

Short communication

Short communication: Surface charring from prescribed burning has minimal effects on soil bacterial community composition two weeks post-fire in jack pine barrens

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ABSTRACT

Prescribed fire – the intentional use of fire to help achieve a land management goal – is becoming increasingly common as a land management practice. Soil physical, chemical, and biological properties can be affected by prescribed fires, but depend on the fire, soil type, residence time and frequency, and may not be changed substantially in low-severity burns. Here, we examined soil bacterial community composition immediately post-fire (15 days) in a sandy jack pine barrens soil in Wisconsin, USA. Soil bacterial communities clustered significantly by sample site ($p < 0.001$) and by soil horizon ($p = 0.048$), but not by whether or not soil samples were visibly burned. There were also no significant differences in total relative abundance at the phylum level in visibly burned vs. not visibly burned soils, and only two significant differences in abundance or variability of individual taxa. Soil properties remained unchanged post-fire and the fire was visibly patchy, suggesting that the low severity prescribed fire most likely had a minimal soil heating effect. Therefore, we suggest the minimal bacterial community composition shifts seen in this study were likely mediated more by plants than by direct heat-killing or changes to soil properties.

1. Introduction

Soil microbial activity drives nutrient cycling processes such as decomposition and mineralization of essential plant nutrients; hence, microbes are essential for maintaining productivity of the soil and its vegetation cover. The microbes that control these critical functions may be affected by fire (1) directly by killing them, (2) indirectly by its effect on soil properties, and (3) indirectly through changes to plant communities (Neary et al., 1999). The relative importance of these processes will depend on the fire, the ecosystem, and time since fire.

First, heat penetration into the soil can affect microbial organisms below the surface (Station, 2008), and varies with depth, where the top horizon will be more affected than the lower horizons (Certini, 2005; González-Pérez et al., 2004; Hart et al., 2005). Some bacteria are adapted to a wide range of temperatures; many species can survive temperatures in the range of 50–400 °C for 2 to 30 min durations (Neary et al., 2008; Switzer et al., 2012; Pingree and Kobziar, 2019). In prescribed fires in Wisconsin in the year 2017, and in habitats similar to the one in this study, the mean temperature was 221 °C (± 115 °C) and the maximum recorded temperature was 597 °C obtained from heat probes placed horizontally 1 cm below the soil surface (Holoubek, N.S.

(personal communication (2017))). The average residence time (number of seconds temperature was > 60 °C) was 166 s (2.77 min), with a maximum residence time of 1019 s (16.98 min) and a minimum residence time of 1 s (Holoubek, N.S. (personal communication (2017))). Hence, with temperatures reached in these prescribed fires, many microorganisms could be killed, but this effect may be limited to the soil surface (Certini, 2005). Second, the effects of fire on soil chemical and physical properties are well-documented (Certini, 2005), and can include altered pH and nutrient levels, and increased hydrophobicity. These changes could promote a different bacterial community composition post-fire (Alcañiz et al., 2018). However, as noted for temperature, these effects are generally reduced in low severity prescribed burns (Neary et al., 1999). Third, plants and microbial communities are highly interdependent; thus, microbes are likely to also be affected by post-fire vegetation community trajectories (Knicker, 2007).

Soil biological properties have been reported to change after fires, including increased or decreased microbial biomass, changes in microbial activities, or microbial community shifts (Catalanotti et al., 2017; Mikita-Barbato et al., 2015; Prendergast-Miller et al., 2017). In a meta-analysis by Holden and Treseder (2013), it was reported that prescribed fire significantly reduced microbial biomass, with response

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ratio (burned/not burned) of 0.67 for soil bacteria across 13 studies employing a range of methods. Microbial community composition also often changes post-fire (Lladó et al., 2018), in some cases likely due to increasing pH of the soils post-fire (Switzer et al., 2012). However, many authors do not report any changes in microbial community composition after a prescribed fire. The low severity of the prescribed fire is often noted as the main reason for the lack of changes of a magnitude that are significantly detectable, within the given experimental design (Alcañiz et al., 2018; Certini, 2005; Fultz et al., 2016; Williams et al., 2012). However, the degree of soil heating is dependent on the fire behavior, and the surface fire behavior may not be directly associated to soil heating. Soil heating is driven by fuel consumption, which in turn, is governed by the fuel load, structure, and availability (Hartford and Frandsen, 1992).

