Mycorrhizal fungi mediation of terrestrial ecosystem responses to global change: mini-review

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ABSTRACT

Mycorrhizal fungi are responsible for most nutrient uptake by the majority of land plants. As such, mycorrhizas are increasingly recognized as important drivers of terrestrial ecosystem processes, and may mediate ecosystem responses to environmental change. Here we review published studies that explicitly address the role of mycorrhizal influence on ecosystem responses such as biogeochemical fluxes and pools, ecosystem productivity, and dominant vegetative growth responses to global change. We find that most studies are of limited duration (≤ 1 yr) and geographical distribution. A strong bias in the literature regarding the location of studied ecosystems, with large parts of the globe, such as highly-weathered soil systems in the tropics, subtropics and warm temperate biomes, accounting for ~30% of the global land base, greatly under-investigated. In terms of mediating ecosystem responses to global change, mycorrhizal–plant symbioses exhibit conflicting responses although some generalities do exist. Plants often shift carbon allocation belowground and the activities of mycorrhizal associates are frequently enhanced at elevated atmospheric CO_2 conditions, but the direct effects for ecosystem dynamics are less clear. Mycorrhizal associations reduce plant stress under drought conditions. How mycorrhizal root colonization responds to nitrogen deposition depends on the type of mycorrhizas and background levels of soil nitrogen and phosphorus. The capacity of mycorrhizas for mediating plant and ecosystem responses to warming are varied, but over 60% of these studies found increased mycorrhizal abundance and decreased mycorrhizal activity with warmer temperatures. This review suggests the role mycorrhizal fungi play in ecosystems responding to global change is not well understood. We emphasize the need for more research in this emerging field, as such responses and ecosystem feedbacks to Earth's climate system are of concern to multiple scientific disciplines and society.

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Introduction

Mycorrhizal symbioses are widespread and common in terrestrial ecosystems around the globe (Smith and Read, 2008), and the symbiotic fungi are often crucial for the uptake of nutrients and water from the soil and transfer to plants (Marschner and Dell, 1994; Clark and Zeto, 2000; Allen et al., 2003; Orwin et al., 2011). In many ecosystems, mycorrhizal fungi are drivers of carbon (C) and nutrient cycling and sequestration (Rillig et al., 2001; Hobbie and Hobbie, 2006; Heinemeyer et al., 2007; Hobbie and Hobbie, 2008; Talbot et al., 2008; Courty et al., 2010; Talbot and Treseder, 2011; Cairney, 2012; Cheng et al., 2012; Heinemeyer et al., 2012; Clemmensen et al., 2013; Treseder and Holden, 2013). Changes in atmospheric conditions, nutrient deposition patterns, and global and regional climate affect ecosystem processes (IPCC, 2007) and mycorrhizal functioning (Treseder, 2004), yet the potential role of mycorrhizal symbioses in mediating ecosystem responses to global change remains underexplored. Here, we review literature published since 1990 addressing roles and responses of mycorrhizal associations for ecosystems such as biogeochemical fluxes and pools, ecosystem productivity, and dominant vegetative growth responses to global change factors. Specifically, we were interested in how ecosystem responses to global change are mediated by mycorrhizal fungi. The goals of this review were: (1) to establish the current state of the science, (2) to identify both strengths and gaps in our knowledge, and (3) to propose suggestions for future research elucidating the roles of mycorrhizas in ecosystem responses to global change. Table 1 summarizes the main findings from our searches.

Most studies addressing potential mycorrhizal mediation of ecosystem responses to global change are of relatively short-term duration (Fig 1) and of limited spatial extent. Published works are generally from mid- to high-latitudes of the Northern Hemisphere, with a strong North American and European bias (Fig 2). Large parts of the globe, such as highly-weathered soil ecosystems in the tropics, subtropics and warm temperate biomes which account for approximately 30 % of the global land base (NRCS, 2005), remain greatly under-investigated. Published works typically address a limited number of mycorrhizal responses and global change drivers (Fig 3A and B).

Of the over 1 400 published references that were found in our Google Scholar and Web of Science searches, only 120, less than 9 %, investigated all three of our criteria of (1) mycorrhizal responses, (2) ecosystem responses, and (3) global change drivers. Most studies assess mycorrhizal mediation of ecosystem responses to global change in only one ecosystem type and location, with the exception of a study contrasting mycorrhizal responses to warming and fertilization in tussock- versus heath-dominated tundra (Clemmensen et al., 2006). Some studies did examine mycorrhizal and ecosystem responses in multiple locations within an ecosystem type (Egerton-Warburton and Allen, 2000; Egerton-Warburton et al., 2007; Thomas et al., 2009; Clemmensen et al., 2013).

Approach

This review encompasses natural ecosystem responses to global change drivers, including responses from laboratory and greenhouse studies using dominant plant species and associated mycorrhizas from natural ecosystems. Agricultural systems are not included in this review. Studies assessing mycorrhizal mediation of ecosystem response to global change (Figs 1–3) were included in this review if they met the following three criteria: (1) global change drivers or treatments, (2) responses of mycorrhizas, and (3) implications for ecosystem functioning such as productivity, species composition, respiration, and biogeochemical cycling. We searched Google Scholar and Web of Science using global change keywords ("Nitrogen deposition," "N deposition," "temperature," "warming," "drought," "moisture," "carbon dioxide," "CO_2," "ozone," "O_3," "ultraviolet," "UV") coupled with "mycorrhiza" and "ecosystem," and excluding "agro" and "agri."

Of the 1 434 citations that were flagged in the search, 120 addressed all three of the selection criteria. Only papers reporting new results are included in our figures, although information from review papers is included in the text. The types of global changes considered in this review include nitrogen (N) deposition; elevated atmospheric carbon dioxide (CO_2), increased tropospheric ozone (O_3); altered ultraviolet radiation (UV); temperature; drought; and "other" such as fire (Fig 3B).

This review considered studies addressing mycorrhizal responses if they directly quantified mycorrhizas (such as changes in root length colonization, abundance, composition) to global change treatments. Secondly we included studies that indirectly addressed mycorrhizas by contrasting responses of dominant plants with specific mycorrhizal associations to infer the role of mycorrhizas in ecosystem response to global change (Thomas et al., 2009; Averill and Finzi, 2011). We did not include papers studying belowground responses to global change that did not distinguish between root and mycorrhizas or among different types of soil microbes without explicitly detailing mycorrhizal responses (Fig 3A).

Studies were only included in this review that quantified an ecosystem response. Types of ecosystem responses include: changes in the dominant plant response (biomass, biomass allocation, demography, physiology, tissue chemistry), soil CO_2 efflux, decomposition, or changes in ecosystem nutrient distribution or cycling including soil N mineralization, nitrification and denitrification. Greenhouse and laboratory studies quantifying mycorrhizal effects on dominant plant responses to global change were included. Finally, we quantified the study duration (Fig 1), longitude and latitude (Fig 2), biome type (Fig 4), and whether the results were from empirical work or from modeling efforts (Fig 5).

