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**PERSPECTIVE**

Australia offers unique insight into the ecology of arbuscular mycorrhizal fungi: An opportunity not to be lost

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Abstract

Typified by ancient soils and unique assemblages of flora, Australia provides opportunities to expand our understanding of arbuscular mycorrhizal (AM) fungi. Despite their ubiquity, key aspects of Australian AM fungal ecology remain buried due to our limited knowledge of their biogeography and their potential adaptation to Australia's environmental conditions. This knowledge gap is particularly extraordinary given that the characteristics of the Australian environment are likely to provide unique insights into AM fungal ecology and evolution. Extensive exploration of the diversity and distribution of AM fungi across the continent is overdue. In pursuit of this goal, ecologists should employ the most effective and pragmatic molecular approaches, while making use of well-curated databases. We urge researchers to examine the biogeography of Australian AM fungi meaningfully, leveraging the distinctive attributes of Australian landscapes, such as the demographics of plant mycorrhizal types and the characteristic interplay with fire. Documenting AM fungal communities across Australia will not only provide unique insights into their ecology but is also pivotal to being able to incorporate these organisms into land management for conservation, restoration and sustainable agriculture.

KEYWORDS

arbuscular mycorrhizal fungi, Australia, dual mycorrhizal, fire ecology, fungal ecology, metabarcoding, SSU

Resumen

Tipificada por suelos antiguos y flora única, el continente Australiano provee una excelente oportunidad para expandir nuestro conocimiento sobre los hongos micorrízicos arbusculares (HMA). A pesar de su presencia casi universal en suelos, aspectos cruciales sobre la ecología de los HMA en Australia se desconocen por el limitado conocimiento su biogeografía y su potencial adaptación a las condiciones ambientales en Australia. Esta brecha en el conocimiento es sorprendente, dado que las características de los ambientes Australianos probablemente proporcionen una oportunidad única para entender la evolución y ecología de HMA. Una caracterización sistemática de la diversidad y distribución de los HMA del continente es un objetivo que ya se debería haber alcanzado. Consideramos que es urgente investigar la biogeografía de HMA en Australia empleando técnicas moleculares efectivas y pragmáticas así como bases de datos especializadas en HMA. Este esfuerzo permitira determinar como los atributos del paisaje australiano han dado forma a las comunidades de HMA, en particular las interacciones entre diferentes tipos

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de micorrizas y el fuego, y generará información útil para su manejo en conservación, restauración de suelos y desarrollo agricultura sostenible en el continente.

INTRODUCTION

Arbuscular mycorrhizal (AM) fungi, as obligate symbionts of terrestrial plants, exhibit a global distribution across diverse ecosystems, encompassing grasslands, forests, deserts and agroecosystems. Tracing back to the dawn of terrestrial plant evolution, their deep roots in evolutionary history lend them a distinctive significance in ecological studies (Brundrett & Tedersoo, 2018; Simon et al., 1993). Today, the AM fungi associate with the vast majority of terrestrial plants, colonizing root systems to acquire carbon while the fungi provide plants with improved access to essential nutrients, particularly phosphorus (Smith & Read, 2008). In addition to increasing plant nutrient uptake, these fungi enhance plant tolerance to various environmental stressors including pathogens and herbivorous insects (Frew et al., 2022). Beyond their direct effects on plant success, AM fungi play important roles in plant community assembly, in maintaining soil structure, and in nutrient and carbon cycling (Powell & Rillig, 2018). Despite their universal presence, critical aspects of AM fungal ecology remain poorly described, underpinned by an incomplete understanding of the drivers and mechanisms of their community assembly and biogeography. This knowledge gap hampers our ability to integrate these crucial organisms meaningfully into applied ecological management.

Australia, with its unique characteristics, offers opportunities to advance our understanding of AM fungal diversity, coevolution, adaptation to stress and potential applications in conservation, restoration and agriculture. Despite the ongoing debate about the uniqueness of Australia's ecology on the global stage (Flores-Moreno et al., 2023), its distinctive biogeography, endemic flora, nutrient-poor soils and significant fire regimes form a landscape ripe for unearthing critical insights into AM fungal ecology.

