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Mycorrhiza

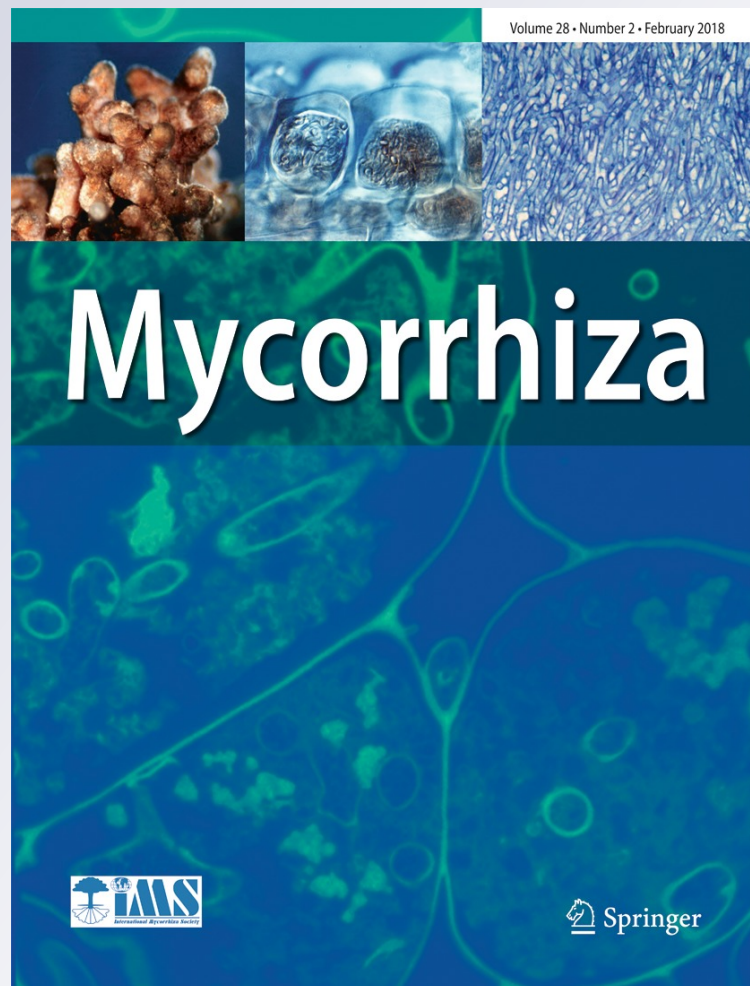
ISSN 0940-6360

Volume 28

Number 2

Mycorrhiza (2018) 28:187-195

DOI 10.1007/s00572-017-0811-y



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Accounting for local adaptation in ectomycorrhizas: a call to track geographical origin of plants, fungi, and soils in experiments

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Received: 7 August 2017 / Accepted: 16 November 2017 / Published online: 27 November 2017
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Abstract Local adaptation, the differential success of genotypes in their native versus foreign environments, can influence ecological and evolutionary processes, yet its importance is difficult to estimate because it has not been widely studied, particularly in the context of interspecific interactions. Interactions between ectomycorrhizal (EM) fungi and their host plants could serve as model system for investigations of local adaptation because they are widespread and affect plant responses to both biotic and abiotic selection pressures. Furthermore, because EM fungi cycle nutrients and mediate energy flow into food webs, their local adaptation may be critical in sustaining ecological function. Despite their ecological importance and an extensive literature on their relationships with plants, the vast majority of experiments on EM symbioses fail to report critical information needed to assess local adaptation: the geographic origin of the plant, fungal inocula, and soil substrate used in the experiment. These omissions limit the utility of such studies and restrict our understanding of EM ecology and evolution. Here, we illustrate the potential importance of local adaptation in EM relationships and call for consistent reporting of the geographic origin of plant, soil, and fungi as an important step towards a better understanding of the ecology and evolution of EM symbioses.

Keywords Community ecology · Evolution · Geographic origin · Soil micro-organisms · Local adaptation · Symbiosis

Introduction

Mycorrhizae contribute significantly to ecosystem functioning through their role in carbon and nutrient cycling (Courty et al. 2010; Van Der Heijden et al. 2008) and can also influence host plant performance by altering plant response to pathogens and competitors (Bever et al. 2001; Rúa et al.

