RESEARCH ARTICLE

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 micorrícica 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 micorrícica 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 micorrícica. 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 micorrícica 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 colonization, 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.

cuando fueron determinadas *ex situ* por medio de bioensayos. Estos resultados sugieren que las magnitudes cambiantes de los efectos del fuego en comunidades fúngicas del suelo pueden ser dependientes del enfoque y método de determinación utilizado. Además el bioma, pero no el tipo de fuego (i.e., incendios *vs* quemas prescritas), fue un moderador significativo de nuestro modelo de categorías, sugiriendo que el bioma podría ser un predictor más útil de la respuesta de la riqueza de especies de hongos post-fuego que el tipo de fuego. Las reducciones post fuego en la riqueza de las especies y en la colonización micorrícica *in situ* disminuyeron logarítmicamente y se aproximaron a cero (i.e., sin ningún efecto) a los 22 y 11 años, respectivamente. Concluimos que el fuego reduce la riqueza de las especies y la colonización micorrícica *in situ*, pero que si las condiciones permiten a las comunidades recuperarse, (por ej., sin un disturbio subsecuente y condiciones de crecimiento favorables), los hongos del suelo son resilientes a escalas de tiempo decenales. La resiliencia de los hongos del suelo contribuye a una rápida recuperación del ecosistema después de un incendio.

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).

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.* 2005*b*). 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.* 2005*b*). 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 (Dhillon *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 inconstancies 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.* 2001, Smith *et al.* 2004, Román and Miguel 2005, Cairney and Bastias 2007), and the degree to which the disturbance frequency and intensity are within the historic range of variability (Hart *et al.* 2005*b*). Fire intensity and severity are well correlated to the amount of combustible fuels (Rothermel 1972, Binkley and Fisher 2012), which is influenced by a suite of factors, including: the ecosystem type or biome, land management practices, and fire type (i.e., wildfire versus prescribed fire). These factors may covary with the response of soil fungal communities to disturbance by fire through their influences on fuel loading and possibly other mechanisms (e.g., fuel continuity, fuel combustibility, etc.; Rothermel 1972, Scott and Burgan 2005).

Differences in fungal response to fire may be simply an artifact of the methods used to evaluate fungal communities. It is well known that fungal communities that have been assessed aboveground (i.e., sporocarps) rarely correspond to their belowground counterparts (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.* 2005*b*), 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 wildland 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 ($n \geq 2$) 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., Martín-Pinto *et al.* 2006), we used the following equation to derive species richness:

