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Review Article

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REVIEW

Nutrient and stress tolerance traits linked to fungal responses to global change: Four case studies

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In this case study analysis, we identified fungal traits that were associated with the responses of taxa to 4 global change factors: elevated CO_2, warming and drying, increased precipitation, and nitrogen (N) enrichment. We developed a trait-based framework predicting that as global change increases limitation of a given nutrient, fungal taxa with traits that target that nutrient will represent a larger proportion of the community (and vice versa). In addition, we expected that warming and drying and N enrichment would generate environmental stress for fungi and may select for stress tolerance traits. We tested the framework by analyzing fungal community data from previously published field manipulations and linking taxa to functional gene traits from the MycoCosm Fungal Portal. Altogether, fungal genera tended to respond similarly to 3 elements of global change: increased precipitation, N enrichment, and warming and drying. The genera that proliferated under these changes also tended to possess functional genes for stress tolerance, which suggests that these global changes—even increases in precipitation—could have caused environmental stress that selected for certain taxa. In addition, these genera did not exhibit a strong capacity for C breakdown or P acquisition, so soil C turnover may slow down or remain unchanged following shifts in fungal community composition under global change. Since we did not find strong evidence that changes in nutrient limitation select for taxa with traits that target the more limiting nutrient, we revised our trait-based framework. The new framework sorts fungal taxa into Stress Tolerating versus C and P Targeting groups, with the global change elements of increased precipitation, warming and drying, and N enrichment selecting for the stress tolerators.

Keywords: Elevated CO_2, Precipitation, Warming, Drying, Nitrogen enrichment, Nitrogen fertilization, Limiting nutrients, Synthesis, Fungal traits, Growth form, Extracellular enzymes, Functional genes, Tissue phosphorus concentration

Introduction

Recent decades have witnessed a discovery stage in fungal ecology, powered in part by advances in high throughput DNA sequencing (Lindahl et al., 2013; Jansson and Hofmockel, 2020). We have learned that fungal communities frequently shift under human-induced global change factors such as elevated CO_2, warming, drought, increased precipitation, and nitrogen (N) enrichment (reviewed in Allison and Martiny, 2008; Castro et al., 2010; Pickles et al., 2012; Treseder et al., 2012; Mohan et al., 2014; Classen et al., 2015; Jansson and Hofmockel, 2020). These changes have now been well-documented in field studies (e.g., Hagedorn et al., 2013; Kerekes et al., 2013; McHugh and Schwartz, 2016; Treseder et al., 2016). Nevertheless, we have a poor understanding of *why* specific fungal taxa respond the way they do (Martiny et al., 2015). For example, why does the abundance of a given taxon increase under elevated CO_2 (or another global change factor) while another decreases? If we understand underlying mechanisms for these shifts, we may better predict fungal contributions to carbon and nutrient cycling under global change.

Global changes could select for (or against) fungal taxa with certain physiological or genetic traits (e.g., Romero-

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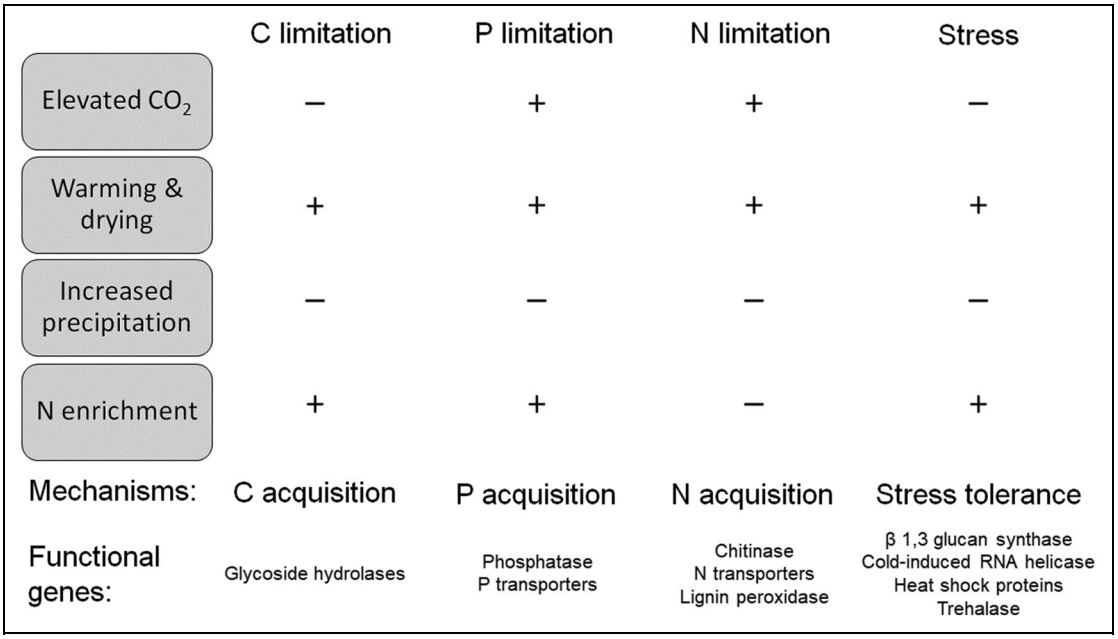

Figure 1. Hypothesized effects of global changes on nutrient limitation of fungal growth and activity. Mechanisms that might underlie fungal responses to nutrient limitation or stress, and related functional genes, are also included. See Table S1 for a complete listing of functional genes. DOI: https://doi.org/10.1525/elementa.2020.00144.f1

Olivares et al., 2021). Here, we focus on traits that enable fungi to acquire and use carbon (C), N, and phosphorus (P) from the environment. Fungi require these nutrients to grow and reproduce (Sinsabaugh et al., 2008; Sinsabaugh et al., 2009; Strickland and Rousk, 2010; Mouginot et al., 2014). Yet, global changes can alter the relative availability of C, N, and P (Vitousek, 2004; Chapin et al., 2011). For instance, elevated CO_2 may alleviate C limitation for fungi by boosting availability of plant C and exacerbate N or P limitation (Chagnon et al., 2013; Johnson et al., 2013). Accordingly, fungi with N- or P-acquisition traits may proliferate under elevated CO_2, while those that invest in C-acquisition traits may decline or remain unchanged (Velicer and Lenski, 1999; Treseder, 2005; Malik et al., 2019). Other global change factors could also alter the relative abundance of C versus N or P, each in their own way.

Global change can also cause environmental stress for fungi, apart from changes in limiting nutrients (Mohan et al., 2014; Lenoir et al., 2016; Morrison et al., 2018; Malik et al., 2019; Garcia et al., 2020). For example, warming (and the drying often associated with it) in arid ecosystems could generate drought stress (Schimel et al., 2007; Manzoni et al., 2012; Homyak et al., 2018). In addition, N enrichment can lead to soil acidification, changes in osmotic potential, or the formation of toxic N-containing compounds such as melanoidins (Broadbent, 1965; Baath et al., 1981; Vitousek et al., 1997; Treseder, 2008; Liu and Greaver, 2010; Lu et al., 2011). Stress tolerance traits may be advantageous under these circumstances.

