

# Fungal communities in soils under global change

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**Abstract:** Soil fungi play indispensable roles in all ecosystems including the recycling of organic matter and interactions with plants, both as symbionts and pathogens. Past observations and experimental manipulations indicate that projected global change effects, including the increase of CO<sub>2</sub> concentration, temperature, change of precipitation and nitrogen (N) deposition, affect fungal species and communities in soils. Although the observed effects depend on the size and duration of change and reflect local conditions, increased N deposition seems to have the most profound effect on fungal communities. The plant-mutualistic fungal guilds – ectomycorrhizal fungi and arbuscular mycorrhizal fungi – appear to be especially responsive to global change factors with N deposition and warming seemingly having the strongest adverse effects. While global change effects on fungal biodiversity seem to be limited, multiple studies demonstrate increases in abundance and dispersal of plant pathogenic fungi. Additionally, ecosystems weakened by global change-induced phenomena, such as drought, are more vulnerable to pathogen outbreaks. The shift from mutualistic fungi to plant pathogens is likely the largest potential threat for the future functioning of natural and managed ecosystems. However, our ability to predict global change effects on fungi is still insufficient and requires further experimental work and long-term observations.

**Key words:** drought, elevated CO<sub>2</sub>, global change, mycorrhiza, nitrogen deposition, warming.

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## INTRODUCTION

Over the past century, CO<sub>2</sub> levels have steadily increased, and global temperatures have risen accordingly. The climate is predicted to continue to change, with increased variability in rain and temperature extremes, both inter- and intra-annually (IPCC 2014, Lee *et al.* 2021), and affect the whole biosphere including soils. In addition to the changing climate, it is the change of global atmospheric nitrogen (N) deposition that is perhaps the most threatening global phenomenon. It has increased from 34 Tg N/y in 1860 to 93.6 Tg N/y in 2016 (Ackerman *et al.* 2019) and is predicted to continue increasing worldwide as the result of human activity. Whether soils will become a source or sink of greenhouse gases under future climate scenarios is difficult to predict due to unclear changes in soil carbon and nitrogen pools, and differences in microbial responses between ecosystems and locations (Jansson & Hofmockel 2020), but there is a justified concern that soils will be heavily affected.

Fungi are eukaryotic microorganisms that play multiple fundamental roles related to the future of soil health. As major decomposers of organic matter, mutualists, or pathogens, fungi significantly influence plant health, carbon mineralisation and sequestration, and act as important regulators of the soil carbon balance (Crowther *et al.* 2016). It is thus important to determine how climate and other global change factors affect future soil fungal communities. The responses of the plant associated guilds to global change factors will likely be of particular interest due to their effects on plant communities. Mycorrhizal fungi act as mutualistic symbionts to plants, providing access to critical nutrients and can ameliorate abiotic stressors associated with climate change, such as heat and drought (Redman *et al.* 2002, Kivlin *et al.* 2013). Plant

pathogenic fungi, on the other hand, may opportunistically attack plant hosts that are under stress due to the rapid change in their environment (Juroszek *et al.* 2020, Desaint *et al.* 2021). Therefore, soil fungi, particularly plant associated guilds, mediate the effects of global change on natural vegetation and agricultural crops in multiple ways.

In addition to direct effects, climate change can indirectly affect soil fungi through shifts in soil chemistry and vegetation structure (Tedersoo *et al.* 2014, Větrovský *et al.* 2019, Zhou *et al.* 2020). It is thus important to understand how global change affects soil fungi. Even though this question has been repeatedly addressed in many contexts and settings in the past, it is still difficult to give a general answer. Soil is the habitat with the highest fungal diversity (Baldrian *et al.* 2021) and generalisations based on the observed response of individual species are difficult. This high diversity is associated with high levels of functional redundancy in the communities of saprotrophic as well as symbiotic fungi (Žifčáková *et al.* 2017). Consequently, loss of some species may in theory be replaced by other taxa. However, the critical level of species loss with consequences for ecosystem processes remains largely unknown. Additionally, the diversity, and dependence on plant hosts, of fungal lifestyles (*i.e.*, free-living saprotrophs, mutualistic symbionts and plant pathogens) affect fungal species responses to climate change.

In this review, we will discuss the links between soils, plants, and fungi to explore the paths by which global change affects fungi and their roles in soils. We will also estimate taxon realised niche space to make predictions about the relative sensitivity of various fungi to global change. Lastly, we will use the accumulated information from experimental manipulations of ecosystems to find general patterns in fungal responses to individual global

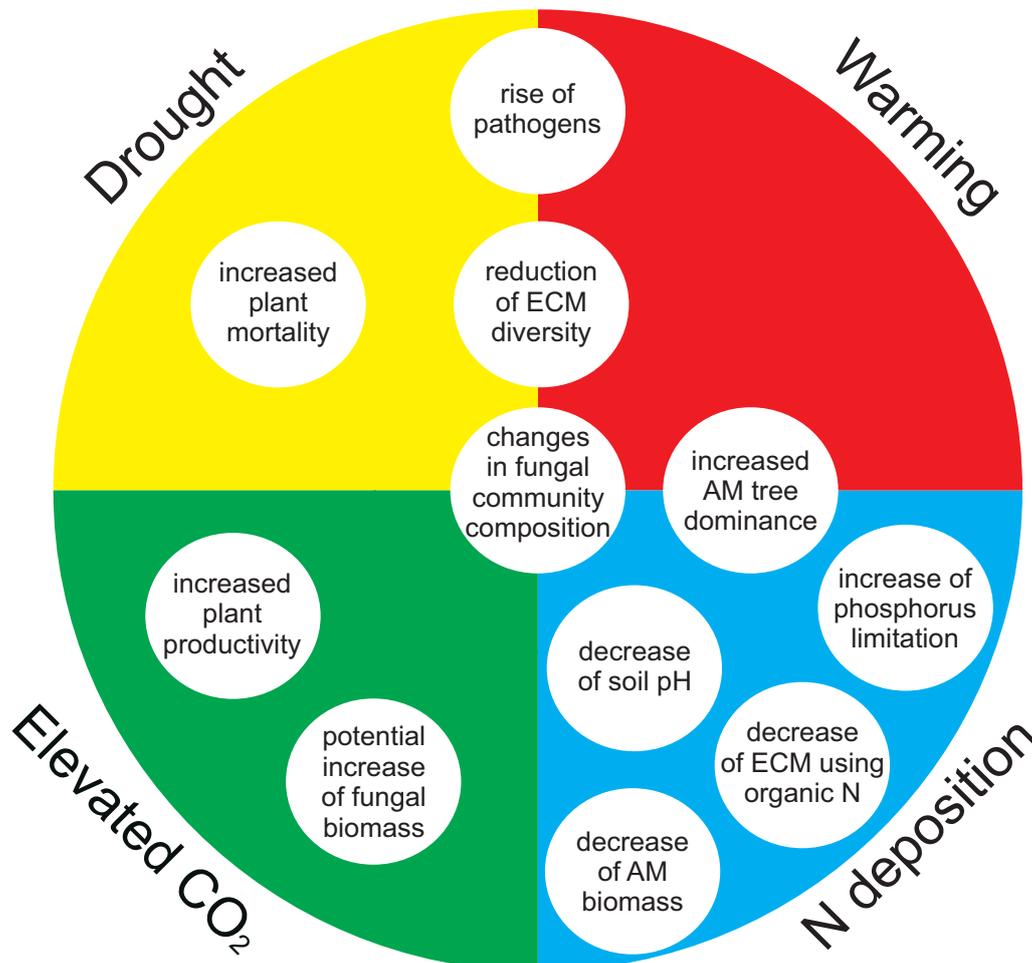
change factors. For simplicity, we will cover only selected global change processes, namely the increasing CO<sub>2</sub> levels, warming, reduction in precipitation and N deposition (Fig. 1) since these effects are general and long-lasting. While there is a whole suite of other important phenomena linked with global change, such as land use change, biological invasions, increased fire frequency or increased phosphorus (P) input, these factors are very often geographically local or appear at limited temporal scales which makes the predictions of their effects on fungi difficult. This review adds to our knowledge of belowground communities' responses to global change by focusing on soil fungi, comparing the possible and current responses of plant pathogens to that of mycorrhizal symbionts, leveraging estimates of fungal guilds realised niches to predict their responses, and only synthesising studies that impose realistic global change manipulations.

## Fungi and their climatic niche

Utilisation of the niche concept is one approach to predicting the response of fungi to climate change: if we understand the constraints for fungal life, we can identify and localise the environments where they can live. The concept of the ecological niche provides a framework for understanding resource partitioning by organisms and emergent patterns of coexistence and distribution (MacArthur & Levins 1967). Realised niches define the conditions under which organisms can survive and reproduce in the presence of biotic interactions while fundamental niches are defined in the absence of biotic interactions. While the realised niche can be derived from

a species' distribution and abundance across habitat properties (Veresoglou *et al.* 2012, Davison *et al.* 2021), characterisation of the fundamental niche is more difficult, because it requires experimental investigation of responses to environmental gradients (Lekberg *et al.* 2007). However, knowing parameters of the fundamental niches of species would be a valuable tool for the prediction of species' responses to changing abiotic environments. The fundamental niche provides information on species' potential responses without the influence of biotic interactions, which must also be expected to change along with abiotic changes (Blois *et al.* 2013).

