

# CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

*Ecology*, 101(4), 2020, e02978  
© 2020 by the Ecological Society of America

## Climate change influences mycorrhizal fungal–plant interactions, but conclusions are limited by geographical study bias

ALISON E. BENNETT <sup>1,5</sup> AND AIMÉE T. CLASSEN <sup>2,3,4</sup>

<sup>1</sup>Department of Evolution, Ecology and Organismal Biology, Ohio State University, Columbus, Ohio 43210 USA

<sup>2</sup>Rubenstein School of Environment & Natural Resources, University of Vermont, Burlington, Vermont 05405 USA

<sup>3</sup>The Gund Institute for Environment, University of Vermont, Burlington, Vermont 05405 USA

<sup>4</sup>Center for Macroecology, Evolution and Climate, The Natural History Museum of Denmark, University of Copenhagen, Copenhagen Ø DK-2100 Denmark

**Citation:** Bennett, A. E. and A. T. Classen. 2020. Climate change influences mycorrhizal fungal–plant interactions, but conclusions are limited by geographical study bias. *Ecology* 101(4):e02978. 10.1002/ecy.2978

**Abstract.** Climate change is altering the interactions among plants and soil organisms in ways that will alter the structure and function of ecosystems. We reviewed the literature and developed a map of studies focused on how the three most common types of mycorrhizal fungi (arbuscular mycorrhizal [AM], ectomycorrhizal [EcM], and ericoid mycorrhizal [ErM] fungi) respond to elevated atmospheric carbon dioxide concentrations (eCO<sub>2</sub>), climatic warming, and changes in the distribution of precipitation. Broadly, we ask how do mycorrhizal fungi respond to climate change, how do these responses vary by fungal type, and how do mycorrhizal traits influence plant adaptation, movement, or extinction in response to climatic change? First, we found that 92% of studies were conducted in the northern hemisphere, and plant host, ecosystem type and study location were only correlated with each other in the northern hemisphere. Second, we show that temperature and rainfall variability had more variable effects than eCO<sub>2</sub> on mycorrhizal fungal structures, but these effects were context dependent. Third, while mycorrhizal fungal types vary in their responses to climate change, it appears that warming leads to more variable responses in ectomycorrhizal than in arbuscular mycorrhizal fungi. Finally, we discuss common traits of mycorrhizal fungi that could aid in fungal and plant adaption to climate change. We posit that mycorrhizal fungi can buffer plant hosts against extinction risk, they can facilitate or retard the dispersal success of plants moving away from poor environments, and, by buffering host plants, they can enable host plant adaptation to new climates. All of these influences are, however, context dependent a finding that reflects the complex traits of mycorrhizal fungi as a group, the diversity of plant species they associate with and the variation in ecosystems in which they reside. Overall, while we point out many gaps in our understanding of the influence of climate changes on mycorrhizal fungi, we also highlight the large number of opportunities for researching plant and mycorrhizal fungal responses to and mitigation of climate changes.

**Key words:** climate changes; ecosystems; elevated carbon dioxide; mycorrhizal fungi; plants; precipitation change; warming.

### INTRODUCTION

Mycorrhizal fungi can regulate plant distribution and productivity and are expected to be important players in

ecosystem responses to, or mitigation of, climate change drivers (Classen et al. 2015). Mycorrhizal fungi are poised to have a large impact on ecosystem responses because they directly influence individual plant function and indirectly impact processes such as plant dispersal and community interactions. For example, prior meta-analyses of one climate change driver, elevated atmospheric carbon dioxide concentrations (eCO<sub>2</sub>), found that eCO<sub>2</sub> promoted mycorrhizal fungi (Treseder 2004,

Manuscript received 27 June 2019; revised 22 November 2019; accepted 5 December 2019. Corresponding Editor: Jason D. Hoeksema.

<sup>5</sup> E-mail: bennett.1242@osu.edu

Alberton et al. 2005). However, whether this promotion translated to plant growth promotion was context dependent and varied with mycorrhizal type (Alberton et al. 2005, Kivlin et al. 2013). Here, we (along with other authors; Mohan et al. 2014, Tedersoo and Bahram 2019) highlight that none of these previous analyses examined geographical variation among studies or mycorrhizal fungal types.

Mycorrhizal fungi are common on the landscape and associate with over 80% of plants in a diversity of managed and unmanaged ecosystems (Smith and Read 2008). In fact, there is overwhelming observational and experimental evidence that mycorrhizal fungi influence a variety of community traits and ecosystem functions, plant productivity and community composition (van der Heijden et al. 1998, Jiang et al. 2017), decomposition, and soil nutrient cycling (Langley et al. 2006, Rosling et al. 2016), soil microbial community composition (Kytaschenko et al. 2017) and soil carbon stabilization, at both local and landscape scales (Clemmensen et al. 2013, Leifheit et al. 2014, Moore et al. 2015a, 2015ba,b, Fisher et al. 2016, Jackson et al. 2017). Here, we explore how the three most common mycorrhizal fungal types, arbuscular, ectomycorrhizal, and ericoid, are influenced by and will influence plant abilities to adapt to climate change.

Like all organisms, mycorrhizal fungal groups have unique suites of traits (Table 1) that mediate the direct impact of climate change on mycorrhizal fungi (Treseder and Lennon 2015). For example, they vary in hyphal exploration type (reviewed in Agerer 2001, Helgason and Fitter 2009, Lilleskov et al. 2011, Peay et al. 2011), and this variation is linked to root density (Bingham and Biondini 2009, Peay et al. 2011), disturbance, and nitrogen availability (Lilleskov et al. 2011, Chen et al. 2018, Treseder et al. 2018) across mycorrhizal types and at the species level (Bukovska et al. 2016). Mycorrhizal fungal species also vary in extra-radical hyphal (ERH) density (Jakobsen et al. 1992, Duan et al. 2011) and turnover (reviewed in Chagnon et al. 2013) all of which may be related to species and genotype level variation in hyphal

fusion rates (Pepe et al. 2016). These traits, and others, are responsive to climatic change (Fernandez et al. 2017). For example, mycorrhizal fungi also vary in melanin content (Wright et al. 1996), and increases in mycorrhizal fungal melanin have been linked to variation in water availability (Deveautour et al. 2019). Increased melanin can also reduce fungal decomposition (Fernandez et al. 2016, Fernandez and Kennedy 2018) and potentially reduce carbon storage (Clemmensen et al. 2015), thus likely feeding back to climate change. In addition, mycorrhizal fungi possess genetic variation in helicase activity (Branco et al. 2017), known to promote cold tolerance in fungi. Variation in mycorrhizal fungal traits can also cascade aboveground to alter plant-species-specific growth rates (Allen et al. 2003, Lopez-Garcia et al. 2014).

Briefly, arbuscular mycorrhizal (AM) fungi form an obligate association with most herbaceous plant species, grasses, broad-leaf tree species and occasionally conifers such as *Sequoia sempervirens*. In return for carbon, AM fungi provide nutrients, water, and trace minerals to host plants. AM fungi are found in every plant habitat, but generally do not produce fruiting bodies, release spores belowground from hyphae and are thus thought to be relatively dispersal limited (Smith and Read 2008), although this may depend on soil disturbance and spore size (see discussion in Mycorrhizal fungal responses to climate change: knowledge and gaps). In contrast, both ectomycorrhizal (EcM) and ericoid mycorrhizal (ErM) fungi form fruiting bodies and often disperse propagules by wind. EcM fungi tend to form associations with a smaller proportion of plant species than AM fungi (Brundrett 2002), but their impact can scale to the landscape because they tend to associate with regionally dominant tree taxa (Steidinger et al. 2019). Like AM fungi, EcM and ErM fungi deliver nutrients and water to the host plant in exchange for carbon. EcM fungi are thought to have a higher host plant specificity (associate with a smaller range of host plants) than AM fungi; while most ErM fungi associate with a narrow group of plants, members of the *Ericaceae*, that are commonly found in ecosystems thought to be most susceptible to climate and land-use change,

TABLE 1. Traits that vary among the three mycorrhizal fungal types explored in this manuscript: arbuscular (AM), ectomycorrhizal (EcM), and ericoid (ErM) mycorrhizal fungi.