We created a framework to predict responses of fungal communities to elevated CO_2, warming, increased precipitation, and N enrichment and then tested the framework on 1 case study for each global change element (Table S1; Hagedorn et al., 2013; Kerekes et al., 2013; McHugh and Schwartz, 2016; Treseder et al., 2016). We acquired data on nutrient and stress tolerance–related traits of the fungal taxa by assessing functional genes in published fungal genomes housed in the U.S. Department of Energy's MycoCosm Fungal Portal (Grigoriev et al., 2014). Then, we used phylogenetic independent contrasts to test for relationships between the global change responses and those functional genes. If fungal taxa respond to global changes depending on nutrient or stress tolerance–related traits, these responses could help us identify broadly applicable mechanisms underlying community shifts. This approach could allow us to use a trait-based framework to predict fungal community shifts in response to future environmental conditions.

Trait-based framework

We based our approach on the idea that fungal taxa should invest more toward acquiring nutrients that limit their growth and reproduction (Read, 1991). Liebig's Law of the Minimum suggests that an organism's activity is constrained by the scarcest nutrient that it requires, even if other required nutrients are readily available (Liebig, 1843). Consequently, fungal taxa that preferentially target the limiting nutrients may displace groups that focus on other, nonlimiting nutrients. The displacement could be particularly strong if evolutionary or physiological tradeoffs apply—if resources invested in acquiring a nonlimiting nutrient cannot be invested in acquiring the limiting nutrient (Velicer and Lenski, 1999; Allison et al., 2010b; Treseder et al., 2011; Malik et al., 2019). Altogether, this framework suggests that the *relative* availability of nutrients selects for or against individual fungal taxa.

Global changes may alter the relative availability of C, N, or P (**Figure 1**). Elevated CO_2 can increase C fluxes from plants to litter and soil, potentially decreasing N and P

availability under certain vegetation types (Staddon et al., 1999; Norby et al., 2001; de Graaff et al., 2006; Hungate et al., 2009; Dieleman et al., 2010; Norby and Zak, 2011). Accordingly, fungi that decompose litter and soil organic matter may become more N- and P-limited and less C-limited. In addition, mycorrhizal fungi may have an advantage under elevated CO_2 since C allocation from host plants to the fungi can increase (Diaz, 1996; Compant et al., 2010). Nitrogen fertilization or anthropogenic N deposition can enrich N supplies to fungi, alleviating N limitation and exacerbating C- and P-limitation (Treseder and Allen, 2002; Johnson et al., 2013; Treseder et al., 2018). Increased precipitation may improve the availability of all 3 nutrients because the water can dissolve and carry the nutrients to the fungi and stimulate decomposer activity (Schimel and Bennett, 2004; Chapin et al., 2011; Manzoni et al., 2012; Manzoni et al., 2014). Warming can stimulate microbial activity when water is not limiting but can lead to higher water evaporation rates and soil drying in some ecosystems (Rebetez and Dobbertin, 2004; Allison and Treseder, 2008; Allison and Treseder, 2011). Consequently, warming could enhance C and N availability in moist ecosystems (Solly et al., 2017a; Solly et al., 2017b), while it could reduce availability of C, N, and P if warming induces moisture limitation (Allison and Treseder, 2011; Parker and Schimel, 2011). We expect that fungal taxa will respond to these shifts in nutrient limitations depending on their nutrient-related traits.

Stress tolerance traits could also influence the distribution of fungal taxa (Malik et al., 2019). Certain global change factors tend to reduce fungal abundance, potentially because the changes create environmental stresses for fungi. Fungal biomass generally declines as N enrichment increases (Treseder, 2008). Warming experiments have varied widely in the extent to which fungal abundance responds, and reductions are more common when warming is accompanied by drying (Chen et al., 2015; Romero-Olivares et al., 2017b; Gao and Yan, 2019). Elevated CO_2 tends to increase mycorrhizal fungal biomass (Treseder, 2004; Dong et al., 2018), so it may alleviate environmental stress for those fungi. Altogether, we predicted that N enrichment and warming (if accompanied by drying) may select for taxa with stress tolerance traits, while elevated CO_2 and increased precipitation may select against them (**Figure 1**).

Methods

Selected traits

Response traits

The extent to which a given fungal group becomes more or less abundant in response to global change can be considered a trait (sensu Lavorel and Garnier, 2002). We quantified response traits as the increase or decrease in relative abundance of a given fungal group in response to a global change factor. For example, if a given fungal group represented 30% of the fungal community under ambient CO_2 controls, but rose to 40% under experimental CO_2 enrichment, its elevated CO_2 response was +10%. In this analysis, positive response traits will indicate proliferation under global change, while negative response traits indicate a reduction.

Functional gene traits

To test our trait-based framework, we focused on functional genes for C, N, and P acquisition and environmental stress tolerance. Certainly, possession of a gene does not confirm that the gene is expressed or translated (Pradet-Balade et al., 2001; Wilmes and Bond, 2006; Myrold et al., 2014). Instead, we consider gene possession an indication that the fungal group has the genetic capacity for that trait. Moreover, gene frequencies or copy numbers can influence the extent to which a trait is expressed (Zhou et al., 2011).

We selected functional genes encoding extracellular enzymes that break down organically bound C for C acquisition (Lynd et al., 2002; Edwards et al., 2008; Martínez et al., 2009), chitin or lignin complexes for N acquisition (Bending and Read, 1997; Cairney and Burke, 1998; Talbot et al., 2012), and C-bound phosphate for P acquisition (Sinsabaugh, 1994). In addition, amino acid permeases, ammonium transporters, nitrate transporters, and phosphate transporters can improve uptake rates of N or P into hyphae (Versaw and Metzenberg, 1995; Nehls et al., 1999; Mitsuzawa, 2006; Slot et al., 2007). For stress tolerance, β-1,3 glucan synthase allows fungi to incorporate this carbohydrate into their cell walls to prevent desiccation and freezing damage (Bowman and Free, 2006; Latgé, 2007). Furthermore, cold-induced RNA helicase and heat shock proteins help improve cold and heat tolerance, respectively (Schade et al., 2004; Owttrim, 2006; Tiwari et al., 2015). Moreover, trehalase produces trehalose, a compatible solute that protects fungi from water loss, freezing damage, and heat shock (Wiemken, 1990; Estruch, 2000). We determined functional gene frequencies (# copies per 10,000 genes) encoding each of these traits by examining 692 published whole fungal genomes representing 111 genera (**Table 1**; Figure S1). We used search terms (**Table 1**) in MycoCosm to identify existing gene annotations (last accessed February 24, 2021; Grigoriev et al., 2014).