2013; Smith and Read 2008). Despite their importance, our understanding of the evolutionary processes that shape and maintain mycorrhizal relationships is limited (Brundrett 2009; Hoeksema 2010; Maherali et al. 2016; Wang and Qiu 2006). Local adaptation, the differential success of genotypes in their native versus foreign environment, is one evolutionary process likely to be important for shaping mycorrhizal

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00572-017-0811-y>) contains supplementary material, which is available to authorized users.

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relationships since they can have profound effects on plant fitness and include fungi with life histories that enable rapid evolution with their host (Kawecki and Ebert 2004). Here, we synthesize literature on ectomycorrhizal (EM) relationships to investigate the potential for local adaptation to shape these associations.

One of the key characteristics of local adaptation is variation in adaptive landscapes which results in the evolution of traits that provide the host an advantage under local environmental conditions regardless of their effect in other environments (Kawecki and Ebert 2004). Soil conditions provide the necessary adaptive landscapes as they can have strong effects on plant growth and be spatially heterogeneous. Ectomycorrhizal (EM) fungi are a biotic component of soils likely to exhibit strong patterns of local adaptation due to the long evolutionary history of plant-fungal interactions (Maherali et al. 2016; Tedersoo et al. 2012a) and the importance of spatially variable soil characteristics in modulating EM symbiosis function (e.g., Kennedy and Peay 2007; Lilleskov et al. 2002). This variation in function creates a dynamic adaptive landscape such that plants may exhibit patterns of local adaptation specific to singular EM fungal species or a community of species functioning similarly. Since EM fungi are extremely diverse (Ryberg and Matheny 2012) and demonstrate wide variation in functional roles such as enzymatic activities (Talbot et al. 2015; Tedersoo et al. 2012b), different capacities to utilize organic and inorganic forms of nitrogen and organic forms of phosphorus (Kranabetter et al. 2015a; Lilleskov et al. 2011; Talbot and Treseder 2010) and different capacities to protect their hosts against pathogens (Bennett et al. 2017), EM fungi may be beneficial across broader swaths of varying environmental characteristics, suggesting they are better suited mutualists in a given area because of their varying functional guilds.

While there is some evidence of local adaptation between partners in the EM symbiosis (Hoeksema and Thompson 2007; Keymer and Lankau 2017; Pickles et al. 2015), including between host, EM fungi, soil, and soil microbiota other than EM fungi, direct tests using reciprocal transplants of different local populations of plants and EM fungi are limited. Local adaptation of plants or fungi to their symbiotic partner(s) is predicated on variation within a species in how they interact with their symbiotic partner(s). Specifically, for local adaptation to be possible, the relationship between plant and fungal performance must vary with plant/fungal population genotype; evidence of such variation exists for EM plants (e.g., Gehring et al. 2014; Karst et al. 2009; Lamit et al. 2016) and fungi (e.g., Branco et al. 2017; Piculell et al. 2008; Rosado et al. 1994). However, the few explicit tests of local adaptation using reciprocal transplants/inoculations of plants, fungi, and/or soil have produced mixed results. For example, the growth of *Pseudotsuga menziesii* was maximized when planted where EM fungal communities were

most similar to those at their sites of origin (Kranabetter et al. 2015b), but three pine species exhibited no evidence of local adaptation to one common EM fungus, *Rhizopogon occidentalis*, in a cross-inoculation experiment (Hoeksema and Thompson 2007). The latter study did find, however, that the EM fungus *R. occidentalis* exhibited a clinal pattern of local adaptation such that EM fungal colonization decreased with increasing geographic distance between plant and fungal populations (Hoeksema and Thompson 2007). Most reciprocal transplant studies also show that climate and/or soil factors are significant predictors of plant and/or fungal performance (e.g., Hoeksema et al. 2012; Kranabetter et al. 2015b; Pickles et al. 2015), demonstrating the importance of the environmental context in shaping local adaptation in the EM symbiosis. Thus, although local adaptation appears to be an important eco-evolutionary process for EM, more comprehensive studies are necessary.