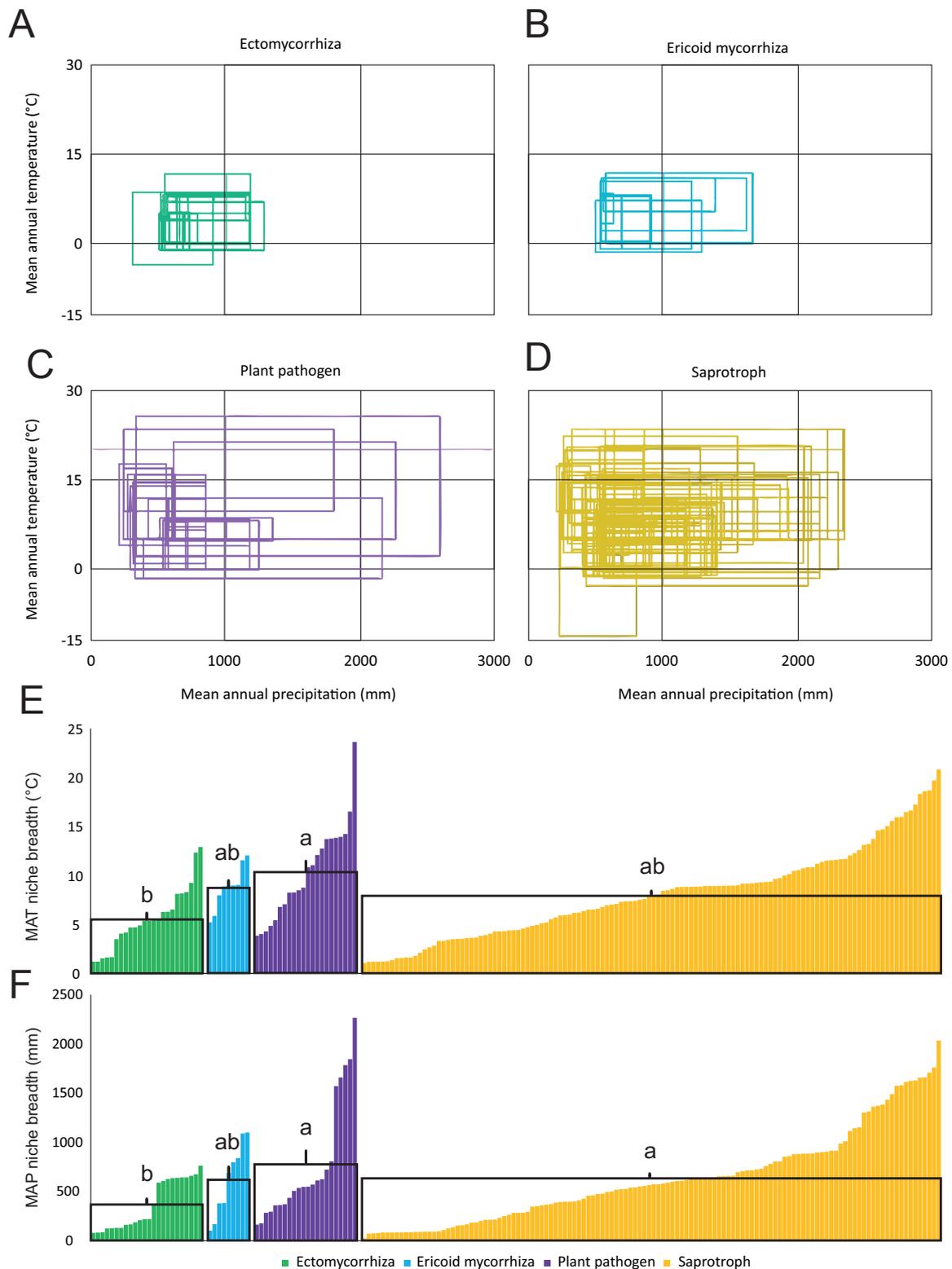
In a global metastudy of soil fungal occurrences using available high-throughput sequencing data, climatic factors contributed, on average, 40–80 % of total explained variability, substantially more than the soil and vegetation properties (Větrovský *et al.* 2019). Though climatic factors are generally found to be among the most important drivers of global fungal composition, their relative importance varies between studies. For example, Bahram *et al.* (2018) found that soil carbon-to-nitrogen ratio was the most important driver of fungal abundance, taxonomic and gene composition while Tedersoo *et al.* (2014) found that soil pH was a major driver of many fungal guilds. Of the climatic factors tested, Větrovský *et al.* (2019) found that mean temperature of driest quarter, precipitation seasonality, mean temperature of wettest quarter, precipitation of coldest quarter and diurnal temperature range were most often the strongest predictors of individual species distributions. Here we used mean annual temperature (MAT) and mean annual precipitation (MAP) to define species realised niches because these metrics are the most widely used and intuitive



**Fig. 1.** Major current and predicted responses to global change factors. Responses to each factor is represented by the location within each section with responses spanning multiple sections indicating the importance of multiple climate change factors.

defining features of biomes and local climates, are known to affect both soil biota and plants (Jetz *et al.* 2012, Thompson *et al.* 2017) and MAT was identified as the strongest predictor of the local distribution of macrofungi within Norway (Wollan *et al.* 2008). If we define the breadth of the realised climatic niche as the range of MAT / MAP where 90 % of occurrences are observed, fungal

species typically inhabit soils within 5–15 °C difference in MAT and 300–1 200 mm difference in MAP (Větrovský *et al.* 2019), although niche breadth varies largely among individual taxa (Fig. 2). When we compared the 200 most common soil fungi (taxa occurring in > 99 samples worldwide) based on their membership in ecological guilds, the mean annual temperature at the location of occurrence



**Fig. 2.** Realised niches of the 200 most frequently observed fungal species in global soils. In panels A–D, each species is represented by a rectangle representing the lower and upper decile of the mean annual precipitation (MAP) and mean annual temperature (MAT) of locations from where it was reported. Colours indicate ecological guild membership: A) green – ectomycorrhizal fungi (n = 24), B) blue – ericoid mycorrhizal fungi (n = 9), C) purple – plant pathogens (n = 22), and D) yellow – saprotrophs (n = 125). The distribution of fungal species niche breadth in E) MAT and F) MAP with color representing guilds and pairwise significant difference between means represented by letters. Individual species are represented with columns. Data from (Větrovský *et al.* 2019).

**Table 1.** Realised niche of fungal guilds of the 200 most common soil fungi from Větrovský *et al.* (2019). The centre of the niche space is represented by the mean guild Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP) while the size is represented by the range of MAT and MAP between the first and the ninth decile of all observations.

Fungal Guild	n	Mean MAT (mean $\pm$ SD °C)	Mean MAP (mean $\pm$ SD mm)	Range MAT (°C)	Range Mean Annual Precipitation (mm)
ectomycorrhizal fungi (ECM)	24	4.8 $\pm$ 2.2	714 $\pm$ 124	5.5	365
ericoid mycorrhizal (ERM) fungi	9	4.9 $\pm$ 1.7	838 $\pm$ 194	8.7	616
saprotrophs	125	7.7 $\pm$ 3.3	809 $\pm$ 249	7.9	630
plant pathogens	22	8.1 $\pm$ 3.7	807 $\pm$ 316	10.3	774

was lowest for ectomycorrhizal (ECM) fungi followed by ericoid mycorrhizal (ERM) fungi, saprotrophs, and plant pathogens while there was less variation between guilds in the observed mean annual precipitation (Table 1). More importantly, the size of the realised temperature and precipitation niche (the range of MAT and MAP between the first and the ninth decile of all observations) was smaller in ECM fungi than in saprotrophs, ERM fungi, and plant pathogens (Table 1; Fig. 2; Větrovský *et al.* 2019). Narrow breadth of the temperature niche in ECM fungi across climatic gradients was also observed within a smaller geographic extent spanning Japan (Miyamoto *et al.* 2018).

Since plant pathogens tend to inhabit warmer areas, and individual species extend both into drier and wetter climates than the ECM fungi (Fig. 2), warming will likely more negatively affect plant-beneficial fungi than plant pathogens (Větrovský *et al.* 2019). Supporting our prediction of increased soil pathogens, a recent global model of current and projected distributions of plant pathogens showed likely increases in pathogen abundance with MAT predicted to be the major driver (Delgado-Baquerizo *et al.* 2020a). Furthermore, there is evidence that the niches of pathogens may lack trade-offs between biotic and abiotic niche breadths (Chaloner *et al.* 2020) and may be more labile than that of plant mutualists such as AM fungi (Bebber & Chaloner 2022) suggesting that pathogens may adapt more rapidly to future climates than plant mutualists. It should be noted that the niche concept can be, in theory, extended to other global change factors as well. For example, the response of ectomycorrhizal fungi to nitrogen availability is known for several taxa (van der Linde *et al.* 2018). However, the limited number of species with reasonable information on their niche breadth, and missing data on local N availability (which exhibits much higher spatial variability than climate), make this concept at present unusable for predicting responses to altered N.

## Ecological guilds of fungi and global change

As already discussed, global surveys of soil fungal occurrences in the GlobalFungi database (Větrovský *et al.* 2020) show that members of various fungal guilds differ in the size of their climatic niche. Moreover, the level of dependence on vegetation varies from obligate biotrophs to free-living fungi. Due to this, global changes are expected to affect various ecological guilds of soil fungi (ECM fungi, AM fungi, ERM fungi, plant pathogens and saprotrophs) differently, affecting their relative share or community composition. These shifts may subsequently result in changes in various ecosystem processes such as decomposition rate or plant performance.

Importantly, climate change-driven shifts in plant communities may lead to shifts in the host availability affecting those fungi that

have a narrow host range. With increasing warming, some alpine communities have seen the replacement of forbs with deep rooted grasses (Liu *et al.* 2018) and increasing nitrogen deposition can lead to reduced species richness though this effect depends on ecosystem characteristics, such as mean annual precipitation (Clark *et al.* 2007). Altered environmental conditions promote not only natural range shifts of plants species (Rudgers *et al.* 2014), but also enable naturalisation of alien plant species outside their native distribution range (Seebens *et al.* 2015). Such events can affect local ecosystems and their fungal components in several ways: by competition for resources, by the introduction of novel fungal species (such as mycorrhizal symbionts or pathogens), or by selective recruitment of root-associating fungal species already present in the local pool by the alien plants (Rudgers *et al.* 2020, Vlk *et al.* 2020a). Because of all these factors, changes in local fungal communities are expected as has been already observed for plant introductions (Vlk *et al.* 2020b).

Due to the complex effects of N on soil chemistry and vegetation, and the fact that mutualistic mycorrhizal fungi mediate its transfer to plants, change in atmospheric deposition is perhaps the factor with greatest importance for guild composition of soil fungi (Fig. 1). Indeed, nitrogen addition to 25 grasslands distributed across four continents led to the increase of fungal pathogens, although it did not significantly affect AM fungi and saprotrophs. These guild level responses were primarily mediated through nutrient-induced shifts in plant communities (Lekberg *et al.* 2021). On the other hand, no consistent shifts in guild composition were observed across N-supplemented forests in the USA (Moore *et al.* 2021).

Among the various aspects of global change, changes in climate lead to severe ecosystem alterations. Forests are already facing increasing lengths of heat waves with unprecedented increases of temperature in high latitudes combined with long drought periods. This high level of climate stress likely increases the vulnerability of forests to disturbances including tree dieback and forest fires (Fig. 1; Allen *et al.* 2010). These severe forest disturbances were shown to result in a shift of fungal communities from those dominated by ectomycorrhizal fungi in undisturbed forests to those dominated by saprotrophs in disturbed forests (Štursová *et al.* 2014, Rodriguez-Ramos *et al.* 2021) as a response to changes in primary productivity.

