FIRE REDUCES FUNGAL SPECIES RICHNESS AND IN SITU MYCORRHIZAL COLONIZATION: A META-ANALYSIS

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ABSTRACT

Soil fungal communities perform many functions that help plants meet their nutritional demands. However, overall trends for fungal response to fire, which can be especially critical in a post-fire context, have been difficult to elucidate. We used meta-analytical techniques to investigate fungal response to fire across studies, ecosystems, and fire types. Change in fungal species richness and mycorrhizal colonization were used as the effect size metrics in random effects models. When different types of methods for assessing fungal species richness and mycorrhizal colonization were considered together, there was an average reduction of 28% in fungal species richness post fire, but no significant response in mycorrhizal colonization. In contrast, there was a 41% reduction in fungal species richness post fire when assessed by sporocarp surveys, but fungal species richness was not significantly affected when assessed by molecular methods. Measured in situ, fire reduced mycorrhizal colonization by 21%, yet no significant response occurred when assessed by ex situ bioas-

RESUMEN

Las comunidades fúngicas del suelo cumplen muchas funciones que ayudan a las plantas a suplir sus demandas nutricionales. Sin embargo, las tendencias generales de respuesta de estos hongos al fuego, que pueden ser especialmente críticas en el contexto del post-fuego, han sido difíciles de dilucidar. Usamos técnicas de meta-análisis para investigar la respuesta de hongos al fuego a través de estudios, ecosistemas, y tipos de fuegos. Los cambios en la riqueza de especies de hongos y colonización micorrílica fueron usados como medida del efecto del fuego en modelos al azar. Cuando los diferentes tipos de métodos para determinar la riqueza de especies de hongos y la colonización micorrílica fueron considerados juntos, se encontró una disminución promedio del 28% en la riqueza de hongos post-fuego, mientras que no hubo respuestas significativas en la colonización micorrílica. En contraste con esto, hubo una reducción del 41% en la riqueza de especies de hongos post-fuego cuando fueron determinados mediante el relevamiento de esporocarpos, mientras que esta riqueza no fue significativamente afectada cuando fue determinada mediante métodos moleculares. Medidos in situ, el fuego redujo la colonización micorrílica un 21%, aunque no hubo una respuesta significativa
says. These findings suggest that the putative magnitude of fire effects on soil fungal communities may be dependent on the approach and assessment method used. Furthermore, biome, but not fire type (i.e., wildfire versus prescribed fire) was a significant moderator of our categorical models, suggesting that biome might be a more useful predictor of fungal species richness response to fire than fire type. Reductions in fungal species richness and in situ mycorrhizal colonization post fire declined logarithmically and approached zero (i.e., no effect) at 22 and 11 years, respectively. We concluded that fire reduces fungal species richness and in situ mycorrhizal coloni- zation, but if conditions allow communities to recover (e.g., without subsequent disturbance, favorable growing conditions), soil fungi are resilient on decadal time scales; the resiliency of soil fungi likely contributes to the overall rapid ecosystem recovery following fire.

**INTRODUCTION**

A common goal of ecosystem management is the restoration and maintenance of critical ecological functions. Many of these processes, including decomposition, nutrient mineralization, and resource acquisition by plants, are moderated by soil fungi (Hobbie and Horton 2007, Baldrian et al. 2012, Phillips et al. 2013). Disturbance by wildfire is widespread globally among terrestrial ecosystems, affecting both aboveground and belowground biotic communities, particularly soil fungi (Bond and Keeley 2005, Bond et al. 2005). The direct effects of extreme temperatures from fire in the upper soil horizons can cause drastic changes in the fungal community even though heat from fire generally only impacts surficial soil layers (DeBano 2000). This preferential sensitivity of fungi (compared to other soil microorganisms) to this form of ecosystem disturbance stems from both fungal intolerance to heat (Dunn et al. 1985, Izzo et al. 2006) and their greater abundance in surficial organic (O) horizons and the upper mineral soil (Baldrian et al. 2012).

**Keywords:** biodiversity, fungi, mycorrhizae, soil ecology

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These direct and selective impacts of fire on soil fungi can potentially alter important ecosystem processes that fungi mediate.

Fungi are also impacted by wildfire through indirect effects on soil properties, which may permeate into deeper soil layers (Jones et al. 2003). For instance, fire generally: decreases canopy cover (due to tree mortality), thus increasing soil insolation (Ballard 2000); decreases surface albedo (by the blackening of soil), thus increasing the relative amount of absorbed shortwave radiation; and decreases soil thickness, and thus insulation of the O horizon due to combustion (Hart et al. 2005b). These indirect effects of fire on the heat balance of soil can alter soil temperature regimes (Binkley and Fisher 2012). Additionally, hydrophobic soil layers are frequently formed by the partial combustion of organic matter (DeBano 2000), which leads to decreased water infiltration and altered soil hydrology. Changes in soil temperature and moisture may affect the phenology of fungal fruiting (Straatsma et al. 2001), mycorrhizal infectivity (Parke et al. 1983), and overall fungal activity (Hamman et al. 2007). Increases in nutrient availability post fire are also likely a driver of fungal community dynamics (Anderson and Menges 1997, Treseder 2004, Bastias et al. 2006). These complex indirect effects of fire on soil physiochemical characteristics, combined with direct heating effects, make it difficult to generalize about fire influences on soil fungal communities from individual studies.

Changes in aboveground vegetation may have the greatest impact on soil fungal communities in later stages of ecosystem recovery (Hart et al. 2005b). Many ectomycorrhizal (ECM) species show some degree of host specificity (Smith and Read 2008); thus, changes in the presence of certain host trees following fire may substantially affect the ECM community. Similarly, decreased woody canopy cover and increased graminoid density following fire can elevate arbuscular mycorrhizal (AM) fungal abundances compared to ECM fungi (Korb et al. 2003). Fire-induced changes to carbon (C) inputs could also alter soil saprobic fungal communities. For instance, increased herbaceous C inputs and reduced lignin-rich woody litterfall post fire (Kaye et al. 2005) could decrease the relative abundance of white-rot fungi (within the class Agaricomycetes) that uniquely produce lignin-degrading enzymes (Hanson et al. 2008, Floudas et al. 2012, Treseder and Lennon 2015). Clearly, aboveground and belowground organismal communities are inextricably linked, such that the succession of fungal communities post fire mimics, at least to some degree, that of plant communities (Frankland 1998). These changes may be long lived, especially if fire induces significant plant mortality.

Inconsistencies in results from individual studies have hindered our ability to make general conclusions about possible linkages among fire, fungi, and ecosystem function. For example, studies have shown that wildfire can have negative (Visser 1995, Martín-Pinto et al. 2006, Hernández-Rodríguez et al. 2013, Motiejūnaitė et al. 2014), neutral (Jonsson et al. 1999, Mah et al. 2001, Chen and Cairney 2002), or positive (Hewitt et al. 2013) effects on fungal diversity. Similarly, many studies have found an overall decrease in mycorrhizal colonization post fire (Dhillion et al. 1988, Rashid et al. 1997, Barker et al. 2013), while other studies have found no effect (Eom et al. 1999) or even increased colonization following fire (Herr et al. 1994, Rincón et al. 2014). Resolving these inconsistencies in fungal response to fire should increase our understanding of decomposition, nutrient cycling, and productivity in post-fire landscapes because of the close coupling between fungi and ecosystem function. For instance, AM species richness strongly controls plant productivity in grassland ecosystems (Gange et al. 1993, van der Heijden et al. 1998, Vogelsang et al. 2006). In deciduous forests, Betula spp. L. plant nutrient concentrations and productivity are posi-
tively correlated with increasing ECM species richness (Baxter and Dighton 2001, Jonsson et al. 2001). Furthermore, laboratory experiments show that species richness of saprobic fungi positively influences decomposition in species-poor environments or on recalcitrant organic substrates (both commonly created in post-fire environments; Setälä and McLean 2004, van der Wal et al. 2013). Differences in mycorrhizal colonization can also have profound impacts on nutrient cycling by influencing nutrient acquisition by their plant hosts (Smith and Read 2008), and changes in the relative proportions between ECM and AM colonization following fire may impact the rates of cycling of these limiting nutrients (Phillips et al. 2013). Clearly, a more unified understanding of how fire influences soil fungal communities would help improve our ability to predict changes in ecosystem function following such disturbances.