EM-associated plant families are important economically, including areas outside their native range where they have been introduced with their fungal associates (Karst et al. 2014; Richardson 1998; Simberloff et al. 2010). Early attempts to plant these families outside of their native range failed until it was discovered that transplanted stock could not survive without soil inoculum obtained from native forests (e.g., Grove and Le Tacon 1993; Perry et al. 1987; Richardson et al. 1994). It is likely that the lack of suitable EM fungi in the Southern Hemisphere delayed the successful establishment of pine forestry until EM fungi were introduced with pines (Dunstan et al. 1998; Nuñez et al. 2009). In turn, these introductions of EM symbionts with wide host ranges may have contributed to the successful establishment of subsequent pine introductions (Pearson 1950). For example, plantations of *Eucalyptus* in the Iberian peninsula appeared to establish successfully without the concurrent introduction of their EM fungi; however, further analysis revealed that many of the EM fungi found in Iberian *Eucalyptus* plantations are of Australian origin, suggesting that these fungi were unintentionally introduced with germplasm into the region from Australia prior to quarantine restrictions, which regulate the introduction of foreign forest soil, spores, or mycelium (Díez 2005).

There are also several examples in which non-native trees have been successfully introduced into existing coniferous EM fungal forests without their soil fungi (Mirov and Hasbrouck 1976). For example, Sitka spruce (*Picea sitchensis*) was introduced from its native range in British Columbia to Ireland and Britain as seed, but is now the most abundant tree species in the region, (O'Hanlon et al. 2013). Similarly, silver fir (*Abies alba*) was introduced from the mountains to the lowlands of Poland as seed but has been shown to establish associations with 81% of the estimated fungal species present in mature native forest stands in the region (Rudawska et al. 2016). As a result, to ensure successful plantings, many non-native EM hosts are either introduced

with their local EM fungi, introduced with native soil containing EM fungal propagules, or inoculated with non-native commercial inocula (Nuñez and Dickie 2014). Thus, there is a potentially rich source of data on the behavior of EM plants and fungi inside and outside their native ranges in which to explore the importance of local adaptation.

Decisions regarding the source of EM fungal inocula required for successful establishment of seedlings in managed forests have revolved around the premise that (1) any EM fungal inoculant is better than none and (2) within a given environment, some EM fungal species that occur naturally are less beneficial than others (Marx et al. 1992). Early recommendations for establishing nurseries of woody plants emphasized the need to inoculate tree seedlings with EM fungi native to the planting site rather than using a fungus that originated from a distant area or different ecosystem type to ensure adequate ecological adaptability to environmental variation (Marx et al. 1992; Trappe 1977). Despite these recommendations, many early mycorrhiza researchers advocated for the use of a single fungal species, *Pisolithus tinctorius*, to ensure successful growth and establishing of EM plants (Marx and Bryan 1975; Marx et al. 1984). This practice propagated throughout the forestry industry largely due to *P. tinctorius*'s broad host distribution, ability to grow well on seedlings and young trees, ease of propagation and manipulation in pure culture, and ability to survive in a wide range of habitats and soils including eroded and mine sites as well as forest, urban, and orchard sites (Cairney and Chambers 1997; Marx 1977; Marx et al. 1992); however, host plant growth responses and other fungal derived benefits varied greatly with fungal genotype (Burgess et al. 1994; Dixon et al. 1987; Lamhamedi et al. 1990), host plant (Marx 1981), and edaphic conditions (Castellano and Trappe 1991; Marx and Bryan 1971). This variation in host benefit to *P. tinctorius* inoculation has largely been attributed to its failure to compete with native EM fungi in plantation soils (Cairney and Chambers 1997; Marx et al. 1984) but may also reflect the importance of considering local adaptation among hosts, their fungi, and soils for understanding the outcome of these interactions.

If local adaptation is important in EM systems, plants should display enhanced growth responses when matched with EM fungi sympatric to their geographic origin and relatively weaker responses when inoculated with fungi allopatric to their geographic origin. On the other hand, examples of successful conifer invasion into exotic habitats with EM fungi from a different continent (Nuñez et al. 2009; Read 1998) suggest either that local adaptation is not important for these interactions, that it occurs rapidly and does not depend on a long evolutionary history, or reflects the robustness of the mutualism. Additionally, the extent to which these patterns extend to non-conifers is less established. In either case, we need information on the geographic origins of plants, fungi, and soils to be able to test these hypotheses.

