Thus, modelling fire behaviour using mycorrhizal type requires additional knowledge regarding the fire system that is common to the ecosystem being examined, since the degree that flammability changes will depend on which trait exhibits the strongest association with flammability in that system. Fire-prone ecosystems characterised by surface fires following the build-up of a flammable litter bed may be more affected by the decomposability of litter from mycorrhizal plants. Alternatively, mycorrhizal fungal effects may play a larger role than previously appreciated for initiation of crown fires given effects on fresh leaf moisture content.

(4) How important is variation within fungal communities of different mycorrhizal types for leaf and litter flammability? – This analysis does not exclude the potential for variation in the composition of mycorrhizal fungal communities from influencing leaf flammability via effects on host fitness and leaf moisture content during, for example, drought stress (Augé, 2001). Substantial leaf trait variation was observed within each mycorrhizal type, which might be associated with variation in the composition or functionality of mycorrhizal fungal communities associated with each host tree. Different mycorrhizal communities are associated with variation in plant nutritional status (Johnson et al., 2010), which is a key component driving the plant economic trait spectrum. More work is also necessary to address the potential for mycorrhizal fungal community variation to affect litter flammability given the potential for mycorrhizal fungal species to vary in their abilities to extract nutrients and water from standing litter (possibly linked to, for example, exploration types; Agerer, 2001) or to resist or recover from fire events (Baar et al., 1999; Peay et al., 2009). Taking a broader view, variation exists among different mycorrhizal types in the strength of observed plant-soil feedbacks, with consequences for the composition of plant and fungal communities (Bennett et al., 2017; Teste et al., 2017). Variation in the strengths of these feedbacks could further influence spatial and temporal variation in leaf and litter traits, with consequences for flammability at the ecosystem level.

To summarise, we observed that classification of Australian tree and shrub species into one of three mycorrhizal types could be used to predict variation in leaf traits associated with measures of leaf flammability. This observation opens the door to mycorrhizal fungi being linked to feedbacks in fire frequency and intensity via direct relationships with their host plants, in addition to previous hypotheses regarding how they may alter flammability of standing litter. We have not demonstrated that mycorrhizal fungi are, in reality, an important component of these feedbacks, but we have suggested further research that could help to determine the role that they play in fire-prone ecosystems.

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Table 1. Comparisons of model fit (using the Bayesian Information Criterion scores) among models with and without direct paths linking mycorrhizal type with measures of leaf flammability, representing statistical associations mediated via unmeasured variables. The best model for each response variable within each material type is that with the lowest score (indicated in bold). All models included paths representing direct effects of mycorrhizal type on leaf traits and, thus, indirect effects of mycorrhizal type on leaf flammability measures. Additional fit measures and model parameters are included in Supplementary Table 2 of the supporting online material.

	Material type		
Direct effects	Fresh	Dried	Senesced
	Log$_{10}$ time to ignition		
leaf traits + ECM-AM + NM	1018.04	266.46	87.59
leaf traits + ECM-AM	1013.69	263.04	84.69
leaf traits + NM	1013.98	265.13	84.62
leaf traits	**1009.62**	**260.87**	**81.37**
	Log$_{10}$ flame duration		
leaf traits + ECM-AM + NM	85.86	49.95	78.27
leaf traits + ECM-AM	82.41	52.85	75.17
leaf traits + NM	82.44	**47.23**	74.96
leaf traits	**79.03**	49.94	**72.32**
	Log$_{10}$ smoulder duration		
leaf traits + ECM-AM + NM	293.45	469.88	495.79
leaf traits + ECM-AM	290.36	468.08	493.56
leaf traits + NM	292.91	467.05	492.46
leaf traits	**289.50**	**464.69**	**490.19**