### Mycorrhizal plant symbionts

Geographic distributions of plants with various mycorrhizal symbioses show climate-driven patterns. Temperature-related factors have been found to be the main predictors of the distributions of plant species forming AM, ECM, and ERM symbiosis. Recent models show AM plants to be favoured by warm climates, while dominance of ECM plants (and to some extent ERM plants) is more favoured by colder climates (Barcelo *et al.* 2019). Ectomycorrhizal symbiosis dominates forests in

which seasonally cold and dry climates inhibit decomposition and is the predominant form of symbiosis at high latitudes and elevation. AM trees dominate in grasslands and the warm-and-wet climates of tropical forests where enhance decomposition is typical (Steidinger *et al.* 2019). Warming can significantly alter the distribution of mycorrhizal host plants, with likely subsequent impacts on the proportion of various guilds of mycorrhizal fungi. In addition to warm climates, AM fungal colonisation has been found to be strongly related to soil carbon-to-nitrogen ratio and highest at sites featuring continental climates with mild summers and a high availability of soil nitrogen (Soudzilovskaia *et al.* 2015). In contrast, the intensity of ectomycorrhizal infection in plant roots maybe more related to soil acidity, soil carbon-to-nitrogen ratio and seasonality of precipitation and is highest at sites with acidic soils and relatively constant precipitation levels (Soudzilovskaia *et al.* 2015). As such, root colonisation by both guilds is predicted to respond to climatic factors and N deposition.

AM fungi primarily rely on inorganic forms of N (Phillips *et al.* 2013) or small organic N compounds (Whiteside *et al.* 2012). In contrast, some ECM fungi are thought to rely more heavily on organic N sources (Phillips *et al.* 2013), having a greater capacity to invest in N-degrading extracellular enzymes that access complex organic forms of N in soil, such as proteins and chitin (Fernandez & Kennedy 2016). ECM fungi are thus more associated with slower decomposition of soil organic matter and increased soil carbon (C) storage (Averill *et al.* 2014, Averill & Hawkes 2016, Fernandez & Kennedy 2016), potentially by competing with free-living soil microbes for organic N resources. These distinctions between AM and ECM fungi lead to two important predictions: (a) that inorganic N inputs to ecosystems will favour AM-associated trees at the expense of ECM-associated trees, and (b) that inorganic N-driven declines in ECM fungal abundance will reduce the belowground C storage capacity of the forest biome (Fig. 1). Indeed, recent nitrogen deposition across USA favoured the expansion of AM trees at the expense of ectomycorrhizal trees, and was spatially correlated with reduced soil carbon stocks (Jo *et al.* 2019). This implies that future changes in nitrogen deposition may further turn the balance between AM and ECM fungi in forest ecosystems (Averill *et al.* 2018).

### **Ectomycorrhizal fungi**

Despite the potential for climate change driven replacement of ECM with AM trees, most ecosystems are dominated by either ECM plant symbionts (in most temperate and boreal forests worldwide) or AM symbionts (in natural grasslands, croplands and tropical forests). Therefore, relative abundance of each guild or the change of within-guild species composition are the most likely responses. While shifts in dominant mycorrhizal type mediated by global changes will likely result in changes in nutrient cycles and soil carbon storage, consequences of potential shifts of within guild species composition are less clear.

Based on the assessment of present climatic drivers of ECM fungal distribution, under future climate scenarios North American *Pinaceae* forests are predicted to see as high as 26 % declines in ECM fungal species richness within 50 years, although there is a high level of regional variation (Steidinger *et al.* 2020). Furthermore, ECM fungal diversity across Japan was also demonstrated to significantly decrease with MAT (Miyamoto *et al.* 2018), suggesting potential decreases with warming. The observation of the ECM fungal community shift on *Betula papyrifera* and *Abies balsamea* saplings in a warming experiment (Fernandez *et al.* 2017) suggests that warming may change the future composition of the ECM fungal subcommunity.

Since N supply to plants is one of the major roles of ECM fungi, N deposition likely affects ECM fungal communities. With increasing nitrogen availability, fungi that obtain nitrogen from complex soil organic sources using metabolically costly pathways – e.g., *Cortinarius*, *Piloderma* and *Tricholoma* – are likely at a disadvantage compared to fungi that use inorganic nitrogen, such as *Elaphomyces* or *Laccaria* (Lilleskov *et al.* 2011). In a large survey of ECM fungi associated with forest trees in Europe, several ECM fungi responded to N throughfall deposition. Fungi that use organic nitrogen tended to be negative indicators for nitrogen deposition, while fungi that use inorganic nitrogen tended to be positive indicators. Conifer specialists – particularly those with abundant hyphae and rhizomorphs – were more negatively affected by increasing nitrogen than generalists and broad-leaf specialists (van der Linde *et al.* 2018). In the future, N deposition will likely affect ECM fungi and promote shifts from nitrophobic species (e.g., *Russula vinosa*, *Lactarius rufus*) to nitrophilic species (e.g., *Scleroderma citrinum*, *Amanita rubescens*, *Russula ochroleuca*) (Fig. 1; van der Linde *et al.* 2018).

In theory, mutualistic fungi could accompany host plants in climate-induced migration (Rudgers *et al.* 2020). In a study of the upward migration of tree individuals above the tree line, low ECM diversity was observed in the roots of migrating trees indicating that the altitudinal shift in the ECM fungal community lags behind climate-driven tree migration. ECM fungal dispersal limitation is thus an important factor controlling this process and possibly retarding vegetation shifts (Alvarez-Garrido *et al.* 2019). Similar conclusions were found in a study of invasive pines that clearly showed plant invasions can be limited by the dispersal of ECM fungi (Nunez *et al.* 2009).

### **Arbuscular mycorrhizal fungi**

Similar to ECM fungi, AM fungi also fully depend on their symbiotic host plants as a sole source of carbon (Tisserant *et al.* 2013) and therefore any environmental shifts may affect abundance, species richness and AM fungal community composition directly as well as indirectly by altering their host plants. A recent review of the response of AM fungal species richness and community composition to various aspects of global change found that elevated CO<sub>2</sub> will likely have no effect on AM fungal richness, and responses to N deposition, warming, and changed precipitation will likely be highly context dependent (Cotton 2018).

The effects of the above-mentioned extrinsic factors associated with global change are translated into community composition of AM fungi via differential responses of each species, which are determined by their intrinsic characteristics, such as specific growth patterns, morphology or anatomy. AM fungi greatly vary in root colonisation traits such as extent and structure (Klironomos & Hart 2002), and soil hyphal traits such as extent, density and structure (Powell *et al.* 2009). Interestingly, the increase of CO<sub>2</sub> concentration, as well as increases in N availability, leads to lower relative abundance of AM fungal taxa from the *Gigasporaceae* and *Diversisporaceae* families, which produce high levels of extraradical mycelia, while relative abundance of the *Glomeraceae* taxa, which are characterised by extensive intraradical colonisation, tend to increase (Cotton 2018). This shift in community traits suggests lower investments in potentially costly nutrient acquisition traits with increasing nutrient availability.

The community level responses to environmental conditions combined with various intrinsic characteristics indicate that niche optima and niche width may differ among the species of AM fungi. Large sampling campaigns, enabled by an onset of high-throughput

sequencing methods, provide sufficient data to model parameters of species ecological niches. While *Acaulosporaceae* has a realised niche optima in low temperature conditions, *Gigasporaceae* has a realised niche optima in high temperature and high precipitation conditions (Davison *et al.* 2021). Additionally, the width of the AM fungal temperature niche appears to be limiting, seeming to be narrower than in other fungal guilds (Větrovský *et al.* 2019, Davison *et al.* 2021). These findings indicate that changes of MAT and MAP can particularly affect the composition of AM fungal communities.

Contrary to diversity, the abundance of AM fungi seems to be more consistently affected by changes in N availability and shifts in CO<sub>2</sub> concentration. While the majority of studies report a decrease in AM fungal abundance with enhanced nitrogen (*e.g.*, Shen *et al.* 2014, Chen *et al.* 2017, Treseder *et al.* 2018, Zhang *et al.* 2018, Han *et al.* 2020, Jia *et al.* 2020a, Ma *et al.* 2021a), a few found no effect (Lilleskov *et al.* 2019, Karst *et al.* 2021). The addition of N can benefit AM fungi if it exacerbates plant P limitation (Johnson 2010), but may be suppressive if nitrophilic, ruderal plants replace plants that allocate more C to AM fungi (Isbell *et al.* 2013). Thus, the responses likely depend on the extent to which nutrient addition alleviates plant deficiencies and alters plant communities. A meta-analysis examining the global effects of nutrient enrichment on AM fungal and plant diversity showed that AM fungal diversity, rate of root colonisation, and extraradical biomass typically decreased with N addition, while spore abundance and hyphal length were unaffected. These results were consistent among forests, grasslands, and agro-ecosystems (Ma *et al.* 2021a).

The short-term fertilisation effect of elevated CO<sub>2</sub> concentrations mostly stimulated AMF abundance (*e.g.*, Treseder 2004, Antoninka *et al.* 2011, Zavalloni *et al.* 2012, Sun *et al.* 2017, Dong *et al.* 2018). Importantly, while stimulation of AM fungal abundance with increased CO<sub>2</sub> is expected, considering that plant productivity depends on nutrient supply by AM fungi, the increase of temperature and shifts in precipitation will likely affect AM fungal abundance thanks to a greater climate niche partitioning of AM fungi.

### Plant pathogens

Analyses of fungal guild niche breadth indicates that plant pathogens may better cope with climate change than other fungal guilds (Chaloner *et al.* 2020). Conditions that affect pathogen overwintering and dispersal are of essential importance due to pathogen lifestyles, survival in soils, and outbreaks triggered by climatic and plant host signals. Global warming in areas with seasonal temperature variation has increased pathogen survival during winters and increased the length of vegetation seasons leading to faster pathogen spread or stronger outbreaks (Harvell *et al.* 2002). As an ongoing consequence of warming, movement of crop pests to higher latitudes has already been observed. Since the 1960s, fungal crop pests were observed to move polewards at a pace of some 5 km/y, more rapidly than most other crop pests (Bebber *et al.* 2013).

Warming appears to be the most important driver of plant pathogen abundance. Climatic factors, especially the MAT and precipitation seasonality were the most important predictors of the relative abundance of plant pathogens across 235 global sites. Under future climate change and land-use scenarios, relative abundance of plant pathogens is predicted to increase (Delgado-Baquerizo *et al.* 2020a). A nine-year warming experiment in a dryland on the Iberian peninsula showed higher relative share of pathogens, higher relative abundance of *Alternaria* and higher absolute abundance of *Alternaria* in warmed plots (Delgado-Baquerizo *et al.* 2020a). While the increase in relative abundance,

or sporulation, of plant pathogens may increase the risk of a disease outbreak, direct causal links may be difficult to find. It is possible that negative responses of mycorrhizal fungi and neutral or positive responses of pathogens to climate change can subsequently manifest in negative responses of vegetation. More importantly, climatic events seem to be predictive factors of fungal disease outbreaks with high humidity and high temperature being the most common factors (Romero *et al.* 2022). Pathogens may also use the opportunity to attack weakened host communities such as forest ecosystems after dieback caused by drought or heat stress (Fig. 1; Anderegg *et al.* 2013).