In lieu of direct tests, investigating the signature of local adaptation through meta-analysis of existing data from experiments manipulating interactions among fungi, plants, and soils may provide a complementary perspective on local adaptation (Hoeksema et al. 2010; Rúa et al. 2016). This technique allows researchers to extend the results of single primary research papers to formulate more comprehensive views on a single topic, understand how results of a single study relate to others from different geographic or ecological systems, and inform future research (Gerstner et al. 2017), making them ideal for understanding local adaptation in mycorrhizas. Additionally, the use of meta-analysis for studying local adaptation in mycorrhizas allows for the synthesis of studies regardless of their intention to study local adaptation, as long as they report the geographic origin of the fungi, plants, and soil. A recent meta-analysis (Rúa et al. 2016) documented the importance of local adaptation in arbuscular mycorrhizal associations and showed greater host plant benefit when plant, fungus, and soil were sympatric compared to allopatric; however, despite evidence for local adaptation in EM associations in some individual manipulative studies (e.g., Hoeksema and Thompson 2007; Keymer and Lankau 2017), similar meta-analyses have not been completed for EM associations.

Using meta-analysis to test for local adaptation

To evaluate the importance of local adaptation for determining plant response to EM fungi, we extended MycoDB, a database of studies measuring plant response to mycorrhizal fungal inoculation (Chaudhary et al. 2016; Rúa et al. 2016). Prior to our effort, MycoDB contained 1026 EM studies from 86 papers. On March 8, 2016, we searched the ISI Web of Science database using the keywords *ectomyc**, *inocul** AND 2010–2016 to identify papers not included in MycoDB. Resulting papers were screened for mycorrhizal-inoculated and non-inoculated control treatments, and whole plant biomass or shoot biomass was extracted. This yielded 573 new studies (individual observations) from 89 papers, resulting in a revised MycoDB database (version 3) containing 1599 EM studies from 175 papers. The Taxonomic Name Resolution Service, v 4.0 [<http://tnrs.iplantcollaborative.org>, Accessed 19Mar 2017] was used to update plant taxon names and eliminate synonyms (Boyle et al. 2013). All data were deposited into Dryad: <https://doi.org/10.5061/dryad.723m1.3>.

This expansion of MycoDB provided data on the geographic origin of plant, soil, and fungal components for 117 studies (from 22 papers), representing only 7% of the overall database. Of the remaining 1482 studies, 496

reported information on geographic origin for two components of the symbiosis (the plant, soil, or fungus; Table S1). Some of these studies used cultivars (13; Table S1) or potting mix (127; Table S1), making them undesirable for examining patterns of local adaptation, but the majority failed to report the origin of the missing component. We did not track studies that only reported the geographic origin of one component of the symbiosis. When possible, we researched isolate numbers for geographic origin or contacted the corresponding author but were largely unsuccessful in obtaining the missing geographic information either because researchers did not reply (most common) or geographic origin was unknown/forgotten.

Analysis

Despite the limitations imposed by the data, we sought to examine the potential for local adaptation to alter the effect of mycorrhizal inoculation on host biomass using a mixed multi-factor meta-analysis. We use this analysis to illustrate the potential such an approach has for informing patterns of local adaptation should information regarding the geographic origin of plants, fungi, and soil used in experiments be reported, but caution against interpreting the results of this analysis too strongly. Four categorical variables were used to capture random effects due to plant taxonomy (PLANTSPECIES), individual observations (EXPERIMENTID), observations that share a non-inoculated control (CTRLSETID), and fungal taxonomy (FUNGALGENERA). To obtain accurate estimates of local adaptation, we used explanatory variables important for shaping mycorrhizal relationships and a variable that identified differences in host response when individual components of the mutualism were sympatric or allopatric to one another (Hoeksema et al. 2010; Rúa et al. 2016): FUNCTIONALGROUP (N-fixing vs non-N-fixing), STERILIZED (yes vs no), NONMYCOCONTROL (microbes added vs not added), PFERTILIZATION (yes vs no), NFERTILIZATION (yes vs no), and ORIGIN (Sympatric vs Allopatric vs Plant-Fungi Sympatric vs Plant-Soil Sympatric). To have enough power to test each predictor variable, we removed studies with characteristics that were poorly represented in the full dataset. For example, only one paper with field studies was appropriate under our criteria so experimental set-up (greenhouse vs field) was not included in the analysis. Thus, the full dataset of 117 studies was culled to 91 studies (from 16 papers), all of which were conducted in the laboratory using single species inoculum. The analysis did not include cases in which the fungus and soil were sympatric but allopatric to the plant. Analyses were conducted using R, version 3.3.3 (R Core Team 2017) and the *rma.mv* function from the *metafor* package

(Viechtbauer 2010) with maximum likelihood estimation of parameters.