Nitrogen deposition

Reactive inorganic nitrogen availability has been rapidly increasing over the last 60 yr primarily due to increased fertilizer usage and fossil fuel consumption (Galloway et al.,

Table 1 − Summary of our published literature search regarding mycorrhizal and ecosystem responses to global change factors. "% of Studies" refers to the studies actually addressing specific responses of mycorrhizas (abundance, activity) and ecosystems (productivity, biogeochemical cycling). Most studies did not address all four response types, and N = 163 here due to some studies addressing multiple global change drivers and/or mycorrhizal/ecosystem responses. We include responses addressed by very limited numbers of studies in order to highlight where future research efforts might focus

Global change driver	Mycorrhizal abundance	% Of studies	# Of studies
N deposition (40 studies total)	Increased	31%	11
	Decreased	44%	16
	No change	25%	9
Elevated atmospheric CO_2 (28 studies total)	Increased	57%	13
	Decreased	9%	2
	No change	35%	8
Elevated tropospheric O_3 (11 studies total)	Increased	60%	6
	Decreased	30%	3
	No change	10%	1
Elevated UV (seven studies total)	Increased	29%	2
	Decreased	14%	1
	No change	57%	4
Increased temperature (45 studies total)	Increased	63%	19
	Decreased	17%	5
	No change	20%	6
Drought (32 studies total)	Increased	43%	3
	Decreased	57%	4
	No change	0%	0

Global change driver	Mycorrhizal activity	% Of studies	# Of studies
N deposition (40 studies total)	Increased	67%	4
	Decreased	33%	2
	No change	0%	0
Elevated atmospheric CO_2 (28 studies total)	Increased	50%	5
	Decreased	40%	4
	No change	10%	1
Elevated tropospheric O_3 (11 studies total)	Increased	0%	0
	Decreased	100%	2
	No change	0%	0
Elevated UV (seven studies total)	Increased	0%	0
	Decreased	0%	0
	No change	100%	1
Increased temperature (45 studies total)	Increased	14%	1
	Decreased	71%	5
	No change	14%	1
Drought (32 studies total)	Increased	27%	4
	Decreased	20%	3
	No change	53%	8

Global change driver	Ecosystem productivity/ Dominant plant growth	% Of studies	# Of studies
N deposition (40 studies total)	Increased	94%	17
	Decreased	0%	0
	No change	6%	1
Elevated atmospheric CO_2 (28 studies total)	Increased	81%	13
	Decreased	6%	1
	No change	13%	2
Elevated tropospheric O_3 (11 studies total)	Increased	13%	1
	Decreased	75%	6
	No change	13%	1
Elevated UV (seven studies total)	Increased	0%	0
	Decreased	75%	3
	No change	25%	1

Table 1 – (continued)

Global change driver	Ecosystem productivity/ Dominant plant growth	% Of studies	# Of studies
Increased temperature (45 studies total)	Increased	65 %	13
	Decreased	15 %	3
	No change	20 %	4
Drought (32 studies total)	Increased[a]	0 %	0
	Decreased	91 %	10
	No change	9 %	1

Global change driver	Biogeochemical cycling rate	% Of studies	# Of studies
N deposition (40 studies total)	Increased	100 %	2
	Decreased	0 %	0
	No change	0 %	0
Elevated atmospheric CO_2 (28 studies total)	Increased	78 %	7
	Decreased	11 %	1
	No change	11 %	1
Elevated tropospheric O_3 (11 studies total)	Increased	33 %	1
	Decreased	67 %	2
	No change	0 %	0
Elevated UV (seven studies total)	Increased	0 %	0
	Decreased	100 %	1
	No change	0 %	0
Increased temperature (45 studies total)	Increased	33 %	6
	Decreased	44 %	8
	No change	22 %	4
Drought (32 studies total)	Increased[b]	0 %	0
	Decreased	93 %	27
	No change	7 %	2

a Myc presence increased productivity/growth in 90 % of studies comparing inoculated & non-inoculated plants.
b Myc presence increased BGC cycling in 66 % of studies comparing inoculated & non-inoculated plants.

2003). The resulting increases in nitrogen deposition have been shown to significantly change ecosystem functioning (Vitousek et al., 1997; Aber et al., 2003; Manning et al., 2006). Several studies have reviewed the effect of nitrogen deposition on mycorrhizal community composition for both ectomycorrhizal (ECM) (Wallenda and Kottke, 1998; Lilleskov et al., 2011) and arbuscular mycorrhizal (AM) fungi (Egerton-Warburton and Allen, 2000; Egerton-Warburton et al., 2007; van Diepen et al., 2011). Although the direct effects of nitrogen deposition on mycorrhizas are well reviewed (Treseder, 2004), the mycorrhizal-mediated impacts on ecosystem responses remain less clear.

Two important groups of mycorrhizas, ECM and AM, are thought to respond differently to increased nitrogen (N) availability (Lilleskov, 2005). ECM are generally considered to be more sensitive to increases in inorganic nitrogen since this group is integral in plant nitrogen uptake (Read, 1991), while AM abundance is not consistently affected by increased nitrogen availability (Lilleskov et al., 2011). In a recent review nitrogen addition thresholds for changes in ECM community composition were 5–10 kg N ha^{-1} yr^{-1}, while thresholds for compositional shifts in AM communities were between 7.8 and 12 kg N ha^{-1} yr^{-1} (Pardo et al., 2011). Yet nitrogen deposition rates, generally between 0.2 and 50 kg N ha^{-1} yr^{-1}, are expected to double between 2000 and 2030 (Reay et al., 2008) exposing a rapidly increasing part of the world's ecosystems to threshold N deposition rates for mycorrhizas.

Many studies have addressed the effect of nitrogen deposition on mycorrhizal functioning and Lilleskov et al. (2011)

provides an excellent review for ECM. Here we address a selection of important findings with implications for ecosystem functioning such as composition of dominant plant species types. Nitrogen fertilization (100 kg N ha^{-1} yr^{-1}) in tall grass prairies increased root colonization and extraradical hyphae production for AM in one study (Eom et al., 1999) while another study found no shifts in colonization, but significant mycorrhizal community composition shifts (Jumpponen et al., 2005). In perennial grassland ecosystems nitrogen fertilization reduced AM abundance and mycorrhizal species richness in phosphorus (P)-rich sites and increased AM abundance and
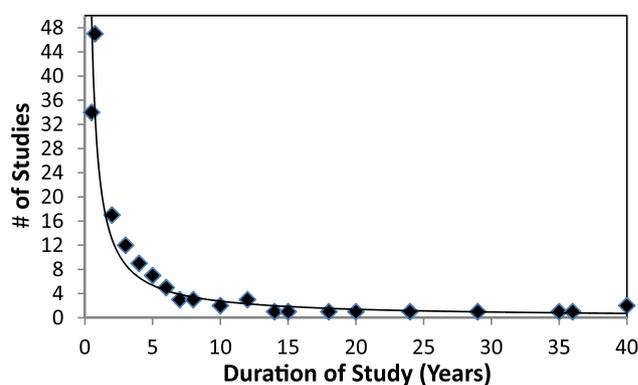