How microbial communities respond to low severity prescribed fires at the surface organic horizon and in the mineral soil is still open to question in pine barrens, an ecosystem frequently affected by fire (Miesel et al., 2012; Myer, 2017). The average stand replacing fire occurs between 8 and 41 years, while surface fires have been noted to occur yearly (Dickmann and Cleland, 2002). Here, we studied the effects of prescribed fire on soil bacteria 15 days after a prescribed fire in a Wisconsin pine barrens, a threatened habitat that supports the world's largest population of the endangered Karner blue butterfly (*Lyciaeides melissa samuelis*) (Myer, 2017). Because of the characteristics of similar prescribed fires as described above, we expected that spatial heterogeneity and differences between the organic (O) and top mineral (A) horizons would be significant factors predicting community composition, while only a small number of taxa would be significant responders to fire.

2. Methods

2.1. Field site, prescribed burn, and soil collection and analysis

The field site and prescribed burn are described in detail in our companion paper, Kranz and Whitman (2019) (greenhouse studies to investigate the effects of fire on jack pine seedling establishment). Coon Fork Barrens is a State Natural Area in Eau Claire County, in west-central Wisconsin, USA, with open jack pine (*Pinus banksiana* (Lamb.)) barrens. Prescribed fire is used as a management tool to help maintain the historical jack pine barrens, and prescribed fires have been used in the area since 2008. The burn unit investigated was 14 ha, and the prescribed fire was conducted on November 7th, 2016. We took advantage of the patchiness of the burn to control for the possible effects of time and location, by choosing pairs of visibly charred and visibly not charred sites. By “patchiness of the burn”, we mean that the mosaic of burning left portions of the plot uncharred, while charring other areas of the plot varying at the sub-meter scale. We also emphasize that our paired samples were visibly charred or not visibly charred; there could have still been some horizontal heat transfer even to the not visibly charred plots. “Visibly charred” samples were clearly blackened at the time of sampling, but we did not perform quantitative assessments of burn severity. We sampled soils for bacterial community composition two weeks after the prescribed burn, choosing this length of time in order to capture the short-term effects of the burn (e.g., to possibly detect reduced abundances of microbes that might have been killed during the fire and allowing enough time for microbes stimulated by the post-burn conditions to increase in abundance). This duration also included one precipitation event (9 mm). We recognize that various other effects of fire (e.g., shifts in vegetation) could take substantially longer to affect microbial community composition (Hart et al., 2005). Six pairs of soil cores were taken in areas that were visibly charred and paired adjacent areas (< 10 cm apart) that were visibly not charred. Soil cores were made from steel piping and measured 5 cm in height and 1 cm inside diameter (Wheatland Tube, Sharon, PA). Cores were placed into Whirl-Pak bags and transported back to the lab on dry ice.

Soils were collected for standard analyses from the same areas as the microbial samples 1 h before and 2 h after the burn (collection and analysis details in Kranz and Whitman (2019) and Supplementary Table 1).

2.2. Bacterial community composition

All twelve cores were divided into O and A horizons, for a total of 24 samples, from which DNA was extracted using a Qiagen (Germantown, MD) DNeasy PowerLyzer Microbial DNA Isolation Kit, following manufacturer's instructions. Samples were amplified in triplicate with bar-coded 515f and 806r primers targeting the V4 region of the 16S rRNA gene (Kozich et al., 2013; Walters et al., 2015). These primers capture archaea as well as bacteria, so archaea are included in our analyses, but because they represent such a small portion of the community, we focus on the bacteria in our discussions throughout. A SeqalPrep Normalization Plate Kit (ThermoFisher Scientific, Waltham, MA) was used to purify and normalize PCR amplicons following manufacturer's instructions. A Wizard SV Gel and PCR Clean-Up System A9282 (Promega, Madison, WI) was used to extract and purify the combined PCR products. The pooled library was submitted to the UW Madison Biotechnology Center (UW-Madison, Madison, WI) for 2 × 250 paired end Illumina MiSeq sequencing. Samples were sequenced on two different runs, with treatments evenly distributed between sequencing runs. See Supplementary Methods for details.

2.3. Data analysis

16S rRNA gene sequences were analyzed using a Jupyter Notebook (Perez and Granger, 2007) using QIIME2 (Bolyen et al., 2018) and dada2 (Callahan et al., 2016) with default settings. Taxonomy was assigned using the SILVA SSU rRNA gene database (SSU Ref NR 99119; Quast et al., 2013). Vegan (Oksanen et al., 2018), phyloseq (McMurdie and Holmes, 2013), and corncob (Martin, 2019) packages were used in R (R Core Team, 2018) for community analysis. We tested for effects of factors (plot, fire, and soil horizon) on community composition using a non-parametric multivariate ANOVA (NPMANOVA) (Oksanen et al., 2018). We tested for differential abundance and differential variability of individual OTUs in visibly burned vs. visibly not burned soils, controlling for sequencing run and soil horizon with a false discovery rate cutoff of 0.05 (Martin, 2019). See Supplementary Methods for more details.