These apparent idiosyncratic responses of soil fungi to fire are often attributed to differences in fire severity among studies (Dahlberg et al. 1997, Jonsson et al. 1999, Horton and Bruns 2001, Fujimura et al. 2004). This is likely due in part to differences in sampling intensity (Horton and Bruns 2001), but may also reflect physiological and phenological differences in the fruiting frequencies of different fungal species. Similarly, estimates of the response of mycorrhizal colonization of plant roots to fire may differ depending on methodology. For example, while fire probably reduces mycorrhizal inocula and host density (Hart et al. 2005b), mycorrhizal colonization assessed using ex situ bioassays, which measure colonization potential in the presence of suitable hosts, may not reflect in situ mycorrhizal colonization in which host species or abundance may be limiting (Perry et al. 1987). Given the myriad of factors that can influence results from individual studies, the application of a robust, quantitative, and synthetic analysis of fire–fungal relationships may help identify characteristic fungal responses to fire and thus help predict associated changes in ecosystem function.

We used meta-analytical techniques to synthesize the saprobic and mycorrhizal fungal community response to fire across wild-land ecosystems, fire types, and assessment methods. The lack of studies on pathogenic or parasitic fungal community response to fire precluded the incorporation of these guilds in our analysis. Using this quantitative approach, we tested the following hypotheses: 1) fire causes an overall reduction in fungal species richness; 2) fire results in an overall reduction in mycorrhizal colonization of plant roots; 3) the apparent impact of fire on soil fungi is influenced by several moderating variables including the fungal guild studied (e.g., AM, ECM, wood-inhabiting fungi, and culturable microfungi), method of measurement, fire type (e.g., wildfire or prescribed fire, a single fire event, or repeated fire), and biome; and 4) the impact of fire on fungal communities diminishes with time since fire. Our overarching
goal was to elucidate previously unidentified trends and factors that contribute to post-fire ecosystem resilience by combining the results from all known studies of fire effects on fungal communities into a single set of statistical analyses.

**METHODS**

**Sources of Data**

Institute for Scientific Information Web of Knowledge (now Clarivate Analytics Web of Science®) and Google Scholar databases were searched for field experiments studying the effects of fire on soil fungal communities using key words such as fung*, fire, wildfire, burn, diversity, richness, and colonization. We used “cited-by” functions from relevant studies to find related papers. Studies were collected for analysis until 21 April 2016. We focused on studies reporting fungal species richness and mycorrhizal colonization in burned versus unburned control treatments, rather than pre fire versus post fire to control for temporal variations in richness and colonization. Although this risks assigning treatment effects to spatial variation, many wildfire studies are conducted post hoc, without pre-fire samples. Therefore, we decided to standardize our data collection by using unburned sites as our control rather than a mix of unburned and pre-fire sites as controls. If an unburned control did not occur, then we used a pre-fire sample as a control, which occurred only in three cases (Olsson and Jonsson 2010, Goberna et al. 2012, Glassman et al. 2015). If a study used a chronosequence without a control, then the latest date of the chronosequence was used as the pre-fire sample. This situation also occurred only in three studies (Treseder et al. 2004, Holden et al. 2013, Sun et al. 2015), and the latest dates were all at least 100-year-old boreal forests. Because our objective was to focus on field-relevant, ecosystem-level implications of fire alone, we excluded laboratory burning simulations and combination thin-burn treatments. Additionally, we limited our analysis to studies with reported replication (n ≥ 2) and mean fungal species richness or mycorrhizal colonization. If studies reported Shannon’s diversity index (H) and evenness (E), but did not report richness (S; e.g., Martin-Pinto et al. 2006), we used the following equation to derive species richness:

\[ S = \frac{e^H}{E} \]  

One of the assumptions of meta-analyses is that each study is independent of the others (Gurevitch and Hedges 1999). Therefore, we only used one data record (nearest to the conclusion of the fire; time = 0) for studies that employed repeated measures from the same experimental unit. However, we assumed independence between time points for studies that also assumed independence between time points (e.g., a fire chronosequence). Although this opens the potential to bias results towards individual studies, no study dominated the dataset (Tables 1 and 2), and relaxing the condition of one record per study allowed the dataset to double in size, increasing the robustness of the meta-analysis.

**Data Acquisition**

The mean fungal species richness or mycorrhizal colonization and number of replicates for both burn and control treatments were recorded. Additionally, for the fungal species richness meta-analysis, we noted the fungal guild studied (e.g., ECM fungi, AM fungi, wood-inhabiting fungi, or culturable microfungi), method of measure (e.g., next-generation sequencing, sporocarp survey, spore morphology, hyphal morphology, or culture morphology), fire type (wildfire or prescribed fire; repeat [<15 yr] or single fire event), biome, and time since fire. Only three biomes
Table 1. Data used in meta-analysis of fungal species richness response to fire, including control replicates \((n_c)\), control mean \((x_c)\), experimental replicates \((n_e)\), experimental mean \((x_e)\), the natural log of the response ratio (\(\ln[R]\)), and change in richness \(\%\).

| Reference               | Guild studied* | Unit of measurement* | Fire type† | Repeat burn? | Years since fire | Biome* | Location | Location | Control replicates \((n_c)\) | Control mean \((x_c)\) | Experimental replicates \((n_e)\) | Experimental mean \((x_e)\) | \(\ln[R]\) | Change in richness \(\%\) |
|-------------------------|----------------|----------------------|------------|--------------|-----------------|---------|-----------|-----------|-----------------------------|-----------------------|-----------------------------|-----------------------------|--------------|---------------------------|
| Barker et al. 2013      | ECM morphotyping + molecular ID | W                  | 3          | TF           | British Columbia, Canada | 15      | 8         | 15        | 6.3                        | –0.2389               | 5.6                        | –0.6932                    | –50.0         |
| Bartoli et al. 1991     | microfungi culture morphology | W                  | 0.01644    | TF           | Italy           | 5       | 2.12      | 5         | 3.2                        | –1.8909               | 5.3                        | –0.3365                    | –28.6         |
| Buscardo et al. 2010    | ECM morphotyping + molecular ID | W                  | 3          | TF           | Portugal        | 11      | 2.6       | 11        | 1.9                        | –0.3032               | 5.6                        | –0.6932                    | –26.2         |
| Dahlberg et al. 2001    | ECM morphotyping + molecular ID | P                  | 0.3        | BF           | Sweden          | 5       | 1.4       | 5         | 0.9                        | –0.5272               | 5.6                        | –0.3365                    | –28.6         |
| Eom et al. 1999         | AM (spore) morphology | P                  | 1          | TG           | Kansas, USA     | 4       | 5.3       | 4         | 3.8                        | –0.3365               | 5.6                        | –0.3365                    | –28.6         |
| Glassman et al. 2015    | ECM morphotyping + molecular ID | W                  | 1          | TF           | California, USA | 25      | 30.5      | 25        | 20                        | –0.4220               | 5.6                        | –0.4220                    | –34.4         |
| Gobena et al. 2012      | All fungi DGGE | P                  | 0.00274    | TG           | Spain           | 10      | 23.5      | 10        | 26.55                      | 0.1208                | 5.6                        | –0.3365                    | –28.6         |
| Girishkan 2016          | microfungi culture morphology | W                  | 1.5        | TF           | Israel          | 3       | 36        | 3         | 23                        | –0.4480               | 5.6                        | –0.3365                    | –28.6         |
| Hernandez-Rodriguez et al. 2013 | All fungi sporocarp survey | W                  | 1          | TG           | Spain           | 6       | 22.1      | 6         | 6.1                        | –1.2827               | 5.6                        | –1.2827                    | –72.3         |
| Holden et al. 2013      | All fungi NGS | W                  | 0          | BF           | Alaska, USA     | 2       | 122.3     | 2         | 121.2                      | –0.0090               | 5.6                        | –0.0090                    | –0.90         |
| Jonsson et al. 1999     | ECM morphotyping + molecular ID | W                  | 62         | BF           | Sweden          | 2       | 22.5      | 2         | 20                        | –0.1178               | 5.6                        | –0.1178                    | –11.1         |
| Jumma and Hart 2011     | WIF sporocarp survey | P                  | 1          | BF           | Finland         | 3       | 18.42     | 3         | 18.68                      | 0.0140                | 5.6                        | 0.0140                     | 1.4           |
| Kipfer et al. 2011      | ECM morphotyping + molecular ID | W                  | 3.5        | TF           | Switzerland     | 5       | 21.2      | 5         | 11.6                      | –0.6030               | 5.6                        | –0.6030                    | –45.3         |
| Kurth et al. 2013       | WIF NGS | W                  | 4          | BF           | Arizona, USA    | 6       | 3.5       | 6         | 1.8                        | –0.6621               | 5.6                        | –0.6621                    | –48.4         |
|                         | WIF NGS | W                  | 9          | TF           | Arizona, USA    | 6       | 3.7       | 6         | 4.3                        | 0.1526                | 5.6                        | 0.1526                     | 16.5          |
|                         | WIF NGS | W                  | 13         | TF           | Arizona, USA    | 6       | 4.8       | 6         | 4.5                        | –0.0728               | 5.6                        | –0.0728                    | –7.0          |
|                         | WIF NGS | W                  | 25         | TF           | Arizona, USA    | 6       | 2.7       | 6         | 5.3                        | 0.6782                | 5.6                        | 0.6782                     | 97.0          |
|                         | WIF NGS | W                  | 32         | TF           | Arizona, USA    | 6       | 3.8       | 6         | 3.8                        | 0.0000                | 5.6                        | 0.0000                     | 0.0           |

