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Meta-analysis

Belowground community responses to fire: meta-analysis reveals contrasting responses of soil microorganisms and mesofauna

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Global fire regimes are shifting due to climate and land use changes. Understanding the responses of belowground communities to fire is key to predicting changes in the ecosystem processes they regulate. We conducted a comprehensive meta-analysis of 1634 observations from 131 empirical studies to investigate the effect of fire on soil microorganisms and mesofauna. Fire had a strong negative effect on soil biota biomass, abundance, richness, evenness, and diversity. Fire reduced microorganism biomass and abundance by up to 96%. Bacteria were more resistant to fire than fungi. Fire reduced nematode abundance by 88% but had no significant effect on soil arthropods. Fire reduced richness, evenness and diversity of soil microorganisms and mesofauna by up to 99%. We found little evidence of temporal trends towards recovery within 10 years post-disturbance suggesting little resilience of the soil community to fire. Interactions between biome, fire type, and depth explained few of these negative trends. Future research at the intersection of fire ecology and soil biology should aim to integrate soil community structure with the ecosystem processes they mediate under changing global fire regimes.

Keywords: fire, soil fauna, soil microorganisms

Introduction

Fire is an important natural disturbance in many ecosystems (Bond and Keeley 2005, Sugihara et al. 2006). Global fire regimes have and continue to shift due to human influences on land use (Marlon et al. 2008) and environmental conditions conducive to fire such as increased lightning strikes (Romps et al. 2014), increased net primary productivity (NPP; Nemani et al. 2003), longer fire seasons (Westerling et al. 2006) and a warmer and drier atmosphere (IPCC 2014). Changing fire regimes have become a significant component of global change (Flannigan et al. 2009, 2013, Moritz et al. 2012) and have feedback potential that may exacerbate climate change (Levine et al. 1995). Given that fire frequency is a long-term driver of soil carbon (C) and nitrogen (N) stocks (Soong and Cotrufo 2015, Pellegrini et al. 2018), it is critical to understand

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the consequences of novel fire regimes for ecosystem structure, function and dynamics.

The literature is replete with studies on the impact of fire on plant communities and the importance of the linkages between plants and soil biota for recovery from disturbance (Wardle et al. 2004, Bond and Keeley 2005, Hart et al. 2005). However, the focus on microorganisms has precluded a comprehensive view of entire soil biological communities and their functions to fire (Zaitsev et al. 2016). Disturbances can exert positive, negative, and neutral effects on soil organisms that are often species specific (Coyle et al. 2017). From the resistance and resilience framework (Holling 1973, Holling and Gunderson 2002), resistant soil communities might exhibit a neutral response to a perturbation and maintain their biomass, abundance, and composition after disturbance while resilient communities change due to disturbance but return to their original structure after some period of time (Allison and Martiny 2008). Resistance requires the survival of individuals via stress tolerance and plasticity (Shade et al. 2012). Resilience depends on population and community persistence, the presence of dormant groups, and dispersal and migration from undisturbed areas (Shade et al. 2012).

Soil biological communities are at the nexus of understanding how ecosystem processes will respond to changing disturbance regimes. Soil organisms play a critical role in ecosystem C and N cycling by regulating decomposition (Seastedt 1984, Brussaard 1998, Wall et al. 2008) and contributing one of the largest C fluxes from the biosphere to the atmosphere, through respiration (IPCC 2014). Soil fauna are recognized as important mediators of belowground biogeochemical cycling (Wardle et al. 2004, Wall and Bardgett 2012), and both trophic (Moore et al. 1988) and non-trophic (Eisenhauer 2010, DeAngelis 2016) community dynamics. However, few studies on the impacts of fire have included both soil microorganisms (bacteria, fungi and Archaea) and soil micro- and mesofauna (e.g. Protozoa, nematodes, microarthropods) in an integrative manner.

Soil communities can be impacted by fire both directly through mortality during the disturbance (Certini 2005) and indirectly through physical, chemical, and biological changes to the soil environment. Such changes include organic matter loss through combustion (Gonzalez-Perez et al. 2004) and erosion (Rumpel et al. 2009, Shakesby 2011, Cotrufo et al. 2016), modification of organic matter quality through the addition of pyrogenic organic matter (Gonzalez-Perez et al. 2004, Knicker 2007, Bird et al. 2015), alterations in plant community composition and subsequent inputs (Hart et al. 2005), loss of soil structure (Mataix-Solera et al. 2011), changes in albedo with consequences for soil moisture dynamics (Beringer et al. 2003, Jin and Roy 2005, Jin et al. 2012), and increases in pH (Certini 2005) – all of which have consequences for soil organisms. Simultaneously, loss of soil organism abundance and diversity during and after fire may change soil food web dynamics and alter the resiliency of entire communities and ecosystems post disturbance. If the effects of fire on soil communities are substantial, shifting fire regimes should have long-term implications for ecosystem function.

We conducted a comprehensive meta-analysis of the literature to answer the following guiding questions: 1) to what extent are soil biota biomasses, abundances, and diversity resistant and resilient to fire disturbance? 2) What are the important controls on soil biota responses to fire? We then integrate our findings into a conceptual framework that highlights important mechanisms driving soil biota responses to fire. We also discuss knowledge gaps in the literature and recommend research priorities for understanding the consequences of changing fire regimes for soil communities and ecosystem processes.

Material and methods

Data acquisition

We conducted a systematic meta-analysis of all relevant peer-reviewed publications to investigate the impact of fire on soil microorganisms, microfauna and mesofauna. Three successive levels of filtering were used to select studies for consideration. First, given the large number of potentially relevant studies, we limited our search to scientific journal articles that were archived in the Web of Science Core Collection database. The final search date was 20 February 2017 and included only publications through 2016. We limited our search to include only peer-reviewed English or English-translated journal articles and excluded book chapters, conference proceedings, talks and presentations, posters, and unpublished datasets from the meta-analysis. With this first level of restrictions we searched the Web of Knowledge Web of Science Core Collection database (<www.webofknowledge.com>) using multiple Boolean search combinations of one of the following fire keywords: fire, wildfire, burn, pyrogenic organic matter; and all of the following soil biota keywords: soil organism, soil microorganism, soil microbe, soil biota, soil animal, soil biodiversity, soil fauna, soil flora, arthropod, microarthropod, nematode, protozoa, bacteria, fungi, acari, collembola, dipluran, proturan, symphylan, archaea, pauropoda, enchytraeid, microbial community. Given that their unique life histories warrant a separate synthesis effort, we considered macrofauna (e.g. surface dwelling arthropods, snails, slugs, earthworms) outside the scope of our study.

The initial search yielded 6058 studies. Next, we used the following a priori acceptance criteria for studies to be included in the meta-analysis before filtering downloaded records: 1) studies must measure the response of one or more soil organism (Table 1) to fire; 2) measured response variables must include either biomass, abundance, richness (e.g. number of species, number of operational taxonomic units), evenness (e.g. Pielou's eveness, Simpson's equitability, Shannon evenness), or diversity indices (e.g. Shannon, Simpson, McIntosh); 3) studies must compare the response(s) of said soil organism(s) between either burned

Table 1. Studies used in meta-analysis of response of soil biota to fire including the soil organism, response parameters, biome, type of fire, sampling depth from ground surface (cm), soil biota quantification method, and number of observations reported in each publication.