3. Results

3.1. Microbial community composition at visibly burned and not visibly burned sites

Bacterial community composition was structured by plot (NPMANOVA on Bray-Curtis dissimilarities, $p < 0.001$, pseudo F-ratio_{5,16} = 2.604) and by horizon (NPMANOVA on Bray-Curtis dissimilarities, $p = 0.048$, pseudo F-ratio_{1,16} = 1.622), but not by whether or not the sample was visibly burned (NPMANOVA on Bray-Curtis dissimilarities, $p = 0.120$, pseudo F-ratio_{1,16} = 1.335) (Fig. 1).

3.2. Identification of fire-responsive bacteria

Bacterial communities in visibly charred and not visibly charred soils (O and A-horizon) were dominated by members of the Actinobacteria, Proteobacteria, Acidobacteria, Planctomycetes, and Verrucomicrobia phyla, but the relative abundances were not significantly different in visibly charred vs. not visibly charred O and A horizons for any phylum ($p > 0.05$; Fig. 2). We also asked whether any specific OTUs were enriched or depleted, or differentially variable in visibly charred soils. We controlled for multiple comparisons, identifying OTUs whose relative abundance increased or decreased

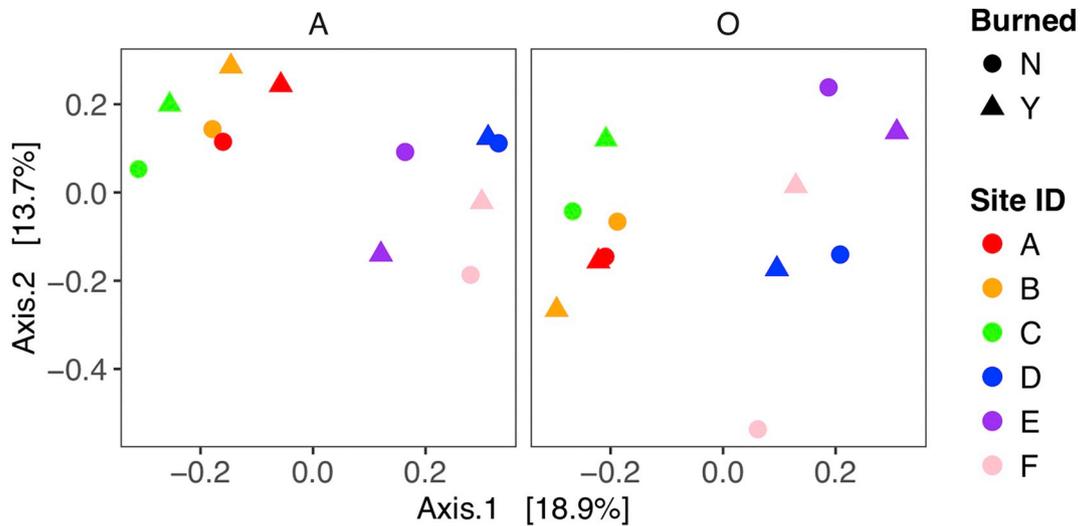


Fig. 1. Principle coordinate analysis (PCoA) of Bray-Curtis distances between bacterial communities (16S). Each point represents an individual sample collected from the field site, colored by paired plot, and separated by A (left panel) and O (right panel) horizon. Triangles represent visibly burned samples and circles represent visibly not burned samples. The first and second principle coordinates account for 18.9% and 13.7% of the total variation, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

significantly in the visibly charred soil as compared to the not visibly charred soil, and controlled for sequencing run and horizon (we will refer to these OTUs as ‘responders’). Using this approach, we found only one OTU that had a significant, negative, response to the prescribed fire (out of 6350 total OTUs). This organism best matched the *Mycobacterium* genus in the SILVA database, but its closest BLAST matches in the NCBI database is *Mycolicibacterium* (100% ID - EU919229.2) (Lee et al., 2010), recently proposed as a new genus previously classified within *Mycobacterium* (Gupta et al., 2018). We found one OTU that was significantly differentially variable in visibly burned soils, that best matched the candidate genus *Xiphenematobacter* in the SILVA database. However, it is only an 88% ID match to the cultured *Xiphenematobacter* isolates, and matches other possible *Verrucomicrobia* taxa at similar % ID.