* AM = arbuscular mycorrhizal fungi; ECM = ectomycorrhizal fungi; WIF = wood-inhabiting fungi
* NGS = next-generation sequencing; DGGE = denaturing gradient gel electrophoresis
* P = prescribed fire; W = wildfire
* TF = temperate forest; BF = boreal forest; TG = temperate grassland; TS = temperate shrubland; TrF = tropical forest
* Fire-resistant propagules (e.g., spores, residual hyphae)
Table 1, continued. Data used in meta-analysis of fungal species richness response to fire, including control replicates ($n_c$), control mean ($x_c$), experimental replicates ($n_e$), experimental mean ($x_e$), the natural log of the response ratio (ln[R]), and change in richness (%).

| Reference                  | Guild studied | Unit of measurement | Fire type | Repeat burn? | Years since fire | Biome | Location          | $n_c$ | $x_c$ | $n_e$ | $x_e$ | ln[R]   | Change in richness (%) |
|----------------------------|---------------|---------------------|-----------|--------------|------------------|-------|-------------------|-------|-------|-------|-------|---------|------------------------|
| Longo et al. 2014          | AM (spore)    | spore morphology   | W         | 0.5          | TF               | Argentina | 10     | 7.5   | 10    | 4.6   | -0.4850 | -38.4                  |
|                            | AM (spore)    | spore morphology   | W         | 0.5          | TF               | Argentina | 10     | 7.7   | 10    | 4.1   | -0.6477 | -47.7                  |
|                            | AM (spore)    | spore morphology   | W         | 0.5          | TF               | Argentina | 10     | 6.9   | 10    | 4.3   | -0.4723 | -37.7                  |
|                            | AM (spore)    | spore morphology   | W         | 0.5          | TF               | Argentina | 10     | 8.4   | 10    | 4.9   | -0.5371 | -41.6                  |
| Mardji 2014                | ECM           | spore morphocarp   | W         | 2 consecutive | TrF             | India    | 4      | 8.75  | 4     | 3.25  | -0.9904 | -62.9                  |
| Martin-Pinto et al. 2006   | All fungi     | sporocarp survey   | W         | 1            | TF               | Spain    | 3      | 22.1  | 3     | 8.8   | -0.9257 | -60.4                  |
|                            | All fungi     | sporocarp survey   | W         | 1            | TF               | Spain    | 3      | 16.9  | 3     | 6.3   | -0.9799 | -62.5                  |
| Motiejūnaitė et al. 2014   | All fungi     | sporocarp survey   | W         | 1            | TF               | Lithuania| 3      | 71.2  | 3     | 23.9  | -1.0930 | -66.5                  |
| Oliver et al. 2015         | All fungi     | NGS                | P         | every 2 yr (winter) | TF           | Georgia, USA | 4      | 668   | 4     | 656.5 | -0.0174 | -1.7                  |
|                            | All fungi     | NGS                | P         | every 3 yr (winter) | TF           | Georgia, USA | 4      | 668   | 4     | 680.5 | 0.0185  | 1.9                   |
|                            | All fungi     | NGS                | P         | every 3 yr (summer) | TF           | Georgia, USA | 4      | 668   | 4     | 659.75| -0.0124 | -1.2                  |
| Olsson and Jonsson 2010    | WIF           | sporocarp survey   | P         | 1            | BF               | Sweden   | 150    | 20    | 150   | 12.2  | -0.5161 | -40.3                  |
| Rinón et al. 2014          | ECM (morphological + molecular ID) | W       | 14           | TF            | Spain          | 3       | 11.9  | 3     | 10.0  | -0.1796 | -16.4                  |
| Robinson and Miguel 2005   | ECM           | morphophyte        | P         | 1            | TF               | Spain    | 3      | 11.9  | 3     | 9.0   | -0.2832 | -24.7                  |
| Smith et al. 2004          | ECM (morphological + molecular ID) | P       | 1            | TF            | Oregon, USA    | 4       | 10.3  | 4     | 10    | -0.0247 | -2.4                  |
|                            | ECM (morphological + molecular ID) | P       | 1            | TF            | Oregon, USA    | 4       | 9.5   | 4     | 1.8   | -1.6917 | -81.6                  |
| Sun et al. 2015            | All fungi     | NGS                | W         | 2            | BF               | Finland  | 10     | 121.5 | 10    | 181.3 | 0.4002  | 49.2                   |
|                            | All fungi     | NGS                | W         | 42           | BF               | Finland  | 10     | 121.5 | 10    | 143.9 | 0.1692 | 18.4                   |
|                            | All fungi     | NGS                | W         | 60           | BF               | Finland  | 10     | 121.5 | 10    | 129   | 0.0599  | 6.2                    |
|                            | All fungi     | NGS                | W         | 60           | BF               | Finland  | 10     | 121.5 | 10    | 130.8 | 0.0738  | 7.7                    |
| Trappe et al. 2009         | ECM           | sporocarp survey   | P         | 3            | TF               | Oregon, USA | 8      | 69    | 8     | 55    | -0.2268 | -20.3                  |
|                            | ECM           | sporocarp survey   | P         | 3            | TF               | Oregon, USA | 4      | 69    | 4     | 81    | 0.1603  | 17.4                   |
|                            | ECM           | sporocarp survey   | P         | 3            | TF               | Oregon, USA | 4      | 69    | 4     | 81    | 0.1603  | 17.4                   |
| Trusty 2009                | ECM (morphological + molecular ID) | W       | 5            | TF            | Montana, USA    | 3       | 2.17  | 3     | 1.58  | -0.3173 | -27.2                  |
| Tuininga and Dighton 2004  | ECM (hyphal morphotype) | P       | every 4 yr   | 0.3           | TF            | New Jersey, USA | 3      | 9.4   | 3     | 9.1   | -0.0389 | -3.8                   |
|                            | ECM (hyphal morphotype) | P       | every 8 yr   | 0.3           | TF            | New Jersey, USA | 3      | 10.6  | 3     | 8.6   | -0.2164 | -19.5                  |
| Xiang et al. 2015          | AM            | NGS                | W         | 1            | BF               | China    | 6      | 74.34 | 6     | 8.68  | -0.5919 | -44.7                  |
|                            | AM            | NGS                | W         | 1            | BF               | China    | 6      | 74.34 | 6     | 12.84 | -0.7641 | -53.4                  |
|                            | AM            | NGS                | W         | 11           | BF               | China    | 6      | 74.34 | 6     | 15.09 | -0.1392 | -13.0                  |
|                            | AM            | NGS                | W         | 11           | BF               | China    | 6      | 74.34 | 6     | 15.85 | -0.4945 | -39.0                  |