Soil organism	Response parameters	Biome	Type of fire	Sampling depth (cm)	Quantification method	No. of observations	Reference
Arthropod	abundance	forest	prescribed	6	Tullgren, direct count	4	Haimi et al. 2000
Arthropod	abundance	forest	prescribed	5	direct count	10	Dress and Boerner 2004
Arthropod	abundance	forest	prescribed	3, 6	high gradient apparatus	4	Berch et al. 2007
Arthropod	abundance	forest	prescribed	NA	Berlese, direct count	2	Camann et al. 2008
Arthropod	abundance	forest	prescribed	NA	Tullgren, direct count	2	Brennan et al. 2009
Arthropod	abundance	forest	prescribed	NA	Tullgren, direct count	1	Dechene and Buddle 2009
Arthropod, Enchytraeid	abundance	forest	prescribed	15	Tullgren, direct count	58	Malmström et al. 2009
Arthropod	abundance	forest	prescribed	5	Tullgren, direct count	3	Grabczynska et al. 2009
Arthropod	abundance	forest	wild	15	Tullgren, direct count	152	Broza and Izhaki 1997
Arthropod	abundance	forest	wild	2	Tullgren, direct count	40	Gongalsky and Persson 2013
Arthropod	abundance	forest	wild	12	Tullgren, direct count	1	Zaitsev et al. 2014
Arthropod	abundance	grassland	prescribed	5	Berlese, direct count	7	Barratt et al. 2006
Arthropod	abundance	grassland	prescribed	20	Tullgren, direct count	3	Whitford and Steinberger 2012
Arthropod	abundance	shrubland	prescribed	8	Berlese, direct count	28	Caruso and Migliorini 2006
Arthropod	abundance	shrubland	wild	6	Tullgren, direct count	1	Shaw 1997
Arthropod	abundance, evenness, diversity	forest	prescribed	NA	Tullgren, direct count	24	Malmström 2012
Arthropod	abundance, richness	forest	prescribed	NA	Tullgren, direct count	48	Malmström et al. 2008
Arthropod	abundance, richness	forest	prescribed	10	Tullgren, direct count	18	Gongalsky et al. 2012
Arthropod	abundance, richness	forest	prescribed	30	direct count	2	Rossi et al. 2010
Arthropod	abundance, richness	grassland	prescribed	30	Tullgren, direct count	6	Doamba et al. 2014
Arthropod	abundance, richness, evenness, diversity	forest	prescribed	10	Tullgren, direct count	4	Huebner et al. 2012
Arthropod	abundance, richness, evenness, diversity	forest	wild	15	high gradient apparatus	4	Cuchta et al. 2012
Arthropod	abundance, richness, evenness, diversity	forest	wild	12	high gradient apparatus	4	Cuchta et al. 2013
Arthropod	richness	grassland	prescribed	15	Berlese, direct count	4	Beyer et al. 2011
Bacteria	abundance	forest	prescribed	15	direct count	7	Song et al. 2004
Bacteria	abundance	forest	wild	5	most probable number dilution series	10	Acea and Carballas 1996
Bacteria	abundance	forest	wild	10	culturing and direct count	2	Khodadad et al. 2011
Bacteria	abundance	forest	wild	5, 15, 25	direct count	30	Kim et al. 2004
Bacteria	diversity	forest	wild	10	DNA	3	de Carvalho et al. 2016
Bacteria	richness, evenness, diversity	forest	wild	1	DNA	6	Sun et al. 2016
Bacteria	richness, evenness, diversity	grassland	prescribed	10	DNA	3	Coolon et al. 2013
Fungi	abundance	agriculture	prescribed	10, 20, 30	direct count	9	Celik et al. 2011
Fungi	abundance	agriculture	prescribed	0, 2, 4, 6, 8, 10, 12, 14, 16, 18, 20	direct count	11	Nasim 2011

(Continued)

Table 1. Continued

Soil organism	Response parameters	Biome	Type of fire	Sampling depth (cm)	Quantification method	No. of observations	Reference
Fungi	abundance	forest	prescribed	15	direct count	14	Johnson 1995
Fungi	abundance	forest	prescribed	15	direct count	6	Dahlberg et al. 2001
Fungi	abundance	forest	prescribed	NA	DNA	21	Mah et al. 2001
Fungi	abundance	forest	wild	10	direct count	8	Vilarino and Arines 1991
Fungi	abundance	forest	wild	15	PCR ITS–restriction fragment length polymorphism	4	Jonsson et al. 1999
Fungi	abundance	forest	wild	NA	direct count	2	Jones et al. 2010
Fungi	abundance	forest	wild	NA	direct count	1	Masaphy and Zabari 2013
Fungi	abundance	forest	wild	20	direct count	2	Moreira et al. 2006
Fungi	abundance	grassland	prescribed	15	direct count	44	Dhillion and Anderson 1993
Fungi	abundance	shrubland	wild	15	direct count	1	Bellgard et al. 1994
Fungi	abundance	shrubland	wild	10	direct count	2	Rashid et al. 1997
Fungi	abundance, richness	grassland	prescribed	25	direct count	7	Gibson and Hetrick 1988
Fungi	abundance, richness, diversity	agriculture	prescribed	15	direct count	3	Wang et al. 2010
Fungi	abundance, richness, diversity	forest	prescribed	NA	direct count	6	Tuininga and Dighton 2004
Fungi	abundance, richness, evenness, diversity	forest	wild	15	direct count	40	Longo et al. 2014
Fungi	biomass	forest	prescribed	10	direct count	1	Waters et al. 1994
Fungi	biomass	forest	prescribed	40	direct count	6	Stendell et al. 1999
Fungi	biomass	forest	wild	1, 3, 5	direct count	6	Akema et al. 2009
Fungi	richness	forest	wild	10	direct count	3	Violi et al. 2008
Fungi	richness	forest	wild	15	direct count	6	Motiejunaite et al. 2014
Fungi	richness	forest	wild	10	rRNA	4	Xiang et al. 2015
Fungi	richness, diversity	forest	prescribed	30	DNA	4	Cowan et al. 2016
Fungi	richness, diversity	forest	wild	20	DNA	12	Buscardo et al. 2015
Fungi	richness, evenness, diversity	agriculture	prescribed	10	direct count	9	de Azevedo et al. 2014
Fungi	richness, evenness, diversity	forest	prescribed	10	DNA	12	Oliver et al. 2015
Fungi, arthropod	biomass, abundance	shrubland	prescribed	5	Tullgren, direct count	42	Rutigliano et al. 2013
Fungi, bacteria	abundance	forest	prescribed	2, 5	culturing	4	Garcia-Oliva et al. 1999
Fungi, bacteria	abundance	forest	wild	NA	direct count	2	Tateishi et al. 1989
Fungi, bacteria	abundance	forest	wild	5	culturing	6	Pourreza et al. 2014
Fungi, bacteria	abundance	grassland	prescribed	15	culturing	48	Dhillion and Anderson 1994
Fungi, bacteria	abundance, biomass	grassland	prescribed	15	quantitative PCR, lipid biomarkers	2	Docherty et al. 2012
Fungi, bacteria	biomass	agriculture	prescribed	10	direct count	2	Aleixo et al. 2014
Fungi, bacteria	biomass	agriculture	prescribed	0.5, 1	substrate-induced respiration	2	Rahkonen et al. 1999
Fungi, bacteria	biomass	forest	prescribed	5, 20	chloroform fumigation	26	Luizao et al. 1992
Fungi, bacteria	biomass	forest	prescribed	NA	chloroform fumigation	1	Fritze et al. 1994
Fungi, bacteria	biomass	forest	prescribed	NA	phospholipid fatty acids	3	Baath et al. 1995
Fungi, bacteria	biomass	forest	prescribed	5	chloroform fumigation	4	Andersson et al. 2004

(Continued)