Results: missing data and emerging biases in ectomycorrhizal research

While EM associations were consistently beneficial for host plants, our tests for patterns of local adaptation indicate no significant effect of geographic origin of components of the mutualism on plant response to inoculation ($Q_M(df_3) = 2.903$, $p = 0.4069$; Fig. 1); however, these tests were severely limited by the number of studies available, which results in low statistical power (Ioannidis et al. 2007). One way to overcome missing data for meta-analysis is to use imputation, which replaces missing data with an estimated value based on other available information (Schwarzer et al. 2015), but this method assumes that at least some of the desired information from a given study is present and complicates interpretation. In this case, imputation of geographic origin data would defeat the purpose of analyses of local adaptation. We argue that the best way to facilitate and maintain biological relevance of meta-analyses on local adaptation in mycorrhizal symbiosis is for researchers to report the exact geographic origin of the plant, soil, and fungi used in an experiment regardless of the overall goal of the experiment.

Even though there was so much missing data, it is likely that researchers know the exact locations of the materials they use in their studies. However, in our experience, it was quite difficult to obtain this information after publication, so we contend that researchers should report the geographic origins of the missing component of the symbiosis in initial publications. In our database alone, this would expand the availability of existing studies fourfold (Table S1). This slight change in researcher behavior would not only allow for broad investigations of local adaptation but also expand the opportunity for additional investigations of EM fungi with meta-analyses. Additionally, reporting results in this way would align mycorrhizal research with current guidelines for reporting ecological results (Gerstner et al. 2017).

Taxonomic bias in the dataset further hampered our overall ability to extend the results. Just as with the whole dataset, the vast majority of studies with complete information utilized plants from just two families, Pineaceae or Myrtaceae (Fig. 2b). Both families contain economically important species that have been planted well outside their native ranges but only represent a fraction of the available plant families which form EM associations (Brundrett 2009). Similarly for fungal genera, 92% of the 117 studies used single species inoculum from a single genus, *Pisolithus* (Fig. 2c), despite estimates indicating there are >250 genera of EM fungi (Tedersoo et al. 2010). This persistence of *Pisolithus* in EM fungal studies likely reflects early recommendations to use *P. tinctorius* in

Fig. 1 With available data, there is no significant effect of local adaptation on plant response to EM inoculation. Values shown are weighted mean effect sizes \pm standard error and number of studies (k) for combinations of plant, fungi, and soil when all are sympatric, allopatric, plant and fungi are sympatric but allopatric to the soil, and plant and soil are sympatric but allopatric to the fungi. The dotted line indicates no response, values above the line indicate positive response to EM inoculation (mutualism), and values below the line indicate negative response to EM inoculation (parasitism)