Trait	AM fungi	EcM fungi	ErM fungi
Distribution	≈100%	≈30%	≈5%
Primary nutrient delivered	phosphorus	nitrogen	nitrogen
External hyphal exploration type	unknown, density varies by species and distance	short, medium, long-distance	unknown?
Root colonization	arum, Paris	Hartig Net	ericoid, arbutoid, monotropoid, cavendishoid
Melanization	spores, hyphae	spores, hyphae	hyphae
Helicase activity	yes	yes	unknown?
Host abiotic tolerance promoted	yes; greatest consistency	yes	unknown

*Note:* Distribution estimates derived from Soudzilovskaia et al (2017), citations for external hyphal exploration type, melanization, helicase activity, and host tolerance are found in the text of the introduction.

such as peatlands, heaths, and the Arctic (Fagundez 2013). Unlike AM fungi (Davison et al. 2015), both ErM and EcM fungi are not found in all habitats, and their distributions are relatively limited by their host plants and/or abiotic conditions (Soudzilovskaia et al. 2017). There is also some overlap between ErM, EcM, and AM fungi as some plant hosts associate with multiple fungal types.

Here, we reviewed the geographic distribution of literature exploring how diverse groups of mycorrhizal fungi respond to elevated atmospheric carbon dioxide concentrations ( $eCO_2$ ), climatic warming, and changes in the distribution of precipitation and highlight patterns in the data as well as gaps in the literature. We end our review with a discussion of how mycorrhizal fungi, and their response to climate change, may influence plant responses to climate change via influencing plant adaptation, extinction, or dispersal.

#### MYCORRHIZAL FUNGAL RESPONSES TO CLIMATE CHANGE: KNOWLEDGE AND GAPS

Mycorrhizal fungal traits should influence their response to climatic changes ( $eCO_2$ , warming, shifting precipitation), yet to date there is no comprehensive synthesis on how broad groups of mycorrhizal fungi may respond to different climate drivers. Here we synthesized the literature to determine the influence of climate changes on AM, ErM, and EcM fungi, and identify knowledge gaps or biases in study geographies as well as research areas and approaches (File S1). We collected and synthesized data from the literature on the influence of warming, increased atmospheric carbon dioxide concentrations ( $[eCO_2]$ ), and increased variability in precipitation on mycorrhizal fungi from manipulative studies. We focused our search on precipitation variation and not precipitation change because recent studies have shown that rainfall variability and extreme events, not solely increased or decreased rainfall, are predicted with climate changes (Knapp et al. 2015). We conducted four Web of Science literature searches. Here we focus on unmanaged ecosystems, thus each of the searches excluded studies in agricultural field systems (NOT “agro\*” NOT “agri”). The first search, 13 October 2017, focused on warming (TOPIC “warming” AND “mycorrhiza\*”) and resulted in 251 studies. The second search, (TOPIC “atmospheric CO2” AND “mycorrhiza\*” NOT “bioenergy”) resulted in 458 papers, the third search (TOPIC “mycorrhiza\*” AND “extreme events”) resulted in 27 papers, and the fourth (TOPIC “mycorrhiza\*” AND “precipitation distribution”) resulted in 38 papers. We removed duplicate papers and distilled the remaining papers down to 150 that met our criteria. We recorded whether, at the last time point of data collection, there was a negative, positive, or neutral influence of the climate change driver on root colonization, extra-radical hyphae (ERH) in soil, biomass (most frequently measured using PLFAs), root community composition (measured with molecular tools), and soil community composition (typically measured with

molecular tools but occasionally measured with spores or sporocarps). We determined whether the value was negative, positive, or neutral by recording whether there was a significant difference between treatments recorded in the paper (nonsignificant differences were recorded as neutral), and, if significant, which direction (positive or negative). We recorded the GPS coordinates for the geographic study location or where the inocula used in the study was collected (if the study was conducted in a greenhouse or in a pot). We also collected data on the type of mycorrhizal fungi (AMF, EcMF, ErMF), plant host(s) and family, host life history characteristics, habitat (forest, grassland, heath [defined as arctic, alpine, and other habitats dominated by ericaceous species], shrubland, desert, aquatic, or arable), type and/or species of inocula, and study location (field, greenhouse, or lab). Altogether we collected 300 data lines for mycorrhizal responses to  $eCO_2$ , 152 data lines for warming, and 19 data lines for variability in precipitation (Data S1).

We formed three hypotheses. Similar to other studies exploring plant ecology, we expect most studies to be located in the northern hemisphere (according to a search on Web of Science on 12 October 2018, 19% of plant ecology studies were conducted in the northern hemisphere) and in North America and Europe (77% from the same search above). This has been posited in two other recent reviews as well (Mohan et al. 2014, Tedersoo and Bahram 2019), but not displayed as in this paper. Second, we expect experimental warming and precipitation variability studies to have a larger direct (negative or positive) impact on mycorrhizal fungi across groups than  $eCO_2$ . We hypothesize that temperature and water availability directly impact soil fungi, whereas  $eCO_2$  impacts fungi indirectly via shifts in plant inputs. Finally, we expect mycorrhizal fungi that occur in regions most likely impacted by climatic change, e.g., ecological range boundaries, arctic ecosystems, to have a stronger positive or negative response to climate change experiments than those in less impacted regions.

#### Study location

The location of studies on climate changes and mycorrhizal fungi (and whether or not studies were in regions likely to experience the greatest climate change impacts) and mycorrhizal fungal type will influence our ability as a scientific community to generalize mycorrhizal fungal responses to future climate changes. Yet, as hypothesized, the majority of studies we identified were conducted in the northern hemisphere, particularly in North America and Europe (Fig. 1). Only 35 experiments from three papers (Baon et al. 1994, Plett et al. 2015, Hortal et al. 2016) were conducted in the southern hemisphere, and most of these data were collected by one group working on EcM fungi (Hawkesbury, New South Wales, Australia; Plett et al. 2015, Hortal et al. 2016). Studies of ErM and EcM fungi were mostly conducted in the northern latitudes of the northern hemisphere. Not a

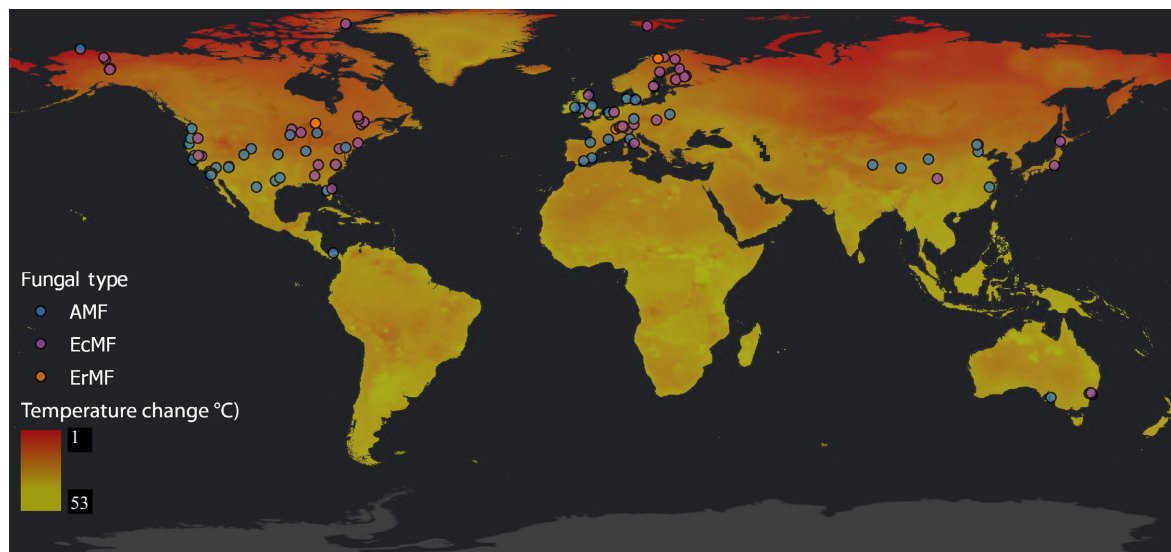


FIG. 1. Distribution of studies exploring mycorrhizal responses to climate change overlaid on a map of projected temperature change in 2050 (Scenario 2.6, IPCC). There are 452 studies across all fungal (ErM, EcM, AM) types, and climate change factors investigated (warming,  $eCO_2$ ) represented on the map.