Table 1. Continued

Soil organism	Response parameters	Biome	Type of fire	Sampling depth (cm)	Quantification method	No. of observations	Reference
Fungi, bacteria	biomass	forest	prescribed	5, 15	direct count	12	Esquilin et al. 2007
Fungi, bacteria	biomass	forest	prescribed	0, 5	phospholipid fatty acids	6	Overby and Hart 2016
Fungi, bacteria	biomass	forest	wild	5	substrate-induced respiration	5	Dumontet et al. 1996
Fungi, bacteria	biomass	forest	wild	5, 10	chloroform fumigation	33	Prieto-Fernandez et al. 1998
Fungi, bacteria	biomass	forest	wild	10	direct count	3	Esquilin et al. 2008
Fungi, bacteria	biomass	grassland	prescribed	5	chloroform fumigation	4	Jensen et al. 2001
Fungi, bacteria	biomass	plantation, shrubland	prescribed	10	phospholipid fatty acids	8	Sun et al. 2011
Fungi, bacteria	biomass	shrubland	wild	5	substrate-induced respiration	1	Halvorson et al. 1997
Fungi, bacteria	evenness, diversity	forest	prescribed	NA	culturing	20	Staddon et al. 1997
Fungi, bacteria	richness, evenness	forest	wild	NA	DNA, quantitative PCR	12	Kennedy and Egger 2010
Fungi, bacteria, microbial	abundance	forest	wild	5	culturing	8	Marozas et al. 2013
Fungi, bacteria, microbial	abundance, biomass	forest	wild	5	chloroform fumigation	156	Mabuhay et al. 2006
Fungi, bacteria, microbial	abundance, biomass	forest	wild	5	culturing, chloroform fumigation, phospholipid fatty acids	7	Barcenas-Moreno et al. 2011
Fungi, bacteria, microbial	biomass	forest	wild	15	fatty acid methyl esters	8	Hamman et al. 2007
Fungi, bacteria, microbial	biomass	forest	wild	2.5, 5	phospholipid fatty acids	24	Lombao et al. 2015
Fungi, bacteria, microbial	biomass	grassland	prescribed	15	phospholipid fatty acids, chloroform fumigation	12	Zhang et al. 2013
Fungi, bacteria, microbial	biomass	grassland	wild	20	phospholipid fatty acids	6	Wang et al. 2016
Fungi, bacteria, microbial	biomass	plantation	wild	5	culturing, chloroform fumigation	6	Kara and Bolat 2009
Fungi, bacteria, microbial	biomass	shrubland	prescribed	5	phospholipid fatty acids	5	Barreiro et al. 2015
Fungi, bacteria, microbial	biomass	shrubland	prescribed	2, 5	phospholipid fatty acids, chloroform fumigation, ergosterol	14	Barreiro et al. 2016b
Fungi, bacteria, microbial	biomass, abundance	shrubland	wild	5	culturing, chloroform fumigation, phospholipid fatty acids	28	Barcenas-Moreno et al. 2016
Fungi, bacteria, microbial, protozoa	biomass, abundance	forest, grassland	wild, prescribed	2.5, 5	chloroform fumigation, fatty acid methyl esters	36	Fultz et al. 2016
Fungi, microbial	abundance	shrubland	wild	NA	culturing	16	Cilliers et al. 2005
Fungi, microbial	biomass	forest	prescribed	5	chloroform fumigation, direct count	40	Rutigliano et al. 2002
Fungi, microbial	biomass	forest	wild	NA	quantitative PCR, chloroform fumigation	6	Waldrop and Harden 2008
Fungi, microbial	biomass	forest	wild	2	ergosterol, phospholipid fatty acids	3	Barreiro et al. 2016a
Fungi, microbial	biomass	forest	wild	15	chloroform fumigation, ergosterol	6	Köster et al. 2016
Fungi, microbial	biomass	shrubland	prescribed	5	chloroform fumigation, direct count	32	Rutigliano et al. 2007

(Continued)

Table 1. Continued

Soil organism	Response parameters	Biome	Type of fire	Sampling depth (cm)	Quantification method	No. of observations	Reference
Fungi, microbial	biomass, evenness, diversity	forest	wild	5	direct count, chloroform fumigation	12	Martin-Pinto et al. 2006
Microbial	abundance	forest	prescribed	15	phospholipid fatty acids	4	Rau et al. 2008
Microbial	biomass	agriculture	prescribed	20	chloroform fumigation	4	Basilio Azevedo et al. 2015
Microbial	biomass	forest	prescribed	5	substrate-induced respiration	10	D'Ascoli et al. 2005
Microbial	biomass	forest	prescribed	10	phospholipid fatty acids	4	Gundale et al. 2005
Microbial	biomass	forest	prescribed	NA	chloroform fumigation	1	Swallow et al. 2009
Microbial	biomass	forest	prescribed	20	substrate-induced respiration	1	Bogorodskaya et al. 2014
Microbial	biomass	forest	prescribed	2.5	chloroform fumigation	14	Palese et al. 2004
Microbial	biomass	forest	prescribed	10	chloroform fumigation	1	Guo et al. 2015
Microbial	biomass	forest	prescribed	10, 20, 40, 60, 80	chloroform fumigation	10	Liu et al. 2015
Microbial	biomass	forest	prescribed	10	chloroform fumigation	4	Shen et al. 2016
Microbial	biomass	forest	wild	10	chloroform fumigation	1	Smith et al. 2008
Microbial	biomass	forest	wild	15	chloroform fumigation	16	Jiang et al. 2012
Microbial	biomass	forest	wild	5	chloroform fumigation	2	Heydari et al. 2016
Microbial	biomass	forest	wild, prescribed	15	chloroform fumigation	6	Grady and Hart 2006
Microbial	biomass	grassland	prescribed	15	chloroform fumigation	10	Liu et al. 2007
Microbial	biomass	grassland	prescribed	10	chloroform fumigation	1	Harris et al. 2008
Microbial	biomass	grassland	prescribed	10	phospholipid fatty acids	1	Jangid et al. 2010
Microbial	biomass	grassland	prescribed	10	chloroform fumigation	6	San Emeterio et al. 2016
Microbial	biomass	shrubland	prescribed	15	chloroform fumigation	6	Liu et al. 2010
Microbial	biomass	shrubland	prescribed	5	chloroform fumigation, substrate-induced respiration	8	Fonturbel et al. 2012
Microbial	biomass	shrubland	wild	2	chloroform fumigation	1	Barreiro et al. 2010
Microbial	biomass	shrubland	wild	4	chloroform fumigation	1	Dannenmann et al. 2011
Microbial	biomass	shrubland	wild	15	chloroform fumigation	5	Hanan et al. 2016
Microbial	biomass, diversity	agriculture	prescribed	18.5	DNA	2	Sul et al. 2013
Microbial	biomass, diversity	shrubland	prescribed	0, 2	chloroform fumigation, average well colour development	36	Fonturbel et al. 2016
Microbial	richness, evenness	forest	prescribed	10	DNA	4	Brown et al. 2013
Microbial, arthropod, nematode, protozoa, enchytraeid	biomass, abundance, richness	forest	wild	15	chloroform fumigation, direct count, Baermann, Tullgren	11	Gongalsky et al. 2016
Nematode	abundance	forest	prescribed	20	Baermann, direct count	12	McSorley 1993
Nematode	abundance	forest	prescribed	10	Baermann, direct count	40	Pen-Mouratov et al. 2012
Nematode	abundance, diversity	forest	wild	10	Baermann, direct count	2	Cerevkova and Renco 2009
Nematode	biomass, abundance, richness, diversity	forest	wild	10	Baermann, direct count	12	Renco and Cerevkova 2015

and non-burned, or pre-fire and post-fire areas; 4) studies must report mean responses, standard deviation or standard error, and sample size.