$$S = \frac{e^H}{E} \quad .\qquad (1)$$

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[a]	Unit of measurement[b]	Fire type[c]	Repeat burn?	Years since fire	Biome[d]	Location	n_c	x_c	n_e	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	−21.3
	ECM	morphotyping + molecular ID	W		3	TF	British Columbia, Canada	15	8	15	4	−0.6932	−50.0
Bartoli *et al.* 1991	micro-fungi	culture morphology	W		0.01644	TF	Italy	5	21.2	5	3.2	−1.8909	−84.9
Buscardo *et al.* 2010	ECM[†]	morphotyping + molecular ID	W		5	TF	Portugal	12	2.5	12	3.1	0.2119	23.6
	ECM[†]	morphotyping + molecular ID	W	2 consecutive	5	TF	Portugal	12	2.5	12	2.6	0.0276	2.8
	ECM[†]	morphotyping + molecular ID	W	2 consecutive	5	TF	Portugal	12	2.5	12	2.2	−0.1188	−11.2
	ECM[†]	morphotyping + molecular ID	W		5	TF	Portugal	11	2.6	11	1.9	−0.3032	−26.2
	ECM[†]	morphotyping + molecular ID	W	2 consecutive	5	TF	Portugal	11	2.6	11	2	−0.2624	−23.1
	ECM[†]	morphotyping + molecular ID	W	2 consecutive	5	TF	Portugal	11	2.6	11	1.6	−0.4608	−36.9
Dahlberg *et al.* 2001	ECM	morphotyping + molecular ID	P		0.3	BF	Sweden	5	1.4	5	0.9	−0.5272	−41.0
	ECM	morphotyping + molecular ID	P		0.3	BF	Sweden	5	2	5	0	NA	NA
Eom *et al.* 1999	AM (spore)	spore morphology	P		1	TG	Kansas, USA	4	5.3	4	3.8	−0.3365	−28.6
Glassman *et al.* 2015	ECM[†]	morphotyping + molecular ID	W		1	TF	California, USA	25	30.5	25	20	−0.4220	−34.4
Goberna *et al.* 2012	All fungi	DGGE	P		0.00274	TG	Spain	10	23.53	10	26.55	0.1208	12.8
Grishkan 2016	micro-fungi	culture morphology	W		1.5	TF	Israel	3	36	3	23	−0.4480	−36.1
	micro-fungi	culture morphology	W		0.5	TF	Israel	3	30	3	20	−0.4055	−33.3
Hernández-Rodríguez *et al.* 2013	All fungi	sporocarp survey	W		1	TG	Spain	6	22.1	6	6.1	−1.2827	−72.3
Holden *et al.* 2013	All fungi	NGS	W		0	BF	Alaska, USA	2	122.3	2	121.2	−0.0090	−0.90
	All fungi	NGS	W		6	BF	Alaska, USA	2	122.3	2	142.1	0.1501	16.2
	All fungi	NGS	W		11	BF	Alaska, USA	2	122.3	2	134.4	0.0943	9.9
	All fungi	NGS	W		23	BF	Alaska, USA	2	122.3	2	117.6	−0.0392	−3.8
	All fungi	NGS	W		54	BF	Alaska, USA	2	122.3	2	108.2	−0.1225	−11.5
	All fungi	NGS	W		90	BF	Alaska, USA	2	122.3	2	99.8	−0.2033	−18.4
Jonsson *et al.* 1999	ECM	morphotyping + molecular ID	W		62	BF	Sweden	2	22.5	2	20	−0.1178	−11.1
Junninen *et al.* 2008	WIF	sporocarp survey	P		1	BF	Finland	3	18.42	3	18.68	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	−45.3
	ECM	morphotyping + molecular ID	W		15.5	TF	Switzerland	7	21.2	7	19.5	−0.0836	−8.0
Kurth *et al.* 2013	WIF	NGS	W		4	TF	Arizona, USA	6	3.5	6	1.8	−0.6621	−48.4
	WIF	NGS	W		9	TF	Arizona, USA	6	3.7	6	4.3	0.1526	16.5
	WIF	NGS	W		13	TF	Arizona, USA	6	4.8	6	4.5	−0.0728	−7.0
	WIF	NGS	W		25	TF	Arizona, USA	6	2.7	6	5.3	0.6782	97.0
	WIF	NGS	W		32	TF	Arizona, USA	6	3.8	6	3.8	0.0000	0.0

[a] AM = arbuscular mycorrhizal fungi; ECM = ectomycorrhizal fungi; WIF = wood-inhabiting fungi
[b] NGS = next-generation sequencing; DGGE = denaturing gradient gel electrophoresis
[c] P = prescribed fire; W = wildfire
[d] 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[a]	Unit of measurement[b]	Fire type[c]	Repeat burn?	Years since fire	Biome[d]	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
	AM (spore)	spore morphology	W		0.5	TF	Argentina	10	7.7	10	4.8	−0.4883	−38.6
Mardji 2014	ECM	sporocarp survey	W	2 consecutive	14	TrF	India	4	8.75	4	3.25	−0.9904	−62.9
Martín-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
	All fungi	sporocarp survey	W		1	TS	Spain	3	26	3	11.7	−0.7978	−55.0
	All fungi	sporocarp survey	W		1	TS	Spain	3	26.1	3	3.8	−1.9158	−85.3
Motiejūnaitė et al. 2014	All fungi	sporocarp survey	W		1	TF	Lithuania	3	71.2	3	23.9	−1.0930	−66.5
	All fungi	sporocarp survey	W		1	TF	Lithuania	3	70.7	3	42.2	−0.5161	−40.3
Oliver et al. 2015	All fungi	NGS	P	every 2 yr (winter)	3	TF	Georgia, USA	4	668	4	656.5	−0.0174	−1.7
	All fungi	NGS	P	every 3 yr (winter)	3	TF	Georgia, USA	4	668	4	680.5	0.0185	1.9
	All fungi	NGS	P	every 3 yr (summer)	7	TF	Georgia, USA	4	668	4	659.75	−0.0124	−1.2
	All fungi	NGS	P	every 6 yr (summer)	10	TF	Georgia, USA	4	668	4	687.5	0.0288	2.9
Olsson and Jonsson 2010	WIF	sporocarp survey	P		1	BF	Sweden	150	2.0	150	1.2	−0.5008	−39.4
Rincón et al. 2014	ECM	morphotyping + molecular ID	W		14	TF	Spain	3	11.9	3	10.0	−0.1796	−16.4
	ECM	morphotyping + molecular ID	W		3	TF	Spain	3	11.9	3	9.0	−0.2832	−24.7
Robinson et al. 2008	All fungi	sporocarp survey	W		1	TF	Australia	4	39.41	4	27.94	−0.3440	−29.1
Román and Miguel 2005	ECM	hyphal morphotype	P		1	TF	Spain	5	6	5	5.2	−0.1431	−13.3
Smith et al. 2004	ECM	morphotyping + molecular ID	P		1	TF	Oregon, USA	4	10.3	4	10	−0.0247	−2.4
	ECM	morphotyping + 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	morphotyping + 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