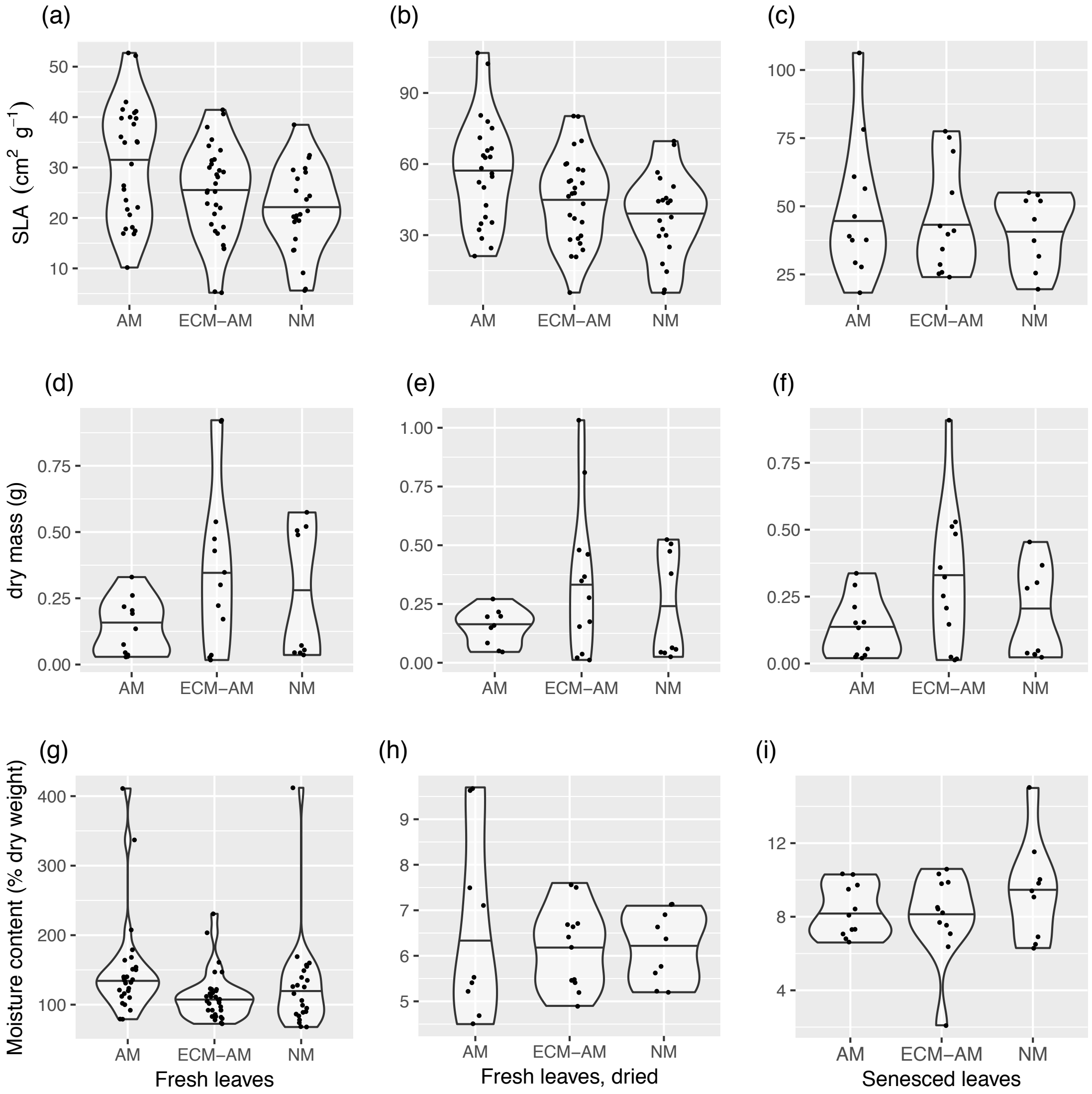

Figure 1. Violin plots demonstrating average trait values associated with leaves sampled from tree and shrub species, classified by mycorrhizal association. Traits were measured on fresh green leaves (a, d, g), dried green leaves (b, e, h), and dried senesced leaves (c, f, i). Width of the plots represent the calculated density at a particular trait value and the horizontal line represents the median observation within each group.