single study was conducted in or using material from Africa, South America, or south Asia, leaving an extensive knowledge gap about how climate changes may influence these organisms in areas of the world expected to be impacted most from climate changes. Further, ErM fungi were by far the least studied group across all climate change factors: we identified 11 lines of data collected from six climate change studies (warming,  $eCO_2$ ; Olsrud et al. 2004, 2010, Arndal et al. 2013, Geml et al. 2015, Asemaninejad et al. 2017, Binet et al. 2017), and all but one (Binet et al. 2017) were conducted in arctic North America or Scandinavia. AM and EcM fungi studies were more common, but study location (field or greenhouse) varied (Appendix S1: Fig. S1). Most warming studies exploring AM (61%) and EcM (75%) fungal responses occurred in the field, whereas,  $eCO_2$  studies were more common in greenhouses: only 36% of AM and 31% of EcM studies were conducted in the field. Our analysis is, however, biased by English language papers found using Web of Science, and thus may underrepresent studies in non-English language journals. However, the paucity of studies on climate change impacts on mycorrhizal fungi in non-northern latitudes was striking.

Plant host and ecosystem types studied were also biased in our review; the majority of studies across all mycorrhizal types were conducted on perennial plants (81% of  $eCO_2$  studies, 86% of warming studies, and 74% of rainfall variability studies). This is not entirely surprising given that EcM and ErM associate predominantly with perennial plants, and long-term field studies generally focus on perennial plants. However, even studies on AM fungi, which often associate with annual plant species, were predominantly conducted on perennials (62% of  $eCO_2$  studies, 85% of warming studies, and

71% of rainfall variability studies, Appendix S1: Fig. S2A,B). Also, only 3% of the studies were conducted on  $C_4$  plants (Appendix S1: Fig. S2C,D). This is concerning for a number of reasons: first, annual plants colonize disturbed habitats and begin succession, thus this research gap will limit our knowledge of the impact of climate changes on young and disturbance-prone ecosystems and early colonizing plants including invasive species. Second, understanding the AM fungal- $C_4$  plant relationship may be crucial for climate change mitigation, because  $C_4$  plants often dominate the tropics and subtropics where the rate and magnitude of climate changes are often predicted to be greatest.  $C_4$  plants are known to rely heavily on AM fungi (reviewed in Bennett et al. 2013) and tolerate higher temperatures, but do not respond as positively to  $eCO_2$  (Antoninka et al. 2009). By contrast,  $C_3$  plants may have a higher photosynthesis rate that does not saturate under tested  $eCO_2$  levels. Thus, an overrepresentation of perennial and  $C_3$  plants associated with AM fungi in research will limit our understanding of AM fungal responses to climate changes and their role in climate change mitigation. Most AM fungal studies were conducted in grasslands (55%), all EcM studies were conducted in forests, and all ErM studies we found were conducted in heaths (Appendix S1: Fig. S3). Few studies were conducted in deserts (Clark et al. 2009, Bell et al. 2014) and non-heath shrublands (Klironomos et al. 1998, Treseder et al. 2003, Allen et al. 2005). These underrepresented ecosystems can have diverse AM fungal communities and rare and endemic ectomycorrhizal fungi (Smith and Read 2008), and thus should be included in research exploring mycorrhizal responses to global change.

Many studies did not measure the direct impact of climate changes on mycorrhizal fungi and mycorrhizal



traits. Most studies (60%) measured root colonization (Appendix S1: Fig. S4). However, mycorrhizal fungi are likely to experience climate changes both directly (via abiotic changes in the soil compartment) and indirectly (via their host plants in the root compartment; Millar and Bennett 2016). Combining AM and EcM results, we identified 26 papers that explored direct and indirect  $eCO_2$ , warming, and altered precipitation effects (see Data S1), and identified only three studies examining root colonization, ERH, and spore production (Klironomos et al. 1996, Antoninka et al. 2009, Yang et al. 2013). Only a small proportion of studies measured fungi outside the root: 19% examined ERH and 5% examined spores or sporocarps. Measuring only one compartment's response limits our understanding of fungal responses to climatic changes, especially fungal fitness and biomass production.

Studies conducted under different experimental conditions, field or greenhouse, show variable responses to the impact of  $eCO_2$  on mycorrhizal fungi (Fig. 2). Only three studies (all conducted in the field) examined ErM fungi. We found that 25% of field manipulations show a positive influence of  $eCO_2$  on EcM fungal root colonization, whereas 40% of greenhouse studies show a non-neutral (positive or negative) influence of  $eCO_2$  on root colonization. Only four EcM fungal studies examined ERH in the field, but 20% of greenhouse studies showed a positive influence of  $eCO_2$  on ERH. AM fungal studies measuring fungi in both root and soil compartments find that root colonization by AM fungi was resilient in the face of  $eCO_2$  as only neutral responses (non-positive or non-negative effects) have been reported for AM fungal root colonization under  $eCO_2$  in the field. However, looking more broadly across all the studies (not just those that measured both root colonization and ERH) we do not observe this negative/neutral pattern: 36% of field studies and 45% of greenhouse studies show a positive influence of  $eCO_2$  on root colonization by AM fungi. Based on studies examining both root colonization and ERH, AM fungi in the soil compartment may be more strongly influenced by  $eCO_2$ , although these effects appear stronger under controlled conditions. This strong  $eCO_2$  driver of AMF response is supported when we look across all studies: 25% in the field and 60% in the greenhouse show a positive influence of  $eCO_2$  on AM fungal ERH. Thus, more studies measuring both root colonization and ERH need to be conducted to understand the response of ecosystems to  $eCO_2$ .

#### *Climate change type*

As predicted by the second hypothesis (both increased temperature and rainfall variability should have a greater range (more positive or negative) of effects on mycorrhizal fungi than under ambient conditions), we found that the effect range (i.e., amount of variability) of warming effects on mycorrhizal fungi was broader than for  $eCO_2$ . However, the broadness of the effect range

was context dependent. Due to the few studies on rainfall variability, we only discuss  $eCO_2$  and warming studies. When looking across mycorrhizal measurements, we found little evidence to support our hypothesis: warming promoted non-neutral (positive or negative) effects in 42% of AM fungal, 63% of EcM fungal, and 43% of ErM fungal studies as compared to 44% of AM fungal, 35% of EcM fungal, and 50% of ErM fungal  $eCO_2$  studies. However, when we examined individual measures of mycorrhizal fungi, we found warming had a greater range of effects on fungi in both root and soil compartments. Studies measuring both colonization and ERH showed stronger influences of warming on ERH, but mostly in the greenhouse and lab. However, few studies measured ERH in any environment limiting our conclusions. Given that temperature likely directly influences ERH, it should not be surprising to observe a more consistent influence of temperature on ERH.

Despite the lack of data dedicated to explaining climate influences on mycorrhizal fungi, we can gain clues by looking at the influence of both climate changes and mycorrhizal fungi on plant growth (often measured as a trait of mycorrhizal fungi). For example, across studies, mycorrhizal type and nitrogen availability are the primary factors predicting  $eCO_2$  fertilization of plants in climate change experiments (Terrer et al. 2016). In particular, there were no differences due to nitrogen availability for plants associated with EcM, but under low nitrogen availability plants associated with AM fungi did not increase growth in response to  $eCO_2$  while AM fungal plants benefited from  $eCO_2$  under high nitrogen availability. This difference may be related to the stronger effects of  $eCO_2$  on AM than EcM fungi.