Lastly, of the remaining studies, we only included those that measured euedaphic soil organisms (i.e. those that spend the majority of their lifespan in the soil habitat). Thus, studies investigating the only effects of fire on litter dwelling and soil surface dwelling organisms were considered outside the scope of our meta-analysis. We included both organic and mineral soils in our analysis. Additionally, when studies presented both microbial biomass C and N, only biomass C was included as it was the more commonly reported of the two parameters. Because some studies only measured microbial biomass using methods that were not able to differentiate between bacterial biomass and fungal biomass (e.g. chloroform fumigation), 'microbial' responses were considered separately from bacterial and fungal responses in the analysis. Similarly, studies that reported changes in fungal communities by means of root colonization (%) were not included and have been synthesized elsewhere by Dove and Hart (2017).

After filtering the initial study set with the above criteria, 131 studies published from 1988 to 2016 remained for further analysis (Table 1). Response data were taken directly from tables, figures and written text. Data were extracted from figures using ImageJ software (Schneider et al. 2012). Within the software, axis scales were defined, and data point locations were measured using the measure function. We extracted both means and standard deviations or standard errors. Additional information that was gathered from the studies included: sample size, response parameter, units, treatment type, time since fire, method of soil biota quantification, qualitative characterizations of fire severity (e.g. light, moderate, or severe), type of fire (e.g. wild versus prescribed), biome, depth of sampling, page number, table or figure number. We categorized the studies into general biome classes (e.g. forest, grassland) rather than regional biomes (e.g. temperate forest, boreal forest) given that an insufficient number of studies reported higher trophic levels (e.g. nematodes, arthropods) or specified the abundance and diversity parameters.

Meta-analysis statistics

All meta-analysis computations were done in R (<www.r-project.org>) using the metafor package (Viechtbauer 2010). We conducted a hierarchical nested meta-regression to account for studies with repeated observations either across time or space (Koricheva et al. 2013). While two is the absolute minimum number of studies required for meta-analysis (Valentine et al. 2010), we only conducted meta-analysis when three or more studies were available. Soil organism by parameter groups (e.g. biomass, abundance) that had less than three studies were only included in 'all studies' analyses (Table 2). To ensure normality in all analyses, we utilized the natural log of the response ratio as the effect size (Hedges et al. 1999) as follows:

$$lnRR = \ln\left(\bar{X}_B\right) - \ln\left(\bar{X}_{NB}\right) \quad (1)$$

where $\bar{X}_B$ is the mean of the burned site and $\bar{X}_{NB}$ is the mean of the non-burned site. We back-transformed the model estimates from the log scale to the linear scale as a measure of percent change due to fire to facilitate interpretation as follows:

$$mean\ \%\ change = (e^b - 1) \times 100\% \quad (2)$$

where b is the *lnRR* model estimate. We first conducted a mixed effects meta-regression on each study to determine an average effect size of fire on each soil organism and parameter.

Table 2. Influence of biome, fire type, burning depth, and quantification method on effect of fire on soil organisms. *k* is the number of observations for each meta-analysis. A dash (–) signifies groups that were not analyzed because they did not meet the minimum study number (3). Values represent p-values of mixed effects meta-regression for each soil organism and parameter group. Significant effects are bolded ($p \leq 0.05$).

						Moderators			
Soil organism	Parameter	*k*	Biome	Fire type	Burning depth	Biome × Fire type	Fire type × Burning depth	Biome × Burning depth	Method
Fungi	biomass	29	0.59	0.19	0.23	**0.02**	0.48	0.30	0.11
	abundance	30	0.77	0.79	0.95	0.70	**0.03**	0.35	0.09
	richness	11	0.43	0.72	0.97	**0.02**	0.45	–	–
	evenness	5	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	–	–	–
	diversity	8	**<0.0001**	0.93	0.23	**<0.0001**	0.14	–	–
Bacteria	biomass	15	0.54	0.84	**0.005**	**0.01**	0.89	0.25	0.93
	abundance	16	0.96	0.96	0.84	0.96	0.87	0.65	0.86
Microbes	biomass	56	0.64	0.44	**0.04**	0.97	**0.04**	0.80	0.70
Nematodes	abundance	5	–	0.86	–	–	–	–	–
Arthropods	abundance	25	0.57	0.89	0.71	0.56	0.88	0.32	–
	richness	9	**<0.0001**	0.44	0.21	0.39	–	–	–
	evenness	4	0.08	0.90	0.98	–	–	–	–
	diversity	4	0.18	0.83	0.98	–	–	–	–

We then used these average effect sizes from each study to conduct a global mixed effects meta-regression on all studies to determine the overall effect of fire on each soil organism and parameter. Taken together, these results were used to guide our interpretation of the effects of fire on the soil community. For example, effect sizes that were not significantly different from zero could be interpreted as a neutral response (e.g. resistant to the fire) or high resilience inasmuch as the group recovered within the time between the fire event and sampling. Likewise, groups that exhibited significantly negative effect sizes might represent non-resistant and non-resilient groups. We conducted a separate nested meta-regression for the 14 studies that measured both fungal and bacterial biomass to determine whether the effect of fire on one group was consistently greater than the effect on the other. We ran the global meta-regression model on the ratio of fungi and bacteria effect sizes, wherein a ratio greater than 1 indicates that the effect of fire on fungi is greater than bacteria. To keep our estimate conservative, we used the larger of the two standard errors of the effect sizes from the meta-regression model of the single studies of bacteria and fungi as inputs into the global meta-regression.

To investigate the effect of biome, type of fire, depth, and quantification method on the effect of fire on soil organisms, we conducted a mixed effects meta-regression with study as the random effect and biome, type of fire, depth and their interactions as categorical moderators. Due to lack of data for each categorical variable and limited statistical power, we did not test the three-way interaction of biome, type of fire, and soil depth. For this analysis, we binned sampling depth from ground surface into three categories: surface ($\leq$ 5 cm), subsoil ($>$ 5 cm), and unknown (sampling depth not reported). We did not analyze depth as a continuous variable because soils were primarily sampled using cores and analyzed across the depth range of the core (e.g. 0–5 cm or 0–20 cm). For studies of richness, evenness, and diversity where the number of observations was limited, we reduced the full model to focus on main effects and interactions that address questions of interest. We conducted an omnibus test of parameters for models that resulted in significant moderators to determine differences between parameter categories (e.g. surface versus subsoil).

To investigate the effect of time since fire on the response of soil biota biomass and abundance to fire, we fit linear mixed effects meta-regression models with study as the random effect and natural log response ratios weighted by variance. We included all observations in studies with multiple observations because time since fire ranged widely both within and between studies. Soil biota richness, evenness, and diversity estimates, as well as microbial abundance, were excluded from the time since fire regression analysis due to insufficient observation numbers. We interpreted positive linear trends of negative effect sizes to represent resilience.

We assessed publication bias using a regression test for funnel plot asymmetry of the global mixed effects meta-regression model described above (Egger et al. 1997). Groups of studies that showed evidence of funnel plot asymmetry ($p \leq 0.05$) were considered to have publication bias and were not included in our interpretation.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.19tb3dp> (Pressler et al. 2018).