Fig 1 – The majority of published studies investigating mycorrhizal mediation of ecosystem response to global change are of short duration. Here, the first point represents studies of < 0.5 yr duration.
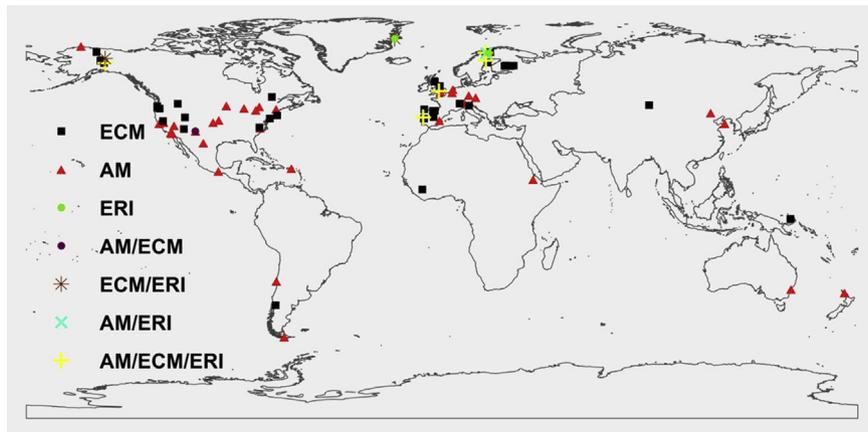
Fig 2 — Global distribution of mycorrhizal studies investigating ecosystem responses to global change, and the type of mycorrhizal association. We found a total of 120 published studies addressed this topic. Figure contains fewer numbers of points, as multiple studies have been published from the same research sites and points overlap. Note that most of the AM studies are laboratory, not field studies. Greenhouse and laboratory studies using dominant vegetation and mycorrhizal associates collected from non-agricultural ecosystems are included as points representing the collection site (not the longitude/latitude of the greenhouse or laboratory).

species richness in P-limited sites (Egerton-Warburton et al., 2007). AM fungal abundance decreased with N enrichment in northern hardwood forests (up to 30 kg N ha^{-1} yr^{-1}) (van Diepen et al., 2007) while shifting to a beneficial community structure for plant growth (van Diepen et al., 2011). Over a natural nutrient gradient in a coniferous forest higher nutrient availability shifted the ecosystem from an ericoid- to an ECM- and, finally, an AM-dominated system (Nilsson et al., 2005). Even though many studies indicate a decline in ECM fungal abundance with increased nitrogen availability (Lilleskov et al., 2011), an increase in morphotype abundance and species richness has also been observed (Rossi et al., 2012).

Although much is known about the response of mycorrhizas to nitrogen deposition, little is known about how shifts in mycorrhizas actually affect the ecosystem. Inoculations with AM fungi from different nitrogen fertilization plots suppressed growth by the shrubland species *Artemisia californica* while enhancing growth by the grassland species *Bromus madritensis*, thus providing a potential mechanism for the large-scale shift from shrubland to grassland in this region (Siguenza et al., 2006a, 2006b). Similar results (Egerton-Warburton and Allen, 2000) were found for the coastal sage brush ecosystem in southern California, where N deposition resulted in altered AM communities with lower species diversity and a general selection for small spore AM species. Reduced AM mutualisms may in part explain the shift in this shrubland towards invasive Mediterranean grasses.

After nitrogen saturation a conifer forest had a significantly lower ECM contribution to plant nitrogen based on natural abundance ^{15}N (Högberg et al., 2011). In a boreal forest low doses of nitrogen deposition (20 kg N ha^{-1} yr^{-1}) increased both root and ectomycorrhizal carbon efflux due to increased biomass, while high doses of nitrogen deposition (100 kg N ha^{-1} yr^{-1}) resulted in significantly reduced rates of root and ectomycorrhizal efflux likely due to decreased

belowground C allocation (Hasselquist et al., 2012). After nitrogen fertilization (100 kg N ha^{-1} yr^{-1}) in a semi-arid woodland ECM-associated *Pinus edulis* (piñon pine) trees had enhanced mortality correlated with a decline in sporocarp production from 20 % of net primary production (NPP) to 0 % (Allen et al., 2010). Foliar N concentrations and N:P ratios indicated the pines had sufficient N, and the increased mortality was most likely due to either or both reduced water transport or diminished P uptake with the decline in ECM. These effects were not observed for AM-associated *Juniperus monosperma* (juniper) trees, suggesting a potential shift in this ecosystem toward AM-associated dominant vegetation. However, in a subalpine grassland AM biomass decreased with fertilization (50 kg N ha^{-1} yr^{-1}) with weekly destruction of mycelium having no effect on plant growth (Blanke et al., 2012), suggesting that as N availability increased grassland plant hosts became less dependent on mycorrhizas for N acquisition.

While 44 % of the studies in our review examining mycorrhizal abundance responses to increased N found declines in abundance, almost a third of the studies documented increased mycorrhizal abundance and a quarter observed no change (Table 1). Thus, while the main tendency is for increased N availability to potentially reduce plant dependence on mycorrhizal N acquisition, and this follows findings from a previous meta-analysis (Treseder, 2004), the reduced dependence on mycorrhizas is by no means a universal response. Similarly, a majority of studies investigating responses of mycorrhizal activity such as nutrient transfer to plants and respiration responses to increased N found increased activity (67 %) while a minority found diminished activity (33 %). However, only six studies in our review addressed potential responses of mycorrhizal activity to elevated N (Egerton-Warburton and Allen, 2000; Egerton-Warburton et al., 2007; Alberton and Kuyper, 2009; Högberg et al., 2011; Weigt et al., 2011; Hasselquist et al., 2012). In contrast to mycorrhizal responses a clear majority of papers (94 %) found increased
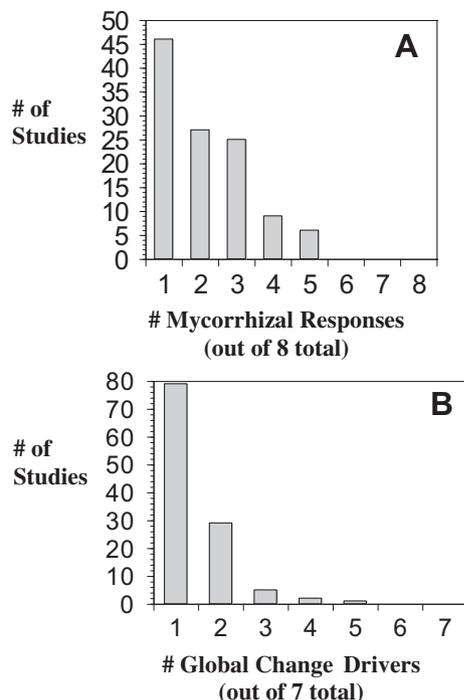
Fig 3 — Comparisons of the number of studies addressing mycorrhizal mediation of ecosystem response to global change (120 total studies) investigated versus the number of (A) mycorrhizal and (B) global change driver variables addressed. (A) Over 36% of studies only investigated one mycorrhizal response. Mycorrhizal response variables were: % root colonization, mycorrhizal abundance per unit soil, other mycorrhizal abundance measure, mycorrhizal composition via morphotyping, mycorrhizal composition from DNA, PLFA composition, hyphal length or density, and "other mycorrhizal variables" including mycorrhizal respiration and nutrient root-transfer. (B) Most studies examined mycorrhizal and ecosystem responses to only one global change driver. The seven drivers included elevated temperature, elevated atmospheric CO_2, drought, enhanced N deposition, increased tropospheric O_3, altered UV-B radiation, and "other" including fire.

ecosystem productivity or dominant plant growth in response to increased N, although the direct role of mycorrhizas for these increases in productivity is not clear.