#### *Mycorrhizal type*

In contrast to our third hypothesis, we found that EcM fungi had a more variable response to climate changes than ErM or AM fungi. For example, as presented above, overall EcM fungi were more likely to show a positive or negative response to warming (63%) than  $eCO_2$  (35%). To further explore this pattern, we conducted a small meta-analysis of 11 AM and 7 EcM fungal studies that measured root colonization under elevated and ambient temperatures.

For this limited meta-analysis, we used studies from a subset of papers collected for our literature review and described above and in File S1. Studies used in the meta-analysis needed to measure root colonization in the greenhouse (due to limited field studies) by both AM fungi and EcM fungi, and provide means or lsmeans, standard deviations or standard errors, and sample sizes. Studies within papers were considered independent observations if they were conducted with different plant or mycorrhizal fungal species. We calculated Hedge's *D* for the difference in colonization between ambient and elevated temperatures, because of the small study numbers, the means were continuous variables, and some

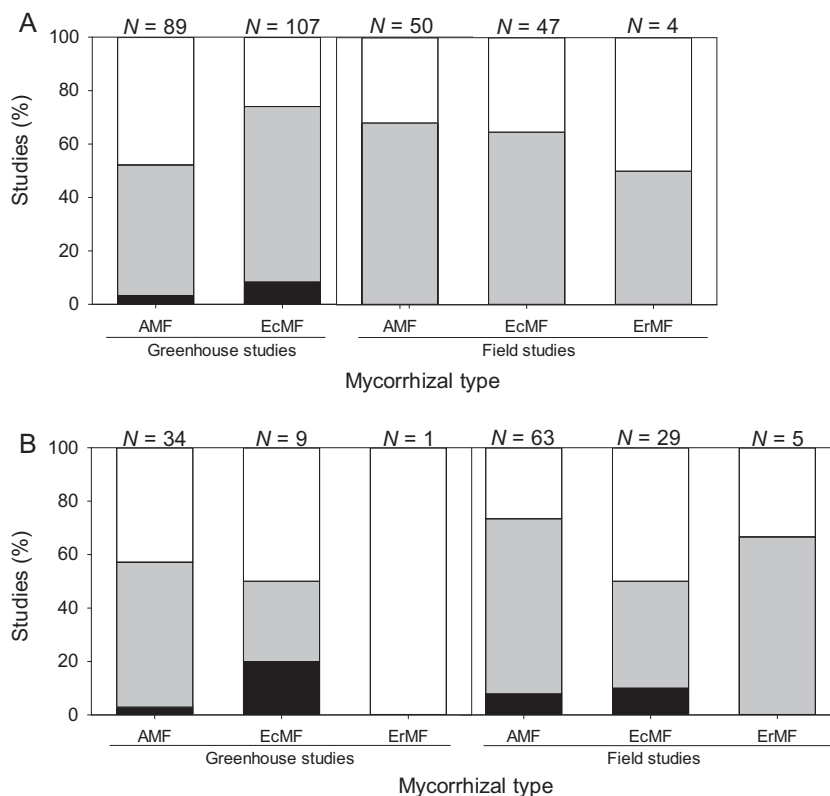


FIG. 2. Range of effects (negative [black], neutral [light gray], positive [white]) of climate changes (A) CO<sub>2</sub> and (B) warming on the three mycorrhizal fungal types (arbuscular mycorrhizal fungi (AMF), ectomycorrhizal fungi (EcMF), an ericoid mycorrhizal fungi (ErMF) and by study location (greenhouse or field).

means equaled zero (eliminating the use of the log response ratio as a potential effect size).

We analyzed variation in effect sizes using OpenMEE (Wallace et al. 2017). We ran a subgroup continuous random effects maximum likelihood model with mycorrhizal type (AM or EcM fungi) as the subgroup. The data used in the meta-analysis are provided as a data sheet supplementary file (Data S2).

Overall, we found there is a relatively strong positive effect of temperature on colonization by mycorrhizal fungi (mean Hedge's *D* estimate = 0.829, 95% CI = 0.258–1.399,  $I^2$  = 68%) driven by a strong positive effect on colonization by AM fungi (mean Hedge's *D* estimate = 1.369, 95% CI = 0.729–2.009,  $I^2$  = 48%). There was little overall influence of temperature on colonization by EcM fungi (mean Hedge's *D* estimate = –0.005, 95% CI = –0.667–0.656,  $I^2$  = 53%), partly due to the range of effects on EcM fungi from positive to negative while the range of effects for AM fungi ranged from neutral to positive. There were not enough independent studies to determine what other factors might have contributed to the greater variation in EcM fungi root colonization response as compared to AM fungi.

Contrary to our expectations, we found many gaps in our understanding of how climatic changes influence

mycorrhizal fungi. There was only a correlation between the ecosystem type of mycorrhizal fungal host plants and different mycorrhizal fungal types in the northern hemisphere, where most of the studies reviewed in this paper were conducted. In addition, our knowledge gaps about ErM fungi and rainfall variability likely limit our ability to predict mycorrhizal fungal responses to climate changes. Also, while both temperature and rainfall variability have greater effects on mycorrhizal fungi, these effects are context dependent and will require greater study before we can confidently make predictions about their impacts. Finally, we incorrectly hypothesized that mycorrhizal growing season length or host plant type would influence the likelihood of climate change impacts on mycorrhizal fungi. Instead, changes driven by direct fungal structure exposure to climate changes, particularly warming, appear to be a stronger predictor of climate change effects on mycorrhizal fungi.

#### HOW MYCORRHIZAL FUNGAL TRAITS AND THEIR RESPONSE TO CLIMATE CHANGES MAY IMPACT A PLANT'S ABILITY TO ADAPT, MOVE, OR GO EXTINCT UNDER GLOBAL CHANGE

Our review reveals large variation in the frequency that different climate change impacts, warming, eCO<sub>2</sub>, changing precipitation, on mycorrhizal fungi have been

studied. This same pattern holds when we examine interactions between plants and mycorrhizal fungi. A meta-analysis of fungal symbiont influences on plant responses to climate changes found drought has been studied two to four times more frequently than other climate drivers (e.g., eCO<sub>2</sub>, warming; Kivlin et al. 2013). In fact, we conducted a Web of Science search (November 2017) on “drought” and “mycorrhiza\*” (not “agro\*” or “agri\*”) resulting in over 62,000 papers. We suspect this bias is in part because drought can be most easily manipulated in a short (experimental) time scale compared to other climate drivers (e.g., warming, eCO<sub>2</sub>).

Given their different life histories and distributions, mycorrhizal fungi should have different influences on plant adaptation to climate change. Plants facing climate change can either adapt, disperse to a more suitable habitat, or go extinct. Mycorrhizal fungi could aid or limit these strategies, and we expect that different mycorrhizal fungal types will have traits or limitations that will cause them to contribute differently to these strategies.

*Mycorrhizal colonization may buffer plants from extinction from climate change*

Mycorrhizal fungi can increase plant tolerance to abiotic stresses associated with climate changes, which should decrease plant extinction risk and provide time for plant dispersal and adaptation. For example, AM fungi can alleviate the negative consequences of rainfall variability (Mohan et al. 2014), due to improved water flow (Delavaux et al. 2017) via increased water use efficiency (Andreo-Jimenez et al. 2015). Increased water uptake and water use efficiency in AM fungal host plants can be accomplished by using hyphae to increase surface area for water absorption (Auge 2001), increased access to small soil pores (Smith and Read 2008), improved apoplastic water flow (Barzana et al. 2012), water uptake via fungal water channels (Maurel et al. 2015), increased stomatal conductance in host plants (Auge et al. 2015), altered host gene expression of drought related genes encoding plant aquaporins (Maurel et al. 2015), and promotion of further AM fungal colonization (Andreo-Jimenez et al. 2015). Greater rainfall variability may alter fungal community composition through the loss of mycorrhizal fungal species only tolerant of drought or increased moisture leaving only more plastic fungi that can tolerate both extremes but may or may not benefit plant partners, which may feedback to alter plant productivity or plant tolerance to change. For example, shifts in seasonality coupled with drought can alter both the abundance and community composition of mycorrhizal fungi (Cregger et al. 2012), which in turn, impacts plant growth (Lopez-Garcia et al. 2014). Thus, mycorrhizal fungi can help plants tolerate rainfall variability.

