The myth of the biological threshold: A review of biological responses to soil heating associated with wildland fire

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A B S T R A C T

Soil heating caused by prescribed or wildland fire commonly focuses on a single biological thermal threshold of 60 °C for the duration of one minute to represent organism death. This metric severely misrepresents the heterogeneity of the soil environment, the physiological attributes and tolerances of organisms, and the complexity of heat transfer through soils. Measurements of biotic death in simulated laboratory experiments render research findings difficult to extrapolate to forest and grassland soils. The disparity between assumed biological responses and the diversity of biological responses after wildland fire events calls for a thorough review of soil biological heating thresholds. In this review, we synthesize and compare research that directly relates soil heating temperature and duration to biological responses, provide relevant models for temperature-duration responses of soil organisms in lieu of a strict threshold, and recommend applications of soil heating data for wildland fire and ecosystem management. For no single study or group of organisms was a threshold of 60 °C for one-minute duration evidenced. All soil organisms reviewed, which included roots, mesofauna, bacteria, fungi, microbial biomass, and soil respiration, displayed both positive and negative responses to soil heating across temperature and duration gradients. We, therefore, discourage the use of the traditionally accepted metric of 60 °C for the duration of one minute. Instead, we present models of duration-temperature relationships of soil biota and invite interdisciplinary efforts from researchers and managers to directly measure biological responses on a case-by-case basis.

1. Soil heating and fire management

The evaluation of wildland fire effects has focused on above-ground indicators of ecosystem structure and function, which tend to be more easily measured than below-ground systems. Yet below-ground systems, including those associated with soil flora and fauna, roots and rhizosphere symbionts, and nutrient, hydrologic, and seed reservoirs, are fundamental to the maintenance and restoration of fire-maintained ecosystems (DeLuca and Sala, 2006; Hart et al., 2005; Oliver et al., 2015; Wardle et al., 2004, 2003). Soil heating resulting from wildland fires, whether applied as prescribed burning or managed wildfires, has potential immediate and long-term impacts on soil processes and constituents.

The mechanism driving fire’s direct (“first order”) biological impacts on soil is the degree to, and duration over, which energy in the form of heat travels through soil and affects soil-dwelling biota. Temperatures reached during wildland fires range from less than 100 °C during low intensity burns to well over 400 °C depending on fuel loads and type, fire behavior, and soil conditions (Busse et al., 2013; DeBano et al., 1979; Hartford and Frandsen, 1992; Massman and Frank, 2004a, 2004b; Raison et al., 1986). The depth and duration soil is heated, and the maximum temperatures reached, is influenced by soil abiotic components (e.g. moisture content, texture, other physical properties) that provide the context for how much energy is transferred and whether heating affects below-ground biotic components (Busse et al., 2014; Frandsen and Ryan, 1986; Massman et al., 2010; Neary et al., 2005). These relationships are complex and are characterized by high spatial variability (Busse et al., 2014), but it stands to reason that soil biota are potentially affected by the range of temperatures reached due to wildland fire-induced heat transfer. Biological temperature tolerances and post-fire conditions alter the degree to which fire impacts soil biota, an important consideration when quantifying first order fire effects on a burned ecosystem.