In natural systems, pathogens appear to be more abundant in resource-rich environments (Reynolds *et al.* 2003, Revillini *et al.* 2016), and nutrient addition (*e.g.* fertilisation) has been linked to increased disease incidence in plants (Walters & Bingham 2007, Veresoglou *et al.* 2013) which may increase the risk of pathogen spread or outbreaks at elevated atmospheric N deposition. The effect of CO<sub>2</sub> increase on pathogens is less clear, however, concentrations of spores of several pathogens were increased by elevated atmospheric CO<sub>2</sub> (eCO<sub>2</sub>) in a *Populus tremuloides* plantation in air and litter. Although the responses of fungi were not uniform, significant increases were found in the potential pathogenic genera *Alternaria*, *Cladosporium* and *Fusarium* (Klironomos *et al.* 1997).

Plant pathogen community composition may not intrinsically affect ecosystems because it is often individual taxa that cause disease outbreaks. The effects of global change on individual plant pathogen taxa may thus be more important than the guild-level effects. Based on historical observations of higher *Alternaria* spp. spore concentrations at warm temperatures, spore concentrations are predicted to increase with warming in the United Kingdom (Maya-Manzano *et al.* 2016) and future climate models suggest increased prevalence of *Alternaria brassicae* in North Germany (Siebold & Tiedemann 2012). In several instances, eCO<sub>2</sub> increased spore production by *Alternaria* spp. several-fold (Klironomos *et al.* 1997, Wolf *et al.* 2010). Considering disease severity, both warming and eCO<sub>2</sub> has been shown to increase *Alternaria* leaf spot severity on rocket, cauliflower and cabbage (Pugliese *et al.* 2012, Siciliano *et al.* 2017).

To conclude, while differential response of ECM fungal species to global changes such as N deposition can be predicted from their extracellular enzymatic capabilities related to organic nitrogen accessibility, response of AM fungi depends on their differential colonisation traits. Species traits of saprotrophs or pathogens related to their response to global changes are much less clear and therefore predictions of global change effects on these two guilds are much more difficult.

### Fungal response to global change factors and lessons learned from manipulated studies

Our present understanding of the response of fungi to global change is based on several lines of support: (1) ecological theory and the predictions based on the known niches of fungal species, (2) predictions of responses to indirect factors affected by global change, such as the change of soil chemistry, vegetation composition, or ecosystem productivity, (3) extrapolation of observations of changes in fungal communities across time and space, (4) experimental simulation of future conditions and the analysis of fungal response. Since there is a lack of long-term observations on soil fungi under conditions of real-time climate

change and the extrapolation of such observations may be problematic, experimental manipulations simulating global change factors appear to be the best tool to predict the future of soil fungi.

Experimental approaches have several limitations that must be considered when interpreting results. Each of the experiments has at least three important aspects that affect the observations: (1) the duration of treatment, (2) the intensity of manipulation, and (3) the local conditions. Over the duration of treatment, several components of the system respond so that direct, and/or indirect, effects change in time and adaptations emerge. The plant communities likely respond first with altered productivity, while change in composition comes later (Smith *et al.* 2009). Importantly, the effects of short-term warming and/or precipitation experiments can be eclipsed by site specific year-to-year variation in climatic conditions. The intensity of manipulation is another critical issue. In many experiments, especially those simulating N deposition, the magnitude of treatments is considerably larger than those predicted by current models. Equally important, the target biome and local condition at the experimental sites can interact with the global change treatments. Moreover, soil fungi as the responding community are extremely diverse in terms of alpha and beta diversity (Baldrian *et al.* 2021) which limits the cross-ecosystem interpretation of community effects. Unfortunately, the experimental results reported so far show high levels of geographic bias with most studies in forests and grasslands of the temperate zone (Tables 2–5). These biases in sampling mean that surprising results from underexplored biomes, such as massive CO<sub>2</sub> fluxes from warmed plots recorded in the Panama tropical rainforest, cannot be ignored. Such fluxes largely exceeded model predictions and indicated high sensitivity of local soil C stocks to warming (Nottingham *et al.* 2020).

Here, we review the results from experimental simulations of climate change factors 1) elevated CO<sub>2</sub>, 2) warming, 3) reduction of precipitation, and 4) increased N deposition (Fig. 1). We ended up with 138 studies that applied realistic treatment types and levels (see each section) and reported at least one of the below response variables (Supp. S1). Though our survey is not exhaustive, we believe it is representative of the current state of knowledge. We decided to focus on the commonly studied fungal responses biomass, diversity, guild share, and changes in community composition. Though these responses are interconnected (*e.g.*, changes in fungal diversity will likely lead to changes in composition), we decided to survey all factors to highlight the current focuses of research into the responses of fungi to climate change factors. The analyses of diversity, guild share, and changes in community composition largely rely on meta-barcoding sequencing, which we recognise as suffering from biases such as primer bias and the use of relative abundances (Quinn *et al.* 2018, Alteio *et al.* 2021), it is still the best tool for understanding fungal communities (Nilsson *et al.* 2018). All recorded responses are taken directly from the results sections and therefore represent current interests in the field.

### Increase of CO<sub>2</sub> concentration

Elevated CO<sub>2</sub> partially underlies global increases in plant productivity (Nemani *et al.* 2003). Furthermore, experimentally elevated atmospheric CO<sub>2</sub> concentrations (eCO<sub>2</sub>) have led to short term increases in plant biomass production, allocation of carbon to roots and to soil (Adair *et al.* 2011) and consequently soil respiration. The higher C allocation belowground can fuel the breakdown of labile organic matter by copiotrophic microorganisms. Therefore, microbial biomass and heterotrophic respiration will likely increase (Fig. 1; Naylor *et al.* 2020). At longer time scales, eCO<sub>2</sub> has been shown to increase microbial decomposition of soil organic matter

(SOM) through priming (van Groenigen *et al.* 2014). Direct effects on individual fungi are unlikely since CO<sub>2</sub> concentration in soil pores is higher than in the atmosphere and varies in space and time.

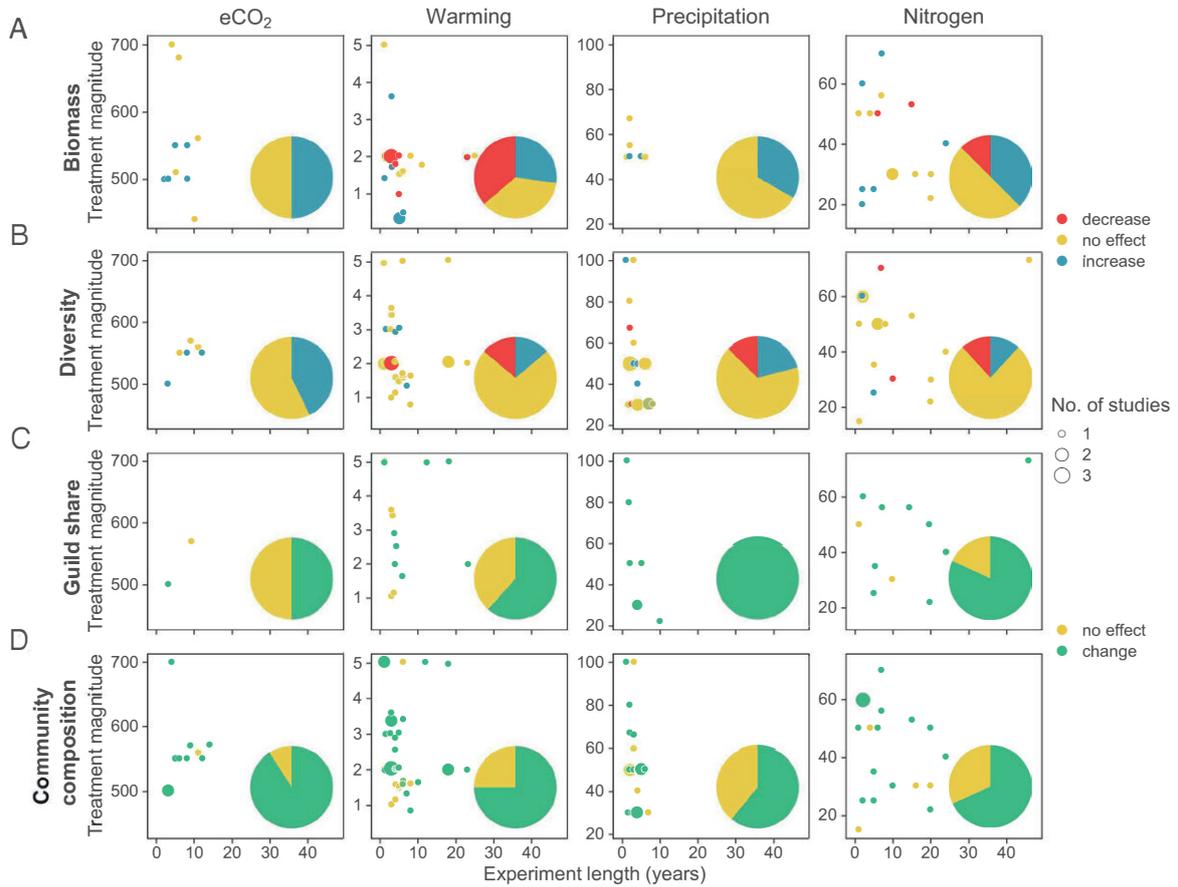
Furthermore, eCO<sub>2</sub> may affect fungal propagation and dispersal. Under an 2x-ambient CO<sub>2</sub> treatment in a *Populus tremuloides* plantation, the concentration of airborne fungal propagules, mostly spores, increased fourfold. Analysis of decomposing leaf litter (likely the main source of airborne fungal propagules) indicated that fungi produced fivefold more spores (Klironomos *et al.* 1997). Furthermore, increased total sporocarp biomass was observed in an eCO<sub>2</sub> experiment (Andrew & Lilleskov 2009). Since fruiting and sporulation is the main mode of dispersal of soil fungi, consequences of this observation – if confirmed in additional systems – may be important.