Results

Distribution of the literature

The majority of studies (75%) included in our meta-analysis focused on soil microorganisms (e.g. bacteria, fungi, microbes), whereas a much smaller percentage (25%) considered soil fauna (e.g. protozoa, nematodes, arthropods). While no studies looked at Archaea alone, they are included in microbial biomass estimates. Studies investigating biomass and abundance were more common (93%) than studies examining aspects of diversity (7%). While studies were distributed across different biomes, the majority of studies were conducted in forests (66%), shrublands (13%), and grasslands (12%). Studies investigating prescribed fires (59%) were more common than wildfires (41%). Sampling depth and soil biota quantification methods varied widely across all studies (Table 1).

Responses of soil biota to fire

Overall, fire had a strong, statistically significant negative effect on biomass (Fig. 1a; $p < 0.0001$) and abundance (Fig. 1b; $p < 0.0001$) estimates of all soil organisms available for meta-analysis except for arthropod abundance ($p = 0.94$). Fire had the greatest overall impact on fungal biomass (–96%; $p < 0.0001$), but the effects of fire on bacterial (–90%; $p < 0.0001$) and overall microbial biomass (–44%; $p = 0.025$), and bacterial (–96%; $p < 0.0001$) and nematode (–88%; $p = 0.005$) abundance were all negative and significantly different than zero (Fig. 1). The effect of fire on microbial abundance (–99%) was greater than that of microbial biomass (–44%), but not significantly different from zero (Fig. 1; $p = 0.07$). For studies that measured both fungal and bacterial biomass, the effect of fire on fungal biomass was significantly greater than the effect on bacterial biomass (fungi effect size: bacteria effect size = 1.62; $p < 0.0001$). Despite differences in quantification approaches and units, the overall effects of fire on soil organism biomass and abundance were similar ($–1.60 \pm 0.22$ versus $–2.07 \pm 0.29$ respectively; Fig. 1).

The effect of fire on fungal (–98%) and arthropod (–97%) richness, fungal (–99%) and arthropod (–99%) evenness, and fungal (–99%), bacterial (–93%), arthropod (–99%) and microbial (–99%) diversity was comparable across all groups, with the exception of bacterial richness (–71%). Fire

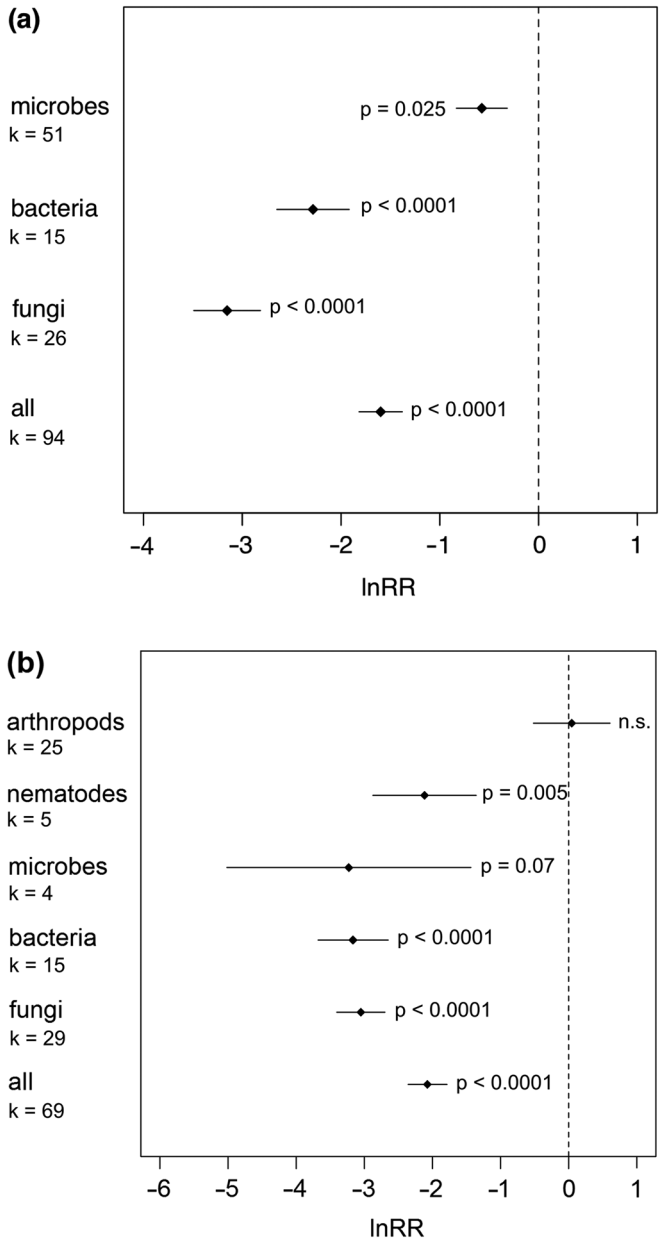

Figure 1. Effect of fire on soil biota biomass (a) and abundance (b). *lnRR* (Eq. 1) is the estimated overall effect size ± SE from meta-regression model. *k* is the number of observations included in each analysis; p-values indicate whether *lnRR* is significantly different from zero (n.s. is not significant). lnRR reported for all studies ('all') include additional studies of nematodes, Protozoa, and enchytraeids analysis in addition to groups presented in figure as there were too few to conduct separate meta-analyses (k < 3).

had a strong negative effect on fungal and arthropod richness (Fig. 2a, $p < 0.0001$), evenness (Fig. 2b, $p < 0.0001$), and diversity (Fig. 2c, $p < 0.0001$), but had no significant effect on bacterial richness ($p = 0.45$) or diversity ($p = 0.09$). In general, the effect sizes of fire on soil organism richness, evenness, and diversity (Fig. 2) were greater than those on biomass and abundance (Fig. 1).

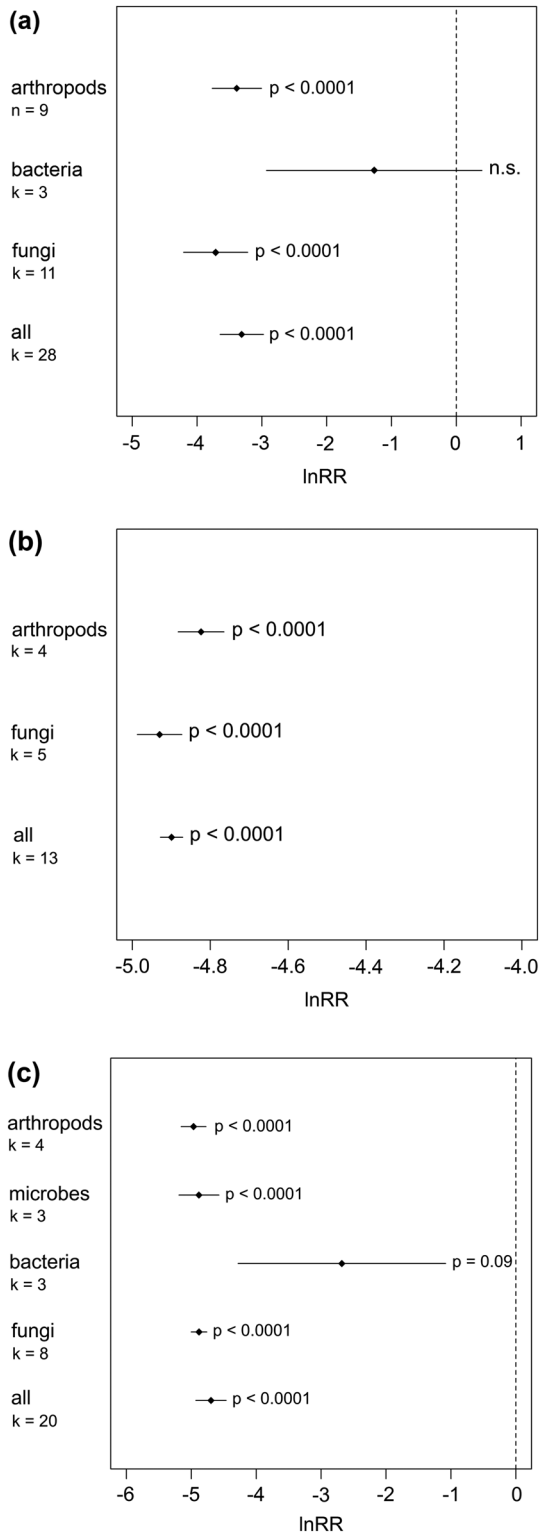

Figure 2. Effect of fire on soil biota richness (a), evenness (b), and diversity (c). *lnRR* (Eq. 1) is the estimated overall effect size ± SE from meta-regression model. *k* is the number of observations included in each analysis; p-values indicate whether the *lnRR* is significantly different from zero (n.s. is not significant). *lnRR*s for 'all' studies were derived as described in Fig. 1.