With the emergence of molecular tools over the last few decades a sophisticated understanding of shifts in mycorrhizal community composition with elevated nitrogen deposition has developed. However, we are just now starting to determine what the consequences of these compositional shifts are for ecosystem functioning. Examples of such ecosystem effects are changes in dominant plant responses (biomass, biomass allocation, demography, physiology, tissue chemistry), soil CO_2 efflux, decomposition, and altered ecosystem nutrient distribution and cycling such as impacts on soil N mineralization, nitrification, and denitrification. Future studies should directly address the link between mycorrhizal performance and ecosystem functioning in response to increased reactive nitrogen. For example, do plants and
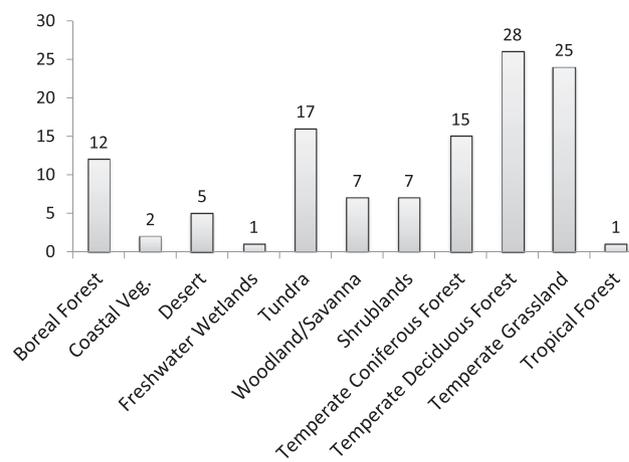

Fig 4 — Number of empirical studies addressing mycorrhizal mediation of ecosystem response to global change in different biome types.

ecosystems become more productive aboveground with increased nitrogen deposition due to less abundant mycorrhizal associates and reduced plant carbon costs, or simply because of the direct fertilization effect of higher N availability?

Atmospheric carbon dioxide

The atmospheric concentration of CO_2 increased from 1995 to 2005 at a rate of ~2 ppm per yr, and is projected to further increase by 40–110% through 2030 (IPCC, 2007). Increasing atmospheric CO_2 will impact functioning of mycorrhizal plants and their fungal associates with potential implications for ecosystem functioning (Rillig et al., 2000; Treseder and Allen, 2000; Parrent et al., 2006; Antoninka et al., 2011; Zavalloni et al., 2012). Direct effects of elevated atmospheric CO_2 on mycorrhizas may be limited because the natural soil environment has very high levels of CO_2 (Andrews and Schlesinger, 2001; Mohan et al., 2007). However, indirect effects due to increased soil nutrient demand by plants are likely to be more widespread (O'Neill et al., 1987; Saxe et al., 1998; Finzi et al., 2007; Johnson et al., 2012; Pickles et al.,
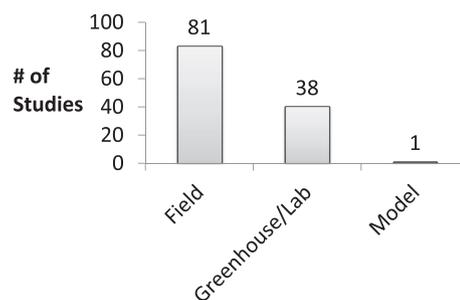

Fig 5 — The number of field, greenhouse/lab, and modeling studies investigating ecosystem responses to global change mediated by mycorrhizal fungal responses.

2012). Under elevated CO_2 treatments, the effects of arbuscular mycorrhizas (AM) for ecosystem response vary among associated plant species (Allen et al., 2005; Clark et al., 2009) and show both enhanced and reduced plant growth, root colonization, and spore and extraradical hyphal production with higher atmospheric CO_2. In contrast, ectomycorrhizal associations generally increase fungal colonization and positive plant growth under elevated CO_2 (Kasurinen et al., 1999; Garcia et al., 2008). The cause of more consistent responses to CO_2 of plants associating with ECM as opposed to AM fungi is not clear, and deserves future research efforts to determine whether this represents a true ecological signal or is an artifact of experimental design.

Studies have investigated effects of enriched atmospheric CO_2 on mycorrhizal host plants and fungi through Free Air Carbon Dioxide Enrichment (FACE) experiments (Phillips et al., 2002; Parrent et al., 2006; Parrent and Vilgalys, 2007; Garcia et al., 2008; Antoninka et al., 2011; Phillips et al., 2012), open top chamber studies (O'Neill et al., 1987; Kasurinen et al., 1999), natural CO_2 gradients (Rillig et al., 2000), and controlled growth chamber experiments (Fransson et al., 2007). Still, the role of mycorrhizas in mediating ecosystem responses to elevated CO_2 remains largely unknown. Arbuscular mycorrhizas hyphal length and root length colonization were not affected under elevated atmospheric CO_2 in a desert environment (Clark et al., 2009). However, in chaparral, the amount of *Scutellospora* and *Acaulospora* hyphae and the protein glomalin present within microaggregates increased with increasing CO_2 (Allen et al., 2005), consistent with previous studies (Rillig et al., 1999; Treseder et al., 2003). Elevated CO_2 increased AM hyphal length in a sandstone grassland, but not in serpentine grassland (Rillig et al., 1999). However, both grassland types experienced increased AM root colonization with higher CO_2 (Rillig et al., 1999). In contrast, in a warm temperate forest elevated CO_2 did not affect AM hyphal length or glomalin stocks, and CO_2 impacts on AM root colonization varied by sampling date (Garcia et al., 2008). In this latter study, ECM root colonization increased in response to elevated CO_2 (Garcia et al., 2008). Other studies have observed no impact of CO_2 for ECM biomass or ECM root colonization (Kasurinen et al., 1999; Parrent and Vilgalys, 2007). Overall fungal abundance in stands comprising both ECM and AM trees has been observed to not respond (Chung et al., 2006) to elevated CO_2.

Changes in salient features like hyphal length, root colonization and nutrient uptake by mycorrhizal fungi in response to elevated CO_2 may profoundly affect ecosystem processes. Plants frequently allocate more resources to mycorrhizal fungi under increased CO_2 (Saxe et al., 1998; Rillig et al., 2000; Treseder, 2004; Johnson, 2010), which may lead to greater extraradical hyphal growth (Sanders et al., 1998; Alberton and Kuyper, 2009; Antoninka et al., 2011; Cavagnaro et al., 2012), glomalin production, and increased soil organic carbon (Treseder and Turner, 2007). However, increased respiration by mycorrhizal fungi and plants may offset any potential soil organic carbon accumulation (Cheng et al., 2012). Furthermore, while conceptual models of plant resource allocation under elevated CO_2 suggest general increases in mycorrhizal activity (Treseder, 2004), the consequences of increased activity such as mycorrhizal respiration (Cheng

et al., 2012), extraradical hyphal growth (Treseder et al., 2003; Rillig, 2004; Garcia et al., 2008), and plant nutrient transfer may differ between and among AM and ECM symbionts (Johnson et al., 2005, 2013).