Study selection

For each of the 4 global change factors, we selected 1 previously published study based on predetermined selection criteria (Table S1). First, we used field-based studies, so that findings could be applicable to an ecosystem setting. Second, we chose studies in which the global change factor was experimentally manipulated in comparison to a control, so we could calculate the response trait based on relative abundance in the experimental versus control treatments. Third, the relative abundance data for each fungal taxon needed to be accessible, either via published databases or directly from authors. Fourth, we focused on studies that characterized fungal communities at the species to genus level to allow greatest flexibility in taxonomic rank analysis. This latter criterion restricted us to studies that sequenced the highly variable ITS1 or ITS2 region. In contrast, we placed

Table 1. Functional genes and their search terms in MycoCosm (Grigoriev et al., 2014). DOI: https://doi.org/10.1525/elementa.2020.00144.t1

Functional Gene	Glycoside Hydrolase (GH) Activity	Search Term
Amino acid permease	n.a.	IPR004762
Ammonium transporter	n.a.	IPR001905
β-1,3 glucan synthase	n.a.	GO:0000148
Chitinase (GH 18)	Chitinase	IPR001223
Crystalline cellulase (AA 9, formerly GH 61)	n.a.	IPR005103
Fungal lignin peroxidase	n.a.	IPR001621
GH 1	β-glucosidase and β-galactosidase	IPR001360
GH 7	Cleave β-1,4 glycosidic bonds in cellulose/β-1,4-glucans	IPR001722
GH 9	Cellulases	IPR001701
GH 12	Endoglucanase	IPR002594
GH 13	Substrates containing α-glucoside linkages	GH13
GH 15	Hydrolyze the non-reducing end residues of α-glucosides	IPR011613
GH 28	Polygalacturonase	IPR00743
GH 31	α-glucosidase	IPR000322
GH 32	Invertase	IPR001362
GH 76	Endo-acting α-mannanases	IPR005198
GH 81	Endo-β-1,3-glucanase	IPR005200
GH 85	Endo-β-N-acetylglucosaminidase	IPR005201
GH 92	Exo-acting α-mannosidases	IPR012939
Heat shock protein	n.a.	IPR002068
Nitrate transporter	n.a.	IPR004737
Phosphatase	n.a.	IPR000560
Phosphate transporter	n.a.	HMMPFAM: PF01384
Cold-induced RNA helicase	n.a.	IPR014014
Trehalase	n.a.	GO:0005991

n.a. = not applicable.

no restrictions on ecosystem type, geography, or sequencing platform (e.g., Illumina or 454). If samples were taken at multiple time points within the same plots, we used the last samplings to allow the longest exposure to the global change treatment. Upon study selection, we contacted the lead authors of the studies and invited them to collaborate on the analysis.

Fungal taxa identification

For most of the studies, we used taxonomic names provided by the investigators unless those taxonomies had been revised after publication. In those cases, we updated taxonomic names to match current names from Index Fungorum (2021, accessed February 24, 2021). For the N enrichment study, Kerekes et al. (2013) had not identified taxa to genus or species. For that study, we used UNITE (Nilsson et al., 2018) to match representative sequences to these taxonomic ranks where possible. Across studies, between 18.2% and 71.2% of taxa were identified to at least the genus level (Table S1).

Experimental designs

Increased precipitation

We calculated responses to increased precipitation using fungal community composition from samples taken at the final sampling (i.e., 30 days after onset of treatments) of the McHugh and Schwartz (2016) study. They collected soil from the top 5 cm of 4 pairs of control and watered plots.

Nitrogen enrichment

Kerekes et al. (2013) characterized fungal taxa in the litter layer in 4 control and four N-fertilized plots.

Warming and drying

Warming and drying responses of taxa were taken directly from supplementary information in Treseder et al. (2016).

They sampled fungi in the litter horizon of 5 control and 5 warmed plots.

Elevated CO_2

We calculated elevated CO_2 responses using data supplied by Hagedorn et al. (2013). They had characterized fungal community composition in 10 blocks of control and elevated CO_2 plots. Each block encompassed 4 plots: a control plot and elevated CO_2 plot, each centered on a *Larix decidua* tree; and a control plot and elevated CO_2 plot, each centered on a *Pinus uncinata* tree. There were 40 plots in total. From each of these plots, they collected soil from 3 horizons: litter layer, F horizon, and H horizon, after 9 plant growing seasons of CO_2 enrichment. The soils were nutrient poor and acidic Ranker or Podzols with a 10- to 20-cm thick organic layer. We calculated mean relative abundances across all soil horizons and both tree species. By combining soil horizons, we obtained a more generalizable pattern of fungal responses than if we had analyzed each horizon separately. On the other hand, it limited our ability to discern horizon-specific responses.

Trait compilation

We compiled the responses of taxa to elevated CO_2, warming and drying, increased precipitation, and N enrichment with functional gene frequencies (Table S2). Specifically, for each response and functional gene trait, we calculated genus-level means (e.g., average response of all taxa within *Boletus*). We chose to take genus-level means instead of species-level means for 2 reasons. First, many taxa were identifiable to genus but not species. Second, the majority of species with response traits were detected in just 1 experiment or did not have whole genomes available in MycoCosm. By taking genus-level means, we were able to compare traits across more taxa. We lost species-level resolution but gained statistical power. Many of the functional gene traits we examined tend to vary most at the order to subphylum levels (Treseder and Lennon, 2015), so we likely captured much of the trait variation with genus-level means.

Relationships between traits

We used phylogenetic independent contrasts to examine relationships between each pairwise combination of response and functional gene traits. Since the global change experiments had sequenced the ITS1 or ITS2 regions, which are highly variable, it was not feasible to construct an accurate phylogeny from these sequences. Instead, we used the fungal phylogeny of Choi and Kim (2017), which was developed from 235 whole genome sequences of fungal strains. We downloaded the phylogeny from Github (2020, accessed March 12, 2020). Of the 111 genera in our dataset, 41 were represented in the phylogeny. For each of the remaining genera, we used the closest taxon in the tree (Table S3). Sixty-one of the genera were assigned to a taxon of the same family or order in the phylogeny. We pruned the tree to remove all taxa not represented in at least 1 case study (Figure S1).

For the phylogenetic independent contrasts, we used the *aotf* function in Phylocom version 4.2 (Webb et al., 2008). This function determined the difference in the values of a specific trait between daughter clades of each node in the phylogenetic tree. It then took a series of correlations of the contrasts between each pairwise combination of traits, minimizing errors along the x and y axes. We used the default parameters for this function, so more recently diverged clades were weighted more in the correlations. Where the correlations included an outlier with large leverage, we ranked the contrasts. We focused on pairwise relationships with r values greater than 0.5 or less than –0.5, which corresponded to an unadjusted $P < 0.00001$ for correlations between functional gene traits. The *aotf* function also identified nodes at which each response trait diverged significantly (Figure S1).