Across the studies we surveyed, eCO<sub>2</sub> experiments report either no change or increased biomass and diversity of all fungi, and only single cases of reduced AM fungal diversity and change in guild composition. Most experiments report change in the fungal community composition but there were no consistent observations of enriched or suppressed taxa (Fig. 3, Table 2). Though we found no clear relationship between fungal responsiveness and experimental length (Figs 3, 4), a meta-analysis of 11 studies found a positive relationship between increased fungal richness due to eCO<sub>2</sub> and experimental length (Veresoglou *et al.* 2016). A recent global meta-analysis found no relationship between experimental length and the responsiveness of fungal biomass, but found that eCO<sub>2</sub> decreased the F/B ratio across 31 studies (Sun *et al.* 2021). In our survey, the longest experiments showed contrasting effects on soil chemistry. A forest-based experiment reported significant decreases in pH, organic matter content, and P and increased water content (Weber *et al.* 2013) which may all potentially affect fungi. However, a grassland experiment of a similar length reported no significant change in soil chemistry (Maček *et al.* 2019).

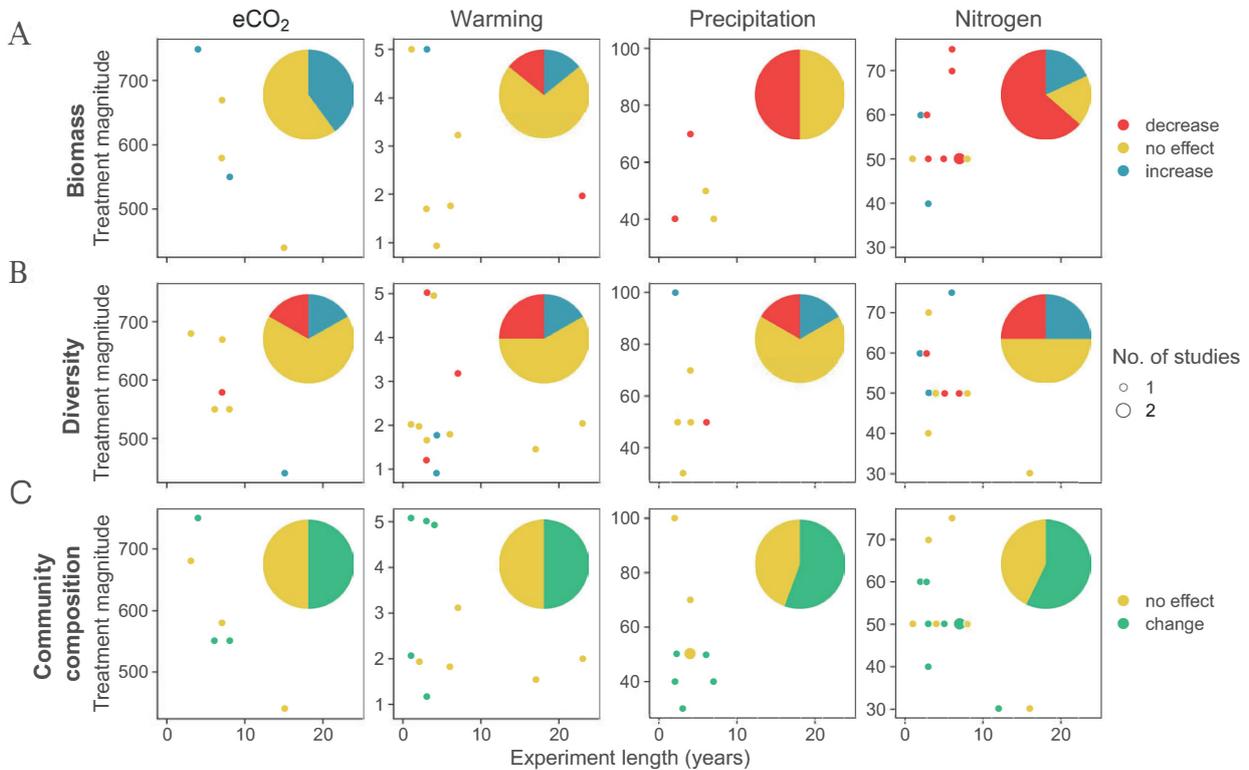
### Warming

In agreement with the increasing catalytic performance of soil enzymes with increasing temperature (Baldrian *et al.* 2013), C turnover across global biomes has been shown to increase with temperature (Carvalhais *et al.* 2014). Temperature sensitivity of soil C loss appears higher in cold regions (Crowther *et al.* 2016, Koven *et al.* 2017) and probably the most extreme response is expected in the permafrost where thawing dramatically increases organic matter transformation and the emissions of CO<sub>2</sub> and CH<sub>4</sub> (Jansson & Tas 2014). The expected C losses are large since the soils in cold regions host large C stocks (Crowther *et al.* 2019, García-Palacios *et al.* 2021). Additionally, warming has led to the loss of plant species unable to tolerate new environmental conditions (Freeman *et al.* 2018) or outcompeted by invaders better adapted to the new conditions (Alexander *et al.* 2015). These shifts in plant species composition may alter the quality of the carbon input into the system (Harte *et al.* 2015). Shifts in fungal saprotroph communities in response to both increased access to extant carbon and novel carbon inputs will have important implications for global responses to climate change (García-Palacios *et al.* 2021).

The responses of soil fungal communities to warming likely depends on the local climatic conditions, such as MAT. Not surprisingly, in the Antarctic, at the lower limit of fungal temperature tolerance, air temperature is the strongest and most consistent predictor of soil fungal diversity and, with current rates of warming, a 30 % increase in fungal diversity is predicted by 2100 (Newsham *et al.* 2016). However, this diversity response to warming is probably not universal since the highest level of fungal diversity



**Fig. 3.** Observations of the effects of selected global change factors on the A) biomass, B) diversity, C) guild composition and D) community composition of total fungi in the context of experimental length and magnitude of treatment. The pie graphs indicate the total share of experiments reporting statistically significant effects (increase, decrease, no change). Treatment intensities are in ppm applied for CO<sub>2</sub>, increase in °C in temperature manipulation, percent reduction in precipitation and kg/ha/y in N addition. For the lists of experiments, see Tables 1–4.



**Fig. 4.** Observations of the effects of selected global change factors on the A) biomass, B) diversity and C) community composition of AM fungi in the context of experimental length and magnitude of treatment. The pie graphs indicate the total share of experiments reporting statistically significant effects (increase, decrease, no change). Treatment intensities are in ppm applied for CO<sub>2</sub>, increase in °C in temperature manipulation, percent reduction in precipitation and kg/ha/y in N addition. For the lists of experiments, see Tables 1–4.

**Table 2.** Effects of experimental CO<sub>2</sub> enrichment on fungi. Manipulations of at least 1 y duration where CO<sub>2</sub> enrichment was not combined with other factors were considered.

Location	Experimental system	Duration of treatment (yr)	CO <sub>2</sub> concentration applied (ppm)	Biomass	Diversity	Guilds share	Community composition	Reference <sup>1</sup>
<b>All fungi</b>								
Asia (China)	cropland	2	500	+			change	Liu <i>et al.</i> (2014)
Asia (China)	cropland	3	500	+	0		change	Liu <i>et al.</i> (2017)
North America (USA)	experimental grassland	3	500		0 / +	change (more AMF)	change	Procter <i>et al.</i> (2014)
Asia (China)	shrubland	4	700	0			change	Jia <i>et al.</i> (2020b)
Europe (Denmark)	shrubland	5	510	0				Haugwitz <i>et al.</i> (2014)
Australia (Australia)	grassland	5	550	+			change	Hayden <i>et al.</i> (2012)
North America (USA)	grassland	6	680	0				Gutknecht <i>et al.</i> (2012)
Europe (Italy)	forest plantation	6	550		0		change	Lagomarsino <i>et al.</i> (2007)
Asia (China)	cropland	8	500	+				Liu <i>et al.</i> (2021a)
North America (USA)	shrubland	8	550	+	+		change	Lipson <i>et al.</i> (2014)
Europe (Switzerland)	experimental forest	9	570		0	no change	change	Solly <i>et al.</i> (2017)
Europe (Germany)	grassland	10	440	0				Guenet <i>et al.</i> (2012)
North America (USA)	forest plantation	11	560	0	0		no change	Dunbar <i>et al.</i> (2014)
North America (USA)	experimental field	12	550		+		change (more Basidiomycota, less Ascomycota)	Tu <i>et al.</i> (2015)
North America (USA)	forest plantation	14	571				change	Weber <i>et al.</i> (2013)
<b>Arbuscular mycorrhizal fungi</b>								
North America (USA)	experimental field	2; 4; 6	550		0		change (more Glomeraceae and Gigasporaceae)	Cotton <i>et al.</i> (2015)
North America (USA)	grassland	3	680		0		no change	Mueller & Bohannan (2015)
North America (USA)	shrubland	3.4–3.9	up to 750	+			change (more Acaulospora and Scutellospora)	Treseder <i>et al.</i> (2003)
Europe (Switzerland)	experimental field	7	600	+ (root colonisation)				Gamper <i>et al.</i> (2004)
North America (USA)	orchard	7	670	0	0			Kimball <i>et al.</i> (2007)
Asia (China)	grassland	7	580	0	-		no change	Zheng <i>et al.</i> (2022a)
North America (USA)	grassland	7	560	+ (soil hyphae)				Antoninka <i>et al.</i> (2011)
Asia (India)	experimental field	8	550	+	0		change	Panneerselvam <i>et al.</i> (2020)
Europe (Germany)	grassland	15	440	0 (root colonisation)	+		no change	Maček <i>et al.</i> (2019)

is predicted in cold areas (Větrovský *et al.* 2019). Similar to soil fungi, the highest diversity of bacteria in global surveys has also been observed at locations with relatively low MAT (around 10 °C; Thompson *et al.* 2017) and temperate regions (Bahram *et al.* 2018), although bacterial biomass in soils does not seem to be affected by warming (Lladó *et al.* 2017).

Short-term and prolonged warming may have differing effects. An initial loss of labile soil carbon in one of the longest running warming experiments in the Harvard Forest was later followed by increased degradation of more recalcitrant carbon compounds. Sustained warming for 26 years resulted in the depletion of soil organic carbon (SOC) with corresponding reductions in microbial biomass (Melillo *et al.* 2017). Based on a meta-analysis, warming initially increases soil respiration, but the magnitude of observed effect declines significantly as warming progresses and in fact, after 10 years of warming, soil respiration in experimentally warmed plots was similar to controls. Microbial acclimation, community shifts, adaptation, or reductions in labile C may ameliorate warming effects on soil respiration in the long-term. Accordingly, long-term soil C losses might be smaller than those suggested by short-term warming studies. The share of experiments where fungal biomass increased versus decreased with warming have been found to be roughly equivalent and no significant change in the fungal to bacterial (F/B) biomass ratio were observed across studies (Romero-Olivares *et al.* 2017). The F/B ratio was also unaffected after 7–25 yr of warming across 12 experiments in the Alpine and Arctic tundra (Jeanbille *et al.* 2021).