[a] AM = arbuscular mycorrhizal fungi; ECM = ectomycorrhizal fungi; WIF = wood-inhabiting fungi
[b] NGS = next-generation sequencing; DGGE = denaturing gradient gel electrophoresis
[c] P = prescribed fire; W = wildfire
[d] TF = temperate forest; BF = boreal forest; TG = temperate grassland; TS = temperate shrubland; TrF = tropical forest
[†] Fire-resistant propagules (e.g., spores, residual hyphae)

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[a]	Unit of measurement	*in situ* or *ex situ*	Fire type[b]	Repeat burn?	Years since fire	Biome[c]	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*	W		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	TF	British Columbia, Canada	18	44.9	18	22.9	−0.6742	−49.0
	ECM	% colonized seedlings	*in situ*	P		0.330	TF	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		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	29.24	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	*in situ*	W		14.00	TF	Spain	3	70	3	81.5	0.1526	16.5
	ECM	% root tips	*in 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_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[a]	Unit of measurement	*in situ* or *ex situ*	Fire type[b]	Repeat burn?	Years since fire	Biome[c]	Location	n_c	x_c	n_e	x_e	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*	W		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
Vilariño 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

[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

(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 am-

biguous (Xiang *et al.* 2015), but we used the reported dominant vegetation (*Larix* spp. Mill.) along with mean annual temperature (−4.7 °C) and precipitation (500 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 yr] or single fire event), biome (e.g., temperate forest, boreal forest, or tem-

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 R^2 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:

$$D = 100(1 - e^{\ln(R)}) \ . \qquad (2)$$

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 $\ln[R] \neq 0$ (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 $\alpha = 0.05$ 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 ($\alpha = 0.05$), 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 R^2_{Meta} values rather than traditional R^2 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 R^2_{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-
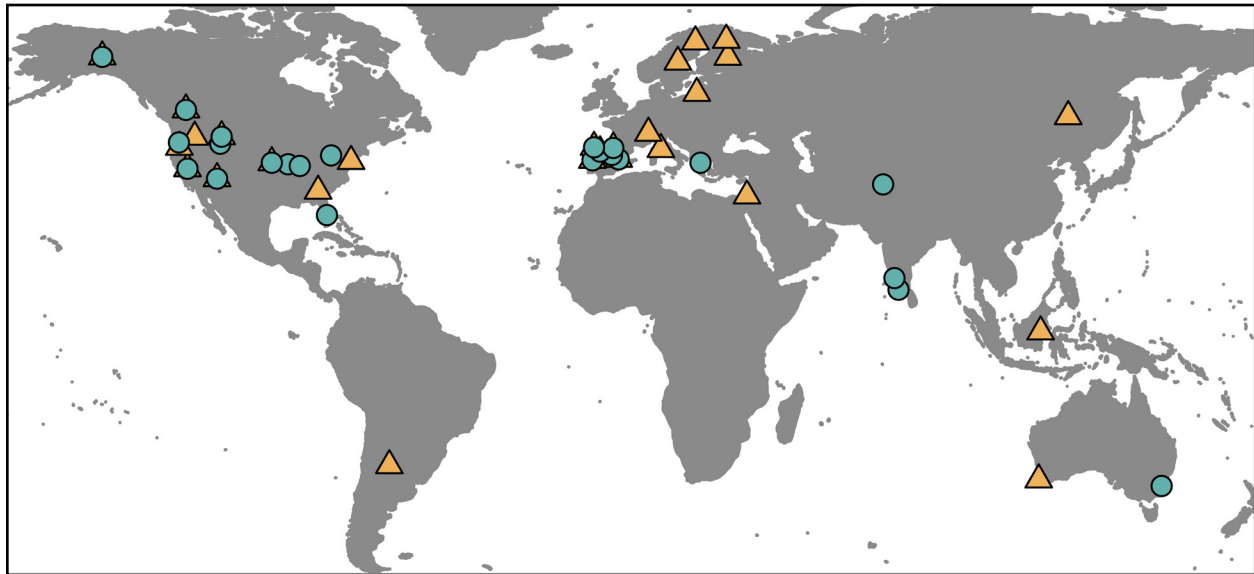
Figure 1. Locations of studies used in the meta-analyses. Circles show locations of studies from which colonization data were extracted; triangles show locations of studies from which richness data were extracted.