To view relationships between all traits included in the case study analysis, we performed a nonmetric multidimensional scaling analysis using the Kruskal Method with a square (similarities) model and 2-dimensional output (SPSS, 2017). The input was the matrix of r values from the phylogenetic independent contrasts (Table S4).

Relationships between traits

Our results were unexpected. The fungal traits sorted into 3 distinct groups based on their relationships to one another (**Figure 2**). Responses to N enrichment tended to be positively related to responses to warming and drying as well as increased precipitation response. Collectively, these response traits clustered with most of the stress tolerance traits: β-1,3 glucan synthase, trehalase, and cold-induced RNA helicase (Group A; **Figure 2**). Thus, we will refer to this group of traits as the "Stress Tolerating Group." A second cluster of traits featured C-targeting enzymes and phosphate transporters (Group B; **Figure 2**). Specifically, crystalline cellulase was positively related to phosphate transporters and GH Families 12 and 81 (endoglucanases). In turn, GH Family 12 was positively related to GH Family 7 (cellulases and β-1,4-glucanases). This group, which we will refer to as "C and P Targeting Group," was distinct from the group that included global change response traits. Altogether, none of our predictions were upheld. In fact, the clustering of increased precipitation response with stress tolerance traits was opposite to its predicted relationship.

Stress Tolerating Group

Why did genera that increased under climate change also tend to possess stress tolerance traits? Bijlsma and Loeschcke (2005) noted that environmental stress is a function of both the *stressor* (e.g., increased precipitation) and the *stressed* (e.g., resident fungal taxa). In other words, environmental conditions that are suboptimal for most fungi could be optimal for local fungi that have adapted to them. For example, although rainfall could alleviate drought stress for many fungi, it might generate environmental stress in fungi adapted to arid ecosystems (Van Gestel et al., 1993; Fierer et al., 2003; Schimel et al., 2007). Perhaps increased precipitation, N enrichment, and warming and drying induced stress because they exposed

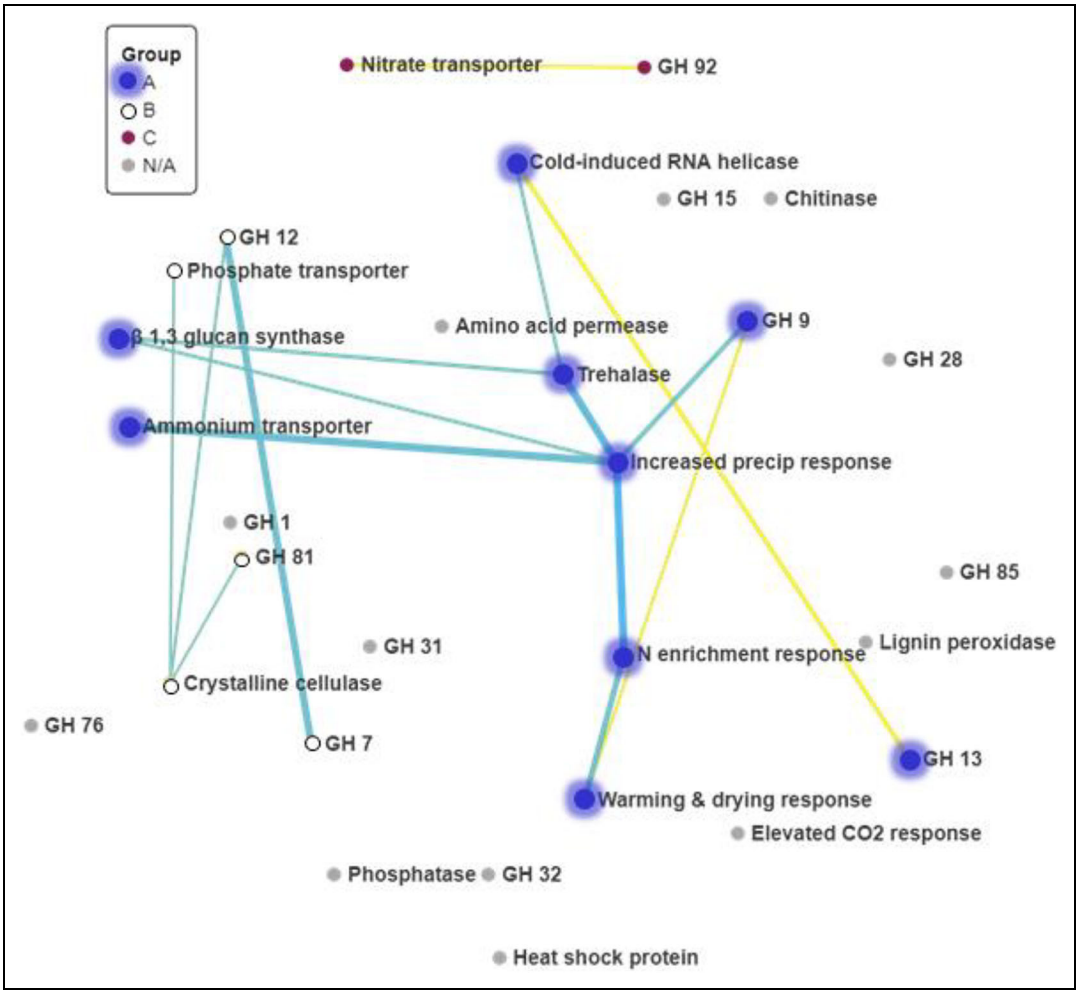

Figure 2. Relationships between traits. Traits are arrayed based on a 2-dimensional nonmetric multidimensional scaling analysis. Traits located closer together tend to be more closely related. Each symbol represents 1 trait. Lines connect traits with phylogenetic independent contrast *r* values greater than 0.5 (cyan) or less than –0.5 (yellow). Line thickness is proportional to $|r|$. A given trait was assigned to a group if it was related (at $|r| > 0.5$) to at least one other trait within the group. "Group A" is highlighted because it includes global change responses. Correlation graphs for each linked pair of traits are below (Group A: **Figures 3**, **4**, and S2; Group B: **Figure 5**; Group C: Figure S3). An interactive version of this figure can be accessed at Polinode (2021). DOI: https://doi.org/10.1525/elementa.2020.00144.f2

fungi to environmental conditions they did not typically experience.