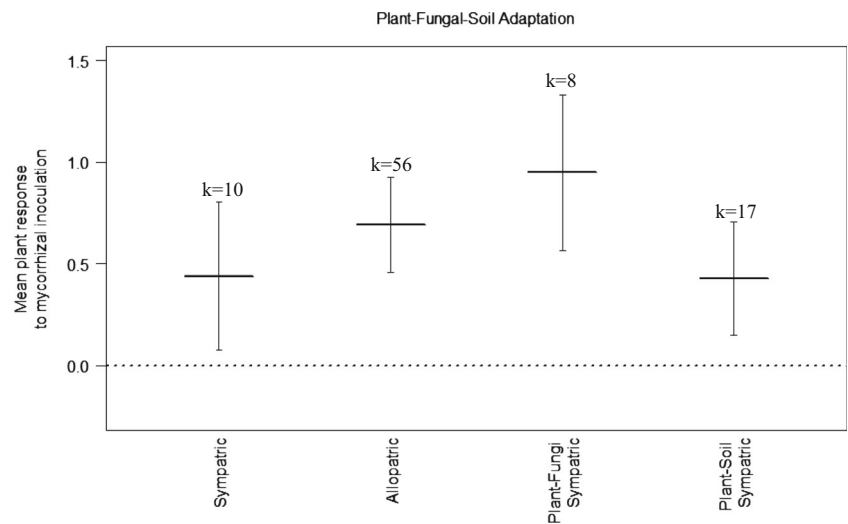
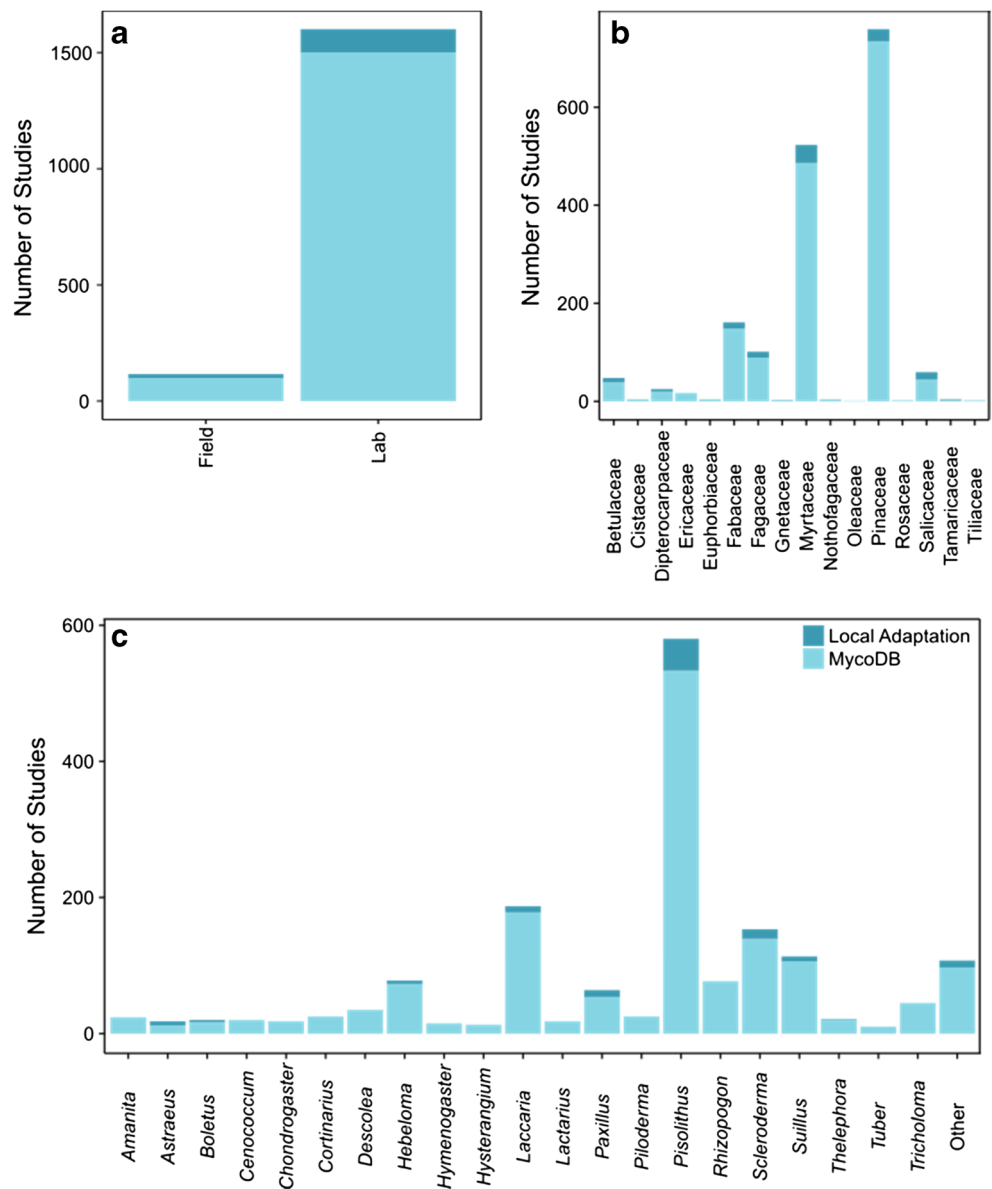


Fig. 2 Number of studies which report the geographic origin of the plant, soil, and fungi as a portion of studies on ectomycorrhizal associations available in the MycoDB database as a function of experimental set-up (a), plant family (b), and fungal genera (c)



plantings but such taxonomic bias undercuts our ability to interpret local adaptation while constraining our general understanding of the EM symbiosis. Thus, we further advocate for EM researchers utilizing inoculation studies to broaden the taxonomic origin of both the hosts and fungi used in such experiments.