Compositional shifts in the AM community occur following CO_2 enrichment (Treseder et al., 2003) and these shifts will likely affect responses by both plants and fungi (Compant et al., 2010). Similar shifts in ECM communities have been proposed (Pickles et al., 2012) and observed (Parrent and Vilgalys, 2007) for ECM fungi. The ECM effect on ecosystem processes is likely to be at least biome-dependent, and potentially varies at even finer spatial scales. For instance, ECM dominate the soil microbial biomass in boreal forests and greatly influence nutrient and carbon cycling in these forests (Hobbie and Hobbie, 2008). However, ECM responses may be poor indicators of ecosystem change in relation to direct CO_2 effects (Cudlin et al., 2007). Instead, enhanced fine root production and increased nitrogen demand by plants may be responsible for changes in mycorrhizal fungi under elevated CO_2 (Finzi et al., 2007; Fransson et al., 2007).

The majority of studies in our review addressing implications of CO_2 for mycorrhizal abundance found either increased mycorrhizal abundance with elevated CO_2 (57 %) or no change in abundance (35 %; Table 1). The general increase in mycorrhizal abundance with elevated CO_2 was similar to a previous meta-analysis (Treseder, 2004). Elevated CO_2 effects on mycorrhizal activity such as nutrient acquisition and respiration were less clear, with studies finding both increased and decreased activity. Similar to N deposition studies, most ecosystems in our review (81 %) became more productive and had higher rates of biogeochemical cycling (78 %) with elevated CO_2, but the direct role of mycorrhizas in mediating these ecosystem responses is not clear.

Finally, effects of increased atmospheric CO_2 on mycorrhizas need to be considered in the context of other changing environmental factors. Altered nitrogen deposition, temperature, moisture availability and other facets of global change all influence ecosystem processes and plant–mycorrhizal interactions (Smith and Read, 2008; Alberton and Kuyper, 2009). Indeed, the most important impact of elevated CO_2 for mycorrhizal mediation of ecosystem processes may be the altered demand for other plant resources. Plants may allocate more carbon belowground to roots and mycorrhizal associates to satisfy the increased demand for nitrogen, phosphorous, and water, although this remains an area requiring further research (Treseder, 2004; Allen et al., 2005; Johnson et al., 2005, 2013). Shifts in plant carbon allocation in response to elevated CO_2, including allocation to mycorrhizal symbionts, will likely have important impacts on ecosystem cycling of nutrients, water and carbon (Gill and Jackson, 2000; Orwin et al., 2011; Vallack et al., 2012; Näsholm et al., 2013; Treseder and Holden, 2013).

Tropospheric ozone (O_3)

Tropospheric ozone is a greenhouse gas and a pollutant of increasing concern in natural systems (Cox, 2003; Karnosky et al., 2007; Mohan et al., 2009). Since ozone pollution is caused by photochemical reactions involving volatile organic

compounds and nitrogen oxides, projections suggest that tropospheric ozone levels will rise as human activity and urbanization increase (Logan, 1985; IPCC, 2007). Elevated ozone has been linked to visible damage to aboveground plant tissues and changes in plant community composition (Ashmore, 2005; Wittig et al., 2009) and in belowground variables such as soil enzymes and microbial communities (Andersen, 2003). However, it remains unclear how ozone affects belowground vegetation and the associated mycorrhizas, and in particular how changes in this symbiotic relationship affect ecosystem-level processes.

Recent studies on mycorrhizas and elevated ozone often focus on ECM, particularly of timber species, and the varied response of these mycorrhizas to ozone. In some cases, the mycorrhizal community becomes more genetically diverse (Haberer et al., 2007) or simply restructured with novel morphotype proportions (Kasurinen et al., 2005; Chung et al., 2006; Grebenc and Kraigher, 2007; Andrew and Lilleskov, 2009). Sometimes, however, observed changes in mycorrhizal community composition and infection rate were transitory (Rantanen et al., 1994; Atkin et al., 2009) or only significant at certain time points throughout treatment (Haberer et al., 2007). In one case, mycorrhizas responded only when severe drought coincided with ozone treatment (Grebenc and Kraigher, 2007). In other studies, ECM diversity has varied with increasing time exposed to ozone fumigation (Edwards and Zak, 2011). Ozone can reduce sporocarp production in ECM species (Andrew and Lilleskov, 2009), indicative of a transition of resources within the fungal structures away from reproduction or simply a reduction in plant-derived carbon to ECM associates. However, this effect varies with fungal species and ozone level (Kasurinen et al., 2005; Andrew and Lilleskov, 2009; Kasurinen et al., 2012). Changes in plant carbon allocation due to ozone are also highly variable (Andersen, 2003), so it remains unclear how these changes affect mycorrhizal colonization and diversity. The general stimulation of mycorrhizal abundance and infection rate in the roots of ozone-treated plants suggests a reaction to mitigate aboveground stress and could be a mechanism to reduce aboveground ozone damage in plants over time. Interestingly, this observation contrasts with the findings of an earlier review on mycorrhizas and global change (Rillig et al., 2002a), possibly because of the increased number of projects in recent years examining ozone responses in commercially important tree species or the maturation of long-term ozone treatment studies, many of which began early in the previous decade.

In our review most studies examining elevated O_3 impacts on mycorrhizal abundance document increases in abundance (60% of studies), while 30% of such studies find decreased abundance. Both studies examining higher O_3 implications for mycorrhizal activity found decreased activity (Chung et al., 2006; Edwards and Zak, 2011). In 75% of published works examining O_3 impacts on ecosystem productivity or dominant plant growth, productivity or growth rates declined. Similarly, two of the three studies looking into elevated O_3 and biogeochemical cycling found decreased cycling rates (Edwards and Zak, 2011; Kasurinen et al., 2012), while the third found increased rates (Grebenc and Kraigher, 2007). However, this represents an obviously limited number of studies and suggests future work is warranted to understand ecosystem

biogeochemistry responses to elevated tropospheric O_3 and the importance of mycorrhizal mediation for ecosystem response.

Finally it is important to consider that changes such as increasing temperatures, CO_2, and O_3 levels will co-occur, and the potential effects on mycorrhizal communities (and, consequently, dominant plant communities) could be a result of their synergism or counteraction. In fact, several studies that have tested the interaction between ozone and CO_2 report that elevated CO_2 levels can dampen the effects of elevated ozone on plant and soil processes, and *vice-versa* (Chung et al., 2006; Andrew and Lilleskov, 2009; Atkin et al., 2009). Increased CO_2 could thus offset ozone-induced aboveground plant stress and subsequent shifts in carbon allocation. This effect has also been observed with warming, wherein ozone enhancement counteracts the benefits of increased temperatures on aboveground plant processes and soil respiration (Kasurinen et al., 2012). Additionally, stimulation of mycorrhizal diversity and colonization from elevated ozone is more dramatic under high stress conditions such as drought (Grebenc and Kraigher, 2007), and nutrient limitation (Rantanen et al., 1994). Overall, recent results on ozone exposure and mycorrhizas suggest that interactive and indirect processes can significantly affect mycorrhizal response to elevated tropospheric ozone, and that these effects vary throughout time and among different tree communities. How these concurrent changes in fungal growth and community structure affect ecosystem-level processes is an area of research that requires more exploration.

Ultraviolet (UV) radiation

Concern about stratospheric ozone depletion in recent decades has led to numerous studies on the effects of ultraviolet radiation in plants (Tevini and Teramura, 1989; Laing, 1991; Reboredo and Lidon, 2012). Most studies of this nature observe aboveground processes such as photosynthesis and biomass production, but fail to consider root and soil changes. Even fewer have directly examined mycorrhizal colonization and growth.