This may have been the case in the increased precipitation manipulation we analyzed. As the climate warms, precipitation regimes change with it (Intergovernmental Panel on Climate Change [IPCC], 2014). On average, precipitation rates are expected to increase globally (IPCC, 2014). In the increased precipitation experiment by McHugh and Schwartz (2016), month-long water additions in an Arizonan semiarid grassland yielded faster soil respiration rates, larger inorganic N pools, and significant shifts in the fungal community. Previous research has indicated that fungal community composition frequently shifts with water availability (Castro et al., 2010; Hawkes et al., 2011; Maestre et al., 2015; Matulich et al., 2015; McHugh and Schwartz, 2015; Gao et al., 2016; He et al., 2017; Zhao et al., 2017; Jansson and Hofmockel, 2020), although not everywhere (Barnard et al., 2013; Jumpponen and Jones, 2014; Zhang et al., 2016a).

In this experiment, water additions may have increased fungal stress. Fungal genera whose relative abundance increased following water additions also dedicated larger proportions of their genomes to trehalase and β-1,3 glucan synthase genes (**Figure 3a and b**). Counterintuitively, water additions to chronically dry soils can be physiologically challenging to microbes (Schimel et al., 2007). As soils dry, microbes tend to accumulate osmolytes to reduce water loss (Harris, 1981). When soils are rewetted, the osmolytes could drive water into their cells, raise internal pressures, and potentially burst the cells (Kieft et al., 1987). Strong cell walls can help offset this risk (Kieft et al., 1987), so reinforcement with β-1,3 glucan might be advantageous in this case. In addition, microbes can quickly remove osmolytes by transforming or excreting them (Wood et al., 2001). It is unclear why fungal genera

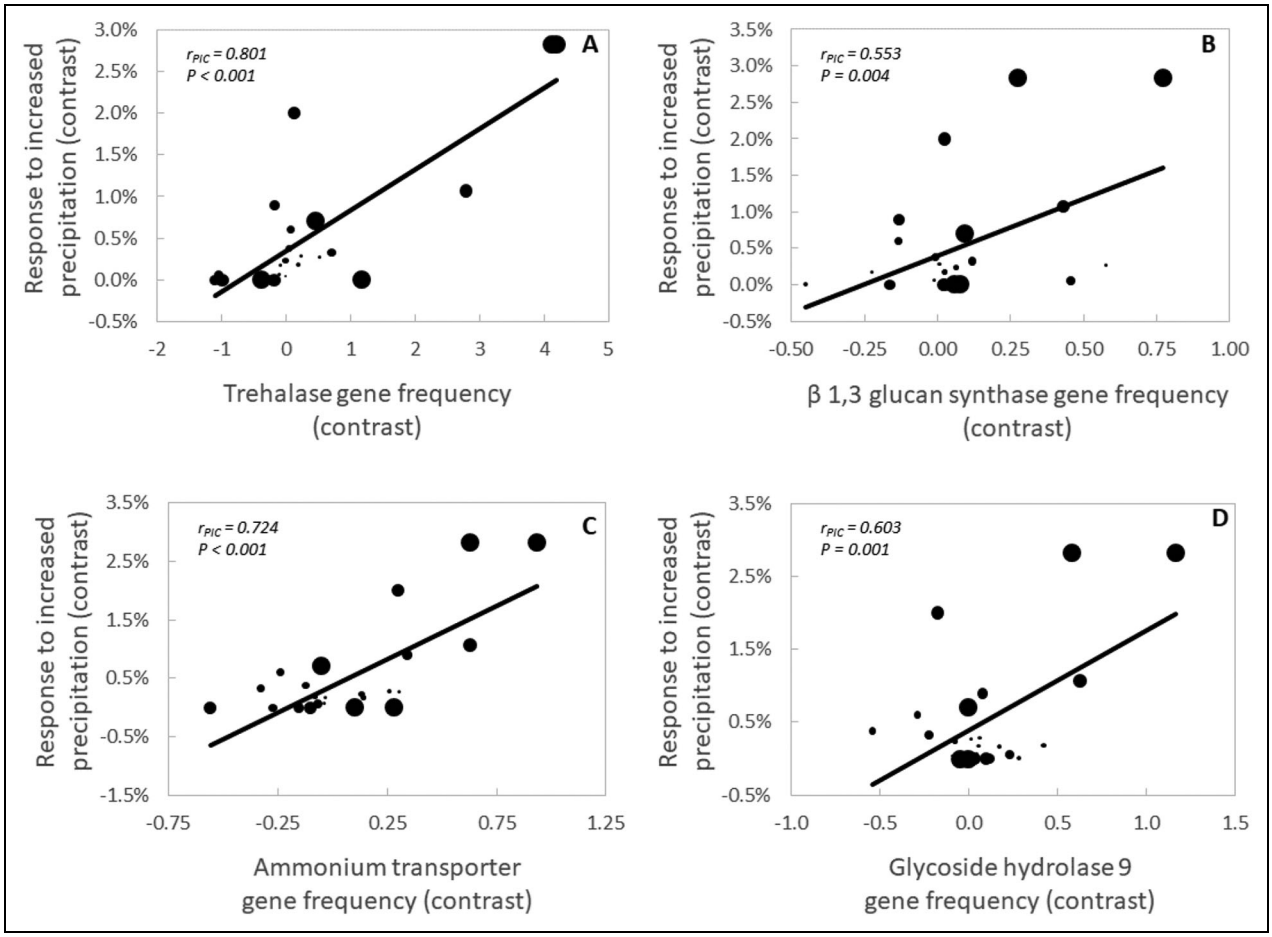

Figure 3. Relationships between fungal responses to increased precipitation versus select functional genes in the Stress Tolerating Group. Symbols represent phylogenetic nodes (Figure S1). Contrasts are differences in trait values between daughter clades of that node. For functional genes, units are number of copies per 10,000 genes. Symbol size is proportional to the node's assigned weight in the analysis. Lines are best fit. *P* values are unadjusted for multiple comparisons. Increased precipitation responses are calculated from McHugh and Schwartz (2016), and gene frequencies are from MycoCosm (Grigoriev et al., 2014). DOI: https://doi.org/10.1525/elementa.2020.00144.f3

with the capacity to construct trehalose tended to perform better in the McHugh and Schwartz (2016) study, given that osmolytes like trehalose can be disadvantageous during rewetting. Perhaps because trehalose production can be reversed upon rewetting, it allowed fungi to tolerate drought stress while allowing them the flexibility to acclimate quickly to changing water availability (Harris, 1981). Gene frequencies for ammonium transporters and cellulases (GH Family 9) were also positively related to responses to increased precipitation (**Figure 3c and d**), possibly because these stress tolerance traits require N for enzyme construction and C for trehalose production.

Trehalase genes coincided with β-1,3 glucan synthase genes and another stress tolerance trait: cold-induced RNA helicase genes (**Figure 4a and b**). In an earlier examination of 157 whole fungal genomes, Treseder and Lennon (2015) had noted that genes for trehalase, β-1,3 glucan synthase, and cold-induced RNA helicases are positively related to one another across the fungal tree of life. Our current analysis of 692 fungal genomes reinforced that observation.