The duration and depth of soil heating may be substantial where fire is reintroduced to long-unburned ecosystems through prescribed fire application as evidenced by impacts to soil microbial processes, and root and rhizosphere communities (Kobziar, 2007; O’Brien et al., 2010; Varner et al., 2007, 2009; Wiggers et al., 2013). Where fire has occurred...
frequently over longer periods of time, soil heating effects on soils are assumed to be relatively benign, and biota may in fact have higher tolerances due to fire acting as a selective agent (DeLuca and Sala, 2006; Jorgensen and Hodges, 1970; Oliver et al., 2015). Where fires result in severe above-ground impacts (e.g. overstory mortality, high consumption of organic soils and downed woody debris), below-ground biological change is rarely measured, but fire effects are often deemed severe if soil temperatures exceed specified thermal intensity benchmarks (Busse et al., 2005; Hartford and Frandsen, 1992; Monsanto and Agee, 2008). Empirical studies of soil biota document a wide range of positive, neutral, and negative responses to wildland fire for many different organisms (Carney and Bastias, 2007; Dove and Hart, 2017; Hart et al., 2005; Kobziar and Stephens, 2006; Taudière et al., 2017; Wang et al., 2012), yet both the scientific and management communities commonly focus on a select group of soil temperatures to pinpoint thresholds where significant biotic repercussions from fire are to be expected (Busse et al., 2014, 2005; Hungerford et al., 1991; Preisler, et al., 2000).

The most frequently referenced threshold submits that soil biota mortality is likely to occur if soil temperatures reach 60 °C or higher for approximately one minute or longer, referred to as the “lethal” level by many (e.g., Busse et al., 2005; Kreye et al., 2013; Preisler, et al., 2000; Swezy and Agee, 1991; Varner et al., 2009). The majority of studies evaluating this threshold cite review papers, symposium reports, or technical reports (Dunn and DeBano, 1977; Hare, 1961; Hungerford et al., 1991; Neary et al., 2005, 1999). One foundational study used as reference for this thermal severity metric, Nelson (1952), does not in fact report results in support of this particular threshold. Notably, the study was not conducted on soil organisms (nor plant roots) but on pine needles. Furthermore, the peer-review process and experimental design of a report from 1952 may not meet modern standards for reproducibility and replication. Similarly, Rosenberg et al. (1971) is often cited, but does not report original heating data or duration of heating for protein denaturation, which makes it difficult to extrapolate to wildland fire heating data and effects on soil biotic communities. Some of the works cited as sources for the threshold suggest that a single measure for assessing soil heating effects is inappropriate, given the variability in responses (e.g., Dunn and DeBano, 1977; Nelson, 1952).

Although it is beyond the scope of this work to trace the pathway which led to the widespread adoption of this thermal severity threshold (i.e. 60 °C for one minute), its general usage is readily evidenced. For example, the First Order Fire Effects Model (FOFEM), a prediction model designed to help fire managers plan for and predict fire effects, has default outputs showing the depth of soil heating where 60 °C was obtained for at least one minute, referred to as “the lethal temperature for living organisms” (Reinhardt, 2003). This and similar programs are designed to inform decision making and planning efforts in regard to a wide variety of forest management actions, which include prescribed fire application, development of post-fire logging specifications, and assessments of fire severity and post-fire rehabilitation needs (Neary et al., 2005; Reinhardt, 2003). Applications centered on a single temperature threshold metric may mislead management activities and, in lieu of direct measurements, the assumption of biological impacts may inhibit the application of fire use for restoration where significant soil heating is predicted. Importantly, such an assumption may also hinder advancement in the mechanistic understanding of wildland fire effects on ecosystem components and processes.

Another presumption regarding fire effects on soil centers on the concept of soil “sterilization.” The term has frequently been used to denote fire’s impacts on soil where above-ground and organic horizon fuel consumption is high (Busse et al., 2005; Heyward, 1939; Massman and Frank, 2004a, 2004b), and soil temperatures reach selected limits, such as those defined for autoclave sterilization of medical devices or the boiling point of water (e.g. Rein et al., 2008). However, the degree to which soil processes, interactions, and ecological functions are impacted by fire vary greatly, which suggests “sterilization” is improbable or at the very least highly localized and ephemeral (Busse et al., 2014; Glassman et al., 2016; Hart et al., 2005; Kurth et al., 2014; Wang et al., 2012). Fire impacts on soil biological processes and consumption have been shown to vary with proximity to vegetation, with a high degree of spatial variability even within small areas (Hille and Stephens, 2005; Kobziar, 2007). Given recent advances in understanding the fine-scale (sub-meter) variability of wildland fire behavior and fuel consumption patterns (O’Brien et al., 2016), it follows that thermal severity is also likely (horizontally as well as vertically) spatially complex and that large-scale extirpation of soil biota would likely only occur under extraordinary circumstances.