Relative to plants and their roots, mycorrhizal fungi tend to have a wider temperature tolerance, which may reflect their ability to produce protective compounds

such as trehalose (Lekberg et al. 2011, Lenoir et al. 2016). However, mycorrhizal temperature tolerances differ among mycorrhizal type (Kilpelainen et al. 2016) and habitat (Antunes et al. 2011); (but see Bunn et al. 2009), and this variation can benefit host plants. AM fungal temperature tolerance could promote greater host tolerance of warming (Bunn et al. 2009, Antunes et al. 2011). Warming can promote both EcM and growth of EcM associated plants in the field (Deslippe et al. 2011). Warming can also influence host plant associations in ways that alter mycorrhizal fungal communities, and these host driven shifts in mycorrhizal fungi, coupled with changes in soil nutrient availability, could lead to significant changes in host plant success especially at the warm edges of plant ranges (Fernandez et al. 2017).

Unlike the other two climate drivers discussed here, warming and precipitation change, eCO<sub>2</sub> may not stress plant–mycorrhizal–fungae interactions. A recent study highlighted that, depending on mycorrhizal fungal type and nutrient availability, mycorrhizal colonization could boost the impact of eCO<sub>2</sub> on plant production via mycorrhizal alleviation of nutrient limitation (Terrer et al. 2016). In low nutrient ecosystems, only EcM fungi significantly stimulated biomass production under eCO<sub>2</sub>, whereas in high nutrient systems both EcM and AM fungi stimulated biomass production under eCO<sub>2</sub>. This result may also be biased by geographic location as most eCO<sub>2</sub> experiments occurred in northern latitudes. Thus overall, eCO<sub>2</sub> should increase growth of mycorrhizal fungal associated host plants and could promote tolerance of other climate change related stresses (Norby and Zak 2011, Solly et al. 2017).

While there have been few direct comparisons, there is evidence that mycorrhizal fungal types vary in how much they buffer plant stress. For example, a meta-analysis found that EcM fungal associated plants had more context dependent responses to climate change than AM fungal associated plants (Kivlin et al. 2013). Overall, given their ability to promote abiotic stress tolerance, mycorrhizal fungi should promote tolerance to climate changes (Kivlin et al. 2013, Mohan et al. 2014), but the type of mycorrhizal fungi and other stresses will likely modify the degree of tolerance. This overall promotion of tolerance to climate changes should reduce plant extinction even in less than optimal environments, but this pattern may be biased toward AM fungi.

*Potential influence of mycorrhizal fungi on plant dispersal under climate change*

As climates change, plants may need to disperse to more suitable habitats, and their dispersal success may depend on mycorrhizal partners (Peay 2016, Wurzbarger et al. 2017). We expect that differences in mycorrhizal fungal distribution and dispersal to influence their host plant dispersal. For example, the relatively ubiquitous distribution of AM fungi may comparatively reduce plant dispersal limitations. AM fungi may be dispersal

limited, although spores can be dispersed by wind (Kivlin et al. 2014) and animals (Mangan and Adler 2002, Nielsen et al. 2016), but these dispersal forms may favor different fungal groups (e.g., small wind-dispersed groups or those that form sporocarps), which likely influences community composition, which in turn, influences plant communities (Mangan and Adler 2002). However, the presence of any AM fungus, even if not the perfect partner, should allow AM fungal host plants a wider dispersal range. For example, AM fungal associations have been seen in two extreme examples of plant dispersal: invasive species (Reinhart and Callaway 2006) and range expanding species (van Grunsven et al. 2014). Thus, we do not expect AM fungi to limit plant dispersal.

In contrast to AM fungi, lack of EcM fungi can limit plant dispersal. For example, work on invasive pines clearly shows invasion can be limited by EcM dispersal (e.g., Nunez et al. 2009). Shrubs are expanding in the Arctic under warming and this expansion is coupled with changes in nutrient cycling and ErM and EcM community compositions (Timling et al. 2012, Geml et al. 2016). The EcM fungi in the Arctic tend to be cosmopolitan and can grow at very low temperatures, thus shifts with warming may reduce the cold-tolerant cosmopolitan fungi and alter this community's ability to facilitate changes with warming (Timling and Taylor 2012). For example, many studies exploring warming in the Arctic find that EcM species of *Russula* increased with warming while other species decline, which could feedback to impact plant growth over time (Deslippe et al. 2011, 2012, Geml et al. 2016). However, when EcM fungi are present warming may promote EcM fungal and shrub expansion (Deslippe et al. 2011, Solly et al. 2017). In addition to lack of inocula, dispersal by Ericaceous plants was hindered by their environmental abiotic conditions. Yet, under the right abiotic conditions, such as high soil moisture, EcM and ErM fungi respond quickly to warming with significant shifts in their community composition (Geml et al. 2016). As a result, we can expect faster dispersal by plants hosting AM fungi in response to climate changes than host plants of ErM or EcM fungi, but the specificity of fungal associations and the shifts in community composition described above across all mycorrhizal fungal types may limit plant productivity in new environments.

#### *Mycorrhizal fungi may promote adaptation of host plants*

We expect all three mycorrhizal types to increase the likelihood of plant adaptation to climate changes. In particular, the promotion of stress tolerance by mycorrhizal fungi should allow temporal space for plant adaptation to climate changes. As a result, we expect that mycorrhizal fungi act as a buffer for plants that find themselves in environments altered by climate change, thereby increasing their "niche" (Peay 2016, Gerz et al. 2018). Under conditions where environmental variation

is common, this "buffering" could allow plants to increase their fitness in suboptimal years; however, this "buffering" could become crucial when climate changes faster than plants can disperse or adapt to their new environment. If mycorrhizal fungi buffer plants against climate changes, then we would expect overall reduced rates of plant extinction and greater prevalence of adaptation in affected environments than expected when we do not account for mycorrhizal fungi. Specifically, it could allow plant species the time needed to adapt to their new environmental conditions.

#### CONCLUSIONS

Here, we highlighted the importance of examining both the response of mycorrhizal fungi and the response of plants associated with mycorrhizal fungi to climate changes; however, the vast majority of studies have, to date, focused on the interaction between these two groups of organisms. As a result, we do not know if the responses of mycorrhizal fungi themselves to future climate changes will limit their promotion of plant tolerance to those same climate changes. Climate changes could also influence dispersal of fungi thereby limiting plant dispersal, and in other cases, we could see phenological shifts in development of fungi and plants that could lead to mismatches that could limit plant productivity and ecosystem services. Some studies separating influences on plants and fungi have pioneered this area of research (Barrett et al. 2014), but there are many opportunities for increasing our understanding of both plant and mycorrhizal fungal responses to climate changes.

#### ACKNOWLEDGMENTS

We thank Jarlath O'Neil-Dunne and the Spatial Analysis Laboratory at UVM for mapping our mycorrhizal distributions under warming. The A. T. Classen lab is supported by the U.S. Department of Energy, Office of Science, Office of Biological and Environmental Research, Terrestrial Ecosystem Sciences Program under Award Number DE-SC0010562 and the Carlsberg Foundation. The A. E. Bennett lab is supported by the Ohio State University. We thank Philip Smith, Kenna Rewcastle, and two anonymous reviewers for comments that improved the manuscript.