Among the studies that do consider mycorrhizas, results have been largely non-significant no matter the treatment — either enhancement or reduction of UV radiation (Newsham et al., 1999; De La Rosa et al., 2003; Kristian et al., 2008). Other results have been inconsistent or indirect. In one study, the effects of reduced UV on mycorrhizas varied between locales (Rinnan et al., 2005), and another noted no overall change in mycorrhizal abundance, but widespread change in morphological structures (Klironomos and Allen, 1995). However, *enhanced* UV-B did lead to decreases in AM colonization in one study on *Carex* sedges in the Netherlands (van de Staaij et al., 2001), contrasting with an earlier study in Argentina that noted a decrease in *Carex*-associated mycorrhizas with *reduced* UV exposure (Zaller et al., 2002). These inconsistencies suggest that additional ecosystem variables (community composition, latitude, soil nutrient levels) in conjunction with UV exposure may play a major role in altering mycorrhizal response.

In our review, 57% of the papers examining elevated UV impacts on mycorrhizal abundance found no significant

changes in overall abundance (Klironomos and Allen, 1995; De La Rosa et al., 2003; Rinnan et al., 2005; Albert et al., 2008), while one documented a decline in abundance (van de Staaij et al., 2001) and two found increases (Klironomos and Allen, 1995; Zaller et al., 2002). Only one published work considered impacts of higher UV on mycorrhizal activity and found no change (Albert et al., 2008). Three of the four studies examining increased UV impacts on ecosystem productivity found productivity decreases (Zaller et al., 2002; De La Rosa et al., 2003; Albert et al., 2008) while the fourth observed no change (van de Staaij et al., 2001). Similarly, the only study in our review to examine UV impacts on ecosystem biogeochemical cycling rates found a reduction at higher UV levels (Albert et al., 2008). Little attention has been given to ecosystem-level processes in UV experiments, with the major ecosystem variable measured often being aboveground and root biomass or dominant plant root:shoot ratios (Klironomos and Allen, 1995; Newsham et al., 1999; Zaller et al., 2002; De La Rosa et al., 2003; Rinnan et al., 2005; Kristian et al., 2008). Future research examining increased UV impacts on mycorrhizal mediation of ecosystem processes is needed, particularly in high-latitude systems most susceptible to the stratospheric "ozone hole."

Temperature

Temperature effects on mycorrhizal functioning can be direct or, more often, indirect via temperature impacts on host plant resource demands, carbon allocation, and soil nutrient biogeochemistry. Previous research in this area attests to the challenges of quantifying the effects of temperature on mycorrhizas and how this translates to ecosystems, largely because the effects on mycorrhizas can be strongly mediated by temperature effects on plant communities. Mycorrhizas may also respond directly to changes in temperature, independent of changes to the plant host (Fitter et al., 2000). Indirect temperature outcomes may result if warming alters rates of soil biogeochemical cycles such as net nitrogen mineralization (Peterjohn et al., 1994; Rustad et al., 2001; Rillig et al., 2002a; Melillo et al., 2011) and nitrification (Butler et al., 2012), thus causing a warming-induced indirect "fertilization effect." It is less clear how particular changes in the mycorrhizal community translate to changes in ecosystem function. However, the mycorrhizal symbioses can potentially mediate changes in ecosystem functioning with climate change (Fitter et al., 2000; Treseder and Allen, 2000; Olsrud et al., 2004, 2010; Garcia et al., 2008; Olsrud et al., 2010; Orwin et al., 2011; Cheng et al., 2012), and can be important for ecosystem carbon storage and cycling (Rillig et al., 2001; Talbot et al., 2008; Phillips et al., 2012; Treseder and Holden, 2013).

Field studies have examined how temperature affects mycorrhizal abundance, but less often have they attributed these changes in biomass or colonization to an ecosystem-scale function such as dominant plant growth, nutrient flux, soil respiration, or decomposition. One study found that with warming an arctic grass species had lower root colonization by AM fungi and increased foliar %N, but no change in aboveground grass cover (Olsrud et al., 2010). The majority of field studies has been conducted in temperate or arctic regions

and remain poorly studied in the rest of the globe, including warm temperate and tropical ecosystems. Ergosterol content, used as a biomass proxy for mycorrhizas, increased in the roots of shrubs associating with ericoid mycorrhizas in response to warming, as well as to increased CO_2 in the heath tundra of Abisko (Olsrud et al., 2004). However, direct examination of the fine roots of these shrub species in the latter study determined an increase in colonization with elevated CO_2, but no effect of warmer temperature for colonization (Olsrud et al., 2010). ECM colonization of *Betula nana* increased in tussock tundra, but did not change in heath tundra in response to warming (Clemmensen et al., 2006). Woody plants of polar regions generally associate with ECM and ericoid fungi, and many temperate trees also associate with ECM fungi, so due to the latitudinal bias in field sites, field data including arbuscular mycorrhizal (AM)-dominated systems are rare (Fig 2) and (Rillig et al., 2002a).

Conversely, laboratory studies focusing on temperature effects on plant–mycorrhizal symbiosis often involve AM mycorrhizas. Mycorrhizal fungi have been considered vectors of plant C input to the soils, however there is evidence that mycorrhizal fungi may also contribute directly to soil C loss through decomposition pathways (Talbot et al., 2008; Cheng et al., 2012; Treseder and Holden, 2013). How mycorrhizal fungi affect the soil carbon balance remains unclear and their role in controlling carbon flow has important consequences with respect to temperature change. Increased temperatures have been shown to affect the allocation of C to fungi which can lead to increased respired C (Hawkes et al., 2008) or an increase in C stored in the soil either via respiratory acclimation or increased growth of the extraradical mycelium (Heinemeyer et al., 2006). In addition, AM colonization has not affected short-term temperature dependence of respiration in AM-associated plants (Atkin et al., 2009). Temperature can also affect the lifespan and morphology of roots and, in turn, affect the turnover of nutrients and carbon additions to the soil (Norby and Jackson, 2000). However, the effect of AM colonization on the root lifespan is plant species-dependent (Atkinson et al., 2003). Increased temperature can enhance carbon allocation to AM fungi, increase acquisition of P, and increase mycorrhizal root colonization rates (Kytoviita and Ruotsalainen, 2007).

In field studies, mycorrhizal abundance often increases with warmer temperatures. In polar regions, increased temperature can promote primary production via lengthened growing season, and with more C to allocate towards mycorrhizas, warmed plants can accumulate more biomass than control plants (van Wijk et al., 2004). In heath tundra ericoid mycorrhizal abundance increased in response to warming (Olsrud et al., 2004). In a tussock graminoid tundra ecosystem at Toolik Lake, ECM colonization increased with increased temperature, and plants shifted allocation to higher shoot biomass (Clemmensen and Michelsen, 2006). Field experiments have documented increases in ECM biomass (Clemmensen et al., 2006) with no change in colonization rate (Clemmensen and Michelsen, 2006) in tussock tundra, which contrasts with increased AM hyphal length and colonization rates in Mediterranean grasslands (Rillig et al., 2002b). In arctic tussock tundra, ECM networks transferred carbon from larger plants to smaller plants, which buffered the smaller plants

against carbon starvation (Deslippe and Simard, 2011). Thus, mycorrhizal networks can buffer plants against carbon deficit resulting from increased temperature and higher plant respiratory cost.