To date, however, there have been limited efforts to exploit this, as such, our knowledge of the diversity and distribution of AM fungi in Australia remains sparse. AM fungi are important to maintaining ecosystem functions and have great potential to support biodiversity conservation and sustainable agriculture, thus it is increasingly important for us to understand them better as we face escalating environmental changes. Here, we highlight the pressing need and significant potential for a deeper exploration of AM fungal communities within the Australian ecological context.

MAPPING AM FUNGI IN AUSTRALIA: MARKER CHOICES AND THEIR IMPLICATIONS FOR AUSTRALIAN RESEARCH

Understanding the spatial and temporal distribution of AM fungi is a fundamental component of their ecology. To effectively manage AM fungal communities and facilitate ecologically sustainable agriculture or restoration efforts, we need to have a grasp on the pool of available taxa and understand the drivers of AM fungal diversity and distribution at the regional and continental scales. Global studies support the notion of a widespread distribution of AM fungi across continents, particularly at higher taxonomic levels (Davison et al., 2015), although it is likely we are underestimating endemism (Stürmer et al., 2018). Nevertheless, ample data exist to substantiate the profound influence of vegetation type, plant community

composition, climate variables such as mean annual precipitation and temperature, and soil factors such as pH and phosphorus on AM fungal communities (Davison et al., 2021; Zobel & Öpik, 2014).

The quest to survey and catalogue AM fungal biogeography has gained momentum since fungal DNA metabarcoding has improved and become increasingly accessible. In recent years, large-scale initiatives have emerged aimed at gathering fungal data across the world, to fill key knowledge gaps (Popkin, 2022; Větrovský et al., 2020). Within an Australian context, the Biomes of Australian Soil Environments (BASE) endeavours is an example of this, which provides valuable insights into soil microbial diversity across various environmental gradients, and has built an impressive library of fungal sequence data for the research community (Bissett et al., 2016). Yet, as such initiatives seek to maximize their coverage of a range of fungal taxa, they predominantly rely on the internal transcribed spacer (ITS) marker within the nuclear ribosomal operon as the 'barcode' of choice (Tedersoo et al., 2022). The ITS region is the most used marker for fungi, including other mycorrhizal groups such as ectomycorrhizal fungi or ericoid mycorrhizal fungi (Tedersoo et al., 2022), but it is not well suited for AM fungi which have highly variable ITS copies (Öpik et al., 2014). While this region can provide species-level resolution, it has high intraspecific variability which can lead to richness overestimations for AM fungi (Bradshaw et al., 2023; Thiéry et al., 2016), and often has very limited recovery of certain families (e.g. Paraglomeraceae, Acaulosporaceae; Lekberg et al., 2018). Furthermore, limited representation and poor curation of AM fungal sequences in ITS databases remains a challenge (Delavaux et al., 2021; Stockinger et al., 2010). Still, as with any barcode marker choice, the usefulness of ITS for AM fungal community surveys is entirely valid depending on research aims and the questions being asked, particularly if the main goal is to assess treatment responses of the dominant AM fungal taxa (Lekberg et al., 2018).

The most frequently used marker for AM fungi is the small subunit (SSU) region which is less variable than the ITS and provides more information about taxon evolutionary relationships (Öpik et al., 2010). This marker consistently provides high recovery of AM fungal sequences across families and is suitable for phylogenetic analyses. While the low variability of the SSU region is understood to limit species-level identification for some groups, the most commonly-used primers yield amplicons with levels of nucleotide variation comparable with those targeting the ITS (Thiéry et al., 2016). Furthermore, with the establishment of the MaarjAM database (Öpik et al., 2010), AM fungal phylogroups were named and coded into the 'virtual taxa' (VT) nomenclature system. This facilitated comparability between studies, and the assigned VT remains consistent. This represents a well-curated and developed database which also contains a wealth of sample metadata, including geographic information. An obstacle in mapping and understanding AM fungal diversity across the environment stems from a lack of comparability among studies that use different markers. Thus, in our opinion, targeting the SSU region and referencing the MaarjAM database is currently the most pragmatic option for ecologists interested in capturing data on AM fungal community composition and diversity from environmental samples in Australia. That said, it is worth noting that other approaches continue to be developed, for example, metabarcoding of the AM fungal large subunit (LSU) region holds a lot of potential. This region allows for better taxonomic resolution than SSU and a new database has recently been established (Delavaux et al., 2021). To date, however, the LSU region was not commonly utilised for sequencing of environmental samples ostensibly due to bioinformatic challenges (Delavaux et al., 2021), but it is likely this region will become more user-friendly in the future.