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 as-

sessed 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 ($\ln[R] = 0.1976 \times \ln[\text{years since fire} + 1] - 0.62$, $R^2_{\text{Meta}} = 0.999$, $P < 0.001$; 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
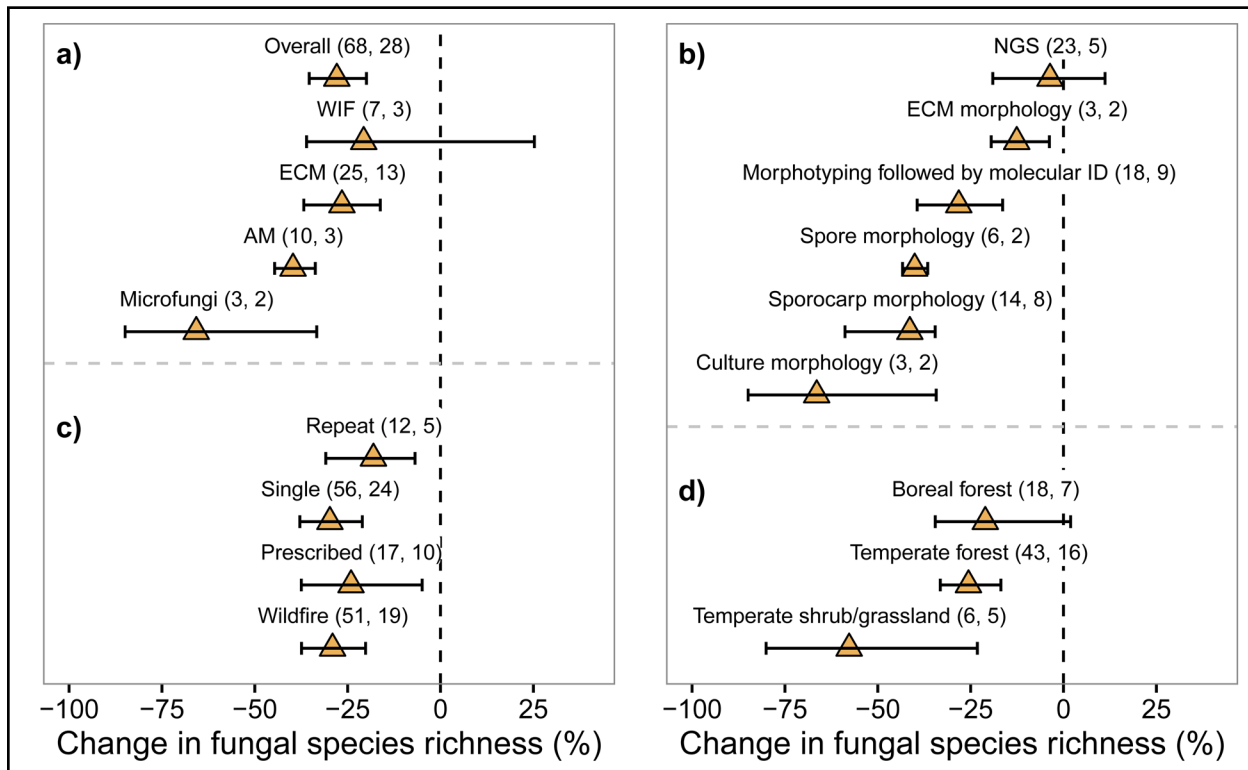
Figure 2. Mean response of fungal species richness to fire overall (groups combined) and (A) among functional guilds, (B) among methods of measurement, C) among fire types and frequencies (not mutually exclusive, and (D) among biomes. Error bars show 95 % bias-corrected bootstrap confidence intervals. Values show data records and number of studies, respectively. Eight studies were not included in the guild categorical model because they studied the richness of all fungal species. Denaturing gradient gel electrophoresis (DGGE) was excluded in the measurement categorical model because only one study (Goberna *et al.* 2012) used this method. Tropical forest was excluded in the biome categorical model because only one study (Mardji 2014) occurred in this biome. WIF = Wood-inhabiting fungi; ECM = ectomycorrhizal fungi; AM = arbuscular mycorrhizal fungi; microfungi = culturable fraction of soil funigi; NGS = next-generation sequencing; ID = identification