A few studies have examined global patterns in mycorrhizal mediation of ecosystem response to global change. Vargas et al. (2010) examined ecosystem CO_2 flux (gross primary production plus ecosystem respiration) and determined it was controlled mainly by inter-annual variations in *temperature* in ECM-dominated systems and by inter-annual variations in *precipitation* in AM-dominated ecosystems. Although mycorrhizal responses are less clear, there is evidence that increased temperature causes plant species to shift biomass from belowground to aboveground production, both in lab studies (Heinemeyer et al., 2006) and field studies (Olsrud et al., 2004; Clemmensen and Michelsen, 2006; Zhou et al., 2011).

Concomitant changes in temperature and other global change drivers (e.g. precipitation, nitrogen deposition, etc.) can further influence plant–mycorrhizal symbioses and drive ecosystem processes. For example, ECM biomass increased in response to warming as well as to NPK fertilization in a tussock tundra ecosystem at Toolik Lake, Alaska, but warming by itself did not significantly influence the ECM biomass in heath tundra at Abisko, Sweden (Clemmensen et al., 2006). Also at Toolik Lake, ECM diversity increased with warming but was slightly reduced with fertilization (Deslippe et al., 2011). ECM-associated *B. nana* exhibited increased biomass and higher aboveground:belowground biomass ratios in response to warming in the tussock tundra system, contrasting with increased belowground allocation and smaller aboveground biomass increase for this species in the heath tundra of Abisko (van Wijk et al., 2004). Indeed, different types of mycorrhizal reactions have also been documented in response to warming and elevated CO_2. In the dwarf shrub tundra system in Abisko, % colonization of heath shrub roots by ericoid mycorrhizas increased in response to elevated CO_2 but exhibited no warming effect (Olsrud et al., 2010). In this same study, AM colonization of grass roots declined in response to warming, and even more so when warming was combined with elevated CO_2 (Olsrud et al., 2010).

In our review of the published literature, warming increased mycorrhizal abundance in 63 % of studies. While 17 % observed decreases, 20 % of studies saw no change in abundance of mycorrhizas with higher temperatures (Table 1). In contrast, mycorrhizal activity in response to rising temperatures generally decreased (71 % of studies), with the remainder reporting a split between increased (14 %) or no change (14 %) in activity. Almost two-thirds of the studies examining ecosystem productivity responses to higher temperature found productivity increases (65 %), while 15 % observed declining productivity and 20 % observed no change. Results on the response of biogeochemical cycling rates to warmer temperatures were mixed, with 44 % of the works observing declines, 33 % finding rate increases, and the remaining 22 % observing no change in rates.

The re-structuring of dominant plant communities can ultimately affect the overall functioning of an ecosystem (Finzi et al., 1998a, 1998b; Mohan et al., 2007; Butler et al., 2012; Hansson et al., 2013). However, changes in ecosystem function may also be mediated by plant–mycorrhizal associations.

Mycorrhizal–plant mutualisms will likely play an important role in mediating the effects of increased global and regional temperatures. Yet there is still a need for better mechanistic understanding of how global change will affect the mycorrhizal–plant symbioses and how this translates to ecosystem functioning. Our ability to make predictions on how ecosystem structure and function are affected with increasing temperatures will depend in part on mycorrhizal fungi and their ability to mediate temperature-induced changes. Multi-factorial approaches, long-term field manipulations, and cross-disciplinary research will help elucidate mycorrhizal and ecosystem responses to rising temperatures.

Altered precipitation – drought

Climate change models project shifting patterns of global precipitation, including decreasing moisture in the tropical and sub-tropical regions and greater moisture at higher latitudes (Trenberth et al., 2007). Increases in episodic rainfall and longer dry periods have been occurring and are projected for many areas of the globe (IPCC, 2007; Kharin et al., 2007). In short, climate change will alter the quantity, frequency and intensity of precipitation for most terrestrial ecosystems (Kreuzwieser and Gessler, 2010; Trenberth, 2011). Longer and drier periods between rainfalls will increase water stress on plants, yet mycorrhizal associations may alleviate drought stress on the host plant (Auge, 2001, 2004; Smith and Read, 2008; Miransari, 2010; Lehto and Zwiazek, 2011). However, the majority of non-agricultural field research focuses on the mycorrhizal response to drought conditions (e.g. fungal community composition, species diversity, colonization percentage and fungal biomass) without reporting the corresponding response of the mature plant community. For practical reasons, manipulative greenhouse and field experiments of forest trees focus on seedling growth and survival, and while dominant plant recruitment is critical for future ecosystem functioning, the effects of seedlings on ecosystem nutrient cycling, forest productivity and hydrology are minimal in comparison to the effects of mature trees (DeLucia et al., 1999; Mohan et al., 2007). Thus, the effects of mycorrhizal relationships on ecosystem processes under drought conditions remain unclear.

The ability of ECM relationships to alleviate drought stress on plants has been demonstrated in both greenhouse and field studies. Greenhouse studies have shown increased above and belowground biomass in ECM seedlings exposed to drought (Koo et al., 2000; Alvarez et al., 2009; Dominguez Nunez et al., 2009), higher photosynthetic rates (Lehto, 1992b), greater stomatal conductance (Davies et al., 1996; Morte et al., 2001), and higher plant tissue concentrations of N and P (Lehto, 1992a; Alvarez et al., 2009). Other studies found plants with ECM showed no benefit (Coleman et al., 1989; Bogeat-Triboulot et al., 2004; Kennedy and Peay, 2007; Kipfer et al., 2012), or even negative impacts (Nardini et al., 2000) from drought. Results drawn from field studies under drought conditions include higher survival for pre-inoculated seedlings following transplantation (Ortega et al., 2004), greater seedling survival from better hydraulic conductance due to greater connectivity to ECM networks (Querejeta et al., 2003; Egerton-Warburton

et al., 2007; Bingham and Simard, 2011; 2012), and positive effects of ECM diversity in stands surviving extreme drought (Azul et al., 2010). Mature trees involved in the ECM symbioses often have extensive root systems extending deep into the soil to access deep water. The ability of mature ECM plants to better acquire nutrients from upper soil horizons during times of drought may even outweigh the benefits of enhanced water uptake (Lehto and Zwiazek, 2011).

The majority of experiments relating AM symbioses and drought conditions are likewise performed under greenhouse conditions, and the results are similar to those reported for the ECM symbioses. The literature relating drought and AM symbioses prior to 2000 is well reviewed by Auge (2001), and we will here only briefly present general trends. Plants in AM symbiosis show increases in biomass (Dixon et al., 1994; Lansac et al., 1995; Birhane et al., 2012), increased photosynthetic rate (Caravaca et al., 2003), greater stomatal conductance (Davies et al., 1996), greater leaf water content (Goicoechea et al., 2004), and improved plant N and P assimilation (Birhane et al., 2012) under drought conditions. Field studies with AM symbioses have primarily used crop species.