†Fire-resistant propagules (e.g., spores, residual hyphae)

AM = arbuscular mycorrhizal fungi; ECM = ectomycorrhizal fungi; WIF = wood-inhabiting fungi

NGS = next-generation sequencing; DGGE = denaturing gradient gel electrophoresis

P = prescribed fire; W = wildfire

TF = temperate forest; BF = boreal forest; TG = temperate grassland; TS = temperate shrubland; TrF = tropical forest
Table 2. Data used in meta-analysis of mycorrhizal colonization response to fire including control replicates \((n_c)\), control mean \((x_c)\), experimental replicates \((n_e)\), experimental mean \((x_e)\), the natural log of the response ratio \((\ln[R])\), and change in colonization (%).

| Reference                  | Guild studied | Unit of measurement | in situ or ex situ | Fire type | Repeat burn? | Years since fire | Biome/Location | n_c | x_c | n_e | x_e | ln[R] | Change in colonization (%) |
|----------------------------|---------------|---------------------|-------------------|-----------|--------------|-----------------|----------------|-----|-----|-----|-----|-------|---------------------------|
| Anderson and Menges 1997   | AM            | % colonized seedlings | ex situ           | P         |              | 0.083           | TF Florida, USA | 10  | 2.2 | 10  | 3.8 | 0.5465 | 72.7                      |
| Bacon et al. 2009          | AM            | % colonized seedlings | ex situ           | P         |              | 33.000          | TF Arizona, USA | 12  | 20  | 12  | 41  | 0.7178 | 105                       |
|                           | AM            | % colonized seedlings | ex situ           | W         |              | 5.000           | TF Arizona, USA | 12  | 7.5 | 12  | 16  | 0.7577 | 113.3                     |
|                           | ECM           | % colonized seedlings | ex situ           | W         |              | 33.000          | TF Arizona, USA | 12  | 60  | 12  | 75  | 0.2231 | 25                        |
|                           | ECM           | % colonized seedlings | ex situ           | W         |              | 5.000           | TF Arizona, USA | 12  | 71  | 12  | 70  | –0.0142 | –1.4                     |
| Barker et al. 2013         | ECM           | % colonized seedlings | in situ           | W         |              | 0.330           | British Columbia, Canada | 18 | 44.9 | 18 | 22.9 | –0.6742 | –49.0                     |
|                           | ECM           | % colonized seedlings | in situ           | P         |              | 0.330           | British Columbia, Canada | 18 | 44.9 | 18 | 26.6 | –0.5238 | –40.8                     |
| Bellgard et al. 1994       | AM            | % root length       | ex situ           | W         |              | 0.083           | TG Australia    | 10  | 35.9 | 10  | 35  | –0.0246 | –2.4                      |
| Bentivenga and Hetrick 1991| AM            | % root length       | in situ           | P         |              | 0.011           | TG Kansas, USA  | 4   | 13.3 | 4   | 11.6 | –0.1382 | –12.9                     |
| Buscardo et al. 2010       | ECM           | % root tips         | ex situ           | W         |              | 5.000           | TF Portugal     | 12  | 55  | 12  | 59.1 | 0.0719  | 7.5                       |
|                           | ECM           | % root tips         | ex situ           | W         | 2 consecutive| 5.000           | TF Portugal     | 12  | 55  | 12  | 60  | 0.0870  | 9.1                       |
|                           | ECM           | % root tips         | ex situ           | W         | 2 consecutive| 5.000           | TF Portugal     | 12  | 55  | 12  | 64.2 | 0.1547  | 16.7                      |
|                           | ECM           | % root tips         | ex situ           | W         | 2 consecutive| 5.000           | TF Portugal     | 11  | 42.5 | 11  | 38.1 | –0.1093 | –10.4                     |
|                           | ECM           | % root tips         | ex situ           | W         | 2 consecutive| 5.000           | TF Portugal     | 11  | 42.5 | 11  | 59.1 | 0.3297  | 39.1                      |
|                           | ECM           | % root tips         | ex situ           | W         | 2 consecutive| 5.000           | TF Portugal     | 11  | 42.5 | 11  | 25.5 | –0.5108 | –40.0                     |
| Dhillion et al. 1988       | AM            | % root length       | in situ           | P         | repeat unspecified | 0.133           | TG Illinois, USA | 10  | 75  | 10  | 39  | –0.6539 | –48.0                     |
| Glassman et al. 2015       | ECM           | % colonized seedlings | ex situ           | W         |              | 1.000           | TF California, USA | 26 | 100 | 22 | 85  | –0.1625 | –15.0                     |
| Hartnett et al. 1994       | AM            | % root length       | in situ           | P         |              | 0.250           | TG Kansas, USA  | 20  | 12.5 | 20  | 15  | 0.1823  | 20.0                      |
| Medve 1985                 | AM            | % root tips         | in situ           | P         |              | 0.330           | TG Pennsylvania, USA | 10 | 70.2 | 10 | 69.9 | –0.0043 | –0.4                      |
| Miller et al. 1998         | ECM           | % colonized seedlings | ex situ           | W         |              | 1.000           | TF Wyoming, USA  | 3   | 38.2 | 3   | 62  | 0.4843  | 62.3                      |
|                           | ECM           | % colonized seedlings | ex situ           | W         |              | 1.000           | TF Wyoming, USA  | 3   | 28.9 | 3   | 55.4 | 0.6507  | 91.7                      |
| Milne 2002                 | ECM           | % root tips         | ex situ           | W         |              | 0.250           | TF Greece       | 3   | 29.2 | 3   | 16.59 | –0.5667 | –43.3                     |
| Raman and Nagarajan 1996   | AM            | % root tips         | in situ           | P         |              | 0.055           | TrF India       | 12  | 53.83 | 12 | 35.92 | –0.4045 | –33.3                     |
| Rashid et al. 1997         | AM            | % root length       | in situ           | W         |              | 0.417           | TG Pakistan     | 10  | 57  | 10  | 23  | –0.9076 | –59.7                     |
|                           | AM            | % root length       | in situ           | W         |              | 0.417           | TG Pakistan     | 10  | 43  | 10  | 20.7 | –0.7311 | –51.9                     |
| Rincón et al. 2014         | ECM           | % root tips         | ex situ           | W         |              | 14.00           | TF Spain        | 3   | 70  | 3   | 81.5 | 0.1526  | 16.5                      |
|                           | ECM           | % root tips         | ex situ           | W         |              | 3.000           | TF Spain        | 4   | 70  | 4   | 61.0 | –0.1383 | –12.9                     |
| Román and Miguel 2005      | ECM           | % root length       | in situ           | P         |              | 1.000           | TF Spain        | 5   | 26.2 | 5   | 18  | –0.3754 | –31.3                     |

\(^a\)AM = arbuscular mycorrhizal fungi; ECM = ectomycorrhizal fungi

\(^b\)P = prescribed fire; W = wildfire

\(^c\)TF = temperate forest; BF = boreal forest; TrF = tropical forest; TrG = tropical grassland; TG = temperate grassland; TS = temperate shrubland
Table 2, continued. Data used in meta-analysis of mycorrhizal colonization response to fire including control replicates \((n_e)\), control mean \((\mu_c)\), experimental replicates \((n_x)\), experimental mean \((\mu_x)\), the natural log of the response ratio \((\ln[R])\), and change in colonization \((\%)\).