Controls on soil biota responses to fire

Biome, burning depth and fire type alone were not good predictors of the response of soil biota biomass and abundance to fire (Table 2). Two exceptions include differences in bacterial and microbial biomass responses between surface and subsoils (Table 2). The effect of fire on bacterial biomass was greater in surface than subsoils (–2.34 ± 1.21 versus 0.07 ± 1.60, respectively; $p = 0.02$). Additionally, the effect of fire on microbial biomass across sampling depth depended on fire type, with prescribed fires resulting in a greater reduction of microbial biomass in subsoils and wildfires having a greater negative effect in surface soils (Fig. 3). We found that prescribed fires had a greater negative effect on fungal biomass in forests than wildfires, while the effects of wildfires and prescribed fires were similar in grasslands and shrublands (Fig. 4). While the overall interaction between biome and fire type is significant for bacterial biomass (Table 2), the omnibus test of parameters did not reveal any significant trend. The significant effect of the interaction between fire type and burning depth on fungal abundance (Table 2) was driven by effect sizes in the 'unknown' burning depth category, and therefore could not be interpreted in an ecological context.

Biome was often a good predictor of fire effects on richness, evenness, and diversity (Table 2). Biome alone was a significant predictor of arthropod richness, while the effect of fire on fungal richness, evenness, and diversity across different biomes depended on the fire type (Table 2). Prescribed fires, rather than wildfires, resulted in a greater reduction in fungal richness (–3.47 ± 0.93 versus –3.31 ± 0.67, respectively; $p < 0.0001$), evenness (–5.13 ± 0.12 versus –4.86 ± 0.06, respectively; $p < 0.0001$), and diversity (–5.05 ± 0.21 versus –4.74 ± 0.23, respectively: $p < 0.0001$) in forests. Arthropod richness was reduced more in grasslands (–5.81 ± 0.92; $p < 0.0001$) than in forests (–3.30 ± 0.63; $p < 0.0001$). Burning depth alone was also a significant predictor of fungal evenness, but this was driven by studies with an 'unknown' burning depth category and therefore could not be further interpreted (Table 2). While many of the main effects or interactions were significant when compiling all studies (i.e. all soil biota groups), the significance of these effects is largely driven by one soil biota group with a greater number of observations included in the meta-analysis (i.e. fungi). As a result, we do not attempt to use results of the all studies category to suggest generalizability across soil biota groups.

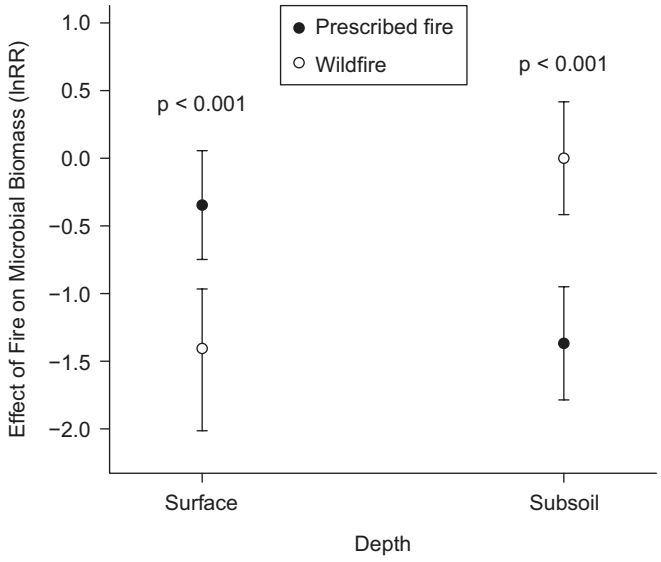

Figure 3. Effect of prescribed fire and wildfire on microbial biomass in surface and subsoils. *lnRR* (Eq. 1) is the estimated overall effect size ± SE from meta-regression model. p-values indicate whether *lnRR* is significantly different from zero.

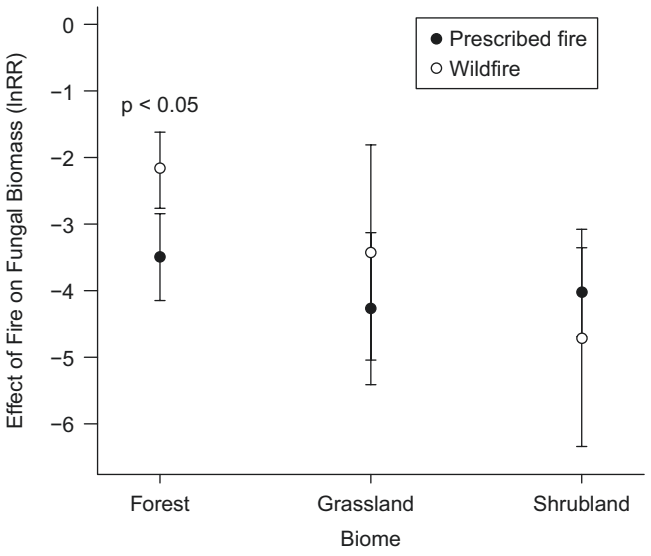

Figure 4. Effect of prescribed and wildfire on fungal biomass in forests, grasslands, and shrublands. *lnRR* (Eq. 1) is the estimated overall effect size ± SE from meta-regression model. p-values indicate whether *lnRR* is significantly different from zero.

Soil biota responses over time since fire

The studies included in the meta-analysis sampled soils between immediately after the fire to 62 years, with an average time since fire of 2 years. Based on the results of linear mixed effects meta-regressions, we found no clear temporal trend of the effect of fire on fungal biomass (marginal $r^2 = 0.06$, $p = 0.72$, $df = 100$), fungal abundance (marginal $r^2 = 0.05$, $p < 0.001$, $df = 233$), bacterial biomass (marginal $r^2 = 0.002$, $p = 0.89$, $df = 8$), bacterial abundance (marginal $r^2 = 0.000007$, $p < 0.001$, $df = 182$), microbial biomass (marginal $r^2 = 0.00002$, $p = 0.87$, $df = 269$) or arthropod abundance (marginal $r^2 = 0.0001$, $p = 0.57$, $df = 348$) over time since disturbance. However, we found a weak, positive relationship between nematode response to fire and time since fire (marginal $r^2 = 0.13$, $p = 0.09$, $df = 5$), suggesting that the effect of fire on nematode abundance decreased with increasing time since fire.