Temperature also alters fungal fruiting with consequences for dispersal. Across Europe, timing of fruiting has been shown to vary by 25 d among latitudes and 30 d among altitudes suggesting a strong temperature effect (Andrew *et al.* 2018). Present-day autumn fruiting of fungi has been shown to occur later than in the past, and the fruiting season length has increased, similar to the vegetation season (Kausserud *et al.* 2012). There has also been shown to be a significant shift in fruiting of saprotrophic and ectomycorrhizal fungi towards higher altitudes in the Swiss Alps between 1960 and 2010 as a consequence of warming (Diez *et al.* 2020).

Warming was the most frequently applied treatment in our survey (47 % of studies) and as such gives the best opportunity for generalisations. Importantly, warming was most frequently reported to alter total fungal biomass and a substantial fraction of the observations indicate negative effects, especially between 3–5 yr of application. In longer-lasting experiments, however, the effects on fungal biomass were less pronounced and AM fungi seem to be even less affected. Both negative and positive effects on total fungal diversity were reported but no effects were reported for experiments running for more than three years; furthermore, the decrease of AM fungal diversity was also observed only in the short term (Figs 3, 4, Table 3). Many individual experiments reported significant effects on fungal guild composition, which were, however, context-dependent. The only exception is the effect on plant pathogens where all reports showed their increase (Table 3). Most warming experiments also reported change in fungal community composition, often within the ectomycorrhizal guild (Fernandez *et al.* 2017, van Nuland *et al.* 2020) and a decrease of the *Glomeraceae* was recorded within the AM fungi (Cao *et al.* 2020a, b). Interestingly, almost all studies with experimental lengths longer than 10 yr or any experimental length with warming treatments larger than 2 °C reported significant changes in fungal community composition. In partial support of our survey, a recent global meta-analysis found that warming decreased fungal richness but that there was no significant effect of experimental

length on this response (Li *et al.* 2022). There were no reports of important changes in soil nutrient content or pH but some of the long-term experiments report the decrease of the F/B biomass ratio (Gutknecht *et al.* 2012) and lower transcription of hydrolytic enzymes (Romero-Olivares *et al.* 2019), two factors that may be connected since fungi are important producers of enzymes in soils (Starke *et al.* 2021).

### **Reduction of precipitation**

Since soil C turnover across global biomes increases with precipitation (Carvalhais *et al.* 2014), any change in precipitation likely affects C cycling. Responses of plant communities to increased variability in precipitation have ranged from high ecosystem stability in the face of intra-annual variability (Jones *et al.* 2016) to increasing functional diversity with increased inter-annual variability (Gherardi & Sala 2015). Even when there is very little recorded change in plant community diversity, significant changes in species composition through reordering have been recorded (Jones *et al.* 2017). While climate models predict both decreases and increases in precipitation across global locations (IPCC 2014), drought effects on ecosystems are likely much more dramatic. Increases in the durations of drought are expected to be a major consequence of future climate and increased desertification is predicted for most semi-arid or arid regions in the coming decades (Huang *et al.* 2016). Based on a recent meta-analysis, terrestrial ecosystem productivity was decreased by drought across all ecosystems (Wang *et al.* 2021a). The response of productivity to drought are more pronounced with higher drought intensity and longer duration, and consistent across biomes and climates. Drought can significantly decrease soil moisture, soil C content, soil C:N ratios, and microbial biomass C, whereas it tends to increase soil pH. The relative proportion of fungal biomass (F/B ratio) however, frequently increases with drought (Delgado-Baquerizo *et al.* 2020b, Wang *et al.* 2021a). The diversity and abundance of soil bacteria and fungi have been shown to decrease in drylands as aridity increased, being largely driven by the negative impacts of aridity on soil organic carbon content (Maestre *et al.* 2015).

Since most global change models predict changes in precipitation, experimental manipulations of precipitation are relatively frequent. Unfortunately, such manipulations are highly diverse and range from reduction and addition to redistribution. Both reduction and addition are frequently combined often without a clear link to a model prediction for the ecosystem under study (Knapp *et al.* 2015). Moreover, many experiments use manipulations that are likely outside the model predictions with reductions or additions > 50 % and the relevance of such manipulations is thus unclear. For simplicity, we surveyed the effects of precipitation reduction since drought seemed to have more profound ecosystem consequences (Table 4).

In our survey, no negative effects of precipitation on total fungal biomass were reported with most experiments reporting no effect on any response variable (Fig. 3, Table 4). In studies of AMF, there was decreased hyphal, spore density, and root colonisation in a forest system in connection with soil acidification (Maitra *et al.* 2019) and a reduction in root colonisation in a perennial cropping system (Emery *et al.* 2022). Reduction of precipitation most frequently did not affect the diversity of fungi and AM fungi and decrease of total fungal diversity was never observed in manipulations lasting three or more years (Figs 3, 4, Table 4). Contrary to our survey, a recent global meta-analysis found that precipitation reduction led to increased fungal richness with the effect size increasing with experimental length, though precipitation reduction had no effect on fungal

**Table 3.** Effects of experimental warming on fungi. Manipulations of at least 1 yr duration where warming was not combined with other factors were considered.

Location	Experimental system	Duration of treatment (yr)	Temperature increase (°C)	Biomass	Diversity	Guilds share	Community composition	Reference
<b>All fungi</b>								
Asia (China)	grassland	1	2.0		0		no change	Zhang <i>et al.</i> (2016a)
North America (USA)	forest	1	5.0		0	change (more plant pathogens, less AMF)	change	Garcia <i>et al.</i> (2020)
North America (USA)	experimental field	1	5.0	0		no change	change	Anthony <i>et al.</i> (2020)
South America (Brazil)	experimental field	1	2.0		0		change (more <i>Hypocreales</i> , less <i>Pleosporales</i> )	de Oliveira <i>et al.</i> (2020)
Asia (China)	forest plantation	1.2	1.4	+				Liu <i>et al.</i> (2021b)
Asia (China)	grassland	1.3	1.0; 2.0		0		change	Xiong <i>et al.</i> (2014)
Asia (South Korea)	forest plantation	1.5	3.0		+		change	Li <i>et al.</i> (2017)
North America (Canada)	grassland	1–2	2.0	0				Bell <i>et al.</i> (2010)
Asia (China)	grassland	1; 2; 4	1.6		0		no change	Shi <i>et al.</i> (2020)
North America (USA)	grassland	1–5	3.0		+		change	Guo <i>et al.</i> (2019)
Asia (China)	cropland	2	2.0	variable	-		change	Liu <i>et al.</i> (2014)
Asia (South Korea)	forest plantation	2.7	3.0		0		change	Li <i>et al.</i> (2018)
Asia (China)	experimental grassland	3	1.5; 2.0		- / 0		change	Zhang <i>et al.</i> (2016b)
Asia (China)	cropland	3	2.0	-	-		change	Liu <i>et al.</i> (2017)
Asia (China)	experimental grassland	3	1.5; 2.0		- / 0		change	Zhang <i>et al.</i> (2017)
North America (USA)	forest	3	1.7; 3.4			no change	change (within ECM community)	Mucha <i>et al.</i> (2018)
North America (USA)	forest plantation	3	1.7; 3.4		0		change (within ECM community)	van Nuland <i>et al.</i> (2020)
North America (USA)	desert	3	2.0	-				Zelikova <i>et al.</i> (2012)
Asia (China)	grassland	3	1.7	+				Ding <i>et al.</i> (2020)
Asia (China)	grassland	3	1.5; 2.0				no change	Zhang <i>et al.</i> (2019)
Asia (Japan)	grassland	3	2.0	-				Yoshitake <i>et al.</i> (2015)
Asia (China)	grassland	3	1.8	-				Ma <i>et al.</i> (2011)
Europe (Switzerland)	forest plantation	3	3.6	+	0	no change	change	Solly <i>et al.</i> (2017)
North America (USA)	grassland	3	1.0		0	no change	no change	Jumpponen & Jones (2014)
Australia (Australia)	shrubland	4	2.9		0 / +	change (more plant pathogens)	change	Birnbaum <i>et al.</i> (2019)
Europe (Spain)	shrubland	4	2.5			change (less ECM)	change (within ECM community)	León-Sánchez <i>et al.</i> (2018)
Asia (China)	grassland	4	1.8	-				Li <i>et al.</i> (2013)

Table 3. (Continued).

Location	Experimental system	Duration of treatment (yr)	Temperature increase (°C)	Biomass	Diversity	Guilds share	Community composition	Reference
Europe (Norway)	tundra	4	0.6–1.1		0	no change	no change	Ahonen <i>et al.</i> (2021)
Europe (Spain)	shrubland	4	2		0	change (less ECM)	no change	Querejeta <i>et al.</i> (2021)
Asia (China)	forest plantation	5	1.5	0	0		no change	Wang <i>et al.</i> (2019)
Europe (Denmark)	shrubland	5	0.3	+				Haugwitz <i>et al.</i> (2014)
Asia (China)	grassland	5	1.0	-				Shao <i>et al.</i> (2018)
Asia (China)	grassland	5	0.3	+				Wang <i>et al.</i> (2017)
Australia (Australia)	grassland	5	2.0	-			change	Hayden <i>et al.</i> (2012)
North America (USA)	forest	6	3.4				change (within ECM community)	Fernandez <i>et al.</i> (2017)
Europe (Norway)	shrubland	6	1.7		0		no change	Lorberau <i>et al.</i> (2017)
Asia (China)	grassland	6	1.6	0	0	change (less AMF)	change (more <i>Dothideomycetes</i> )	Che <i>et al.</i> (2019)
North America (USA)	woodland	6	5.0		0		no change	Gehring <i>et al.</i> (2020)
North America (USA)	grassland	6	1.0			change (less AMF)		Gutknecht <i>et al.</i> (2012)
Asia (China)	shrubland	6	0.5	+				Song <i>et al.</i> (2021)
Asia (China)	grassland	7	1.3		0 / +		change	Yu <i>et al.</i> (2019)
Many (Many)		7–25	0.5–2.0	0				Jeanbille <i>et al.</i> (2021)
Asia (China)	cropland	8	2.0	0				Liu <i>et al.</i> (2021a)
Asia (China)	grassland	8	1.6		0		no change	Peng <i>et al.</i> (2020)
Antarctica (Antarctica)	desert	8	0.8	+	0		change	Kim <i>et al.</i> (2018)
North America (USA)	forest	10	1.6				change	Romero-Olivares <i>et al.</i> (2019)
Asia (China)	grassland	11	1.8	0				Zhang <i>et al.</i> (2015)
North America (USA)	forest	12	5.0	-		change (less AMF)	change	Frey <i>et al.</i> (2008)
North America (USA)	grassland	18	1.5–2.0		0		change	Geml <i>et al.</i> (2015)
North America (USA)	grassland	18	1.0–5.0		0	change (more plant pathogens and saprotrophs)	change (within <i>Ascomycota</i> )	Semenova <i>et al.</i> (2015)
North America (USA)	grassland	18	1.5–2.0		0		change	Geml <i>et al.</i> (2021)
North America (USA)	grassland	23	2.0	0 / -	0	change (more AMF)	change	Kazanel <i>et al.</i> (2019)
<b>Arbuscular mycorrhizal fungi</b>								
North America (USA)	experimental field	1	5.0	0			change	Anthony <i>et al.</i> (2020)
Europe (Germany)	cropland	1	2.0		0		change	Wahdan <i>et al.</i> (2021)
Asia (China)	grassland	2	2.0		0		no change	Wei <i>et al.</i> (2021)
Asia (China)	grassland	3	0.5–1.2		-		change	Shi <i>et al.</i> (2017)
Asia (China)	forest plantation	3	5.0	+ (root colonisation)	-		change (less <i>Glomeraceae</i> )	Cao <i>et al.</i> (2020b)