These 3 traits may form part of a multifaceted "environmental stress response," which has previously been defined for ascomycetes (Gasch and Werner-Washburne, 2002; Gasch, 2007). In an environmental stress response, hundreds of stress tolerance–related genes are expressed when fungi are exposed to a stressor such as heat shock. After the environmental stress response has commenced, the fungus is then tolerant of other stresses it has not been previously exposed to, such as extreme pH (Gasch, 2007; Gasch and Werner-Washburne, 2002). At the same time, other genes, including those involving carbohydrate metabolism, are repressed, ostensibly to divert resources to stress tolerance traits (Gasch, 2002; Zakrzewska et al., 2011). This type of trade-off may also have been apparent in the negative relationship we observed between cold-induced RNA helicase and α-glucosidase (GH Family 13) genes (**Figure 4c**). If trehalase, β-1,3 glucan synthase, and cold-induced RNA helicases were indeed part of a larger environmental stress response, then it is possible that an unidentified stress response trait—

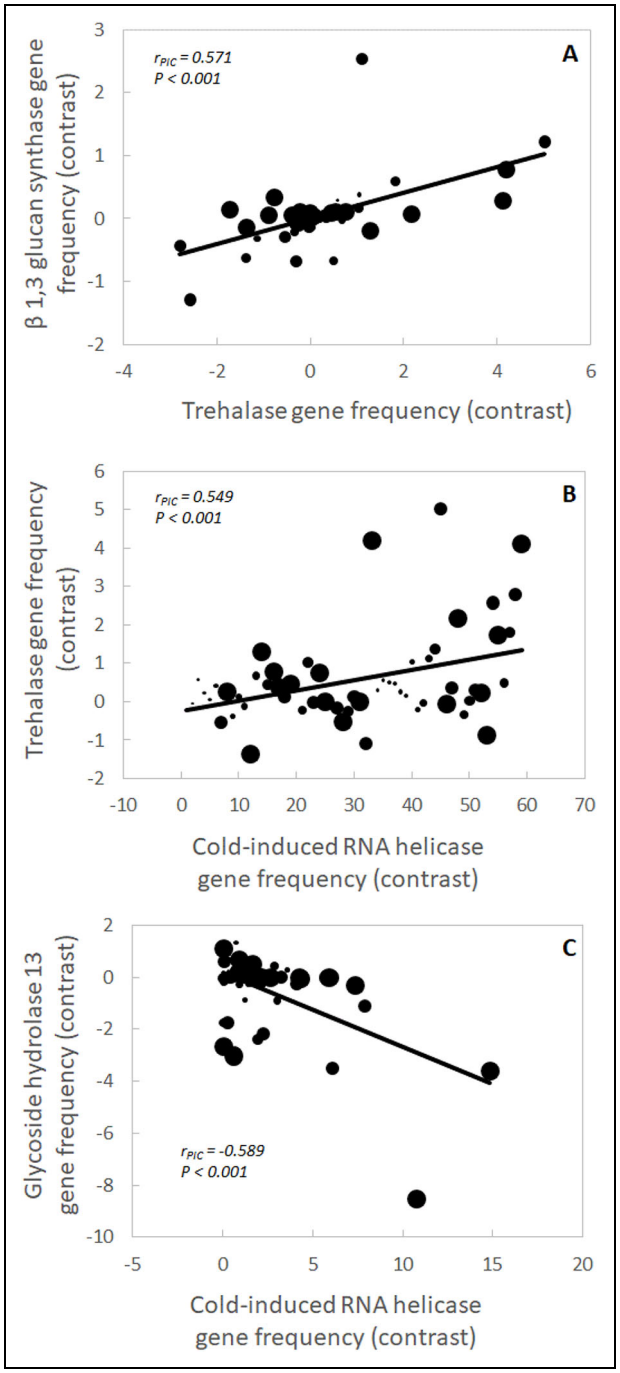

Figure 4. Relationships between functional genes in the Stress Tolerant Group. Symbols represent phylogenetic nodes (Figure S1). Contrasts are differences in trait values between daughter clades. Units are number of copies per 10,000 genes. Symbol size is proportional to the node's assigned weight in the analysis. Lines are best fit. *P* values are unadjusted for multiple comparisons. Data are from MycoCosm (Grigoriev et al., 2014). DOI: https://doi.org/10.1525/elementa.2020.00144.f4

other than trehalase—was driving tolerance for increased precipitation.

Responses to N enrichment and warming and drying also belonged to the Stress Tolerating Group. Specifically, fungal genera that responded positively to N enrichment in the Kerekes et al. (2013) tropical forest experiment also tended to respond positively to increased precipitation and warming and drying (Figure S2a and b). In this site, N additions had reduced soil pH from 5.1 to 4.9, which may have contributed to fungal stress (Corre et al., 2010). Nitrogen enrichment shifts fungal community composition (Johnson, 1993; Egerton-Warburton and Allen, 2000; Allison et al., 2008; Allison et al., 2010a; Entwistle et al., 2013; Amend et al., 2016; Morrison et al., 2016; Jia et al., 2017; Chen et al., 2018) more often than not (Porras-Alfaro et al., 2011; Cassman et al., 2016; McHugh et al., 2017). In a temperate forest in the northeastern United States, N fertilization favors stress-tolerant fungi and those with higher gene frequencies of ammonium transporters and amino acid permeases (Morrison et al., 2018; Romero-Olivares et al., 2021). Our finding that responses to N enrichment in the tropical forest tended to cluster with stress tolerance and ammonium transporter genes was consistent with those from the temperate forest.

With respect to warming and drying in the boreal forest study, departures from ambient temperature or moisture (or both) might have been stressful for local fungi. In the boreal forest experiment, warming increases evapotranspiration and dries the topsoil by about 22% (Allison and Treseder, 2008). As a result, fungal abundance declines (Allison and Treseder, 2008). After 8 years, the fungal community in surface litter had shifted significantly (Treseder et al., 2016; Romero-Olivares et al., 2017a). Moreover, decomposition rates of the litter slowed, especially for cellulose (Romero-Olivares et al., 2017a). Metatranscriptomic profiles of the fungal community in this experiment indicate that warming and drying induces the expression of cell maintenance genes while repressing the expression of GH genes, potentially owing to trade-offs between stress tolerance and decomposition (Romero-Olivares et al., 2019). In addition, fungi belonging to known stress-tolerant taxa displayed higher gene transcription rates in the warming and drying treatment compared to controls (Romero-Olivares et al., 2019). These findings mirror those reported from the Hubbard Brook Experimental Forest in the northeastern United States, where warming combined with intensified freeze/thaw cycles selected for stress-tolerant genes in fungi and bacteria (Garcia et al., 2020).