Publication bias

Our meta-analysis focused on published peer-reviewed journal articles and some degree of publication bias against results archived elsewhere is unavoidable. Within our dataset, the regression test for funnel plot asymmetry (Egger et al. 1997) revealed evidence for publication bias in studies of nematode abundance ($p < 0.0001$; $k = 5$), bacterial richness ($p = 0.0005$; $k = 3$), and microbial diversity ($p = 0.01$; $k = 3$). These groups also had a low number of studies available for meta-analysis and the results were therefore not included in our interpretation.

Discussion

Soil mesofauna are more resistant to fire than soil microorganisms

The significant negative effect of fire was consistent across microbial taxa and parameters considered in this meta-analysis suggesting that soil microbial communities are not resistant to fire. These results align with expectations from the literature and previous syntheses that soil microbial communities can be both directly and indirectly negatively affected by fire (Dooley and Treseder 2012, Dove and Hart 2017). The primary direct effect of fire is mortality of soil organisms during the event. We found that, across all studies, the effect of fire on fungal biomass is greater than its effect on bacterial biomass (Fig. 1a). This trend remains consistent when considering only the 14 studies that measured both bacterial and fungal biomass suggesting that bacteria are more resistant to fire than fungi. However, when considering abundance, our results show that fire affects both fungal and bacterial abundance to a similar degree (Fig. 1b) likely due to differences in quantification methods for fungi and bacteria (e.g. sporocarps versus culturing). The effect of fire on microbial abundance was greater than that of microbial biomass, but this observation is based on only four studies of microbial abundance and likely depends on differences in quantification methods for abundance and biomass. With respect to fungal richness, our results (Fig. 2a) are consistent with those of a recent synthesis of fungal diversity in fire-affected ecosystems (Dove and Hart 2017), confirming that fungal richness decreases with fire. These findings confirm the widely held view that fungi are more sensitive to fire than bacteria. Previous evidence suggests that this is due to both the lower thermal tolerance of fungi and, for mycorrhizal fungi, the mortality of plant hosts during fire (Neary et al. 1999).

Unlike fungi, bacterial richness was not significantly different between burned and unburned sites (Fig. 2a). However, only three studies of bacterial richness were available for meta-analysis and we found evidence for publication bias. Thus, our understanding of how fire affects bacterial richness remains unresolved. In general, far fewer studies investigated the effect of fire on aspects of belowground diversity than biomass or abundance measures (25% versus 75% of studies, respectively). While we found that the overall effect of fire on belowground diversity is strongly negative, this finding is based on a limited number of studies and additional research is needed to validate this negative effect across different taxa and ecosystems.

Our results indicate that the effect of fire on soil mesofauna (nematodes and arthropods) is weaker than for microorganisms (bacteria, fungi, microbes), but far fewer studies were available for mesofauna than for microorganisms (Fig. 1). There are clear differences in the morphologies, physiologies and ecologies between microorganisms and soil mesofauna that could explain these results. Soil mesofauna, particularly arthropods, are larger, possess greater vagility and tend to occupy higher trophic positions than microorganisms. Soil arthropods appear to be either resistant to or highly resilient to fire as their abundance did not significantly increase or decrease with fire (Fig. 1b). Soil arthropod richness, evenness, and diversity did decrease significantly with fire (Fig. 2) but the number of studies available is limited (Table 1). While it has been shown that soil arthropods have differential susceptibilities to fire and asynchronous recovery times (Malmström et al. 2009), we were not able to discern this effect in our dataset. Soil arthropods are more agile than other invertebrates and have the ability to move about soil pore spaces in search of more favorable conditions. However, dispersal ability is species specific and distance traveled belowground tends to be low (Lehmitz et al. 2012). Some taxa (e.g. oribatid mites) are more heavily armored than others (e.g. Collembola), which results in greater protection against increased temperatures during fire (Malmström 2008). Soil arthropod communities may be resistant to fire because they are able to either withstand or escape high soil temperatures by migrating to unburned patches or deeper into the soil. The spatial heterogeneity of soil after a fire is an important control on soil arthropod community recovery with unburned refugia harboring greater abundance and diversity of soil arthropods (Gongalsky and Zaitsev 2016). Soil arthropods that survive in unburned patches or deeper in the soil profile may serve as colonizing populations for recovering arthropod communities (Zaitsev et al. 2014). Depending on the rate of recolonization, this may result in no net difference in arthropod abundance estimates between burned and non-burned plots by the time of sampling.

Omnivory is common among soil arthropods (Moore et al. 1988) and thus arthropods have a wide array of prey options available which may allow for greater survival as prey resources become limiting after a fire. When considered in a food web context, the resistance of soil arthropods to fire may result in an increase in top–down pressure on their microbial prey that may exacerbate microbial sensitivity to fire and contribute to their limited recovery. However, few studies investigate the effect of fire on microorganisms, fauna and their interactions in a food web context. Thus, the implications of fire resistant soil arthropods for top–down controls on microbial communities remains speculative and unresolved.

Soil microorganisms are not resilient to fire

Not only is the negative effect of fire on soil biota generally consistent across taxa and biomes, the response remains consistent over time since disturbance. We found a weak relationship ($r^2 = 0.13$, $p = 0.09$, $df = 5$) between nematode abundance response and time since fire, but these data are subject to publication bias. For all other groups, we found no clear temporal signal of soil biota recovery after fire suggesting that microbial communities are not particularly resilient to fire. The majority of the studies included in this meta-analysis sampled soil biological communities within 10 years after fire (two years on average), but even a decade after fire, we find no consistent evidence for a trend towards recovery of soil biological communities. While a few studies found a positive effect on soil biota at some time points, the majority of response ratios were negative, regardless of soil biota group or time since fire. The negative effect of fire on soil biota biomass and abundance may persist over a decade, as observed in both arthropod (Malmström 2012) and fungal communities (Treseder et al. 2004). Our results align with meta-analyses by Dove and Hart (2017) and Dooley and Treseder (2012) who found limited evidence of recovery of fungal richness and microbial biomass in less than 10 years. A recovery trend of microbial biomass was found in Boreal forests (Dooley and Treseder 2012) and fungal richness across sites (Dove and Hart 2017), but these effects were not realized until 10–20 years or more after the fire. If soil biological communities are not resilient to fire within a decade, the predicted increase in fire frequency (Moritz et al. 2012) may further hinder the recovery of soil communities and the important ecosystem processes they regulate.

Biome, burning depth and fire type are poor predictors of soil biota responses

Our synthesis provides some evidence for ecosystem and fire parameters to drive soil biota responses to fire. However, biome, burning depth, fire type, and quantification method were overall inadequate predictors of soil biota responses (Table 2). Many of the other physical, chemical, and biological mechanisms that likely control soil biota responses to fire (e.g. pH, organic matter quantity and quality, soil temperature and moisture, plant community composition, soil food web interactions) were not measured or reported consistently across the literature and thus could not be included as moderators in our meta-analysis. Instead, discussions of variation in soil biota responses to fire in the literature have focused primarily on differences in ecosystem types (Dooley and Treseder 2012, Dove and Hart 2017), fire severity (Gongalsky 2006, Malmström 2010), fire type (Dove and Hart 2017), and measurement technique (Dooley and Treseder 2012, Dove and Hart 2017). Although biome, burning depth, and fire type could not explain much of the variation in soil biota responses (Table 2), a few patterns emerged from our analyses that serve as starting points for future research.

We found that fire had a stronger negative effect on bacterial biomass in surface soils than in subsoils. This result confirms previous observations that burning depth plays an important role in determining the degree to which soil biological communities suffer direct mortality due to fire (Neary et al. 1999). Depending on fire severity, some fires may only burn the top few centimeters of the soil surface (Neary et al. 1999) and samples that are taken down to greater depths may dilute the signal of the response of soil microbial communities to fire.

