Global mycorrhizal fungal range sizes vary within and among mycorrhizal guilds but are not correlated with dispersal traits

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Abstract

Aim: Mycorrhizal fungi associate with the majority of plant species with large consequences on ecosystem nutrient, carbon and water cycling. Two main types of mycorrhizal fungi, arbuscular mycorrhizal (AM) fungi and ectomycorrhizal (EM) fungi, dominate terrestrial ecosystems. Most global distribution modelling of AM and EM associations describe the distribution of AM and EM plants, and not fungi directly. However, significant functional trait variation occurs within AM and EM fungal guilds. Therefore, modelling range sizes and determinants of these ranges of fungi directly is likely to create spatial maps that are a better proxy of ecosystem function than guild-level lumping of AM and EM plant distributions.

Location: Global.

Taxa: Arbuscular mycorrhizal and ectomycorrhizal fungi.

Methods: Here I calculated the ranges of 164 AM and 67 EM fungal taxa at the global scale and related range sizes to differences in spore sizes as a proxy of dispersal potential. If dispersal limitation affects range sizes, I expected that EM fungi with smaller spores would have larger ranges than AM fungi with larger spores. If spore size was not related to range size, this would indicate factors other than passive dispersal control global mycorrhizal fungal ranges.

Results: Overall, AM fungal taxa had larger ranges than EM fungal taxa. AM fungi also had larger spore sizes than EM fungi. Range sizes within both AM and EM fungal taxa were phylogenetically conserved; closely related AM and EM fungi have similar range sizes. Closely related EM fungi also had similar spore sizes. However, spore size was not related to range size for either mycorrhizal fungal guild after phylogenetic correction, except for EM fungi in the Northern hemisphere.

Main Conclusions: These findings provide evidence that range size for both mycorrhizal fungal guilds is for the most part not determined by dispersal limitation, suggesting instead that environmental tolerance or plant host distributions determine mycorrhizal fungal ranges. Future surveys of the same plant species across environmental gradients will elucidate abiotic versus host plant influence on mycorrhizal fungal niches.

Keywords

arbuscular mycorrhizal fungi, biogeography, dispersal limitation, ectomycorrhizal fungi, macroecology, niches
1 | INTRODUCTION

Mycorrhizal fungi associate with over 90% of plant taxa and provide key benefits for plants including nutrient and water uptake (Smith & Read, 2008) and protection from pathogens (Sikes, Cottenie, & Klironomos, 2009). Two main types of mycorrhizal fungi, arbuscular mycorrhizal (AM) fungi and ectomycorrhizal (EM) fungi, dominate most terrestrial ecosystems. AM fungi originated ca. 480 million years ago, whereas EM fungal lineages have evolved multiple times from saprotrophic fungal clades ca. 183 million years ago (Lutzoni et al., 2018). These mycorrhizal fungal types also differ in function, with AM fungi largely accessing inorganic nutrients in soils while EM fungi can decompose organic forms of N and P, leading to different nutrient use strategies among plant hosts of the two groups (Averill, Bhathagar, Dietze, Pearse, & Kivlin, 2019). In addition, while host specificity of mycorrhizal fungal associations are still unresolved (Opik & Peay, 2016), general differences are recognized between AM and EM fungi. Many AM fungi lack specific plant host associations (Veresoglou & Rillig, 2014) and associate with at least 70% of plant taxa (Bueno et al., 2017; Soudzilovskaja et al., 2019). In contrast, EM fungi can specialize at the level of plant genera or even species (Matheny et al., 2009; Tedersoo et al., 2008; Toju, Yamamoto, Tanabe, Hayakawa, & Ishii, 2016) and associate with approximately 2% of plant taxa (Tedersoo & Brundrett, 2017). In addition, species concepts vary among AM and EM fungi. AM fungi are typically grouped into virtual taxonomic units (VTXs) based on 97% sequence identity in the highly conserved SSU gene region sensu Opik et al. (2010), which may represent genetic variation at coarser taxonomic levels than species (Bruns & Taylor, 2016) and artificially inflate “species” ubiquity. EM fungal species delineations are more resolved via grouping at 97% sequence identity of the variable ITS2 locus (Koljalg et al., 2013), which may result in narrowed “species” ranges. Finally, most AM fungi are probably asexual (Kokkoris & Hart, 2019) and therefore their range sizes may not be hindered by lack of suitable fungal mating types. In contrast many EM fungi, especially in the Basidiomycota, require two compatible mating types in order to create viable lineages of sexual spores (Horton, 2017).