#### LITERATURE CITED

- Agerer, R. 2001. Exploration types of ectomycorrhizae: A proposal to classify ectomycorrhizal mycelial systems according to their patterns of differentiation and putative ecological importance. *Mycorrhiza* 11:107–114.
- Alberton, O., T. W. Kuyper, and A. Gorissen. 2005. Taking mycocentrism seriously: Mycorrhizal fungal and plant responses to elevated CO<sub>2</sub>. *New Phytologist* 167:859–868.
- Allen, E. B., M. E. Allen, L. Egerton-Warburton, L. Corkidi, and A. Gomez-Pompa. 2003. Impacts of early- and late-seral mycorrhizae during restoration in seasonal tropical forest, Mexico. *Ecological Applications* 13:1701–1717.
- Allen, M. F., J. N. Klironomos, K. K. Treseder, and W. C. Oechel. 2005. Responses of soil biota to elevated CO<sub>2</sub> in a chaparral ecosystem. *Ecological Applications* 15:1701–1711.



- Andreo-Jimenez, B., C. Ruyter-Spira, H. J. Bouwmeester, and J. A. Lopez-Raez. 2015. Ecological relevance of strigolactones in nutrient uptake and other abiotic stresses, and in plant-microbe interactions below-ground. *Plant and Soil* 394:1–19.
- Antoninka, A., J. E. Wolf, M. Bowker, A. T. Classen, and N. C. Johnson. 2009. Linking above- and belowground responses to global change at community and ecosystem scales. *Global Change Biology* 15:914–929.
- Antunes, P. M., A. M. Koch, J. B. Morton, M. C. Rillig, and J. N. Klironomos. 2011. Evidence for functional divergence in arbuscular mycorrhizal fungi from contrasting climatic origins. *New Phytologist* 189:507–514.
- Arndal, M. F., M. P. Merrild, A. Michelsen, I. K. Schmidt, T. N. Mikkelsen, and C. Beier. 2013. Net root growth and nutrient acquisition in response to predicted climate change in two contrasting heathland species. *Plant and Soil* 369:615–629.
- Asemaninejad, A., R. G. Thorn, and Z. Lindo. 2017. Experimental climate change modifies degradative succession in boreal peatland fungal communities. *Microbial Ecology* 73:521–531.
- Auge, R. M. 2001. Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza* 11:3–42.
- Auge, R. M., H. D. Toler, and A. M. Saxton. 2015. Arbuscular mycorrhizal symbiosis alters stomatal conductance of host plants more under drought than under amply watered conditions: a meta-analysis. *Mycorrhiza* 25:13–24.
- Baon, J. B., S. E. Smith, and A. M. Alston. 1994. Phosphorus uptake and growth of barley as affected by soil temperature and mycorrhizal infection. *Journal of Plant Nutrition* 17:479–492.
- Barrett, G., C. D. Campbell, and A. Hodge. 2014. The direct response of the external mycelium of arbuscular mycorrhizal fungi to temperature and the implications for nutrient transfer. *Soil Biology & Biochemistry* 78:109–117.
- Barzana, G., R. Aroca, J. A. Paz, F. Chaumont, M. C. Martinez-Ballesta, M. Carvajal, and J. M. Ruiz-Lozano. 2012. Arbuscular mycorrhizal symbiosis increases relative apoplastic water flow in roots of the host plant under both well-watered and drought stress conditions. *Annals of Botany* 109:1009–1017.
- Bell, C. W., D. T. Tissue, M. E. Loik, M. D. Wallenstein, V. Acosta-Martinez, R. A. Erickson, and J. C. Zak. 2014. Soil microbial and nutrient responses to 7 years of seasonally altered precipitation in a Chihuahuan Desert grassland. *Global Change Biology* 20:1657–1673.
- Bennett, A. E., T. J. Daniell, and P. J. White. 2013. Benefits of breeding crops for yield response to soil organisms. Pages 17–27 in F. J. de Bruijn, editor. *Molecular microbial biology of the rhizosphere*. Wiley-Blackwell, Hoboken, New Jersey, USA.
- Binet, P., S. Rouifed, V. E. J. Jassey, M. L. Toussaint, and G. Chiapusio. 2017. Experimental climate warming alters the relationship between fungal root symbiosis and Sphagnum litter phenolics in two peatland microhabitats. *Soil Biology & Biochemistry* 105:153–161.
- Bingham, M. A., and M. Biondini. 2009. Mycorrhizal hyphal length as a function of plant community richness and composition in restored northern tallgrass prairies (USA). *Rangeland Ecology & Management* 62:60–67.
- Branco, S., et al. 2017. Continental-level population differentiation and environmental adaptation in the mushroom *Suillus brevipes*. *Molecular Ecology* 26:2063–2076.
- Brundrett, M. C. 2002. Coevolution of roots and mycorrhizas of land plants. *New Phytologist* 154:275–304.
- Bukovska, P., M. Gryndler, H. Gryndlerova, D. Puschel, and J. Jansa. 2016. Organic nitrogen-driven stimulation of arbuscular mycorrhizal fungal hyphae correlates with abundance of ammonia oxidizers. *Frontiers in Microbiology* 7:15.
- Bunn, R., Y. Lekberg, and C. Zabinski. 2009. *Arbuscular mycorrhizal* fungi ameliorate temperature stress in thermophilic plants. *Ecology* 90:1378–1388.
- Chagnon, P.-L., R. L. Bradley, H. Maherali, and J. N. Klironomos. 2013. A trait-based framework to understand life history of mycorrhizal fungi. *Trends in Plant Science* 18:484–491.
- Chen, W. L., R. T. Koide, and D. M. Eissenstat. 2018. Root morphology and mycorrhizal type strongly influence root production in nutrient hot spots of mixed forests. *Journal of Ecology* 106:148–156.
- Clark, N. M., M. C. Rillig, and R. S. Nowak. 2009. Arbuscular mycorrhizal fungal abundance in the Mojave Desert: Seasonal dynamics and impacts of elevated CO<sub>2</sub>. *Journal of Arid Environments* 73:834–843.
- Classen, A. T., M. K. Sundqvist, J. A. Henning, G. S. Newman, J. A. M. Moore, M. A. Cregger, L. C. Moorhead, and C. M. Patterson. 2015. Direct and indirect effects of climate change on soil microbial and soil microbial-plant interactions: What lies ahead? *Ecosphere* 6:21.
- Clemmensen, K. E., A. Bahr, O. Ovaskainen, A. Dahlberg, A. Ekblad, H. Wallander, J. Stenlid, R. D. Finlay, D. A. Wardle, and B. D. Lindahl. 2013. Roots and associated fungi drive long-term carbon sequestration in boreal forest. *Science* 339:1615–1618.
- Clemmensen, K. E., R. D. Finlay, A. Dahlberg, J. Stenlid, D. A. Wardle, and B. D. Lindahl. 2015. Carbon sequestration is related to mycorrhizal fungal community shifts during long-term succession in boreal forests. *New Phytologist* 205:1525–1536.
- Cregger, M. A., C. W. Schadt, N. G. McDowell, W. T. Pockman, and A. T. Classen. 2012. Response of the soil microbial community to changes in precipitation in a semiarid ecosystem. *Applied and Environmental Microbiology* 78:8587–8594.
- Davison, J., et al. 2015. Global assessment of arbuscular mycorrhizal fungus diversity reveals very low endemism. *Science* 349:970–973.
- Delavaux, C. S., L. M. Smith-Ramesh, and S. E. Kuebbing. 2017. Beyond nutrients: a meta-analysis of the diverse effects of arbuscular mycorrhizal fungi on plants and soils. *Ecology* 98:2111–2119.
- Deslippe, J. R., M. Hartmann, W. W. Mohn, and S. W. Simard. 2011. Long-term experimental manipulation of climate alters the ectomycorrhizal community of *Betula nana* in Arctic tundra. *Global Change Biology* 17:1625–1636.
- Deslippe, J. R., M. Hartmann, S. W. Simard, and W. W. Mohn. 2012. Long-term warming alters the composition of Arctic soil microbial communities. *FEMS Microbiology Ecology* 82:303–315.
- Deveautour, C., Chieppa, J., Nielsen, U. N., Boer, M. M., Mitchell, C., Horn, S., Power, S. A., Guillen, A., Bennett, A. E., and Powell, J. R. 2019. Biogeography of arbuscular mycorrhizal fungal spore traits along an aridity gradient, and responses to experimental rainfall manipulation. *Fungal Ecology*. in press <https://doi.org/10.1016/j.funeco.2019.100899>
- Duan, T. Y., E. Facelli, S. E. Smith, F. A. Smith, and Z. B. Nan. 2011. Differential effects of soil disturbance and plant residue retention on function of arbuscular mycorrhizal (AM) symbiosis are not reflected in colonization of roots or hyphal development in soil. *Soil Biology & Biochemistry* 43:571–578.
- Fagundes, J. 2013. Heathlands confronting global change: drivers of biodiversity loss from past to future scenarios. *Annals of Botany* 111:151–172.
- Fernandez, C. W., and P. G. Kennedy. 2018. Melanization of mycorrhizal fungal necromass structures microbial decomposer communities. *Journal of Ecology* 106:468–479.