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-
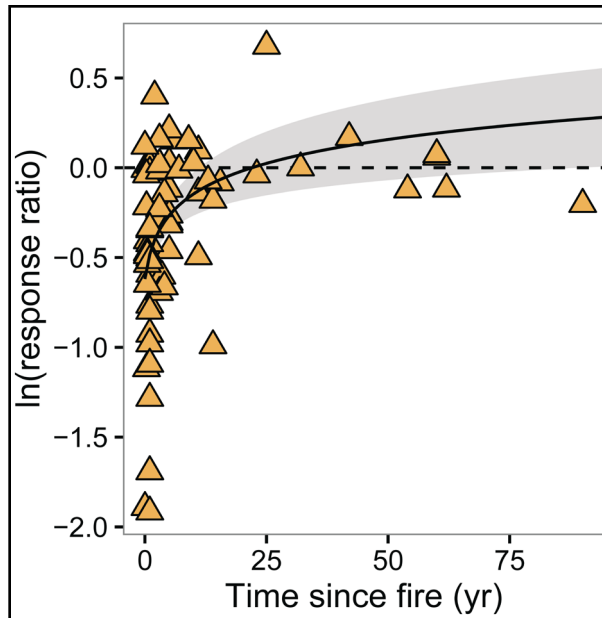
Figure 3. Mean responses of fungal species richness (ln[response ratio]) as a function of time since fire. Solid line represents best-fit meta-regression (ln[response ratio] = 0.1976 × ln[years since fire + 1] − 0.62), the shaded area shows the 95% bias-corrected bootstrap confidence interval around the line, and the dashed line shows no response (i.e., ln[response ratio] = 0).

Figure 4. (A) Mean response of mycorrhizal colonization to fire overall (groups combined) and between ectomycorrhizal (ECM) and arbuscular mycorrhizal (AM) fungi, and (B) mean responses of mycorrhizal colonization to fire assessed in situ or by ex situ bioassays. Error bars show 95% bias-corrected bootstrap confidence intervals. Numbers show data records and number of studies, respectively.

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 × ln[years since fire + 1] − 0.2971, R^2_{Meta} = 0.31, P = 0.003; Figure 5). 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_{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 × ln[years since fire + 1] − 0.4646; R^2_{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).
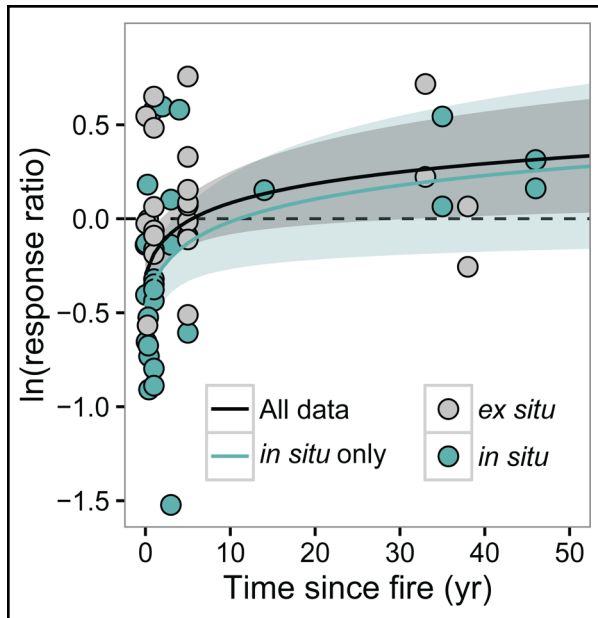
Figure 5. Mean responses of overall mycorrhizal colonization and in situ mycorrhizal colonization (ln[response ratio]) as a function of time since fire. Solid black line represents best-fit meta-regression of overall mycorrhizal colonization (gray and blue circles; ln[R] = 0.1588 × ln[years since fire + 1] − 0.2971), and gray shaded area shows the 95 % bias-corrected bootstrap confidence interval around the line. Solid blue line represents best-fit meta-regression of *in situ* mycorrhizal colonization (blue circles; ln[R] = 0.1870 × ln[years since fire + 1] − 0.4646), and blue shaded area shows the 95 % bias-corrected bootstrap confidence interval around the line. The dashed line shows no response (i.e., ln[response ratio] = 0).

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, physiochemi-

cal 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.* 2005*b*, 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 abo-

veground 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 Romme 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.* 2005*b*). 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.* 2005*a*); 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.* 2005*b*, 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 (Bentivenga 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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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	0.419
	Boreal forest	−5.4	−49.1 to 38.6	6	1	
	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.