Continued advances in soil microbiology and fire ecology provide a complex perspective on biological responses to wildland fire-induced soil impacts (Baynes et al., 2012; Butenko et al., 2017; Cutler et al., 2017; Dixon et al., 1995; Korobushkin et al., 2017; Long et al., 2014). The disparity between traditionally assumed biological responses induced by elevated soil temperatures and the variety of biological responses after wildland fire events calls for a thorough review of soil biological heating thresholds in order to better characterize potential consequences and to help guide fire management activities. The purpose of this review is to (1) consolidate peer-reviewed research that directly relates soil heating temperatures and duration of heating to soil-dwelling organism responses, (2) present models for temperature-duration responses of soil organisms, and (3) provide recommendations for applications of soil heating data.

2. Approach and criteria for reviewed published works

This review compiled peer-reviewed primary research studies that quantified responses of soil-dwelling organisms and roots in relation to elevated temperatures. In order to provide a succinct compilation of isolated and direct effects of heating on soil biota, we limited our search criteria to only those organisms and excluded responses such as seed germination, soil nutrients, physical soil parameters, and effects on tree boles, stems, and leaves. Only twenty-three peer-reviewed research papers provided reproducible data of biological responses directly paired with soil temperatures, meeting the criteria for inclusion in this review (Table 1). In one instance, soil temperature data was derived from a separate publication (DeBano and Klopatek, 1988). Data included a variety of direct and indirect measures of biological responses to soil heating and were included if temperatures were directly measured in relation to the response. Soil respiration rates have been used in numerous studies as a broad indicator of soil biota response to heating from wildland fire, although the sources of the response are not typically differentiated (i.e. autotrophic and heterotrophic sources), especially in field studies (Godwin et al., 2017; Kreye et al., 2013). Studies all included controls to distinguish any background changes in independent variables from those induced by soil heating.

To provide a basis for comparison among the studies, the various biological responses were reported here as a percent difference relative to the unheated control values with the following formula:

\[
\frac{(tr - c)}{c} \times 100 = \Delta R \ (\%)
\]

where \(c\) = the biological response of the unheated control treatment, \(tr\) = the biological response at an elevated temperature treatment, and \(\Delta R\) = the percent difference of the biological response at the elevated temperature treatment relative to unheated control treatment (+ infinity to −100%). Where survival was measured, a −100% difference in biological response (\(\Delta R\)) corresponds to 100% mortality. For other measures of biological response (CFU, % mycorrhizal colonization, soil respiration, microbial biomass) a −100% value corresponds to a complete cessation of that response relative to a control. A mortality “threshold temperature” was reported where studies measured biological responses across any temperature gradient in order to define a temperature range (1–200 °C increments) at which −100% \(\Delta R\) was
Temperatures selected for evaluation in these studies did not follow a consistent logical approach across studies, nor were they consistently scaled to approximate typical wildland fire induced soil heating temperatures. Temperatures from some studies conducted in the laboratory were determined using thermocouples in soils at various depths during heating (DeBano and Klopatek, 1988; Dunn et al., 1979; Izzo et al., 2006; Kipfer et al., 2010; Pattinson et al., 1999), but the majority of studies exposed samples to air or water temperatures over extended periods of time and assumed soil organism temperatures reached.

All studies reviewed were used to calculate percent biological responses across temperature and heating duration. We excluded one data point that tested a duration of 24 h and found a > 100% ΔR which far exceeded the lower duration -100% ΔR in the same study (Labad et al., 1975). Due to the design of some studies, biological responses were included that were related only to maximum temperatures and durations (Dunn et al., 1979; Klopatek et al., 1988; Pattinson et al., 1999). Data from studies where specific identities of fungi and bacteria were not reported (Díaz-Raviña et al., 1992; Labeda et al., 1975) were included in both bacterial and fungal data analyses. All data are provided in the Appendix Table A1 and were analyzed in the R environment (R Core Team, 2016).