Carbon and Phosphorus Targeting Group

The C and P Targeting Group of traits was centered on crystalline cellulose genes (Auxiliary Activity Family 9; Levasseur et al., 2013; **Figure 2**). This enzyme family releases cellulose chains from highly crystalline or cross-linked structures, which tend to be recalcitrant (Harris et al., 2010; Langston et al., 2011). Fungal genera with relatively strong capacities for crystalline cellulase production tended to be capable of glucan breakdown as well (**Figure 5a and c**, GH Families 12 and 81). Moreover, gene frequencies for endoglucanase production (GH Family 12) were positively related to those for GH Family 7, which breaks β-1,4 glycosidic bonds in cellulose and β-1,4-glucan (**Figure 5d**; Shoemaker et al., 1983; Teeri et al., 1983; Ilmen et al., 1997). This suite of carbohydrate-targeting

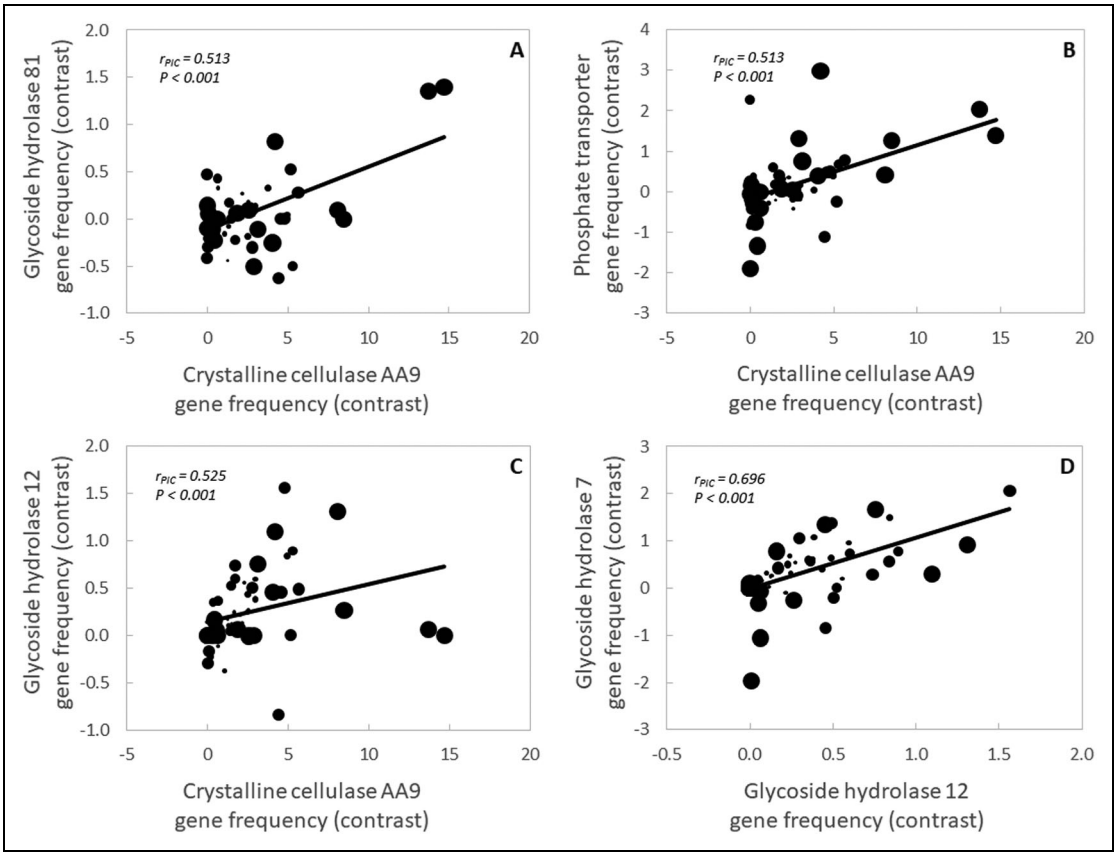

Figure 5. Relationships between functional genes in the C and P Targeting Group. Symbols represent phylogenetic nodes (Figure S1). Contrasts are differences in trait values between daughter clades. Units are number of copies per 10,000 genes. Symbol size is proportional to the node's assigned weight in the analysis. Lines are best fit. *P* values are unadjusted for multiple comparisons. Data are from MycoCosm (Grigoriev et al., 2014). DOI: https://doi.org/10.1525/elementa.2020.00144.f5

genes may form a decomposer lifestyle in fungi, distinct from a stress tolerance lifestyle. Previous studies have noted that C-targeting extracellular enzymes tend to coincide within fungal taxa (e.g., Eastwood et al., 2011; Floudas et al., 2012; Riley et al., 2014; Treseder and Lennon, 2015).

Phosphate transporters were also linked to this trait group. Specifically, gene frequencies of phosphate transporters were positively related to those of crystalline cellulase (**Figure 5b**). Fungi use P to build DNA, RNA, adenosine triphosphate, and phospholipids (Elser et al., 1996). Fungi might invest in P uptake to meet stoichiometric demands associated with increased C use (Sinsabaugh et al., 2008; Sinsabaugh et al., 2009; Sinsabaugh et al., 2016).

Unlinked trait: Responses to elevated CO_2

Several traits were not strongly linked to any others, so they did not belong to any group here. Responses to elevated CO_2 in alpine treeline was one example. Unlike the other response traits, it did not cluster with the Stress Tolerating Group. The numbers of sequences and identified taxa from this experiment were comparable to the other experiments (Table S1), so lack of statistical power is not a likely explanation. In this study, an increase in CO_2 concentrations from approximately 370 ppm (ambient) to 563–600 ppm (elevated) yields no significant change in fine root biomass or soil fungal biomass (Hagedorn et al., 2013). Likewise, the soil fungal community does not shift significantly at the operational taxonomic unit (i.e., species) level (Hagedorn et al., 2013). In fact, soil bacterial communities may have been more sensitive to elevated CO_2 than are fungi, given that bacterial composition shifts marginally significantly (Hagedorn et al., 2013). In this ecosystem, temperature limitation of plants may constrain their responses to elevated CO_2 (Dawes et al., 2011), which in turn may minimize effects on belowground C supplies and progressive nutrient limitation. Essentially, fungi in this system may have experienced little change in environmental conditions under elevated CO_2.

This case study may not be representative of other elevated CO_2 studies. Elsewhere, mycorrhizal fungi frequently become more abundant (Treseder, 2004; Dong et al., 2018). Likewise, fungal community composition often shifts (Weber et al., 2011), sometimes owing to increases in fine root production (Lipson et al., 2014). These CO_2 effects in other ecosystems might be more readily linked to stress tolerance, resource acquisition, or other lifestyles.