| Reference                  | Guild studied | Unit of measurement | Fire type | Repeat burn? | Years since fire | Biome | Location            | \(n_e\) | \(\mu_c\) | \(n_x\) | \(\mu_x\) | \(\ln[R]\) | Change in colonization \((\%)\) |
|----------------------------|---------------|---------------------|-----------|--------------|------------------|-------|---------------------|------|--------|------|--------|---------|-------------------------------|
| Schoenberger and Perry 1982| ECM           | % root tips         | ex situ   | W            | 38.000           | TF    | Oregon, USA         | 4    | 74.6   | 4    | 57.8   | -0.2552 | -22.5                         |
|                            | ECM           | % root tips         | ex situ   | W            | 38.000           | TF    | Oregon, USA         | 4    | 74.4   | 4    | 79.5   | 0.0663  | 6.9                           |
| Senthilkumar et al. 1995   | AM            | % root tips         | in situ   | P            | 0.083            | TrG   | India               | 4    | 51.25  | 4    | 45    | -0.1301 | -12.2                         |
| Tipton 2016                | AM            | % root length       | in situ   | P            | 1.000            | TG    | Missouri, USA       | 4    | 33     | 5    | 59     | 0.5810  | 78.8                          |
|                            | AM            | % root length       | in situ   | P            | 2.000            | TG    | Missouri, USA       | 4    | 33     | 2    | 60     | 0.5978  | 81.8                          |
|                            | AM            | % root length       | in situ   | P            | 4.000            | TG    | Missouri, USA       | 4    | 33     | 3    | 59     | 0.5810  | 78.8                          |
|                            | AM            | % root length       | in situ   | P            | 5.000            | TG    | Missouri, USA       | 4    | 33     | 2    | 18     | -0.6061 | -45.5                         |
| Torres and Honrubia 1997   | ECM           | % root tips         | ex situ   | W            | 1.000            | TF    | Spain               | 10   | 91.1   | 10   | 97.1   | 0.0641  | 6.6                           |
|                            | ECM           | % root tips         | ex situ   | W            | 1.000            | TF    | Spain               | 10   | 91.1   | 10   | 75.6   | -0.1871 | -17.1                         |
| Treseder et al. 2004       | ECM           | % root length       | in situ   | W            | 3.000            | BF    | Alaska, USA         | 10   | 28.5   | 10   | 6.2    | -1.5216 | -78.2                         |
|                            | ECM           | % root length       | in situ   | W            | 35.000           | BF    | Alaska, USA         | 10   | 28.5   | 10   | 49.2   | 0.5449  | 72.5                          |
|                            | ECM           | % root length       | in situ   | W            | 46.000           | BF    | Alaska, USA         | 10   | 28.5   | 10   | 39.0   | 0.3131  | 36.8                          |
|                            | AM            | % root length       | in situ   | W            | 3.000            | BF    | Alaska, USA         | 10   | 30     | 10   | 33.2   | 0.1026  | 10.8                          |
|                            | AM            | % root length       | in situ   | W            | 35.000           | BF    | Alaska, USA         | 10   | 30     | 10   | 32.1   | 0.0664  | 6.9                           |
|                            | AM            | % root length       | in situ   | P            | 46.000           | BF    | Alaska, USA         | 10   | 30     | 10   | 35.3   | 0.1624  | 17.6                          |
| Trusty 2009                | ECM           | % colonized seedlings| in situ   | W          | 5.000            | TF    | Montana, USA        | 3    | 99.6   | 3    | 90.8   | -0.0925 | -8.8                          |
| Vásquez-Gassibe et al. 2016| ECM           | % root tips         | ex situ   | W            | 1.000            | TF    | Spain               | 5    | 42.53  | 5    | 40     | -0.0613 | -5.9                          |
|                            | ECM           | % root tips         | ex situ   | W            | 1.000            | TF    | Spain               | 5    | 42.53  | 5    | 39.82  | -0.0891 | -8.5                          |
| Vilarino and Arines 1991   | AM            | % root length       | in situ   | W            | 1.000            | TF    | Spain               | 3    | 51     | 3    | 23     | -0.7963 | -54.9                         |
|                            | AM            | % root length       | in situ   | W            | 1.000            | TF    | Spain               | 3    | 51     | 3    | 33     | -0.4353 | -35.3                         |
|                            | AM            | % root length       | in situ   | W            | 1.000            | TF    | Spain               | 3    | 51     | 3    | 37     | -0.3209 | -27.5                         |
|                            | AM            | % root length       | in situ   | W            | 1.000            | TF    | Spain               | 3    | 51     | 3    | 21     | -0.8873 | -58.8                         |
|                            | AM            | % root length       | in situ   | W            | 1.000            | TF    | Spain               | 3    | 51     | 3    | 36     | -0.3483 | -29.4                         |

AM = arbuscular mycorrhizal fungi; ECM = ectomycorrhizal fungi
P = prescribed fire; W = wildfire
TF = temperate forest; BF = boreal forest; TrF = tropical forest; TrG = tropical grassland; TG = temperate grassland; TS = temperate shrubland

(e.g., temperate forest, boreal forest, or temperate shrubland and grassland) contained sufficient replication \((n \geq 2)\) to be included in the meta-analysis (Table 1). We combined temperate shrublands and grasslands into the same biome category because of an insufficient number of studies in each of these biomes for robust inter-biome statistical comparisons (two for temperate shrubland and one for temperate grassland). We justify this grouping because both have relatively low aboveground biomass and a higher frequency of fire disturbance than boreal or temperate forests (Chapin et al. 2011). Only one biome classification was ambiguous (Xiang et al. 2015), but we used the reported dominant vegetation \((Larix\) spp. Mill.) along with mean annual temperature \((-4.7^\circ\text{C})\) and precipitation \((500\text{ mm})\) to classify the study site as a boreal forest (Whittaker 1970). For the mycorrhizal colonization meta-analysis, we recorded the fungal guild studied (e.g., ECM fungi or AM fungi), whether the response was assessed in situ or using ex situ bioassays (i.e., method; in situ bioassays were excluded from analysis due to lack of studies), fire type (wildfire or prescribed fire; repeat \([<15\text{ yr}]\) or single fire event), biome (e.g., temperate forest, boreal forest, or temperate shrubland).
perate grassland), and time since fire. We included all measures of mycorrhizal colonization for our analysis including percent colonized seedlings, percent root tips colonized, and percent root length colonized. When means were presented in graphical format, we used Web Plot Digitizer 3.5 to extract data (Rohatgi 2014).

Statistical Analysis

Random effects models were used to determine the significance of fungal species richness and mycorrhizal colonization response to fire. All cumulative and categorical analyses were conducted in MetaWin 2.1 (Rosenberg et al. 1997), and continuous analyses were conducted in R (R Development Core Team 2008) using the Metafor package (Viechtbauer 2010). We used R for the continuous analyses because MetaWin does not report R² or Akaike information criterion (AIC) statistics, which allows for the statistical comparison between models (i.e., linear versus logarithmic meta-regression).

The effect size was calculated as the natural log of the response ratio (ln[R]). The response ratio (R) is the mean of the treatment response (X_{treatment}) divided by the mean of the control (X_{control}) (Hedges et al. 1999). For example, if ln[R] = 0, then there is no treatment effect. Post analysis, effect sizes were converted to percent difference (D) using the equation:

\[
D = 100(1 - e^{\ln(R)}) .
\]

We weighted the effect sizes by the number of replicates (n) instead of the inverse variance (as is common in some meta-analyses) because many studies did not report standard deviation (SD) or standard error (SE) of the mean. We assumed that effect size records with higher replication were a stronger estimate of the population mean. Making this assumption allowed us to maximize sample size and improve the robustness of our analysis.

A random effects model was used to determine if ln[R] ≠ 0 (i.e., fire had a significant effect). We calculated bias-corrected bootstrap 95% confidence intervals (CIs) for each mean ln[R]. If CIs did not overlap with 0, then effects were considered significant at the α = 0.05 level. Additionally, we used categorical random effects models to compare responses to fire among fungal guilds, methods of measurement, fire types, and biomes. If the categorical model showed significant differences among groups (α = 0.05), then CIs were used to interpret multiple comparisons of group means; if CIs did not overlap, then groups were considered significantly different.

Continuous random effects models (meta-regressions) were conducted to determine if effect size varied with time since fire. Following Aloe et al. (2010), we report R²_{Meta} values rather than traditional R² based on ordinary least squares (OLS), because the assumption of equal variances needed for OLS does not hold in meta-regression (i.e., effect sizes are weighted). The statistic R²_{Meta} describes the proportional reduction in the amount of heterogeneity in the model after including moderators, and it is useful for interpreting the practical significance and comparing the fit of competing meta-regression models (López-López et al. 2014).