We found that microbial biomass is more susceptible to wildfire in surface soils, whereas the effect of prescribed fires is greater in subsoils (Fig. 3). The observed decrease in microbial biomass in subsoils after prescribed fires could be driven by changes in the fungal community. In forests, we found that prescribed fires have a greater negative effect on fungal biomass and diversity than wildfires (Fig. 4). We did not see a difference in the effect of fire on fungal biomass in grasslands and shrublands (Fig. 4). We speculate that this may be because their management results in similar severity of prescribed burns and wildfires. A number of studies included in the meta-analysis were prescribed fires that were set after clear cutting the forest (Baath et al. 1995, Mah et al. 2001, Malmström et al. 2008). Fires and tree removal during clear cutting shift plant community composition and thus influence the rhizosphere and rhizosphere interactions (Moore 1988, Wall and Moore 1999), particularly mycorrhizal associations. Thus, the greater negative effect of prescribed fire on fungal biomass may be driven by studies investigating post-clearcut burning. Mycorrhizal colonization also decreases after fire when measured in situ (Dove and Hart 2017) and may explain the decreases in fungal and microbial biomass in both surface soils and subsoils. Regardless of fire type, low severity fires result in high tree survival and shallow depth of burn into mineral soil in which mycorrhizal colonization and diversity can persist (Dahlberg et al. 2001) but we were not able to test an effect of fire severity due to a limited availability of studies. When considering fire regimes, rather than recovery from single fires, our perspective on the resistance and resilience of soil communities changes. Repeated burning overall may not affect fungal richness (Dove and Hart 2017), but distinct fire-adapted fungal communities do develop in frequently burned forests (two- and three-year intervals; Oliver et al. 2015).

Our analysis found that fire reduces arthropod richness to a greater degree in grasslands than in forests (Table 2). Forest litter and soil horizons often have a lower bulk density than grassland soils (Keen et al. 2011), allowing for greater ease of movement for arthropods to traverse deeper into the soil to evade high temperatures during fire. Oribatid mites possess exoskeletons that are more resistant to higher soil temperatures (Malmström 2008) and are common in forests, while less armored microarthropods (e.g. collembola, prostigmatid mites) are common in grasslands (Maraun and Scheu 2000), though both kinds of microarthropods can be found in either ecosystem. Mycorrhizal associations

play a key role in structuring grassland plant communities (Hartnett and Wilson 2002) and many soil microarthropods are fungal feeders (Hunt et al. 1987, Schneider et al. 2004). The observed reduction in arthropod richness may be a consequence of direct effects of fire on plant communities and their mycorrhizal associations with cascading effects to their microarthropod consumers. However, mycorrhizae also play important roles in both temperate (Read et al. 2004) and tropical forests (Rillig et al. 2001), suggesting that these mechanisms are likely also at play in regulating arthropod richness after fire in forest ecosystems.

Knowledge gaps and research priorities

Our synthesis revealed two major knowledge gaps: 1) the biotic mechanisms by which soil food webs are influenced by fire and, 2) approaches to studying the responses of soil biota to fire in the context of global change. As with much of the soil ecology literature (Coyle et al. 2017), there is a clear gap in our understanding of how higher trophic levels respond to fire (Zaitsev et al. 2016). It is necessary to consider taxa in higher trophic levels and how they interact with primary consumers and the rest of the food web when seeking to understand shifts in ecosystem function to fire. In fact, trophic interactions within the soil food web have been shown as useful predictors for soil organism vulnerability to disturbance (Hedlund et al. 2004). However, our literature review turned up only two studies that considered the effects of fire on Protozoa, and while slightly more studies were found for nematodes and arthropods (Table 1), higher trophic levels are underrepresented in the literature in comparison to microorganisms (bacteria, fungi, Archaea). Further, most studies only considered one type of soil organism, and those that did consider more than one did not integrate these findings into a community or food web framework, precluding a strong connection to changes in belowground functioning.

While not the focus of this meta-analysis, an aboveground-belowground linkages framework is a promising approach to improve our understanding of soil biological responses to fire and consequences for ecosystem function. Links between soil organisms and plant communities can be used to predict soil organism vulnerability to disturbance, particularly for soil biota that are directly associated with plants (i.e. mycorrhizae; Hedlund et al. 2004). Such an aboveground–belowground linkages framework has been evoked as a way to approach restoration of post-fire systems (Kardol and Wardle 2010). Despite our understanding of the importance of aboveground–belowground linkages and plant–soil feedbacks for understanding community dynamics and ecosystem function (Bardgett and Wardle 2010), efforts to explain soil biota responses to fire have largely focused on short-term changes to the physical and chemical soil environment. Understanding the consequences of longer term shifts in forest plant communities for soil microbial community responses to fire has been noted as an important research need (Hart et al. 2005), but links to higher trophic levels in soil food webs are seldom discussed.

The majority of the studies included in this meta-analysis only considered the effect of a single fire event on soil biota. While understanding the short-term implications of a single fire on belowground communities is important, the nature of fire regimes (frequency, severity, size and timing) is shifting as a result of climate change (Flannigan et al. 2009, 2013, Moritz et al. 2012). The effect of fire on fungal richness does not differ between single and repeated burns (Dove and Hart 2017), but distinct fungal communities develop under frequently burned and unburned sites (Oliver et al. 2015). Understanding how fungal communities change under different fire regimes is an important first step. We currently do not have sufficient data to determine the consequences of shifting fire frequency, severity, seasonality, size and duration on the structure and function of the entire belowground community or the physical, chemical and biological interactions that give rise to these responses. Further, fire frequency has important ecosystem consequences for soil C and N stocks (Pellegrini et al. 2018). As with many disturbances, understanding the effect of a single fire on an ecological community and its processes cannot simply be extrapolated additively to multiple, repeat fires. Similarly, fire regimes are not shifting in isolation of other global changes and therefore must be included in investigations of ecosystem responses to global change. In particular, whether fire will render soil communities more or less susceptible to other global changes (e.g. precipitation shifts, warming, nitrogen deposition) remains an open question. When fire is included as a treatment in fully factorial experimental designs investigating other global changes, responses of plant communities and abiotic factors, rather than soil communities, tend to be the focus (Henry et al. 2006, Koerner and Collins 2014, but see Allison et al. 2010 and Docherty et al. 2012).

Given the knowledge gaps identified above, we suggest the following avenues for impactful future research at the intersection of fire disturbance ecology and soil biology:

1) Further investigate the effect of fire on soil fauna.
2) Consider multiple microbial and faunal taxa in a single study and, where possible, the entire soil food web.
3) Identify biotic mechanisms for recovery after fire, both for the soil food web and the interactions between plant and soil communities, and determine in which biomes and under what conditions biotic or abiotic mechanisms are the most important drivers of soil communities after fire.
4) Investigate how disturbance regimes, rather than single disturbances, restructure belowground communities, and identify consequences for ecosystem processes.
5) Utilize both experimental and observational approaches to explore the interactive effects of fire with other global changes.

Moving forward, soil ecologists could take a more comprehensive view of belowground communities by considering both food web interactions and aboveground-belowground linkages that may influence the response of recovery of soil biota to fire. This approach can be readily applied to other types of disturbance. Studies that link responses of soil

communities to changing fire regimes with ecosystem processes such as decomposition and biogeochemical cycling will bring us closer to predicting and quantifying the consequences of climate-induced shifts in fire regimes for ecosystem function.

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Author contributions – YP and MFC conceived of the idea for the work. YP conducted the meta-analysis. YP wrote the manuscript with the contribution of JCM and MFC.
Conflicts of interest – The authors do not have any conflicts of interest to report.

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