**Table 3.** (Continued).

Location	Experimental system	Duration of treatment (yr)	Temperature increase (°C)	Biomass	Diversity	Guilds share	Community composition	Reference
Asia (China)	grassland	3	1.2–1.7	0	0			Yang (2013)
Asia (China)	forest plantation	4	5.0		0		change (more <i>Gigasporaceae</i> , less <i>Glomeraceae</i> )	Cao <i>et al.</i> (2020a)
Asia (China)	grassland	4.3	1.8		+			Kim <i>et al.</i> (2015)
Asia (China)	grassland	4.3	0.9	0 (soil hyphal density)	+			Kim <i>et al.</i> (2014)
Asia (China)	grassland	6	1.8	0 (soil hyphal and spore density)	0		no change	Gao <i>et al.</i> (2016)
Asia (China)	grassland	7	1.5–3.2	0	-		no change	Zheng <i>et al.</i> (2022a)
Asia (China)	grassland	17	1.5		0		no change	Shi <i>et al.</i> (2021)
North America (USA)	grassland	23	2.0	0 / -	0		no change	Kazenel <i>et al.</i> (2019)

**Table 4.** Effects of experimental reduction of precipitation on fungi. Manipulations of at least 1 y duration where reduction of precipitation was not combined with other factors were considered.

Location	Experimental system	Duration of treatment (yr)	Reduction of precipitation (%)	Biomass	Diversity	Guilds share	Community composition	Reference <sup>1</sup>
<b>All fungi</b>								
North America (USA)	grassland	1	100		0		change	McHugh & Schwartz (2015)
Asia (China)	grassland	1	50		0		no change	Zhang <i>et al.</i> (2016a)
North America (Brazil)	experimental field	1	100		+	change (more selected plant pathogens)	no change	de Oliveira <i>et al.</i> (2020)
Asia (China)	forest plantation	1.2	50	0				Liu <i>et al.</i> (2021b)
Asia (Korea)	forest plantation	1.5	30		0		change	Li <i>et al.</i> (2017)
North America/ Australia (USA/ Australia)	grassland	1–2	50	0 / +	variable	change (less AMF)	change	Ochoa-Hueso <i>et al.</i> (2018)
Asia (China)	grassland	1–2	30; 50		0		no change	Yang <i>et al.</i> (2021b)
Asia (China)	cropland	1–2	30; 50		0		no change	Sun <i>et al.</i> (2020)
Asia (China)	grassland	1–2	20; 40; 60				change	Zhao <i>et al.</i> (2016)
Australia (Australia)	grassland	1; 2; 3	50		+		change	Ochoa-Hueso <i>et al.</i> (2020)
Asia (China)	grassland	1; 2; 4	50		+		change	Shi <i>et al.</i> (2020)
North America (USA)	grassland	1–5	50		-		change	Guo <i>et al.</i> (2019)

Table 4. (Continued).

Location	Experimental system	Duration of treatment (yr)	Reduction of precipitation (%)	Biomass	Diversity	Guilds share	Community composition	Reference <sup>1</sup>
Asia (China)	forest	2	67	0	-		change (more Basidiomycota, less Ascomycota)	Zhao <i>et al.</i> (2017)
Asia (China)	grassland	2	40; 80		0	change (more pathogens, less AMF)	change	Huang <i>et al.</i> (2021)
Europe (Belgium)	forest plantation	2	45–55	0				Hicks <i>et al.</i> (2018)
Asia (South Korea)	forest plantation	2.7	30		-		change	Li <i>et al.</i> (2018)
North America (USA)	grassland	2–3	66				change	Lagueux <i>et al.</i> (2021)
Asia (China)	grassland	3	0–100		0		no change	Wu <i>et al.</i> (2020)
Asia (China)	grassland	3	30; 60		0		no change	Wang <i>et al.</i> (2020a)
Australia (Australia)	shrubland	4	30		0	change (more ECM and plant pathogens)	change	Birbaum <i>et al.</i> (2019)
Europe (Spain)	shrubland	4	30		0	change (less ECM)	change (within EMF community)	León-Sánchez <i>et al.</i> (2018)
North America (USA)	grassland	4	40		0/+		no change	Narayanan <i>et al.</i> (2021)
Asia (China)	grassland	5	50		0	change (more plant pathogens)	change	Wang <i>et al.</i> (2020b)
Europe (Denmark)	shrubland	5	50	+				Haugwitz <i>et al.</i> (2014)
North America (USA)	woodland	6	50	0	0		no change	Gehring <i>et al.</i> (2020)
Asia (China)	grassland	6	50		0		change	Xiao <i>et al.</i> (2020)
Asia (China)	forest	7	30		0		no change	Zhang <i>et al.</i> (2021)
Asia (China)	grassland	7	30		0			Jia <i>et al.</i> (2017)
Asia (China)	forest	8	30		+			Yan <i>et al.</i> (2021)
North America (USA)	forest	10	22			change		Romero-Olivares <i>et al.</i> (2019)
<b>Arbuscular mycorrhizal fungi</b>								
Australia (Australia)	experimental grassland	1; 2; 3; 4	50				0	Deveautour <i>et al.</i> (2020)
Asia (China)	experimental field	2	100		+		0	Zhong <i>et al.</i> (2021)
North America (USA)	experimental grassland	2	40	- (root colonisation)			change	Emery <i>et al.</i> (2022)

Table 4. (Continued).

Location	Experimental system	Duration of treatment (yr)	Reduction of precipitation (%)	Biomass	Diversity	Guilds share	Community composition	Reference <sup>1</sup>
Australia (Australia)	experimental grassland	2.3	50		0		change	Deveautour <i>et al.</i> (2018)
Asia (China)	grassland	3	30		0		change	Wang <i>et al.</i> (2021c)
Asia (China)	forest	4	70	- (hyphal and spore density, root colonisation)	0		0	Maitra <i>et al.</i> (2019)
Asia (China)	forest plantation	4	50		0		0	Cao <i>et al.</i> (2020a)
Asia (China)	grassland	6	50	0	-		change	Zheng <i>et al.</i> (2022b)
North America (USA)	shrubland	7	40	0			change	Weber <i>et al.</i> (2019)

diversity (Li *et al.* 2022). Importantly, precipitation reduction typically shifted the share of fungal guilds with the reduction of AM fungi and increase of plant pathogens being frequently reported. Changes in fungal community composition were also relatively frequent (Table 4). Increase of the F/B ratio was observed in a heathland experiment (Haugwitz *et al.* 2014). Changes in soil chemistry were typically not found, not even for the long-lasting experiments.

### Increased atmospheric N deposition

Many plant communities are N limited (LeBauer & Treseder 2008), and additional N can thus promote plant productivity if P content is non-limiting (Fay *et al.* 2015). Additionally, N deposition may reduce plant species richness though this effect depends on ecosystem characteristics, such as MAP (Clark *et al.* 2007). For example, N addition may increase plant species richness in ecosystems with high MAP (Komatsu *et al.* 2019). In addition to effects on vegetation, N has multiple effects on soil chemistry, including acidification (Lekberg *et al.* 2021). Though a recent global meta-analysis found that N reduced overall soil fungal richness (Zhou *et al.* 2020), the effects of N deposition on soil fungi can be, like plant community responses, context dependent. Across N-addition studies in the US forests, fungal biomass and richness increased with simulated N deposition at sites with low ambient deposition but decreased at sites with high ambient deposition (Moore *et al.* 2021). Along local fertility gradients, total fungal biomass was highest in soils with the lowest nutrient availability and tree productivity (Nilsson *et al.* 2005). Higher N availability promotes bacterial growth due to their higher N demand. Especially in the N-limited boreal soils, N addition results in a decrease of the F/B ratio by 25–70 % (Frey *et al.* 2004, Wallenstein *et al.* 2006, Maaroufi *et al.* 2015).

There appears to be a general consensus that N deposition increases soil C sequestration due to the decline in SOM decomposition via the reduction of fungal abundance and decomposer activity in many different soil environments, including temperate and boreal forests (Frey *et al.* 2014, Maaroufi *et al.* 2015). Since, similar to plants, many fungi respond to P availability in soil and it is an important driver of fungal abundance in soils without N limitations (Odriozola *et al.* 2021), increased N content may act on fungal productivity and community composition indirectly through P limitation (Fig. 1).

Within our survey, the goal of the majority of N addition experiments was to simulate predicted increases in atmospheric

deposition, but many used unreasonably high amounts of fertilizer, ignored ambient N deposition rates, and virtually none of them referenced a model that predicts future deposition, whose extent shows high local variation. It is currently estimated that the vast majority of forests are subject to total N deposition lower than 25 kg N/ha/y (Schwede *et al.* 2018) and it is unrealistic to expect that the increase in future is several-fold. We have thus considered only the results of experiments where N addition was lower than 75 kg N/ha/y.

The effects of N addition on fungal biomass in soil were variable. For AM fungi, decreased spore density, root colonisation, and biomass were much more frequent than positive effects (Fig. 4). In forest ecosystems, decrease of fungal biomass and root colonisation appears typical (Ma *et al.* 2021b). Both increases and decreases in diversity of fungi or AM fungi were observed (Figs 3, 4, Table 5). This lack of consistency in diversity responses is somewhat supported by the effects of increased N on fungal richness varying between global meta-analyses with increased N either decreasing richness or having no effect (Zhou *et al.* 2020, Li *et al.* 2022). Changes in the representation of fungal guilds were a common consequence of N addition. In most long-term N addition experiments, the share of ECM fungi was significantly reduced (Table 5) with a shift to nitrophilic taxa such as *Rusula vinacea* (Morrison *et al.* 2016, Tahovská *et al.* 2020). The consequences of longer N enrichment (> 4 yr) were relatively complex and include acidification and increased N availability (Choma *et al.* 2017, Wang *et al.* 2021b), decreased F/B ratio (Gutknecht *et al.* 2012, Wang *et al.* 2015) and decreased activity of enzymes decomposing recalcitrant plant biopolymers lignin and cellulose (Freedman *et al.* 2015, Hesse *et al.* 2015). Although vegetation responds to N addition as well, the change of soil chemistry appeared to be the immediate driver of fungal community composition (Zheng *et al.* 2014, Zhou *et al.* 2020, Wang *et al.* 2021b).