RESULTS

Fire Effects on Fungal Species Richness

Overall, 68 records across 29 studies were considered suitable for meta-analysis (Table 1; Figure 1). Across studies, fire significantly reduced fungal species richness by an average of 28% (95% CI: −35% to −20%; Figure 2a). Additionally, heterogeneity within studies was not statistically significant (Q_T = 68.3, P = 0.434), indicating that fungal species richness responses to fire were consistent even though individual studies may not have had a significant effect (i.e., CIs encompassing 0). Our meta-analysis incorporated studies that inves-
tigated fire effects on different fungal guilds (Table 1). All guilds assessed except for wood-inhabiting fungi (WIF) showed significant negative response to fire (Figure 2a). The overall categorical model found marginally statistically significant differences among guilds ($P = 0.080$).

Six different methods of measuring fungal species richness were analyzed in the meta-analysis (Table 1). Negative response to fire was apparent for all measurement methods except next-generation sequencing (Figure 2b), and the model found significant differences among groups ($P = 0.002$). Richness assessed using culture morphology and sporocarp surveys showed the greatest response to fire, with average reductions of 66% (95% CI: $-85\%$ to $-34\%$) and 41% (95% CI: $-59\%$ to $-35\%$), respectively.

Repeat burning (within 15 years) reduced the negative effect on fungal species richness by almost half compared to single burns (average response of $-18\%$ and $-30\%$, respectively), but this difference was not statistically significant ($P = 0.274$). This lack of statistical significance may be due to low statistical power given the few studies ($n = 10$) that have assessed the impacts of repeated burning on fungi (Figure 2c). Similarly, we were unable to detect a significant difference between wildfire and prescribed fire ($P = 0.603$). Nevertheless, we did find significant differences in fungal species richness response to fire across biomes ($P = 0.010$; Figure 2d), with temperate shrublands and grasslands showing the greatest mean reduction (95% CI: $-80\%$ to $-23\%$) and boreal forests showing a non-significant reduction (95% CI: $-35\%$ to 2%).

We found a statistically significant and positive logarithmic correlation between the response ratio of fungal species richness and time since fire ($\ln[R] = 0.1976 \times \ln[\text{years since fire}] + 0.62$, $R^2_{\text{Meta}} = 0.999$, $P < 0.001$; Figure 3). At time = 0, the mean reduction in fungal species richness was calculated as $-46\%$ (SE = 7%, $P < 0.001$), and the negative effect size was reduced logarithmically, crossing zero (i.e., no effect) at year 22.

**Fire Effects on Mycorrhizal Colonization**

Fifty-one records across 24 studies were used for our meta-analysis of fire effects on mycorrhizal colonization (Table 2). Across all
studies and records, mycorrhizal colonization post fire was not significantly affected by fire (95% CI: −20% to 1%; Figure 4a). Heterogeneity was not statistically significant ($Q_T = 46.9, P = 0.600$), indicating that mycorrhizal colonization responses to fire were consistent even though individual studies may have had a significant effect. When analyzed separately by mycorrhizal type (i.e., ECM and AM), no significant post-fire effect was found for either type (Figure 4a). Additionally, the effect of fire on mycorrhizal colonization was not statistically significantly different among fire types or biomes (Appendix 1).

There was a significant difference between fire effects on mycorrhizal colonization measured in situ and in ex situ bioassays ($P = 0.006$; Figure 4b). Mycorrhizal colonization was reduced on average by 21% following fire (95% CI: −36% to −2%) when assessed in situ, while a non-significant 11% increase (95% CI: −3% to 29%) in post-fire mycorrhizal colonization was observed when using ex situ bioassays. Due to this difference, categorical models (guild, unit of measurement, fire type, and biome) were re-analyzed using only records measured in situ to determine if categorical differences would then emerge; how-
ever, statistical significance for each categorical model remained unchanged (Appendix 2).

Similar to our results for fungal species richness, we found a statistically significant and positive logarithmic correlation between the response ratio for mycorrhizal colonization and time since fire ($\ln[R] = 0.1588 \times \ln[\text{years since fire} + 1] - 0.62$), the shaded area shows the 95% bias-corrected bootstrap confidence interval around the line, and the dashed line shows no response (i.e., $\ln[\text{response ratio}] = 0$).

At time = 0, mean reduction in mycorrhizal colonization was calculated as $-26\%$ (SE = 10\%, $P = 0.003$), and the negative effect size was reduced logarithmically crossing zero (i.e., no effect) at year 5. Because mycorrhizal colonization assessed in situ showed a significantly greater negative response to fire than methods using ex situ bioassays, we ran a separate continuous model that included method as a predictor variable. In this model, both method ($P = 0.019$) and time ($P = 0.005$) were significant moderators of mycorrhizal colonization response to fire ($R^2_{\text{Meta}} = 0.45; P = 0.001$). Furthermore, only using data from studies that measured mycorrhizal colonization response to fire in situ, we found that at time = 0, mean reduction in mycorrhizal colonization was calculated as $-37\%$ (SE = 12\%, $P = 0.003$). The negative effect size was reduced logarithmically crossing zero (i.e., no effect) at year 11 ($\ln[R] = 0.1870 \times \ln[\text{years since fire} + 1] - 0.4646; R^2_{\text{Meta}} = 0.32; P = 0.011$; Figure 9). Time was not a significant predictor of mycorrhizal colonization response to fire for studies that used ex situ bioassays ($P = 0.267$).
DISCUSSION

Fire Effects on Fungal Species Richness

The meta-analytical model supported our hypothesis that fungal species richness is negatively impacted by fire. Fire likely eradicates fungal species that cannot withstand intense heat, reducing species richness to those species that have the ability to survive fire through fire-resistant propagules (Horton et al. 1998, Baar et al. 1999). Furthermore, physiochemical changes in the soil environment and shifts in vegetation composition following fire likely select for species able to best compete under fire-altered conditions (Hart et al. 2005b, Cairney and Bastias 2007). Given that fungal diversity generally is positively related to decomposition rates (Setälä and McLean 2004, van der Wal et al. 2013) and aboveground productivity (van der Heijden et al. 1998), reduced fungal species richness likely contributes to the decreases in these ecosystem processes commonly observed post fire (Dore et al. 2010, Holden et al. 2013, Toberman et al. 2014). However, the magnitude of this response probably also depends on the functional redundancy of the soil microbial community, in which functions that are performed by many species are not altered by differences in diversity (Nielsen et al. 2011).

The impact of fire on fungal species richness varied across fungal guilds, indicating that fire affects soil fungi differentially within terrestrial ecosystems. Although the overall categorical model did not suggest a difference in species richness among fungal guilds post fire, the species richness in all individual guilds except for WIF was negatively impacted by fire (denoted by negative 95\% CIs that did not overlap with 0). Wood-inhabiting fungi may have responded differently to fire because fire may have increased the variety of habitats (i.e., niches) available for this fungal guild compared to the other fungi. For instance, depending on the severity of fire, downed coarse woody debris (DCWD) may increase, and partial charring of wood may increase overall surface area for fungal colonization within this material (Pietikäinen et al. 2000). Many studies have found that DCWD availability positively correlates with WIF diversity (Nordén et al. 2004, Abrego and Salcedo 2013, Persiani et al. 2015), and experimentally enhanced DCWD has been shown to increase WIF species richness (Dove and Keeton 2015), while declines in DCWD have reduced WIF species richness (Bader et al. 1995).
Hence, if fire maintains or increases DCWD available to pioneer fungal species, then WIF species richness will likely be resistant to fire disturbance (Berglund et al. 2011). As terrestrial ecosystem functioning is impacted by the activities of several different soil fungal guilds (e.g., mycorrhizal fungi increase plant nutrient acquisition, white-rot fungi regulate lignin degradation), understanding the disparate effects of fire on these guilds is essential for predicting how these various respective functions are affected by fire.