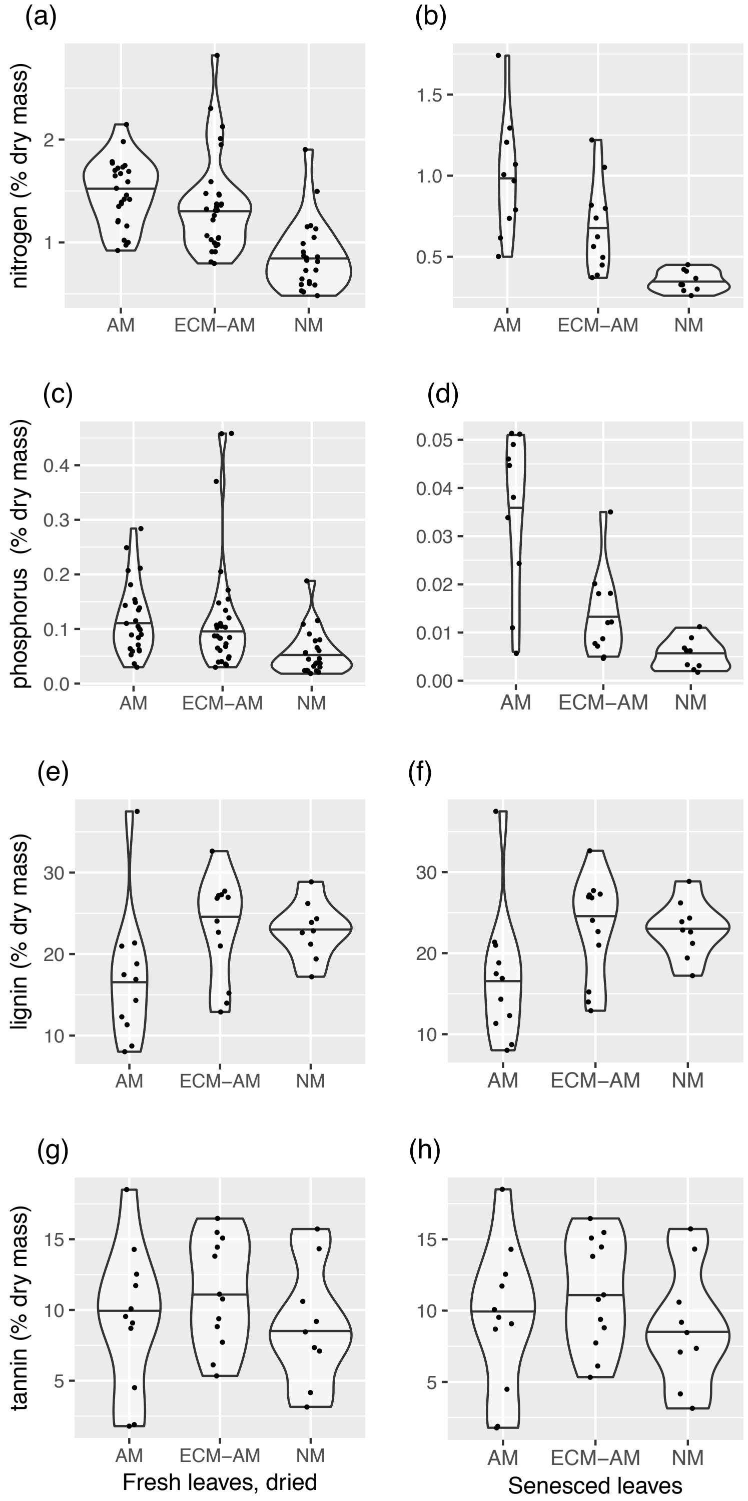

Figure 2. Violin plots demonstrating average trait values associated with leaves sampled from tree and shrub species, classified by mycorrhizal association. Traits were measured on dried green leaves (a, c, e, g) and dried senesced leaves (b, d, f, h). See figure 1 caption for further details.