### Table 1

Study designs and response variables for the 23 experiments included in this review. CFUs = colony forming units. Additional information can be located in Appendix Table A1.

<table>
<thead>
<tr>
<th>Organism</th>
<th>Response variable</th>
<th>Heating method</th>
<th>Time of measurement after heat treatment</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Roots</td>
<td>Shoots area (^{-1})</td>
<td>Water bath</td>
<td>8 weeks</td>
<td>Flinn and Pringle (1983)</td>
</tr>
<tr>
<td>Roots</td>
<td>Percent mortality</td>
<td>Water bath</td>
<td>4 months</td>
<td>Ursic (1961)</td>
</tr>
<tr>
<td>Roots</td>
<td>Percent survival</td>
<td>Water bath</td>
<td>1 week, 2 weeks, 3 weeks</td>
<td>Zeleznik and Dickmann (2004)</td>
</tr>
<tr>
<td>Mesofauna</td>
<td>Percent survival</td>
<td>Humidity controlled heat chamber</td>
<td>48 h</td>
<td>Hodkinson et al. (1996)</td>
</tr>
<tr>
<td>Mesofauna</td>
<td>Abundance in organic matter</td>
<td>Oven</td>
<td>Immediate</td>
<td>Malmsø (2008)</td>
</tr>
<tr>
<td>Mesofauna</td>
<td>Percent relative frequency survival</td>
<td>Humidity controlled heat chamber</td>
<td>Immediate</td>
<td>Vannier (1994)</td>
</tr>
<tr>
<td>Mesofauna</td>
<td>Survival</td>
<td>Humidity controlled heat chamber</td>
<td>Immediate</td>
<td>Megdje (1965)</td>
</tr>
<tr>
<td>Fungi, bacteria, microbial biomass, respiration</td>
<td>Fungal and bacterial CFUs, basal respiration, normalized respiration, specific respiration</td>
<td>Muffle furnace</td>
<td>30 days</td>
<td>Badía and Martí (2003)</td>
</tr>
<tr>
<td>Fungi, bacteria, microbial biomass, respiration</td>
<td>Biomass, fungal and bacterial PLFA, fumigation-extraction and substrate induced respiration, basal respiration</td>
<td>Muffle furnace</td>
<td>Immediate</td>
<td>Bárceñas-Moreno and Bååth (2009)</td>
</tr>
<tr>
<td>Fungi and bacteria</td>
<td>Fumigation-extraction, microbial CFU, fungal hyphae</td>
<td>Muffle furnace</td>
<td>Immediate</td>
<td>Díaz-Raviña et al. (1992)</td>
</tr>
<tr>
<td>Fungi and bacteria</td>
<td>CFUs</td>
<td>Muffle furnace</td>
<td>Immediate</td>
<td>Guerrero et al. (2005)</td>
</tr>
<tr>
<td>Fungi and bacteria</td>
<td>CFUs</td>
<td>Experimental burn</td>
<td>Immediate</td>
<td>Dunn et al. (1979)</td>
</tr>
<tr>
<td>Fungi and bacteria</td>
<td>Percent survival, CFUs</td>
<td>Water bath</td>
<td>2 days or less</td>
<td>Dunn et al. (1985)</td>
</tr>
<tr>
<td>Fungi</td>
<td>Percent colonization, species richness</td>
<td>Drying oven</td>
<td>8 months</td>
<td>Izzo et al. (2006)</td>
</tr>
<tr>
<td>Fungi</td>
<td>Mean and total number of species</td>
<td>Drying oven</td>
<td>6 months</td>
<td>Kipfer et al. (2010)</td>
</tr>
<tr>
<td>Fungi</td>
<td>Percent colonization</td>
<td>Infrared lamps</td>
<td>24 h</td>
<td>DeBano and Klopatek (1988) and Klopatek et al. (1988)</td>
</tr>
<tr>
<td>Fungi</td>
<td>Percent colonization</td>
<td>Heating element</td>
<td>2 weeks</td>
<td>Patterson et al. (1999)</td>
</tr>
<tr>
<td>Fungi</td>
<td>CFUs</td>
<td>Water bath</td>
<td>Immediate</td>
<td>Warcup and Baker (1963)</td>
</tr>
<tr>
<td>Fungi</td>
<td>CFUs</td>
<td>Oven and kiln</td>
<td>33 days</td>
<td>Chambers and Attiwill (1994)</td>
</tr>
<tr>
<td>Fungi</td>
<td>Species richness and proportion of active spores</td>
<td>Drying oven</td>
<td>Immediate</td>
<td>Peay et al. (2009)</td>
</tr>
<tr>
<td>Microbial biomass and respiration</td>
<td>Fumigation-extraction and basal respiration</td>
<td>Muffle oven</td>
<td>Immediate</td>
<td>Choromanska and Deluca (2002)</td>
</tr>
<tr>
<td>Microbes</td>
<td>CFUs</td>
<td>Oven</td>
<td>Immediate</td>
<td>Labeda et al. (1975)</td>
</tr>
<tr>
<td>Bacteria</td>
<td>CFUs</td>
<td>Controlled heat chamber</td>
<td>Immediate</td>
<td>Murrell and Scott (1966)</td>
</tr>
</tbody>
</table>