The ability of mycorrhizal symbioses to alleviate drought conditions has been investigated in greenhouse studies and a handful of field transplant experiments. Importantly, the results of many greenhouse studies may not be scalable to ecosystem processes as results vary according to plant and fungal species (and genotypes) involved in the interaction (Garbaye and Guehl, 1997; Jany et al., 2003; Johnson et al., 2012). Similarly, field studies indicate important effects of plant genotype in response to drought and mycorrhizas (Bingham and Simard, 2013). Large-scale field studies are likely required to adequately investigate ecosystem effects of mycorrhizal symbioses under drought conditions. It is likely impossible (or at least extremely difficult) to manipulate mycorrhizal colonization in long-term field experiments; however, the use of tracer elements and stable isotope analyses (Hobbie et al., 2000; Hobbie and Colpaert, 2003) following rainfall exclusion and trenching can provide indirect evidence for the role of mycorrhizas under variable moisture conditions in the natural environment. Yet large-scale manipulative field experiments are needed to elucidate the direct effects of mycorrhizal symbioses for ecosystem processes under increased soil moisture extremes.

In summary, impacts of drought on mycorrhizal abundance in our review were mixed, with 57 % of studies finding decreased and 43 % observing increased mycorrhizal abundance with diminished soil moisture (Table 1). Over half of the studies (53 %) examining drought impacts on mycorrhizal activity found no change in rates, with the remainder nearly split between increased (27 %) and reduced (20 %) rates. The vast majority of studies observed drought to reduce ecosystem productivity or dominant plant growth (91 %), and no study in this review observed increased productivity with drought conditions. However, drought studies provide the best example of direct manipulation of mycorrhizas presence or abundance on ecosystem response to global change. In 90 % of the studies, mycorrhizas increased productivity under drought conditions when compared to non-mycorrhizal plants. Similarly, while drought directly diminished rates of biogeochemical cycling in 93 % of the studies, in 66 % of these

studies biogeochemical rates were higher under drought conditions when plants were inoculated with mycorrhizas compared with non-mycorrhizal plants. Clearly mycorrhizas help alleviate drought stress for plants and ecosystems, and this role will likely become more important as drought frequency and intensity increase.

Conclusion and future work

It is clear that potential mycorrhizal mediation of ecosystem responses to global change requires further study. Thus far we have only a limited number of studies of generally short-term duration (Fig 1), limited geographical distribution (Fig 2), a general consideration of only one or two global change drivers (Fig 3B), and a strong bias in the published literature toward temperate forests and grasslands (Fig 4). For forested systems, studies are often limited to tree seedlings.

Longer term studies explicitly addressing mycorrhizal and ecosystem responses to global change would greatly improve our ability to forecast system and biome responses to environmental change. Now that we have some long-term ecosystem-scale global change experiments, later results could be compared with earlier investigations of mycorrhizal-ecosystem response. For example, while 60 % of post-1990 published papers on O_3 impacts observed increases in mycorrhizal root colonization (Table 1), this contrasts with an earlier O_3 review which found, over the shorter term, a general reduction in mycorrhizal colonization with higher O_3 (Rillig et al., 2002a). Although not explicitly mycorrhizal in nature, an example of the importance of long-term ecological investigation comes from the original soil warming experiment at Harvard Forest. Whereas over the first several years of the experiment soil CO_2 efflux increased dramatically with 5 °C warmer soil temperatures, by year 10 of the experiment the warmed soil CO_2 efflux rates no longer significantly differed from those of the control plots (Peterjohn et al., 1994; Melillo et al., 2002). Potential roles of mycorrhizas for this shift are just beginning to be explored.

Similarly, most studies pertaining to potential mycorrhizal mediation of ecosystem responses to global change address only one global change factor (Fig 3B). Yet other studies have found that ecosystem response to one global change driver may be affected by response to a second global change factor, as in investigations of elevated atmospheric CO_2 and O_3 (Kasurinen et al., 1999; Chung et al., 2006), temperature and O_3 (Kasurinen et al., 2012), and CO_2 and N additions (Tingey et al., 2005; Parrent et al., 2006; Parrent and Vilgalys, 2007; Alberton and Kuyper, 2009; Parrent and Vilgalys, 2009; Antoninka et al., 2011). Therefore, we included papers that examined single global change factors but also investigated the number of papers that considered two or more global change drivers (Fig 3B), and encourage more multi-factor experimental approaches.

An important point is that most of these studies did not manipulate mycorrhizas independently of the global change driver (for example, directly manipulating the colonization status of mycorrhizal plant associates), so much of the findings thus far are correlative rather than causal. However, inoculation with AM fungi and responses to N fertilization in two studies exhibit the direct effects of mycorrhizas for plant responses to

increased N and demonstrate the role of reduced AM abundance for observed shifts in shrublands to grassland dominance (Siguenza et al., 2006a, 2006b). One field study examining N fertilization impacts in subalpine grassland directly manipulated mycorrhizal abundance by disturbing hyphae around target plant roots (Blanke et al., 2012). This study found that N fertilization decreased AM biomass, but weekly destruction of mycelium had no effect on the growth of the dominant plants, suggesting plant hosts became less dependent on mycorrhizal nutrient acquisition under higher N conditions.

In addition, a number of greenhouse laboratory studies have examined roles of mycorrhizal associates for dominant plant responses have done so by contrasting the responses of plants with and without mycorrhizas to drought (Lehto, 1992b; Lansac et al., 1995; Koo et al., 2000; Morte et al., 2001; Querejeta et al., 2003; Ortega et al., 2004; Gonzalez-Monterrubio et al., 2005; Dominguez Nunez et al., 2008; Alvarez et al., 2009; Azul et al., 2010; Bingham and Simard, 2011; Birhane et al., 2012; Kipfer et al., 2012) and increased temperatures (Delucia et al., 1997; Atkinson et al., 2003; Kytoviita and Ruotsalainen, 2007; Atkin et al., 2009; Reininger and Sieber, 2012). In 90 % of studies, dominant plant biomass was higher under drought conditions when plants were colonized by mycorrhizas (Table 1). On the other hand, studies that examine temperature effects on growth of plants with and without mycorrhizas do not show a clear trend. Increased temperature had no effect on *Pinus ponderosa* (ponderosa pine) biomass upon inoculation with ECM fungi (Delucia et al., 1997) but had a positive effect on *Picea abies* (Norway spruce) and *Pseudotsuga menziesii* (Douglas-fir) with ECM fungi, and Douglas-fir biomass was higher at higher temperature when inoculated (Reininger and Sieber, 2012). Mycorrhizas affect a number of plant physiological processes with elevated temperatures. Plant roots inoculated with mycorrhizas had higher rates of respiration in *Plantago* (plantain) when grown in elevated temperatures (Atkin et al., 2009). However, cold acclimated non-AM plants exhibited higher rates of respiration compared to inoculated plants (Atkinson et al., 2003), suggesting that mycorrhizas affect plant cold acclimation. Mycorrhizas enhanced plant P capture with elevated temperature in two arctic herbs, although mycorrhizal colonization did not affect plant biomass (Kytoviita and Ruotsalainen, 2007).

Investigation in under-studied parts of the globe, such as the Neotropics, Asia, Africa and the Southern Hemisphere would enhance our ability to make global-scale predictions. Further, recent work suggests the role of mycorrhizal fungi for ecosystem-scale processes such as system carbon loss and sequestration is an emerging and important area for earth system science (Talbot et al., 2008; Orwin et al., 2011; Cheng et al., 2012; Phillips et al., 2012; Treseder and Holden, 2013). Direct investigation of mycorrhizal and ecosystem responses to changing planetary conditions will thus be of interest across scientific disciplines with direct implications for society.

Acknowledgments

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