There is also substantial functional variation among taxa within AM- and EM fungal guilds. For example, AM fungi in the Gigasporaceae and Glomeraceae generally produce more hyphae outside of roots (in soils) versus inside of roots respectively (Hart & Reader, 2002; Powell et al., 2009). Trade-offs in growth form among AM fungal lineages may result in functional variation in resource competition, disturbance tolerance or stress tolerance (Chagnon, Bradley, Maherali, & Klironomos, 2013). For example, fungi in the Diversisporaceae have greater access to soil nutrients and fungi in the Glomeraceae tend to compete with pathogens for space in the root, resulting in different benefits for the host plant (Phillips et al., 2019; Treseder et al., 2018). Additional trade-offs may occur for resource acquisition of nitrogen versus phosphorus among AM fungal lineages (Treseder et al., 2018). Similar distinctions occur among EM fungal lineages where some clades (e.g. *Lactarius* spp.) excel at overall decomposition of organic matter (Baldrian, 2006; Martin, Kohler, Murat, Veneault-Fourrey, & Hibbett, 2016) and others are specialized to decomposition of specific organic substrates (e.g. lignin or tannin) (Martin et al., 2016; Shah et al., 2016; Talbot, Martin, Kohler, Henriessat, & Peay, 2015). Moreover, some trait trade-offs follow more traditional expectations from plant-based ecological theory (Grime, 1979), including clades that can be more competitive (e.g. *Helvella* spp.) and others (e.g. *Suillus* spp.) that can disperse farther within local ecosystems (Smith, Stedinger, Bruns, & Peay, 2018).

The large functional variation between and within AM and EM fungal guilds has led to many studies of how mycorrhizal fungal guilds might impact ecosystem functions such as carbon storage, nutrient cycling and litter decomposition across space (e.g. Averill et al., 2019; Averill, Turner, & Finzi, 2014; Keller & Phillips, 2019; Sulman et al., 2019). Historically, most biogeographic maps of mycorrhizal associations relied on host plant mycorrhizal types (Barcelo, Bodegom, & Soudzilovskaia, 2019; Bueno et al., 2017; Steidinger et al., 2019). Recently, both plant and mycorrhizal fungal distributions have been considered together (Toussaint et al. 2020), but focus has remained on patterns of alpha- and beta diversity and not on individual mycorrhizal fungal distributions. If functional variation within the AM or EM fungi is large, then using host plants or even mycorrhizal fungal diversity as a proxy for mycorrhizal fungal function will be insufficient for predicting terrestrial ecosystem carbon and nutrient cycling now and into the future. Instead, incorporating distributions of mycorrhizal fungal taxa and their functional traits with models of mycorrhizal plant types may provide the most promise for linking mycorrhizal symbioses to ecosystem function.