**3. Mortality thresholds for soil organisms**

Eleven studies established a temperature and duration threshold value (as defined above) for roots, mesofauna, fungi, bacteria, microbial biomass, and soil respiration rates (Bárceñas-Moreno and Bååth, 2009; Díaz-Raviña et al., 1992; Dunn et al., 1985; Flinn and Pringle, 1983; Guerrero et al., 2005; Hodkinson et al., 1996; Malmsø, 2008; Peay et al., 2009; Ursic, 1961; Vannier, 1994; Zeleznik and Dickmann, 2004). In instances where a mortality threshold was identified, we found a significant (p < 0.001) and negative correlation (Spearman’s \( \rho = -0.4 \)) between log-transformed temperature and duration ranging from 0.5 to 120 min and 35 °C to 800 °C (Fig. 1). Organism and environmental factors influenced threshold values, such as season of collection time, relative humidity, soil moisture content, species, ecosystem type, and time after heat treatment (Table A1).

For no single study or group of organisms was a consistent threshold of 60 °C for one-minute duration evidenced. Plant roots displayed mortality thresholds between 0.5 and 120 min within a range of temperatures between 48 °C and 65 °C (Flinn and Pringle, 1983; Ursic, 1961; Zeleznik and Dickmann, 2004). Soil fungi and bacteria mortality thresholds were reported for temperatures from 60 °C to 400 °C and 80 °C to 400 °C for 2–30 min durations, respectively, but the majority of data points occur at 15 and 30 min durations (Bárceñas-Moreno and Bååth, 2009; Dunn et al., 1985; Guerrero et al., 2005; Peay et al., 2009). Only one study determined a mortality threshold for microbial biomass, which occurred at 160 °C for 30 min (Díaz-Raviña et al., 1992). Similarly, a single soil respiration rate threshold was reached when soils were heated to 200 °C for 15 min (Bárceñas-Moreno and Bååth, 2009).
4. Soil organism responses to heating

All reviewed studies related one or more biological response (ΔR) to soil temperatures that could conceivably be reached during a wildland fire and across a wide range of elevated temperature durations (Busse et al., 2013; DeBano et al., 1979; Hartford and Frandsen, 1992; Massman and Frank, 2004a, 2004b; Raison et al., 1986). Organisms ranged in ΔR91, ΔR95+5, and ΔR71–75 from +8000% to −100%, extending over a temperature range of 35 °C to 800 °C, and for durations from 0.5 min to 400 min (Fig. 2, Table A1). Similar to mortality thresholds, temperature (log-transformed) was also negatively correlated to duration (Fig. 2, p < 0.05, Spearman’s ρ = −0.13).