### Combined effects and model predictions

Current models predict that the effects of global change factors will act simultaneously in most terrestrial habitats and the resulting effect of global change thus reflects their combination. Furthermore, shifts in plant community composition are likely determined by interactions between multiple climate change drivers (Avolio *et al.* 2021). Between 1990 and 2014, global heterotrophic soil respiration

**Table 5.** Effects of experimental N addition on fungi. Manipulations where N was added in a mineral form with the aim to simulate atmospheric deposition that lasted at least for 1 yr and where N addition was not combined with other factors were considered. Manipulations or treatments where N addition exceeded 75 kg N/ha/yr were not considered as highly exceeding projected N deposition increase; + denotes that the experiment also included treatment(s) with higher N addition level(s).

Location	Experimental system	Duration of treatment (yr)	N addition (kg N/ha/yr)	Biomass	Diversity	Guilds share	Community composition	Reference
<b>All fungi</b>								
North America (USA)	shrubland	1	7; 15		0		no change	Mueller <i>et al.</i> (2015)
Asia (China)	grassland	1	50; +		0		change	Li <i>et al.</i> (2020a)
North America (USA)	experimental field	1	50	0		no change	no change	Anthony <i>et al.</i> (2020)
North America (Canada)	grassland	1–2	20	+				Bell <i>et al.</i> (2010)
Asia (China)	shrubland	2	60		0		change	She <i>et al.</i> (2018)
Asia (China)	forest	2	30; 60; +	+	+	change (more AMF)	change (more <i>Basidiomycota</i> )	Li <i>et al.</i> (2019a)
Asia (China)	wetland	2	30; 60; +		0		change	Li <i>et al.</i> (2020b)
Asia (China)	forest	2	25	+			change	Guo <i>et al.</i> (2021)
Asia (China)	grassland	3	15; 30; 50; +		0			Zhang <i>et al.</i> (2018)
Europe (Czech Republic)	forest	4	50	0			no change	Choma <i>et al.</i> (2020)
Asia (China)	grassland	5	35		0	change (less AMF)	change	Wang <i>et al.</i> (2020b)
Asia (China)	forest	5	25	+	+	change (more saprotrophs)	change	Zhao <i>et al.</i> (2020)
Asia (China)	forest	6	50; +	-	0		change (less <i>Ascomycota</i> )	Wang <i>et al.</i> (2021b)
North America (USA)	grassland	6	70				change (less AMF)	Gutknecht <i>et al.</i> (2012)
Asia (China)	forest	6	50; +		0		no change	Li <i>et al.</i> (2019b)
Asia (China)	experimental field	7	35; 70; +	+	-		change	Wang <i>et al.</i> (2015)
North America (USA)	experimental grassland	7	28; 56; +	0		change (less AMF)	change	Li <i>et al.</i> (2021)
Asia (China)	forest	8	50		0			Yan <i>et al.</i> (2021)
North America (Canada)	forest	10	30	0		no change	no change	Wu <i>et al.</i> (2021)
North America (Canada)	experimental field	10	30; +	0	-		change	Tosi <i>et al.</i> (2021)
Europe (United Kingdom)	wetland	14	8; 25; 56			change (less ERM)		Vesala <i>et al.</i> (2021)
Asia (China)	grassland	15	18; 53; +	-	0		change (more <i>Eurotiomycetes</i> and <i>Sordariomycetes</i> )	Chen <i>et al.</i> (2019)
North America (USA)	forest	16	30	0			no change	Hesse <i>et al.</i> (2015)
North America (USA)	forest	20	30	0	0		no change	Freedman <i>et al.</i> (2015)
North America (USA)	forest	20	50; +			change (less ECM, more saprotrophs)	change (more nitrophilic ECM)	Morrison <i>et al.</i> (2016)
Europe (Switzerland)	forest	20	22	0	0	change (less ECM)	change	Frey <i>et al.</i> (2020)
Europe (Sweden)	forest	23; 46	34; 73		0	change (less ECM)		Choma <i>et al.</i> (2017)

Table 5. (Continued).

Location	Experimental system	Duration of treatment (yr)	N addition (kg N/ha/yr)	Biomass	Diversity	Guilds share	Community composition	Reference
Europe (Sweden)	forest	24	40	+	0	change (more saprotrophs)	change (more nitrophilic ECM)	Tahovská <i>et al.</i> (2020)
<b>Arbuscular mycorrhizal fungi</b>								
North America (USA)	experimental field	1	50	0			no change	Anthony <i>et al.</i> (2020)
Asia (China)	forest	2	30; 60	+ (root colonisation)	+		change	Liu <i>et al.</i> (2021c)
North America (USA)	shrubland	2.8	60	- (spore density)	-		change (more <i>Glomus</i> , less <i>Gigaspora</i> and <i>Scutellospora</i> )	Egerton-Warburton & Allen (2000)
Asia (China)	forest plantation	3	40; +	+ (root colonisation)	0		change (more <i>Gigasporaceae</i> )	Cao <i>et al.</i> (2020b)
Asia (China)	grassland	3	50; +	- (root colonisation)	+		change	Jiang <i>et al.</i> (2018)
North America (USA)	grassland	3	70		0		no change	Mueller & Bohannan (2015)
Asia (China)	forest	4	50		0		no change	Zhao <i>et al.</i> (2018)
Asia (China)	experimental field	5	50; +	-	-		change	Zhu <i>et al.</i> (2018)
Asia (China)	grassland	6	15; 75	- (spore density)	+		no change	Zheng <i>et al.</i> (2014)
North America (USA)	grassland	6	70	- (biomass)				Gutknecht <i>et al.</i> (2012)
Asia (China)	grassland	7	50; +	- (root colonisation)	0		change	Lu <i>et al.</i> (2020)
Asia (China)	grassland	7	50; +	- (root colonisation, biomass)	-		change	Chen <i>et al.</i> (2017)
Asia (China)	grassland	8	25; 50	0	0		no change	Li <i>et al.</i> (2015)
North America (USA)	forest	12	30				change (more <i>Glomus</i> )	van Diepen <i>et al.</i> (2011)
North America (USA)	forest	16	30		0		no change	van Diepen <i>et al.</i> (2013)

and its ratio to total soil respiration increased, probably in response to the combined effects of global change factors (Bond-Lamberty *et al.* 2018). This suggests that climate-driven losses of soil carbon are currently occurring across many ecosystems, with a detectable and sustained trend emerging at the global scale, although the underlying mechanisms cannot be easily identified. Simulation of the global change effects until the year 2090 using available data from 1950 indicates that climate change acts mostly indirectly, through other environmental variables, *e.g.*, changes in the soil pH (Guerra *et al.* 2021). The effects of global change factors on fungi thus may depend either on the relative importance of each individual factor under local conditions or on the combined effects of multiple factors.

## CONCLUSIONS

While ongoing climate change has had seemingly no dramatic effects on soil fungal communities, and neither fungal biomass nor fungal diversity in soils appear to be dramatically affected, experiments simulating the main global change effects predict significant shifts in fungal community composition and the share of fungal guilds. The differences in the size of the realised niche of plant-beneficial ECM fungi compared to that of plant pathogens suggests that the fitness of vegetation may decrease as ecosystems experience increased spread of plant pathogens and potentially higher frequencies of outbreaks. This issue is perhaps the one that deserves most attention (Fig. 1). Interestingly, responses of soil fungi to various aspects of global change can be predicted based on different ecological features. While differential responses of

ECM fungal species to global changes such as N deposition can be predicted from their extracellular enzymatic capabilities related to organic nitrogen accessibility, response of AM fungal species depends on their differential colonisation traits.

Global change effects on ecosystems are highly context dependent and there are undoubtedly ecosystems where changes will be more pronounced. Where global change relieves existing limitations, such as the coldest or N-limited areas, novel limitations will arise, such as increased desertification or induced P-limitation, respectively. Unfortunately, these systems are rarely the subject of research. Experimental manipulations in underexplored systems are thus most welcome.

Although the experiments combining multiple factors are relatively frequent (Yang *et al.* 2021a), they are in most cases applying unrealistic treatment intensities and so far too rare to allow generalisations. Since global change factors act in combination and their effects are not simply additive (Rillig *et al.* 2019), it would be more than welcome to see results of long-term manipulations based on complex predictions of multiple global change factors for given localities. Since it will never be possible to perform manipulations everywhere, long term collection of observational data is needed that would help to describe trends in the soil mycobiome. Global and regional initiatives intending to capture all available types of fungal community data, combined with paired environmental metadata, across time (Andrew *et al.* 2017, Větrovský *et al.* 2020) have the potential to scale our understanding of global change effects on soil fungi to a global level.

## DECLARATION ON CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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**Supplementary Material:** <https://studiesinmycology.org/>

**Supp. S1.** Selection criteria for the inclusion of studies describing effects of global change manipulation on fungi.

## SUPP. S1

### Selection criteria for the inclusion of studies describing effects of global change manipulation on fungi

Source Database: **Web of Science**

Keywords: **TOPIC:** (nitrogen addition OR nitrogen enrichment OR nitrogen deposition OR nitrogen fertilization OR nitrogen input OR nitrogen application OR CO<sub>2</sub> enrichment OR CO<sub>2</sub> manipulation OR FACE experiment OR warming OR experimental warming OR precipitation rainfall OR precipitation manipulation) **AND TOPIC:** (microbial community OR fungal community fungal OR diversity OR fungal response community composition), **FROM** 1945-2021

Last search: 15-11-2021

Total: 773 papers

- checking the criteria below by reading the abstracts:
- the experiment is done directly to terrestrial ecosystems
- laboratory incubation studies were excluded
- effect of Nitrogen, CO<sub>2</sub>, warming, altered precipitation is observed alone and we are sure that the effects are due to the considered factor only (without interaction with other factors)
- focus on global fungal communities or AMF communities

Total: 204 papers suitable

- reading the methods and results:
- aim must be to simulate global change effects and not efficiency of fertilizer or temperature for example
- Provide information about at least one of this fungal characteristics: fungal community composition, fungal biomass, or fungal activity
- manipulation of at least one year duration

Total: 139 included

*(i.e., 25 CO<sub>2</sub> + 38 precipitation + 41 N + 63 warming = 167 because some papers have multiple factors)*