4. Discussion

4.1. Site heterogeneity plays a larger role in structuring soil bacterial community composition than surface charring of prescribed fire over the short term

Because the prescribed fire was a disturbance to the ecosystem, and the study site is relatively level, uniform in soil color, and has no obvious trends in plant vigor across the landscape, we were somewhat surprised that spatial heterogeneity was the most important factor for structuring microbial communities ($p < 0.001$). This supports the observation that site-level variation is one of the major characteristics that determines the biological properties of fire-affected soils, in addition to the fire itself, fuel load, and soil moisture (Alcañiz et al., 2018; Certini,

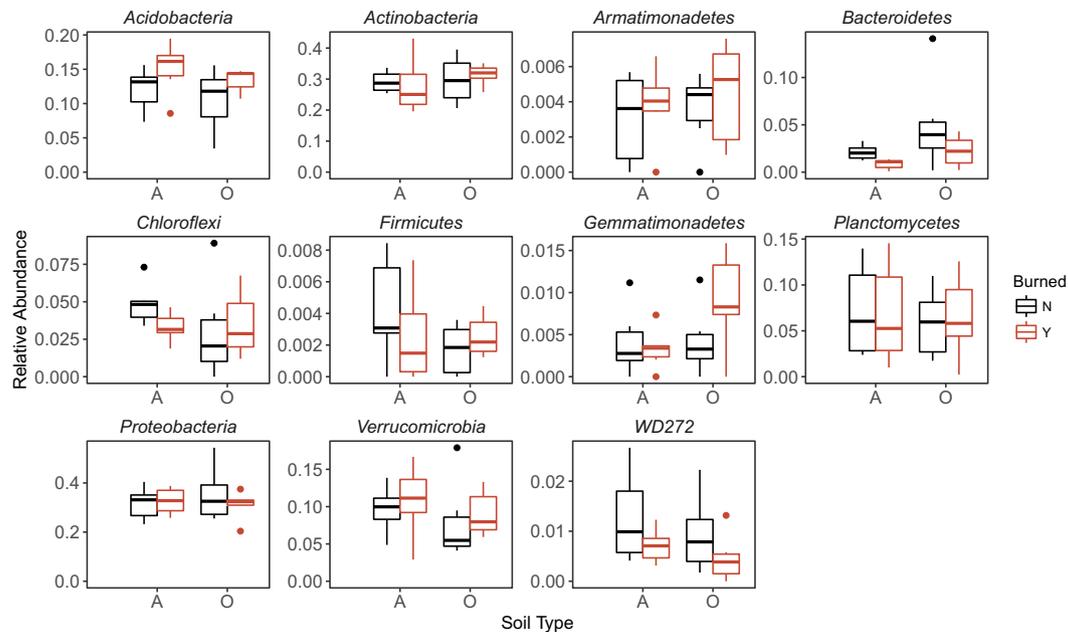


Fig. 2. Relative abundance of top ten most abundant bacterial phyla for A-horizon (A) and O-horizon (O) soil from burned (N, black) and not burned (Y, red) cores. No differences between groups within a phylum are statistically significant ($p > 0.05$, ANOVA). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2005), and indicates that site-level heterogeneity can eclipse fire effects in low-severity prescribed burns. The study site was an open jack pine barrens (described in detail in Kranz and Whitman (2019)), dotted with jack pines, so the samples' differential proximity to specific plants could also be contributing to the strong effect of location on microbial community composition. Larger trees are often the driving force in creating spatial variability in soil through cycling of nutrients, microclimates, and the rhizosphere zone (Alcañiz et al., 2018). Specifically, aboveground forest characteristics post-fire, such as tree scoring, have been noted as a major driver of soil microclimates and soil carbon cycling. Samples taken closer to these points could easily have different community compositions than those adjacent to other plants (Kobziar, 2007).

The soil properties on which microbes depend to thrive and which structure microbial community composition, such as pH or nutrient availability, can vary at fine spatial scales in the field (Baldrian, 2000; Lladó et al., 2018). Previous studies have observed that within-site sample variance commonly attributed to random error is often spatially dependent at smaller scales, due to factors such as micro-topography (Hook et al., 1991; Lechowicz and Bell, 1991; Robertson et al., 1993; Robertson et al., 1999; Webster, 1985;). For example, Liu et al. (2018) investigated soil nutrient shifts post-fire in grasslands based on micro-topography. While the authors found that fire significantly increased SOC, total N, NH_4^+ , and P, they also observed that micro-topography affected the soil nutrient distributions, with higher nutrient contents in lower sloping areas (Liu et al., 2018). When interpreting microbial community shifts post-fire, micro-topography is a factor that should be considered, particularly in cases where burn severity is low.