Revisiting the trait-based framework

We revised our trait-based framework to center links between stress tolerance traits and responses to increased

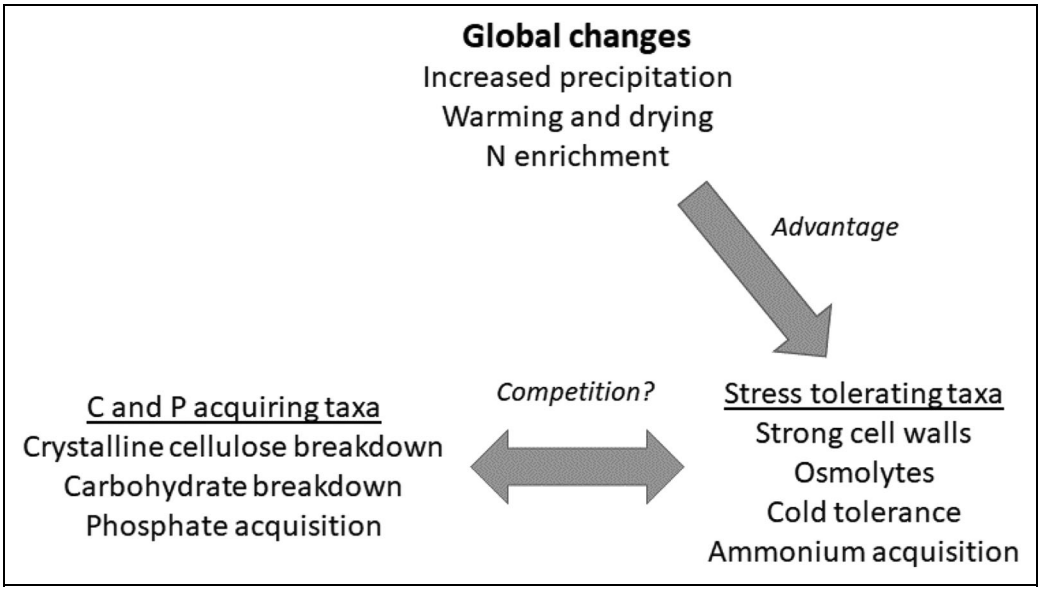

Figure 6. Revised trait-based framework relating global changes to the relative abundance of fungal taxa and their functional gene traits. DOI: https://doi.org/10.1525/elementa.2020.00144.f6

precipitation, N enrichment, and warming and drying (**Figure 6**). We suggest that taxa with strong cell walls (from β-1,3 glucose), osmolytes (e.g., trehalose), and cold tolerance (via cold-induced RNA helicase) may have an advantage under these conditions. The advantage may be conferred by these specific stress tolerance traits or by a larger environmental stress response with which they co-occur (Gasch and Werner-Washburne, 2002; Gasch, 2007).

In contrast, C- and P-acquisition traits may be disadvantageous under these circumstances. If stress-tolerating fungi compete for space or resources with C and P acquiring fungi, the latter group may become less prevalent. Furthermore, GH 13 genes (α-glucosidases) were negatively related to cold-induced RNA helicase genes (**Figure 4c**), which implies that investment in C acquisition might trade off with stress tolerance. On the other hand, if competition or trade-offs are not significant, the C and P acquiring taxa may not necessarily decline in absolute abundance upon exposure to increased precipitation, N enrichment, or warming and drying. Nevertheless, fungal species are known to compete with one another (Boddy, 2000; Fukami et al., 2007; Kolesidis et al., 2019). It would be worth investigating whether stress tolerators compete with decomposers under natural settings (Cray et al., 2013; Ho et al., 2017; Malik et al., 2019).

Another question to explore is the timescale during which stress tolerance might be advantageous under global change. If stress is induced when fungi are exposed to unfamiliar environmental conditions, will the stress decline once fungi acclimate or adapt? Here, the increased precipitation experiment was relatively brief—the water additions lasted for 1 month (McHugh and Schwartz, 2016). By comparison, N enrichment had been maintained for 9 years at the time of sampling (Kerekes et al., 2013). Moreover, the warming and drying experiment had been ongoing for 8 years. In laboratory settings, fungi can adapt or acclimate to new conditions within hours to months (Dettman et al., 2008; DeAngelis et al., 2010; Romero-Olivares et al., 2015; Zhang et al., 2016b). However, we might expect these mechanisms to operate more slowly in the field, where conditions can be less optimal, and stress levels are less extreme or abrupt (Leuzinger et al., 2011; Gao et al., 2020). In addition, direct, immediate effects of the global change itself need not be the only sources of stress for fungi. Indirect effects via shifts in the plant community, changes in soil texture, disturbance, or other intermediate processes could sustain stress over a longer time.

The revised trait-based framework suggests potential consequences of global changes for fungal contributions to nutrient cycling (sensu Lavorel and Garnier, 2002; Chagnon et al., 2013; Treseder and Lennon, 2015; Ho et al., 2017; Malik et al., 2019). In ecosystems exposed to increased precipitation, N enrichment, or warming and drying, we might expect that β-1,3 glucan incorporation into fungal cell walls will increase owing to its contributions to stress tolerance. β-1,3 glucan forms cross-linkages with chitin (Cabib, 2009), forming a recalcitrant C complex that may remain in the soil after the fungi die (Klis, 1994; Treseder and Lennon, 2015). This process could augment soil C storage. Conversely, as C and P targeting fungi use the products of extracellular cellulases, they essentially convert a portion of the cellulose-C to CO_2. If competition with stress-tolerating fungi reduce the abundance of C and P targeting fungi, then the fungal community may produce less CO_2 via this process. If competition is not significant, however, this may not be a consequence. Next generation trait-based models can use these trait linkages to predict ecosystem dynamics under global change (Follows et al., 2007; Allison, 2012; Allison, 2014; Wieder et al., 2015).

Conclusions

In summary, we found that stress tolerance traits were positively related to the responses of fungal genera to 3

types of global change: increased precipitation, N enrichment, and warming and drying. Capacity for C and P acquisition seemed less critical, as functional genes for these traits were less strongly linked to global change responses. Although we had expected that ability to capture limiting nutrients under global change would influence responses of fungal genera, we found little evidence to support this notion. We developed a revised trait-based framework predicting that increased precipitation, N enrichment, and warming and drying will generate stress in fungi and select for taxa with stress tolerance traits. Stress-tolerating fungi may outcompete C and P targeting fungi if space or resources are limiting. Essentially, elements of global change—even those that might otherwise seem beneficial to fungi like increased precipitation—may generate environmental stress and select for stress-tolerating fungi.

Data accessibility statement

The following datasets were generated:

Trait database, uploaded as Table S2 of this publication.

Supplemental files

The supplemental files for this article can be found as follows:

Figures S1– S3. PDF
Table S1. PDF
Tables S2–S4. xlsx

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Competing interests

The authors declare no competing interests.

Author contributions

Performed data assimilation and analysis and developed the conceptual framework: KKT, CJA, LAC, MEG, ALK, KGL.

Helped write the manuscript, with KKT leading: All authors.

Provided data and intellectual contributions: FH, JFK, TAM, EFS.

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