- Fernandez, C. W., J. A. Langley, S. Chapman, M. L. McCormack, and R. T. Koide. 2016. The decomposition of ectomycorrhizal fungal necromass. *Soil Biology & Biochemistry* 93:38–49.
- Fernandez, C. W., N. H. Nguyen, A. Stefanski, Y. Han, S. E. Hobbie, R. A. Montgomery, P. B. Reich, and P. G. Kennedy. 2017. Ectomycorrhizal fungal response to warming is linked to poor host performance at the boreal-temperate ecotone. *Global Change Biology* 23:1598–1609.
- Fisher, J. B., S. Sweeney, E. R. Brzostek, T. P. Evans, D. J. Johnson, J. A. Myers, N. A. Bourg, A. T. Wolf, R. W. Howe, and R. P. Phillips. 2016. Tree-mycorrhizal associations detected remotely from canopy spectral properties. *Global Change Biology* 22:2596–2607.
- Geml, J., L. N. Morgado, T. A. Semenova, J. M. Welker, M. D. Walker, and E. Smets. 2015. Long-term warming alters richness and composition of taxonomic and functional groups of arctic fungi. *FEMS Microbiology Ecology* 91:13.
- Geml, J., T. A. Semenova, L. N. Morgado, and J. M. Welker. 2016. Changes in composition and abundance of functional groups of arctic fungi in response to long-term summer warming. *Biology Letters* 12:20160503.
- Gerz, M., C. G. Bueno, W. A. Ozinga, M. Zobel, and M. Moora. 2018. Niche differentiation and expansion of plant species are associated with mycorrhizal symbiosis. *Journal of Ecology* 106:254–264.
- van Grunsven, R. H. A., T. W. Yuwati, G. A. Kowalchuk, W. H. van der Putten, and E. M. Veenendaal. 2014. The northward shifting neophyte *Tragopogon dubius* is just as effective in forming mycorrhizal associations as the native *T. pratensis*. *Plant Ecology & Diversity* 7:533–539.
- van der Heijden, M. G. A., J. N. Klironomos, M. Ursic, P. Moutoglis, R. Streitwolf-Engel, T. Boller, A. Wiemken, and I. R. Sanders. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* 396:69–72.
- Helgason, T., and A. H. Fitter. 2009. Natural selection and the evolutionary ecology of the arbuscular mycorrhizal fungi (Phylum Glomeromycota). *Journal of Experimental Botany* 60:2465–2480.
- Hortal, S., J. R. Powell, J. M. Plett, A. Simonin, and I. C. Anderson. 2016. Intraspecific competition between ectomycorrhizal *Pisolithus microcarpus* isolates impacts plant and fungal performance under elevated CO<sub>2</sub> and temperature. *FEMS Microbiology Ecology* 92:11.
- Jackson, R. B., K. Lajtha, S. E. Crow, G. Hugelius, M. G. Kramer, and G. Pineiro. 2017. The ecology of soil carbon: Pools, vulnerabilities, and biotic and abiotic controls. *Annual Review of Ecology, Evolution, and Systematics* 48(1):419–445.
- Jakobsen, I., L. K. Abbott, and A. D. Robson. 1992. External hyphae of vesicular-arbuscular mycorrhizal fungi associated with *Trifolium subterraneum* L.1. Spread of hyphae and phosphorus inflow into roots. *New Phytologist* 120:371–380.
- Jiang, J., J. A. M. Moore, A. Priyadarshi, and A. T. Classen. 2017. Plant-mycorrhizal interactions mediate plant community coexistence by altering resource demand. *Ecology* 98:187–197.
- Kilpelainen, J., M. Vestberg, T. Repo, and T. Lehto. 2016. Arbuscular and ectomycorrhizal root colonisation and plant nutrition in soils exposed to freezing temperatures. *Soil Biology & Biochemistry* 99:85–93.
- Kivlin, S. N., S. M. Emery, and J. A. Rudgers. 2013. Fungal symbionts alter plant responses to global change. *American Journal of Botany* 100:1445–1457.
- Kivlin, S. N., G. C. Winston, M. L. Goulden, and K. K. Treseder. 2014. Environmental filtering affects soil fungal community composition more than dispersal limitation at regional scales. *Fungal Ecology* 12:14–25.
- Klironomos, J. N., M. C. Rillig, and M. F. Allen. 1996. Below-ground microbial and microfaunal responses to *Artemisia tridentata* grown under elevated atmospheric CO<sub>2</sub>. *Functional Ecology* 10:527–534.
- Klironomos, J. N., M. Ursic, M. Rillig, and M. F. Allen. 1998. Interspecific differences in the response of arbuscular mycorrhizal fungi to *Artemisia tridentata* grown under elevated atmospheric CO<sub>2</sub>. *New Phytologist* 138:599–605.
- Knapp, A. K., D. L. Hoover, K. R. Wilcox, M. L. Avolio, S. E. Koerner, K. J. La Pierre, M. E. Loik, Y. Q. Luo, O. E. Sala, and M. D. Smith. 2015. Characterizing differences in precipitation regimes of extreme wet and dry years: implications for climate change experiments. *Global Change Biology* 21:2624–2633.
- Kyaschenko, J., K. E. Clemmensen, E. Karlton, and B. D. Lindahl. 2017. Below-ground organic matter accumulation along a boreal forest fertility gradient relates to guild interaction within fungal communities. *Ecology Letters* 20:1546–1555.
- Langley, J. A., S. K. Chapman, and B. A. Hungate. 2006. Ectomycorrhizal colonization slows root decomposition: the post-mortem fungal legacy. *Ecology Letters* 9:955–959.
- Leifheit, E. F., S. D. Veresoglou, A. Lehmann, E. K. Morris, and M. C. Rillig. 2014. Multiple factors influence the role of arbuscular mycorrhizal fungi in soil aggregation—a meta-analysis. *Plant and Soil* 374:523–537.
- Lekberg, Y., J. Meadow, J. R. Rohr, D. Redecker, and C. A. Zabinski. 2011. Importance of dispersal and thermal environment for mycorrhizal communities: lessons from Yellowstone National Park. *Ecology* 92:1292–1302.
- Lenoir, I., J. Fontaine, and A. L. H. Sahrhoui. 2016. Arbuscular mycorrhizal fungal responses to abiotic stresses: A review. *Phytochemistry* 123:4–15.
- Lilleskov, E. A., E. A. Hobbie, and T. R. Horton. 2011. Conservation of ectomycorrhizal fungi: exploring the linkages between functional and taxonomic responses to anthropogenic N deposition. *Fungal Ecology* 4:174–183.
- Lopez-Garcia, A., C. Azcon-Aguilar, and J. M. Barea. 2014. The interactions between plant life form and fungal traits of arbuscular mycorrhizal fungi determine the symbiotic community. *Oecologia* 176:1075–1086.
- Mangan, S. A., and G. H. Adler. 2002. Seasonal dispersal of arbuscular mycorrhizal fungi by spiny rats in a neotropical forest. *Oecologia* 131:587–597.
- Maurel, C., Y. Boursiac, D. T. Luu, V. Santoni, Z. Shahzad, and L. Verdoucq. 2015. Aquaporins in plants. *Physiological Reviews* 95:1321–1358.
- Millar, N. S., and A. E. Bennett. 2016. Stressed out symbiotes: hypotheses for the influence of abiotic stress on arbuscular mycorrhizal fungi. *Oecologia* 182:625–641.
- Mohan, J. E., et al. 2014. Mycorrhizal fungi mediation of terrestrial ecosystem responses to global change: mini-review. *Fungal Ecology* 10:3–19.
- Moore, J. A. M., J. Jiang, C. M. Patterson, M. A. Mayes, G. S. Wang, and A. T. Classen. 2015a. Interactions among roots, mycorrhizas and free-living microbial communities differentially impact soil carbon processes. *Journal of Ecology* 103:1442–1453.
- Moore, J. A. M., J. Jiang, W. M. Post, and A. T. Classen. 2015b. Decomposition by ectomycorrhizal fungi alters soil carbon storage in a simulation model. *Ecosphere* 6:1–16.
- Nielsen, K. B., R. Kjoller, H. H. Bruun, T. K. Schnoor, and S. Rosendahl. 2016. Colonization of new land by arbuscular mycorrhizal fungi. *Fungal Ecology* 20:22–29.
- Norby, R. J., and D. R. Zak. 2011. Ecological lessons from Free-Air CO<sub>2</sub> Enrichment (FACE) experiments. *Annual*