As expected, our meta-analyses demonstrated that the impact of fire on fungal richness changed depending on the method used to evaluate fungal species presence. These methods probably assess different fractions of the fungal community because they evaluate the presence of fungi on different temporal and spatial scales. For instance, sporocarp surveys oversample species that fruit more often than those with other life history strategies. Furthermore, because fungal fruiting is highly dependent on temperature, moisture, and other chemical parameters (Fogel 1976, Zak and Wicklow 1978, Straatsma et al. 2001), most of which are modified by fire disturbance (Neary et al. 1999), treatment effects assessed by sporocarp surveys may be indicative of changes to fruiting conditions rather than the fungal communities themselves. Some fungal taxa, such as Pezizales, increase greatly in sporocarp abundance following fire (Petersen 1970). Yet, high numbers of sporocarps of Pezizales or other fungal taxa following fire may not be representative of their belowground abundance (Fujimura et al. 2004), and sporocarp surveys do not capture the non-fruiting diversity of fungi (Jonsson et al. 1999, Horton and Bruns 2001). Alternatively, belowground sampling and DNA sequencing techniques do not sample the same spatial extent as sporocarp surveys. Horton and Bruns (2001) reviewed five studies that sampled aboveground and belowground and found that <0.1% of the area that was sampled visually for aboveground sporocarps was sampled belowground. Diminished sampling intensity through soil coring and sequencing techniques may limit the ability to detect treatment effects such as fire. Given this apparent tradeoff (i.e., fruiting phenology effects versus sampling intensity), we suggest multiple approaches be employed for evaluating the response of fungal species richness to disturbances such as fire (e.g., Fujimura et al. 2004).

Our meta-analysis suggested that fungal richness was unaffected by fire type, a surprising result given numerous individual studies that found that higher severity burns diminish fungal diversity to a greater degree (Dahlberg et al. 2001, Smith et al. 2004, Rincón and Pueyo 2010, Hewitt et al. 2013, Persiani and Maggi 2013, Motiejūnaitė et al. 2014). The lack of significance in our meta-analytical study may be due to high variability in fire severity within each category (i.e., wildfire versus prescribed fire). For example, prescribed burning in temperate climates during different seasons (e.g., spring burns compared to fall burns) can result in large differences in fire severity within the same terrestrial ecosystem, which may result in disparate fungal responses (Smith et al. 2004). Furthermore, wildfires vary greatly in severity both within a given fire and among different fires depending on fuel loading and weather conditions (Albini 1976). Therefore, simple generalizations of fungal response to fire based on fire type may be inadequate if the severity of the burn is not measured. We recommend that future studies measure burn severity (e.g., dNBR; Miller and Thode 2007) as well as other fire characteristics (e.g., fire weather, fuel moisture, etc.) to more accurately compare the effects of fire on fungal communities across studies.

Our hypothesis that repeat fires (<15 yr) would influence fungal species richness response to fire was not supported by the meta-analysis. We speculate that heterogeneity within this category and low sample size of repeat fire (n = 12; 5 studies) likely contributed
to this result. We expected that repeated fire would have a smaller effect on fungal species richness than single fire events because fuel loadings are generally lower after a single burn, thus subsequent burns are generally lower in severity and higher in patchiness (Fernandes and Botelho 2003). Lower fire severity, in turn, should reduce heat-induced fungal mortality, and greater patchiness in fire effects should preserve post-fire refugia (Bastias et al. 2006). Furthermore, repeated fire best mimics natural processes in dry, fire-dependent ecosystems (commonly found in the western USA and globally); thus, it is likely that repeated fire in these ecosystems creates conditions that help maintain fungal diversity (i.e., increased patchiness and plant diversity; Bruns 1995, Buscardo et al. 2010, Oliver et al. 2015). However, the severity of repeat fires may not always be lower than single fire events. For instance, high severity fires in areas with long histories of fire suppression could result in increased shrub colonization with an increased likelihood of high-severity fire in subsequent burns (Coppoletta et al. 2016). Furthermore, our analysis combined repeat wildfires and prescribed fires into the same group across all biomes; separating this analysis by fire type or biome was not feasible given the lack of repeat fire studies. This amalgamation likely increased within-group heterogeneity, reducing our ability to distinguish differences between single and repeated fires. Frequent repeat fires may be necessary to maintain ecological benefits derived from prescribed fire at the individual ecosystem scale (Fernandes and Botelho 2003); yet, the global impact of repeated fire on soil fungal communities is still unclear. Future studies of fire impacts on soil fungal communities should include repeated fire in their experimental design.

We speculate that the significant difference in fungal species richness response among biomes is due to differences in the natural fire behavior within each biome rather than adaptations of the fungal community at the ecosystem scale. We expected that the smallest effects of fire on fungal species richness would be present in ecosystems with fungal species most adapted to fire (i.e., frequent-fire biomes). However, the greatest effects were found in the temperate shrubland and grassland biome, which should include fungal species that are adapted to more frequent fire than those found in biomes that have infrequent fire, such as boreal forests. This unexpected result could be due to greater within-landscape variability in burn severity that occurs in wetter than in drier ecosystems (Turner and Rome 1994). Such mixed-severity fires have unburned patches that serve as refugia for plants and fungi during disturbance, and thus greater heterogeneity in burn severity could have maintained higher fungal species richness post disturbance. Furthermore, the majority of studies in boreal forests took place in Pinus sylvestris L. forests of Fennoscandia, which burn historically at low severities.

Our results suggest that biome might be a more useful predictor of fungal response to fire than fire type, given that our meta-analysis found a significant difference in fire effects on fungal species richness among biomes but not among fire types (at least in broad categories such as wildfire versus prescribed fire). However, while the temperate forest biome is well represented in our analyses, few studies describe fungal species richness response to fire in other biomes. The combination of shrubland and grassland together into a single biome in our analysis also could have altered the significance of biome on fungal diversity response to fire. However, it is unlikely that combining these two groups contributed to a false-positive result because such a merger should only increase the variation within the group. This finding underpins the need to evaluate the effects of fire on fungi within each biome. Hence, future studies of fungal response to fire should prioritize underrepresented biomes such as temperate grassland, chaparral, boreal forest, and savanna.
Fire Effects on Mycorrhizal Colonization

Our meta-analysis showed that fire did not significantly affect mycorrhizal colonization when analyzed across a diverse array of studies. We expected fire to negatively influence overall mycorrhizal colonization through fire-induced mortality of mycorrhizal inocula, changes to soil physiochemical characteristics, or shifting plant species composition from mycorrhizal to non-mycorrhizal, ruderal post-fire plant communities (Hart et al. 2005b). Soil heating can drastically reduce active mycelium, especially in upper soil layers (Cairney and Bastias 2007). Additionally, host plant mortality eliminates the energy source (in the form of plant-derived photosynthates) for most mycorrhizal fungi. Thus, post-fire inoculum is derived primarily from the pre-fire sporebank rather than residual mycelia (Baar et al. 1999, Glassman et al. 2015). Although fungal spores show differential resistance to heat (Izzo et al. 2006), temperatures of 65 °C for extended periods of time (>5 min), which are commonly reached in the upper soil layers of both prescribed fires and wildfires (Neary et al. 1999), can completely denature even the most heat-resistant propagules (Peay et al. 2009). Furthermore, changes in soil chemistry (e.g., pH and nutrient availability) may influence belowground allocation of plant photosynthates to fungal symbionts. For example, increases in inorganic nitrogen (N) availability through fire-induced mineralization (St. John and Rundel 1976) may reduce mycorrhizal colonization similarly to what occurs following N fertilization (Treseder 2004). However, given the diversity of biomes, methods, fire types, and guilds studied, the high variation in responses among studies (SD = 44%) may have led to a non-significant overall response.

We predicted that fire would increase AM colonization relative to ECM colonization because increases in post-fire canopy openings would create new habitat for herbaceous AM plant hosts (MacKenzie et al. 2004). A shift in the host plants aboveground would thus drive a shift in the dominance of mycorrhizal symbionts belowground. Although this shift in dominance from ECM to AM colonization following fire has been shown in two individual studies (Korb et al. 2003, Treseder et al. 2004), the vast majority of studies used in this analysis only studied the effect of fire on one of these mycorrhizal guilds. Hence, we were unable to detect changes in the dominance of mycorrhizal guilds. We suggest that future studies assess both ECM and AM colonization because changes in the relative dominance of these guilds may have profound implications for post-fire ecosystem nutrient cycling (Phillips et al. 2013).