One of the main initial processes controlling the distribution of many microorganisms is dispersal limitation (Hanson, Fuhrman, Horner-Devine, & Martiny, 2012). While historical paradigms of microbial biogeography suggested that dispersal limitation did not apply to microorganisms (Baas Becking 1934), more recent evidence suggests that spore traits (Kivlin, Winston, Goulden, & Treseder, 2014), wind patterns (Tipton et al., 2019), seasonality (Peay & Bruns, 2014), life history strategies (Horton, 2017) and the location of spore origination (Egan, Li, & Klironomos, 2014; Peay, Garbelotto, & Bruns, 2010a; Peay, Kennedy, Davies, Tan, & Bruns, 2010b; Peay, Schubert, Nguyen, & Bruns, 2012) all affect how far fungi will disperse in the atmosphere. Thus, dispersal limitation should affect range sizes at the global scale assuming airborne passive dispersal is the main dispersal vector of mycorrhizal fungi and any of these factors influence how far a fungal propagule disperses. Alternatively, spore size may be inversely related to dispersal distance (sensu Davison et al., 2018) if larger spores are more likely to germinate (Norros, Karhu, Norden, Vahatalo, & Ovaskainen, 2015) or withstand resource limitation (Halbwachs, Hiellmann-Clausen, & Bassler, 2017). If mycorrhizal fungal spores are actively dispersed, then metrics of dispersal limitation can be applied to mycorrhizal fungal ranges sizes.

Here I address how spore size and phylogenetic history independently and jointly affect range sizes of AM and EM fungal taxa. I collected data on geographic distributions of AM and EM fungal taxa...
at the global scale to determine taxon-specific range sizes and the influence of dispersal limitation on those ranges. If dispersal limitation affects range sizes, I expected EM fungi to have larger ranges than AM fungi, given EM fungal spores are mainly produced by mushrooms aboveground and are smaller (79–20,100 μm²) than AM fungal spores (154,000–55,750,000 μm²). Alternatively, if spore size is not related to range size, I expected AM fungi to have larger ranges given that they originated over 200 million years before EM fungi and have a wider plant host breadth than EM fungi.

2 | MATERIALS AND METHODS

2.1 | Data collection

AM fungal occurrences were collected from the MaarjAM database (Opik et al., 2010) and supplemented with a GenBank search using ‘Glomeromycotina’ completed on 06.06.2019. Only records with geographic locations were included in the final dataset. AM fungal sequences of the 18S rRNA gene were clustered into virtual taxonomic units (VTX) following Opik et al. (2010). For EM fungi, I used the Tedersoo et al. (2014) global survey of 365 locations sequenced at the ITS2 locus and clustered into operational taxonomic units (OTUs) at 97% sequence similarity. For both datasets only mycorrhizal fungal taxa sampled from at least 20 geographic locations were retained in the final analysis. This limited the dataset to 164 AM fungal taxa and 67 EM fungal taxa. While this may limit interpretation to common or widespread fungi, because molecular methods of fungal analysis have only been developed in the last two decades, sampling effort at the global scale is still low and low sampling effort may bias range size estimates. However, range size varied 290-fold for EM fungi and 59-fold for AM fungi, suggesting that this sampling effort is sufficient to capture both narrowly and broadly distributed mycorrhizal fungal taxa.

2.2 | Range sizes

Commonly applied estimates of range sizes, such as convex hulls, can overpredict range sizes by including gaps in distributions (Burgman & Fox, 2003). To mitigate errors in range size calculations, I calculated range sizes in several ways. First, I calculated range sizes using alpha hulls in the range Builder package v 1.4 (Rabosky et al., 2016) where hulls included 95% of datapoints and were trimmed to include only terrestrial areas followed by polygon area calculation with rgeos v 0.4.3 (Bivand, Rundel, Pebesma, Hufthammer, & Bivand, 2014). Second, I calculated latitudinal range and midpoints of all datapoints using raw values. Finally, I calculated absolute latitudinal range and midpoint values for all data together and the Northern and Southern hemispheres separately. These approaches for calculating range sizes are complementary and allowed me to examine commonality in mycorrhizal fungal ranges while mitigating some common pitfalls of underrepresentation (e.g. fewer samples in the Southern versus. Northern hemisphere).