- Review of Ecology, Evolution, and Systematics 42(42):181–203.
- Nunez, M. A., T. R. Horton, and D. Simberloff. 2009. Lack of belowground mutualisms hinders Pinaceae invasions. *Ecology* 90:2352–2359.
- Olsrud, M., J. M. Melillo, T. R. Christensen, A. Michelsen, H. Wallander, and P. A. Olsson. 2004. Response of ericoid mycorrhizal colonization and functioning to global change factors. *New Phytologist* 162:459–469.
- Olsrud, M., B. A. Carlsson, B. M. Svensson, A. Michelsen, and J. M. Melillo. 2010. Responses of fungal root colonization, plant cover and leaf nutrients to long-term exposure to elevated atmospheric CO<sub>2</sub> and warming in a subarctic birch forest understory. *Global Change Biology* 16:1820–1829.
- Peay, K. G. 2016. The mutualistic niche: Mycorrhizal symbiosis and community dynamics. *Annual Review of Ecology, Evolution, and Systematics* 47(47):143–164.
- Peay, K. G., P. G. Kennedy, and T. D. Bruns. 2011. Rethinking ectomycorrhizal succession: are root density and hyphal exploration types drivers of spatial and temporal zonation? *Fungal Ecology* 4:233–240.
- Pepe, A., M. Giovannetti, and C. Sbrana. 2016. Different levels of hyphal self-incompatibility modulate interconnectedness of mycorrhizal networks in three arbuscular mycorrhizal fungi within the Glomeraceae. *Mycorrhiza* 26:325–332.
- Plett, J. M., A. Kohler, A. Khachane, K. Keniry, K. L. Plett, F. Martin, and I. C. Anderson. 2015. The effect of elevated carbon dioxide on the interaction between *Eucalyptus grandis* and diverse isolates of *Pisolithus* sp is associated with a complex shift in the root transcriptome. *New Phytologist* 206:1423–1436.
- Reinhart, K. O., and R. M. Callaway. 2006. Soil biota and invasive plants. *New Phytologist* 170:445–457.
- Rosling, A., M. G. Midgley, T. Cheeke, H. Urbina, P. Fransson, and R. P. Phillips. 2016. Phosphorus cycling in deciduous forest soil differs between stands dominated by ecto- and arbuscular mycorrhizal trees. *New Phytologist* 209:1184–1195.
- Smith, S. E., and D. J. Read. 2008. *Mycorrhizal Symbiosis*. Third edition. Academic Press, New York, New York, USA.
- Solly, E. F., B. D. Lindahl, M. A. Dawes, M. Peter, R. C. Souza, C. Rixen, and F. Hagedorn. 2017. Experimental soil warming shifts the fungal community composition at the alpine tree-line. *New Phytologist* 215:766–778.
- Soudzilovskaia, N. A., S. Vaessen, M. van't Zelfde, and N. Raes. 2017. Global patterns of mycorrhizal distribution and their environmental drivers. Pages 223–235 *In* L. Tedersoo, editors. *Biogeography of mycorrhizal symbiosis*. Springer International Publishing, Cham, Switzerland.
- Steidinger, B. S., et al. 2019. Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. *Nature*, 569, 404.
- Tedersoo, L., and M. Bahram. 2019. Mycorrhizal types differ in ecophysiology and alter plant nutrition and soil processes. *Biological Reviews* 94:1857–1880.
- Terrer, C., S. Vicca, B. A. Hungate, R. P. Phillips, and I. C. Prentice. 2016. Mycorrhizal association as a primary control of the CO<sub>2</sub> fertilization effect. *Science* 353:72–74.
- Timling, I., and D. L. Taylor. 2012. Peeking through a frosty window: molecular insights into the ecology of Arctic soil fungi. *Fungal Ecology* 5:419–429.
- Timling, I., A. Dahlberg, D. A. Walker, M. Gardes, J. Y. Charcosset, J. M. Welker, and D. L. Taylor. 2012. Distribution and drivers of ectomycorrhizal fungal communities across the North American Arctic. *Ecosphere* 3:25.
- Treseder, K. K. 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO<sub>2</sub> in field studies. *New Phytologist* 164:347–355.
- Treseder, K. K., and J. T. Lennon. 2015. Fungal traits that drive ecosystem dynamics on land. *Microbiology and Molecular Biology Reviews* 79:243–262.
- Treseder, K. K., L. M. Egerton-Warburton, M. F. Allen, Y. F. Cheng, and W. C. Oechel. 2003. Alteration of soil carbon pools and communities of mycorrhizal fungi in chaparral exposed to elevated carbon dioxide. *Ecosystems* 6:786–796.
- Treseder, K. K., E. B. Allen, L. M. Egerton-Warburton, M. M. Hart, J. N. Klironomos, H. Maherali, and L. Tedersoo. 2018. Arbuscular mycorrhizal fungi as mediators of ecosystem responses to nitrogen deposition: A trait-based predictive framework. *Journal of Ecology* 106:480–489.
- Wallace, B. C., M. J. Lajeunesse, G. Dietz, I. J. Dahabreh, T. A. Trikalinos, C. H. Schmid, and J. Gurevitch. 2017. OpenMEE: Intuitive, open-source software for meta-analysis in ecology and evolutionary biology. *Methods in Ecology and Evolution* 8:941–947.
- Wright, S. F., M. Franke-Snyder, J. B. Morton, and A. Upadhyaya. 1996. Time-course study and partial characterization of a protein on hyphae of arbuscular mycorrhizal fungi during active colonization of roots. *Plant and Soil* 181:193–203.
- Wurzbarger, N., E. N. J. Brookshire, M. L. McCormack, and R. A. Lankau. 2017. Mycorrhizal fungi as drivers and modulators of terrestrial ecosystem processes. *New Phytologist* 213:996–999.
- Yang, W., Y. Zheng, C. Gao, X. H. He, Q. Ding, Y. Kim, Y. C. Rui, S. P. Wang, and L. D. Guo. 2013. The arbuscular mycorrhizal fungal community response to warming and grazing differs between soil and roots on the Qinghai-Tibetan Plateau. *PLoS ONE* 8:e76447.

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2978/supinfo>