Where mycorrhizal colonization was assessed (using in situ indices or ex situ bioassays) significantly influenced the response of mycorrhizae to fire, suggesting that greenhouse-based or growth-chamber-based evaluations of mycorrhizal responses to disturbances may not be representative of in-field impacts. These differences likely reflect the discrepancy between actual colonization and inoculum potential post fire. For instance, mycorrhizal colonization potential assessed by bioassay is conducted under near-ideal environmental conditions. However, fire also affects soil abiotic conditions such as irradiance, temperature, and moisture (Neary et al. 1999), which also may indirectly affect mycorrhizal colonization (Parke et al. 1983, Perry et al. 1987). Additionally, the use of “bait” plants typically employed in ex situ bioassays may not accurately reflect the colonization potential by the native plants on site (Sýkorová et al. 2007). Fine-root density may also be reduced post fire (Smith et al. 2004, Hart et al. 2005a); thus, discrepancies in root density between in situ and ex situ approaches may also explain observed differences in mycorrhizal colonization response to fire among studies. Because there was no effect of fire on mycorrhizal colonization via ex situ bioassay, but fire significantly reduced mycorrhizal colonization when as-
sessed in situ, we speculate that fire reduces mycorrhizal colonization primarily because of unfavorable changes in environmental and host-density conditions in the field rather than due to direct reductions in fungal inocula. Regardless of the mechanism, our results suggest that the evaluation of the response of the mycorrhizal community to fire may be strongly dependent on the assay used.

**Fungal Resilience to Fire**

Our hypothesis that fire effects on fungal species richness and mycorrhizal colonization would diminish over time was supported by the meta-analysis, suggesting that the fungal community is relatively resilient to disturbances such as fire. For fungal species richness and in situ mycorrhizal colonization, a continuous logarithmic model fit the data in which effect sizes were most negative soon after fire and approached zero after 22 yr and 11 yr, respectively. Nevertheless, results from individual studies that followed fungal species richness or mycorrhizal colonization post fire over time showed a wide range in temporal responses. For instance, using a fire chronosequence of stand-replacing fires in southwestern US Pinus ponderosa Douglas ex. C. Lawson forests, Kurth et al. (2013) found that WIF species richness recovered to unburned richness values after about nine years. However, the recovery in both mycorrhizal and saprobic fungal species richness took 41 years after a stand-replacing wildfire in a Pinus banksiana Lamb. chronosequence (Visser 1995). Such discrepancies in rates of fungal species richness recovery from disturbance among studies are likely a combination of differences in the direct effects of fire severity on fungal mortality and differences in the complex suite of indirect effects of fire on soil fungi (Hart et al. 2005b, Cairney and Bastias 2007). Similarly, while studies that used fire chronosequences (3 yr to 46 yr) found an increase in mycorrhizal colonization with time since fire (Treseder et al. 2004, Rincón et al. 2014), those that followed a site for <1 yr after a fire showed no change (Hartnett et al. 1994) or a continued decline in mycorrhizal colonization over time (Bentivengena and Hetrick 1991, Bellgard et al. 1994, Anderson and Menges 1997). Changes in mycorrhizal colonization measured within one year following fire may represent seasonal variation in mycorrhizal colonization rather than a fire effect, as suggested by corresponding temporal changes in mycorrhizal colonization in unburned control plots (Anderson and Menges 1997). Our meta-analyses used only the first sample date post fire when studies sampled the same site repeatedly over time to prevent violation of data independence (Gurevitch and Hedges 1999). Therefore, it is not surprising that our temporal meta-regressions of fungal species richness or mycorrhizal colonization following fire across different studies may not be representative of results from individual studies that followed these changes over time from the same site, or from space-for-time substitutions (i.e., fire chronosequences).

**CONCLUSION**

By aggregating data from multiple ecosystems, fire types, and sampling methods, we showed that soil fungal communities (species richness and mycorrhizal colonization) are adversely affected by fire. However, short-term negative effects diminish quickly over time, returning to pre-fire levels within one to two decades. This finding has major implications for ecosystem recovery post disturbance (Perry et al. 1989), as soil fungal communities are drivers of aboveground diversity (van der Heijden et al. 1998) and other important ecological functions and services (Ingham et al. 1985, Finlay 2008, van der Wal et al. 2013). Future studies should investigate linkages between post-fire fungal communities and ecosystem function to develop a mechanistic understanding of ecosystem processes in post-fire environments.
Our meta-analyses also revealed significant moderators of fungal species richness response to fire. Although quantifying disturbance-driven changes in fungal species richness is valuable from a biodiversity perspective, it is perhaps more important to quantify specifically how the structure of soil fungal communities change in response to disturbance. For instance, although Chen and Cairney (2002) found that overall fungal species richness did not change post fire, they found that species assemblages changed from mainly ECM to AM fungi, with possible commensurate changes in nutrient cycling processes (Phillips et al. 2013). Furthermore, our analyses suggest that mycorrhizal colonization following fire is driven mainly by indirect, post-fire environmental changes rather than the direct effects of fire-induced fungal mortality. This finding suggests that resource managers may be able to manipulate site conditions post fire to make them more conducive to post-fire mycorrhizal colonization of new plant propagules. Nevertheless, small sample sizes and underrepresented taxa, biomes, and fire types limit the inferential power of our conclusions from both meta-analyses. Further studies of fire effects on fungi in novel environments, targeting underrepresented fungal guilds and life stages, are needed to comprehensively assess the role of fire in shaping soil fungal communities. Additionally, we recommend that future studies document burn severity (e.g., dNBR; Miller and Thode 2007), as well as other important fire characteristics (e.g., fire weather, fuel moisture), to provide the necessary context for improving our mechanistic understanding of the role of fire in sustaining soil fungal communities and the ecosystems they support.

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1. Introduction

1.1. Literature Review

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### Appendix 1. Results of statistical comparisons among groups for the response of overall mycorrhizal colonization to fire.

| Comparison        | Group          | Mean effect size (%) | 95% CI       | Records\(^a\) | Number of studies | P-value |
|-------------------|----------------|----------------------|--------------|---------------|-------------------|---------|
| Fire type         | Prescribed fire| −0.50                | −23.3 to 28.1| 12            | 9                 | 0.341   |
|                   | Wildfire       | −9.43                | −23.8 to 5.1 | 39            | 15                |         |
| Repeat fire       | Repeated       | −10.5                | −44.9 to 20.8| 5             | 2                 | 0.935   |
|                   | Single         | −7.10                | −20.2 to 8.6 | 46            | 22                |         |
| Biome\(^*\)       | Temperate forest| −3.93                | −17.6 to 10.9| 32            | 14                | 0.358   |
|                   | Boreal forest  | −5.39                | −50.1 to 39.1| 6             | 1                 |         |
|                   | Temperate grassland| −14.7                | −37.6 to 15.5| 11            | 7                 |         |

\(^a\) Number of data records for each group.
\(^*\) Two studies were omitted because there were not enough records for tropical forest (Raman and Nagarajan 1996) and tropical grassland (Senthilkumar et al. 1995) for a statistical comparison.

### Appendix 2. Results of statistical comparisons among groups for the response of *in situ* mycorrhizal colonization to fire. Comparison between repeat fires and single fire events was not made due to insufficient studies.

| Comparison      | Group          | Mean effect size (%) | 95% CI       | Records\(^a\) | Number of studies | P-value |
|-----------------|----------------|----------------------|--------------|---------------|-------------------|---------|
| Guild           | ECM            | −26.9                | −54.5 to 9.2 | 9             | 5                 | 0.616   |
|                 | AM             | −17.8                | −32.1 to 0.7 | 20            | 10                |         |
| Fire type       | Prescribed     | −6.5                 | −25.7 to 17.9| 11            | 8                 | 0.219   |
|                 | Wildfire       | −28.5                | −46.2 to −6.1| 18            | 6                 |         |
| Biome\(^*\)     | Temperate forest| −35.2                | −43.8 to −23.0| 11            | 5                 |         |
|                 | Boreal forest  | −5.4                 | −49.1 to 38.6| 6             | 1                 | 0.419   |
|                 | Temperate grassland| −15.6                | −40.7 to 19.5| 10            | 6                 |         |

\(^a\) Number of data records for each group.
\(^*\) Two studies were omitted because there were not enough records for tropical forest (Raman and Nagarajan 1996) and tropical grassland (Senthilkumar et al. 1995) for a statistical comparison.