2.3 | Phylogeny

Separate phylogenies were created for AM and EM fungi using representative sequences for each VTX and OTU respectively. For each guild, sequences were trimmed to equal length and aligned with MAFFT and placed into a maximum likelihood phylogeny using RAxML (Appendix 1). This process was iterated until the best alignment and phylogeny were obtained using PASTA (Mirarab et al., 2015). Sequences for AM fungi were derived from the 18S gene sequences available in MaarjAM (Opik et al., 2010). Sequences for EM fungi were obtained from Tedersoo et al. (2014) from the ITS2 variable region. While variable, the ITS2 phylogeny was monophyletic with the exception of one Russula species which grouped with a sister genus Lactarius. Because these genera are closely related within the same family, this is unlikely to influence the overall phylogenetic model (see below).

2.4 | Spore size traits

Spore sizes (height, width, length) for AM fungi were obtained from Aguilar-Trigueros, Hempel, Powell, Cornwell, and Rillig (2019). When VTX were not represented, I used the mean value at the genus level. The same EM fungal spore traits were collated from the primary literature (see Appendix S2). Spore volumes were then calculated based on the volume of an ellipsoid.

2.5 | Statistics

Differences in range size between each mycorrhizal fungal guild were determined using a univariate ANOVA with the fixed factor of mycorrhizal fungal type. Because hyphal exploration types, nutrient acquisition and response to global change are often conserved within mycorrhizal fungal genera (Chagnon et al., 2013;Phillips et al., 2019;Treseder et al., 2018), I also used univariate ANOVAs to determine how spore size and range sizes varied among genera within each mycorrhizal fungal guild when a genus contained at least three representative fungal taxa.

I tested if spore volume or range size metrics were phylogenetically conserved using Blomberg’s K in the Picante package v 1.7 in R (R Core Team, 2018). Phylogenetic signal was tested separately for AM and EM fungi since the phylogeny for each group was created with a different marker gene.

My main goal was to understand if spore volume was related to any metric of range size. I tested for these univariate relationships separately for EM and AM fungi with phylogenetic generalized least squares (PGLS) approach to account for phylogenetic signal in fungal
traits using the Caper package v 1.0.1 (Orme et al., 2012) in R (R Core Team, 2018).

3 | RESULTS

3.1 | Range sizes

Overall, AM fungi had 3.43x larger ranges by area ($F = 192.400, p < .001$, Figure 1a) and 1.44× larger latitudinal ranges than EM fungi ($F = 130.200, p < .001$, Figure 1b). Because species definitions may vary among fungal guilds, I also calculated range size for each EM fungal genus. Even in this case, AM fungal taxa had larger areal range sizes ($F = 4.487, p = .035$), but not latitudinal ranges ($F = 1.848, p = .175$), than EM fungal genera.

3.2 | Spore sizes

Spore volumes were on average 2028× larger for AM fungal taxa compared to EM fungal taxa ($F = 16.19, p < .001$, Figure 2).

3.3 | Phylogenetic signal in spore and range size traits—species level

Closely related EM fungi had similar spore sizes ($K = 0.764, p < .001$). In addition, closely related EM fungi also had more similar range sizes based on area ($K = 0.332, p = .034$), and latitudinal ranges overall ($K = 0.326, p = .012$), and in the Northern ($K = 0.316, p = .018$) and Southern hemispheres ($K = 0.414, p = .037$). Closely

FIGURE 1 Global areal range size for AM fungal and EM fungal guilds (a) and latitudinal range of AM and EM fungal guilds (b) with means ± 1 SE. Each point is a single fungal taxon. AM fungi have larger global ranges than EM fungi [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 2 Spore size for AM fungal and EM fungal guilds with means ± 1 SE. Each point is single fungal taxon. AM fungi have larger spore sizes than EM fungi [Colour figure can be viewed at wileyonlinelibrary.com]
related AM fungi had similar range sizes when calculated by area \((K = 0.178, p < .001)\), and overall latitudinal range \((K = 0.152, p = .044)\). In addition, closely related AM fungal taxa had more similar latitudinal means in their ranges \((K = 0.178, p < .001)\). Spore sizes within AM fungi were not phylogenetically conserved \((K = 0.197, p = .143)\).