The studies available for analysis had additional sources of bias important for understanding patterns of local adaptation. Although EM associations occur on six continents (Read 1991), most of the studies suitable for our analysis used soil, fungi, or plants from Australia (30% of the studies), Asia (21%), or Europe (22%) (Fig. 3). This was also true for the origin of the fungal inocula used in the study as the majority of studies used inocula from Australia (27%), Asia (24%), and Europe (21%). Interestingly, this pattern changed when plant origin was considered as the overwhelming majority of studies used plant material from Asia (48%) or Europe (21%) while only a small percentage of the material was from Australia (6%). Studies with North American origins represented 16% (soil and fungi) and 14% (plant) of available studies. This pattern partially contrasts with previous research examining geographical biases in ecological studies which found that, based on land area, both Africa and Asia (as well as South America and the Middle East) are understudied relative to studies from Europe and North America (Martin et al. 2012). This suggests that research with EM fungi may have a different set of biases than the ecological literature as a whole.

An additional limitation highlighted by our study is the experimental set-up of most EM studies. An overwhelming majority, 85% of the 117 studies, were conducted in the laboratory (or greenhouse) as opposed to the field (Fig. 2a).

While laboratory and greenhouse studies can provide important insight into the patterns of local adaptation, to more fully understand its role in shaping EM relationships, field studies which utilize a wider range of fungal and plant genera are necessary.

Conclusion

What seemed like a large available data set is reduced because of lack of reporting of key information in studies resulting in a dataset limited in the types of plants and fungi included, their geography and the manner in which they were studied. This call for detailed documentation of fungal origin is not new to the field, beginning with early studies of EM fungal physiology which noted the need to identify the origin of fungal isolates being tested or researched (Ammirati 1979; Trappe 1967; Trappe 1977). Close to 50 years later, we are still advocating for researchers to fully document their source material. In the current study, our ability to determine whether patterns of local adaptation are widespread or reflect geographic differences was drastically limited by the geographic limitations imposed by the available studies. Understanding patterns of local adaptation in EM associations has the potential to not only address the high variability in ecological outcomes of these associations (Hoeksema et al. 2010; Karst et al. 2008; Read 1991), but also have significant implications for using mycorrhizal inoculation in horticulture and forestry, as knowledge of patterns of local adaptation can aid in species and habitat management decisions. Furthermore, understanding the role local adaptation played in the past could inform how



Fig. 3 Geographic origins of the plant, soil, and fungi reported for local adaptation studies of ectomycorrhiza in MycoDB. Point size reflects number of studies. Inset reflects the number of studies available per continent

current global change (e.g., species introductions (Wolfe et al. 2010), atmospheric nitrogen deposition, and climate change) will affect these associations in the future. To further understand the role of local adaptation for structuring this important symbiosis, we advocate for not only more direct tests of local adaptation, particularly in the field, but also through comprehensive meta-analysis. To facilitate this, we highlight the need for reporting the geographic origin of the plant, soil, and fungi involved in EM inoculation studies, regardless of the overall goal of the study, which would not only increase the number of studies available for meta-analyses but also extend the ability to interpret the importance of results.

Further limitations in taxonomic diversity and study conditions highlight important gaps in EM research which are limiting our overall understanding of this important symbiosis. Our recommendations for improving reporting procedures and outcomes echoes that of other ecological researchers (Gerstner et al. 2017), but is particularly important for mycorrhizal relationships whose outcomes are highly context dependent. While the individual limitations described here are problematic, taken together, they restrict our ability to use meta-analysis to evaluate patterns of local adaptation for EM relationships in a realistic biotic and abiotic context. The reporting and experiment modifications we suggest here will allow for a more complete understanding of both the ecological and evolutionary underpinnings of EM systems.

Funding information This work was supported by start-up funds from the Wright State University to MAR, a NSERC Discovery Grant and Canada Research Chair to PMA, a NSERC Industrial Research Chair to JK and National Science Foundation grants to JDH (award #1119865) and CAG (award #EF-1340852).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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