As most initiatives in Australia seek to map fungal communities, and not only AM fungi, they understandably opt to sequence fragments of the ITS region, but with this, they sacrifice the advantages of SSU metabarcoding for AM fungi. We contend this is sub-optimal if we are to build a reliable dataset of AM fungal diversity across Australia. We lack the wealth of reliable biogeographic data on AM fungi for Australia that we might expect, and this represents an important barrier to progress. While best-practice approaches to capture and survey AM fungal diversity will continue to develop and improve (Delavaux et al., 2021), we urge Australian ecologists to appreciate the benefits of SSU sequencing in their environmental surveys, so we can build our knowledge-base of AM fungal diversity across Australia (Figure 1a).

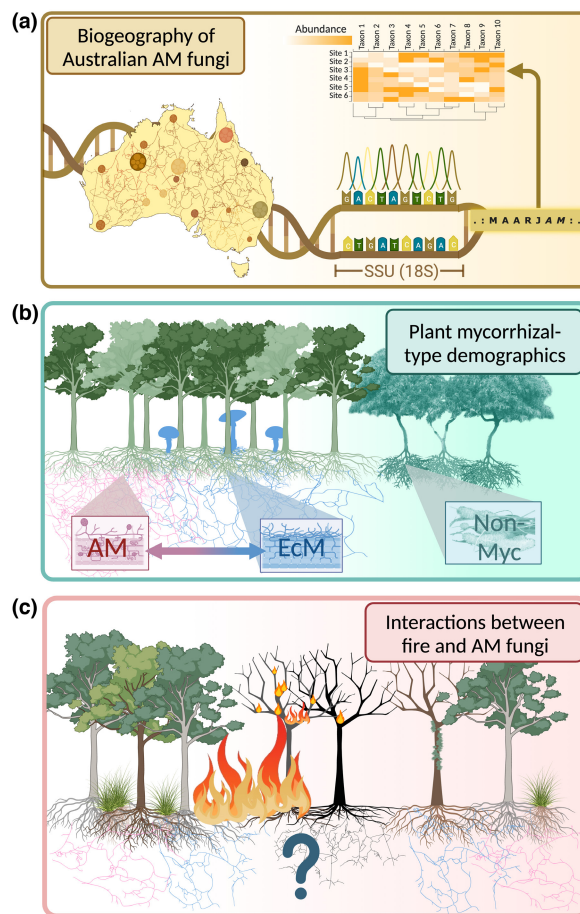


FIGURE 1 Key opportunities for research on Australian arbuscular mycorrhizal (AM) fungi: (a) Opportunity to build biogeographic data on AM fungal diversity and distribution, we advocate using DNA metabarcoding of the small subunit (18S) region and referencing the MaarjAM database to help build a dataset of Australian AM fungal diversity and distribution. (b) Opportunity for novel insight into the ecological roles of AM fungi as Australia is a hot spot for certain plant nutrient uptake strategies including dual-mycorrhizal plants (able to form arbuscular mycorrhizas and ectomycorrhizas [EcM]) and diverse non-mycorrhizal (Non-Myc) plant strategies, which may suggest the role of AM fungi in Australia will be different to other continents. (c) Australia has been called the fire continent, yet we have very little knowledge of how fire affects AM fungal communities, or what role AM fungi play the ecosystem recovery from fire. This represents an opportunity for researchers to explore the interactions between fire and AM fungi. Created using BioRender.

CHARACTERISTICS OF AUSTRALIA OFFER INSIGHT INTO AM FUNGAL ECOLOGY

Australia, while not a global outlier in terms of its ecology (Flores-Moreno et al., 2023), boasts unique characteristics. Its distinctive biogeography and remarkably high species endemism, with 93% of plants found exclusively within its borders, are attributed to the continent's long-standing geographic isolation (Orians & Milewski, 2007). Moreover, Australia has experienced limited glaciation compared to most terrestrial landscapes in the northern hemisphere. Although the continent has undergone transformations over the millennia, such as the drying out of its landmass, it is renowned for harbouring the oldest continental crust on Earth, characterized by highly leached and nutrient-poor soils (Johnson, 2009).