### 3.4 Phylogenetic signal in spore and range size traits—genus level

Within guilds, spore sizes varied among AM fungal genera \((F = 37.73, p < .001)\), Figure 3a). Despite significant variation in spore volumes among AM fungal genera, neither range sizes calculated by area \((F = 0.973, p = .445)\), Figure 3b), latitudinal ranges \((F = 1.765, p = .109)\), nor in the Southern hemisphere \((F = .152, p > .05)\) nor in the Northern \((F = 1.564, p = .124)\) hemispheres alone varied among AM fungal genera.

EM fungal genera also varied in spore size \((F = 10.540, p < .001)\), Figure 3a), but areal ranges of EM fungi did not differ among genera \((F = 1.564, p = .124)\), Figure 3b). Similarly, EM fungal latitudinal range sizes did not vary overall \((F = 1.676, p = .092)\), when calculated using absolute latitude \((F = 0.51, p = .936)\), in the Southern \((F = 1.819, p = .130)\) or Northern hemisphere \((F = 1.133, p = .364)\).

### 3.5 Relationships between spore size and range size

Despite AM fungi having larger ranges and larger spore sizes than EM fungi, within both guilds spore size was unrelated to range size calculated by area \((AM R^2 = .006, p = .961; EM R^2 = .037, p = .082)\), Figure 4a,b) or by latitudinal range \((AM R^2 = .006, p = .768; EM R^2 = .023, p = .135)\) after phylogenetic correction. However, EM fungal taxa with smaller spores tended to have larger latitudinal ranges in the Northern hemisphere \((R^2 = .132, p = .003)\). This pattern disappeared, however, after two narrow-ranged, but high spore volume taxa in the *Humaria* genus were removed.

### 4 DISCUSSION

AM fungal taxa had larger distributions than EM fungal taxa. However, within both AM and EM fungal guilds closely related taxa had similar range sizes, suggesting some influence of shared functional trait determination of range sizes. One clear way that closely related fungal taxa may have similar range sizes is if they have similar spore sizes that determine the ability of passive air-borne dispersal. However, spore size was not related to most range size metrics for either mycorrhizal fungal guild. Instead, AM fungi had larger spores and larger ranges than EM fungi. Spore size may not relate to range size if passive wind is not the main dispersal vector for mycorrhizal fungal spores. Many AM fungi may rely on passive dispersal via seawater (Davison et al., 2018) or active animal dispersal vectors (Mangan & Adler, 2000) and recent evidence suggests that migratory birds may co-disperse AM fungi and seeds across continents (Correia, Heleno, Silva, Costa, & Rodriguez-Echiverria, 2019), which may explain their large range.
sizes compared to mostly wind dispersed EM fungi (Peay et al., 2012, but see Halbwachs, Brandl, & Bassler, 2015). Prolonged passive wind dispersal of smaller, epigeous produced (Kivlin et al., 2014) or melanized (Gessler, Egorova, & Belozerskaya, 2014) spores may explain why spore size was negatively correlated to range size of EM fungi in the Northern hemisphere. Alternatively, EM fungi with smaller spores may have higher UV or desiccation tolerance, allowing for longer air transport (Tipton et al., 2019).