4.2. Bacterial community compositions in visibly charred vs. visibly not charred patches were not significantly different two weeks after prescribed fire

As prescribed fires become a more common land management tool, efforts to understand the impact of these disturbances on soil microbial dynamics are needed. Prescribed fires are often low severity fires, and can have different effects on soil ecosystems from wildfires (Alcañiz et al., 2018; Certini, 2005; Grady and Hart, 2006; Neary et al., 1999). In our study, the location of the soil sample within the landscape (plot ID) was the strongest predictor of differences in bacterial community composition, likely due to vegetation cover, microclimate, and micro-topography (Alcañiz et al., 2018; Certini, 2005; Sun et al., 2016). However, despite specifically selecting paired visibly charred vs. visibly not charred sites, the prescribed fire in this study had no significant effect on overall bacterial community composition two weeks post-fire (Fig. 1). This was consistent with our hypothesis: prescribed fires are generally low severity fires, and several other studies of prescribed burns have detected no or little significantly measurable change in community composition (Alcañiz et al., 2018; Blankenship and Arthur, 1999; Fultz et al., 2016; Williams et al., 2012). Further reflecting this low severity, there were no significant differences between most pre-burn (1 h before the fire) and post-burn (2 h after the fire) soil properties (Supplementary Table 1), which suggests that the (limited) soil bacterial response to low severity fires such as these may be primarily mediated by plants, rather than due to direct death from the heat or changes to soil properties (Hart et al., 2005).

The findings from several studies suggest that the fire return interval may play an important role in determining bacterial community composition (Mikita-Barbato et al., 2015; Neary et al., 2008; Pellegrini et al., 2017; Williams et al., 2012). Thus, although we did not find significant differences at the whole-community level in this study, different fire regimes or return intervals might have different results. Additionally, prescribed fires are generally designed for plant community and fuel loading management (Keeley, 2009). It is possible that the effects of prescribed fire that are mediated through changes to plant communities (e.g., changes in the quantity, quality, and competition for

nutrients, or changes in mutualisms) may be as or more important than the short-term effects of fires on microbes (e.g., direct fire-induced mortality or changes to soil chemical properties) (Hart et al., 2005). The review by Dooley and Treseder (2012) reports that prescribed fires led to non-significant changes in microbial biomass when compared to wildfires. The authors speculate this is because wildfires are often more severe than prescribed fires. Lower severity fires elicit less of a bacterial response because the burn (lower temperatures and/or lower residence time) consumes less aboveground biomass and SOM. Overall, our results suggest this prescribed fire had minor effects on the whole community within the first 2 weeks post-fire, with changes limited to a small number of taxa. However, because we analyzed DNA, rather than RNA, proteins, or functional parameters such as N mineralization or respiration, there could have been changes in microbial activity that we did not detect, even though the overall community composition did not seem to change at the DNA level.

Even when we looked at the level of single OTUs, there were very few significant effects of fire. The OTU that was less abundant in visibly charred samples is from the proposed genus *Mycolicibacterium*, which is thought to contain mostly environmental saprotrophs that are generally non-pathogenic (Gupta et al., 2018). However, we do not know substantially more about this organism beyond that that would allow us to speculate on why it may have decreased in relative abundance after a fire. Similarly, the differentially variable OTU does not match any well-characterized organisms. Future investigations might work to strengthen our understanding of the bacterial fire-response framework (Hart et al., 2005), including direct death from fire exposure, response to fire-induced changes to the soil environment, and response to fire-induced changes to the plant environment. This last factor may be the most important driver of any post-fire changes to microbial community composition in low severity prescribed fires such as the one studied here, and this effect may take longer than two weeks post-fire for effects to emerge.

Declaration of Competing Interest

We have no conflict of interest to declare.

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Appendix A. Supplementary data

Supplementary information is available for this paper. Sequencing data are available at the NCBI SRA database, under accession numbers PRJNA556207. Code and data associated with this paper are available at https://github.com/WhitmanLab/Jack_Pine/. Supplementary data to this article can be found online at <https://doi.org/10.1016/j.apsoil.2019.07.004>.

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