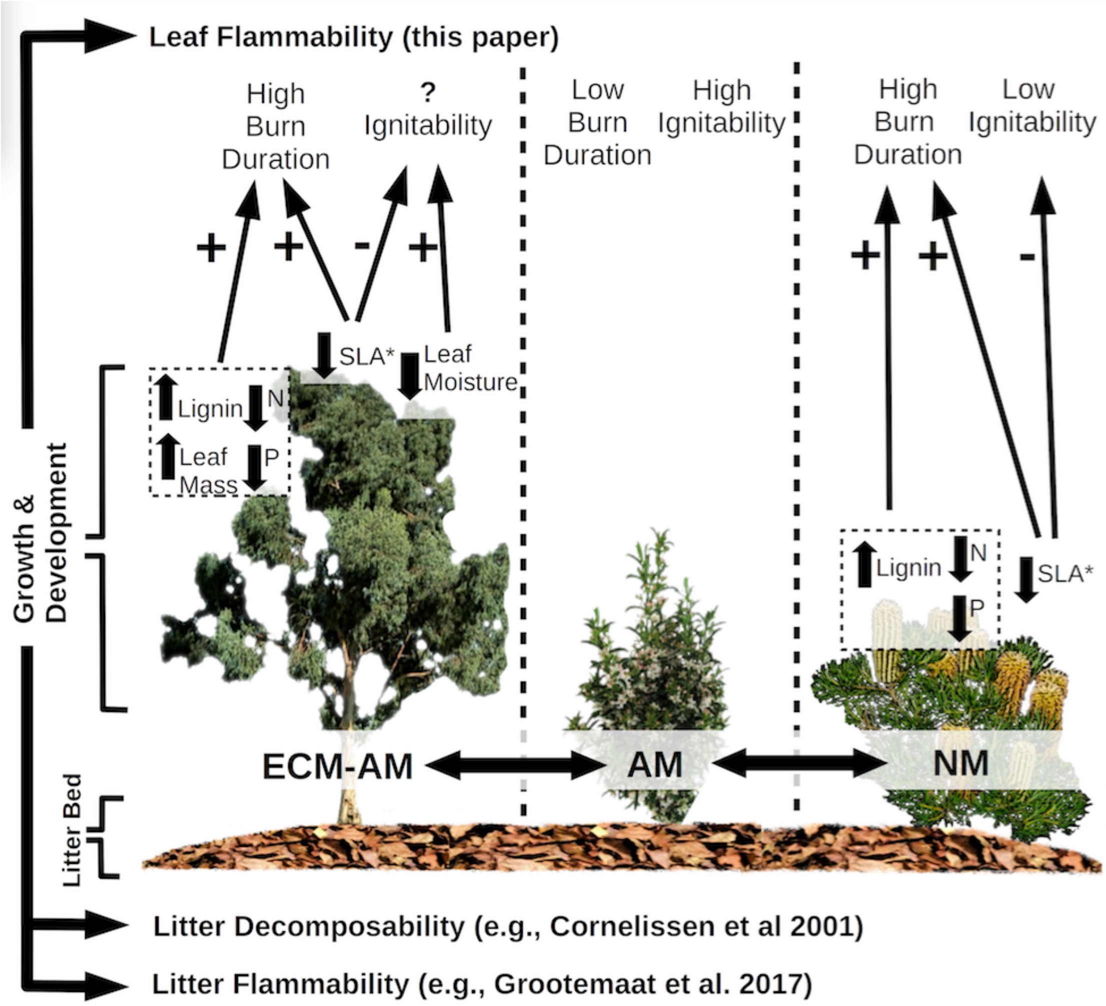

Figure 3. Conceptual figure summarising the relationships between differences in tree and shrub mycorrhizal type, leaf traits, and leaf flammability. Evolution of the ECM-AM and NM association from AM ancestors are related to shifts in leaf traits that increase burn duration, but have weak or uncertain effects on leaf ignitability. These trait shifts also have consequences for litter decomposability (e.g., Cornelissen et al. 2001) and litter bed packing, which influences litter flammability (e.g., Grootemaat et al. 2017).