Another phylogenetically conserved trait within mycorrhizal fungal guilds may be the breadth of environmental conditions under which mycorrhizal fungal taxa can persist. In this case, AM fungi may have larger range sizes because they have broader environmental tolerances than EM fungi. AM fungi have been isolated from ecosystems ranging from deserts (Mohammad, Hamad, & Malkawi, 2003) to rainforests (Gaudarrama & Alvarez-Sanchez, 1999), and myriad ecosystems in between (Kivlin, Hawkes, & Treseder, 2011). Moreover, most individual AM fungal taxa have been sequenced from 4 to 5 different ecosystems (Opik et al., 2010). In contrast, EM fungi mostly originate from temperate (Talbot et al., 2014), boreal (Read, Leake, & Perez-Moreno, 2004) or tropical forests (Peay, Baraloto, & Fine, 2009) with some species isolated from in artic and alpine ecosystems (Gardes & Dahlberg, 1996).

Fundamental niches of mycorrhizal fungi may be structured by the abiotic environment with further restriction of realized mycorrhizal fungal niches by host availability. Thus, distributions of both AM and EM fungi may be restricted by the distributions of their plant hosts (Steidinger et al., 2019). AM fungi typically have broader host ranges compared to EM fungi (Matheny et al., 2009; Opik et al., 2010; Veresoglou & Rillig, 2014), allowing AM fungi to persist in more geographic locations than EM fungi. Parsing environmental versus plant host influence on below-ground mycorrhizal fungi is difficult because mycorrhizal plant distributions are also influenced by abiotic climatic drivers (Barcelo et al., 2019). Ultimately, global surveys of multiple plant hosts across a variety of ecosystems will resolve the abiotic versus biotic component of mycorrhizal fungal niches. While large-scale mycorrhizal fungal surveys are becoming common (e.g. Davison et al., 2015; Tedersoo et al., 2014), sampling effort is still low (~400 locations), precluding a generalizable framework of mycorrhizal fungal distributions.

In addition to these data limitations, several other constraints should be considered. Mycorrhizal fungal species definitions based on DNA similarity are notoriously in flux depending on sequencing region, taxonomic clade and sequencing technology (Hibbett et al., 2017). In this dataset AM fungi were defined as VTXs following Opik et al. (2010) and EM fungi were classified at 97% sequence identity of the ITS2 variation region as in Tedersoo et al. (2014). When AM fungi in particular are defined as virtual taxonomic units (e.g. VTXs) this may better reflect genus- or family-level genetic differences (Bruns & Taylor, 2016, but see Opik, Davison, Moora, Partel, & Zobel, 2016). However, in the current study, AM fungal range sizes were still larger than the range size for entire EM fungal genera, adding robustness to this finding. Furthermore, recent evidence suggests that even genotypes of the same AM fungus are widespread among continents (Savary et al., 2018), indicating that species definitions may not influence geographic range. Moreover, in a comparison of species distribution models of a common AM fungus, *Rhizophagus irregularis* (VTX00114), defined by VTX or per cent DNA similarity from 97% to 99.5% shared bases in the 18S region, Kivlin, Muscarella, Hawkes, and Treseder (2017) found little difference in niche envelopes based on taxonomic resolution. Finally, neither gene region nor DNA similarity influenced community patterns of AM fungal assemblages at the global scale (Kivlin et al., 2011). Nevertheless, these results should be interpreted with these species definitions in mind.

## 5 Conclusion

Overall, I found little indication that dispersal limitation measured as a proxy of spore size is the main driver of mycorrhizal fungal distributions at the global scale. Instead range sizes were phylogenetically conserved both within AM and EM fungal lineages. This suggests that either other mechanisms of dispersal are occurring or that filtering by abiotic or biotic factors influences mycorrhizal fungal range size dynamics. Future modelling including these environmental imprints on mycorrhizal fungal distributions will elucidate the relative influence of dispersal limitation versus abiotic and biotic filtering on mycorrhizal fungal distributions.

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### Data Availability Statement

The data that support the findings of this study are openly available in DRYAD at https://doi.org/10.5061/dryad.b8gth78v

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The Kivlin Laboratory (https://kivlinlab.github.io) specializes on the biogeography of microorganisms, how microbial communities affect ecosystem processes and how microbial distributions and function will shift with global change.

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