The relationship between temperature and duration of biological responses (ΔR) across soil organisms was primarily driven by roots (Fig. 3b, p < 0.0001, Spearman’s ρ = −0.49) and bacteria (Fig. 3c, p < 0.001, Spearman’s ρ = −0.56). Mesofauna (Fig. 3a), fungi (Fig. 3d), microbial biomass (Fig. 3e), and soil respiration rates (Fig. 3f) showed no significant relationship between temperature and duration of biological responses. However, the data for microbial biomass and soil respiration were only reported at one to three durations and likely do not reflect biological response patterns across a broader duration gradient.

5. Limitations and applications of review findings

Across all soil organisms addressed here, biological thresholds derived in this review were influenced by environmental, methodological, and biological factors (e.g. species, relative humidity, collection season, time after heat treatment, soil type, heat source, response variable) as evidenced by the range in temperatures and durations even among studies assessing the same type of soil biota (Figs. 1–3, Table A1). Where temperature and duration windows were deduced to provide a mortality threshold, the original studies show influencing factors that greatly limit inferences and applications beyond the study parameters (Tables 1 and A1). Study designs of the majority of reviewed literature also limit the extrapolation of these data to in-situ scenarios, where biotic and abiotic interactions are likely to influence biological responses (Tables 1 and A1).

Positive responses (+ΔR) displayed across all soil microorganisms illustrate the capacity of these organisms to resist and recover from temperatures above the traditionally accepted threshold for living soil organisms (i.e. 60 °C for 1 min) (Figs. 2 and 3, Table A1). The data provided in this review caution against extrapolating a mortality threshold and generalizing across life forms or environmental conditions. It is also essential to make a distinction between the mortality of an individual organism and the response of a community of organisms to soil heating, the latter of which is likely to result in above-ground and below-ground functional responses to fire (Zhang et al., 2010).

Microbes, for example, provide essential ecosystem services such as decomposition and carbon (C) cycling, nutrient cycling, controls on greenhouse gas fluxes, soil structure and maintenance, and biological population control (Graham et al., 2016; Ogliazzi et al., 2016; Paul, 2014). These diverse, abundant, and adaptable organisms are likely to be integral drivers of resilience and recovery in fire-affected ecosystems, especially as natural and human-induced changes to disturbance regimes continue. The responses of bacteria, fungi, and microbial processes in relation to heating temperatures do little to provide a consistent and, therefore, useful threshold temperature and duration for wildland fire management planning and predictions (Figs. 1–3). An adequate understanding of microorganism responses to soil heating is essential for appropriate prediction of fire effects.