Consequently, Australian plant populations exhibit unique characteristics in their nutrient acquisition strategies (Figure 1b). Australia serves as a centre of diversity of plants having evolved non-mycorrhizal strategies like cluster roots or carnivorous nutrition to thrive in such challenging conditions (Lambers et al., 2011). In addition to this, much of Australia is dominated by vegetation with uncommon or even ambiguous mycorrhizal status. For instance, many plant species are putatively able to form both arbuscular mycorrhizas and ectomycorrhizas (Teste et al., 2020). Australian *Melaleuca* and *Acacia* species often exhibit these dual mycorrhizal associations, hosting both AM fungi and ectomycorrhizal fungi simultaneously to varying degrees. On the other hand, *Eucalyptus* species are often associated with the arbuscular mycorrhizal symbiosis when they are seedlings or under specific conditions, but they predominantly form ectomycorrhizal associations as they become mature trees. As such, Australia has been identified as a 'hot-spot' for plants with this dual mycorrhizal status (Teste et al., 2020). Considering these plant mycorrhizal-type demographics (i.e. how the different mycorrhizal types are distributed and organized in the landscape; Figure 1b), comprehensively mapping AM fungal communities across Australia is likely to provide unique insight into the ecology and evolution of mycorrhizal symbioses. These unique population characteristics also necessitate more ecologists and mycorrhizal scientists to work across multiple mycorrhizal systems, which is perhaps less important in other continents where most vegetation is considered to form only one form of mycorrhizal association.

In addition to the unique make-up of plant mycorrhizal types, Australia's relationship with fire is considered a defining characteristic (Figure 1c). Australia is often referred to as the 'fire continent' due to its high susceptibility to bushfires (Bradstock et al., 2002). Thus, we cannot explore ecological interactions in Australia without also considering the potential role of fire. Throughout history, fire has played a pivotal role in shaping Australia's landscapes, influencing ecosystem dynamics, carbon and nutrient cycling, and the composition of plant and animal communities at various scales. Yet our understanding of the interactions between fire and fungi, particularly in Australia, remains limited (Fox et al., 2022). While some research on this topic exists, the scarcity of data hinders our ability to make accurate predictions about how fire shapes fungal communities across the diverse Australian landscapes. Notably, the interactions between fire and AM fungi in Australia continue to be mostly ignored. As we strive to comprehend the implications of changing fire regimes on Australian biodiversity, it is crucial to underscore the fundamental role that mycorrhizal fungi play in supporting plant diversity and ecosystem functions (Powell & Rillig, 2018). Despite this importance, we do not know whether AM fungi have adapted to the fire-prone landscapes of Australia, or if they provide specific functional benefits

to vegetation in these environments. These outstanding questions will become increasingly critical as the continent is faced with bushfires of increasing frequency and intensity, and as regions not well-adapted to fire face more frequent fire events (Abram et al., 2021).

CONCLUSION

Australia presents a unique and untapped opportunity to deepen our understanding of AM fungal ecology, its complex interplay with diverse vegetation types, and its adaptation to fire-prone ecosystems. Despite its ecological richness and unique features, this potential has been largely overlooked. The distinctive biogeography of Australia, coupled with the unique nutrient acquisition strategies of its vegetation along with its characteristic relationship with fire, all underscore the need for a more refined approach to mycorrhizal research.

The lack of robust biogeographic data on AM fungi in Australia is a significant barrier to progress. Thus, mapping AM fungal communities across the continent and sharing these data openly is necessary not only to advance our understanding of AM fungal ecology but to support conservation efforts, sustainable agriculture, and the prediction of ecosystem responses to environmental change. By doing so, we can make the most of the untapped potential that Australia offers for advancing mycorrhizal ecology and contribute to global efforts to understand and conserve our world's complex and invaluable biodiversity.

AUTHOR CONTRIBUTIONS

Adam Frew: Conceptualization (lead); writing – original draft (lead). **Carlos A. Aguilar-Trigueros:** Conceptualization (supporting); writing – original draft (supporting); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

There are no data associated with this paper.

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