Roots and root associations also provide essential functions in forest soils (e.g. below-ground C storage, nutrient cycling, soil structure, etc.) and have been correlated with overstory mortality or growth reduction after wildfires and prescribed fires (O’Brien et al., 2010; Varner et al., 2007). Although the connection between post-fire overstory tree vigor and fine roots is often cited, we were only able to locate two studies that directly related root vitality of forest conifers to measured soil temperatures and durations (Ursic, 1961; Zeleznik and Dickmann, 2004). Only one of these studies (Zeleznik and Dickmann, 2004) employed an in-situ approach that incorporated rhizosphere processes and interactions. In this study, complete mortality was not reached for all temperature treatments above the threshold temperatures, which varied with duration of heating and time of observation after heat treatment (Zeleznik and Dickmann, 2004). In the same study, compared to an in-situ experimental prescribed fire where soil surface temperatures were above 60 °C for ~15 min, fine root production and mortality were not affected (Zeleznik and Dickmann, 2004). Although our review only encompasses plant roots, which do not represent all plant tissues, the empirical data do not support the assumption of ubiquitous plant tissue death occurring at 60 °C for one minute. Mortality of plant roots was shown to occur both above and below this threshold (Fig. 1) and some species showed a positive response after heating (Fig. 3, Table A1). This topic clearly deserves further experimentation with a focus on in-situ study designs that incorporate critical rhizosphere interactions. Due to the small pool of studies available, we do not recommend extrapolation of these temperature and duration thresholds beyond their experimental parameters (e.g. tested temperature and duration, species, season, etc.).
This review elucidates a nuanced relationship between heating and biota with complexities that are not adequately addressed in the current body of knowledge. Although we sought to identify thresholds via a comparison of all qualifying studies, variability factored more heavily than emergent measures of central tendency, which should caution their application. If, for example, these findings were applied to predict the soil biota effect of an experimental fire that induced soil heating temperatures over 60 °C for 27 min on average (±75 min) (e.g. Varner et al., 2009), one might expect 100% mortality of plant roots, soil bacteria, fungi may double or undergo 100% mortality, microbial biomass C may decrease by 50–100%, shrub and conifer roots would be expected to undergo 20–100% mortality, and soil respiration rates may double or completely cease. Collectively, soil biological responses to heating, as reported by studies that directly measure these responses, do not provide consistent results for strict ecological predictions of fire effects using a single temperature and duration threshold. However, temperature-duration patterns across organisms that measured 100% mortality (Fig. 1) allow us to infer that the mortality of soil biota is likely to occur at lower temperatures when duration of heating is longer, and conversely, mortality is likely to occur at higher temperatures when duration of heating is minimal.

6. Conclusions

Soil heating evokes complex responses from plant roots and microbial communities, which suggests that a single biological threshold is an inappropriate measure of soil heating effects. Yet this over-simplified concept has been widely adopted for assessments of prescribed and wildfire effects. Soil heating affects soil biota directly, as a product of temperature and duration of heating, but also indirectly in
conjunction with physiochemical properties (e.g. soil moisture, soil type, spatial extent and scale) and biological attributes of specific soil organisms and communities (e.g. abundance, community interactions, mobility, acclimation). Interactions and processes ongoing in the soil environment are also likely to affect biotic survival, which were not measured by the majority of the reviewed studies. We, therefore, suggest that researchers and managers avoid using a biological threshold metric until sufficient evidence supports the existence of central tendencies in the data. Instead, simple measures of soil biota that combine soil processes and the attributes of the biotic community (abundance and structure) will provide more useful and appropriate guidance that is specific to each ecosystem. Furthermore, obtaining soil heating data is only one step towards linking biological responses to fire effects. Researcher and managers have not yet devised an adequate methodology or metric to represent the additive effects of soil heating over time. Soil heating, parallel to consecutive doses of drugs, should represent cumulative and additive effects (Smith et al., 2016), as well as the potential influence of soil heating in selecting for fire adapted species. These findings should encourage interdisciplinary research efforts that explicitly pair soil biotic changes and soil heating temperatures in order to better understand the integrated above- and belowground responses to wildland fire.

Fig. 3. Percent difference relative to controls (ΔR₁, ΔR₁₋₁₉, and ΔR₁₋₁₉₀) in mesofauna (a, N = 54), plant roots (b, N = 75), bacteria (c, N = 59), fungi (d, N = 85), microbial biomass (e, N = 19), and respiration (f, N = 25) responses over a temperature and duration gradient. A small amount of noise was added to both axes in order to aid in visualization of all points (a: 0.1, b: 5.0, c: 3.0, d: 3.0, e: 0.1, f: 0.1). The dotted lines denote the common threshold metric of 60 °C and one-minute duration.
7. Competing interests

The authors declare no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2018.10.032.

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