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Long-term soil fungal community recovery after fire is impacted by climate change

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ABSTRACT.—Though much is known about fungal importance to forest health, there is very little information abou factors that impact recovery times of soil fungal communities after a fire. Soil samples were taken from burn sites one ecotype of temperate coniferous forest in Utah over a 20-year chronosequence. Sites were selected from ava historic burns and were similar in plant community structure, elevation, slope, and aspect. Fungal DNA from these ples was compared to soil from paired unburned sites nearby to measure community similarity and estimate soil f recovery rates. Differences between paired burned and unburned sites remained fairly stable over a decadal time overall, but fungal community structure was found to recover more quickly in areas with a higher average annual perature. A significant positive correlation in community recovery was seen in areas with a difference of as little a per year. The only other environmental variable that significantly interacted with time since burn was annual mea cipitation. As global temperatures increase, alpine fires are increasing as well, but these results suggest that fung munity recovery time will be shortened under new climate scenarios.

RESUMEN.—A pesar de que se conoce mucho acerca de la importancia de los hongos para la salud de los bosque existe escasa información sobre los factores que influyen en el tiempo de recuperación de la comunidad fún suelo después de un incendio. Se tomaron muestras de suelo de lugares quemados dentro de un ecotipo de bosqu plado de coníferas en Utah a lo largo de una cronosecuencia de 20 años. Los lugares se seleccionaron de entre las mas históricas disponibles y que fueron similares en cuanto a su aspecto, estructura de la comunidad vegetal, ele y pendiente. El ADN fúngico de estas muestras se comparó con el del suelo de lugares cercanos no quemados co objetivo de medir la similitud de la comunidad y estimar las tasas de recuperación de los hongos en el suelo. En g las diferencias entre los sitios comparados quemados y no quemados se mantuvieron estables a lo largo de una e tiempo decenal. No obstante, se encontró que la estructura de la comunidad fúngica se recuperó más rápidament áreas con temperatura media anual más alta. Se observó una correlación positiva significativa en la recuperación comunidad en áreas con una diferencia de tan sólo dos grados Celsius por año. La otra variable ambiental que int significativamente con el tiempo transcurrido desde la quema fue la precipitación media anual. A medida que aun las temperaturas globales, también aumentan los incendios alpinos. Sin embargo, los resultados de este estudio s que el tiempo de recuperación de la comunidad fúngica se acortará bajo los nuevos escenarios climáticos.

The effect of fires on belowground microbial communities has received increased attention in the past decade due to the importance of microbes to overall ecosystem recovery. Soil microbes interact with plants during disturbance recovery to shape resource availability, community assembly, and successional trajectories (Knelman et al. 2015, Weidner et al. 2015, Sikes et al. 2016). Ecosystem recovery from fire disturbance is thus dependent on microbes that facilitate plant succession either directly via obligate symbioses (Dickie et al. 2017) or indirectly via processes such as resource liberation and soil stabilization (Claridge et al. 2009, Fuentes-Ramirez et al. 2018, Bonner et al. 2019). For the purposes of this project, we define “recovery” as resemblance to a nearby unburned plot. It is assumed that no fungal community can be fully “recovered” given that communities are always changing. Unburned fungal communities are also under constant flux, but as burned communities begin to more closely resemble adjoining unburned sites, we treat this as “recovery” in the sense that fire effects are beginning to give way to other site-level forces such as edaphic properties and plant community influences.

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Currently, the reported effects of fire on belowground microbial communities have few consistencies other than a general agreement that full recovery to prefire conditions takes place on a decadal timescale (Treseder et al. 2004, Holden et al. 2013, Köster et al. 2014). Reported differences between studies include varied recovery times for bacteria and fungi (Bárcenas-Moreno and Bååth 2009, Bárcenas-Moreno et al. 2011) and divergent effects of fire on microbial diversity and abundance in differing biomes (Allison et al. 2010, Dove and Hart 2017, Hansen et al. 2019). Most studies have focused on time since fire as the main effect in their particular ecosystems, and the contrasting details about microbial recovery could be specific to the climatic and edaphic properties of the biomes in which they were observed.

Warmer and drier conditions in many ecosystems due to climate change are increasing the frequency and impact, and decreasing the predictability, of wildfires (Flannigan et al. 2009, Abatzoglou and Williams 2016). Thus, it is important to continue building knowledge of how soil microbes respond to fires. Furthermore, it is important to understand not only how future climate scenarios alter fire regimes, but whether they will alter the recovery responses of microbial communities in those systems.

Here, we conducted an observational study along a 20-year fire chronosequence, comparing paired burned and unburned sites along an annual mean temperature gradient in the Wasatch and Uinta montane ecoregion dominated by pinyon pine (*Pinus edulis*) and juniper (*Juniperus osteosperma*) forests in Utah, USA. This ecosystem is expected to continue warming at a faster rate than most other biomes, with a 20-year projected climate that includes an annual mean temperature of 2 °C above baseline according to the IPCC AR5 regional synthesis report (Barros et al. 2014). The study design allowed us to test the hypothesis that a warmer climate could alter belowground microbial recovery rates after fires within a single biome.

METHODS

Overview

A range of historic fire events was used to select 11 forested regions of Utah that had burned between 1 and 20 years prior to our study. Each burned site was paired with an adjacent unburned site to serve as controls, giving us a total of 22 sites. Sites were selected to maximize similarity across a range of environmental variables. At each site, we collected burned and unburned soil from the organic horizon of 3 locations, measured canopy and ground cover vegetation, and collected vegetation samples for identification and herbarium curation. We used meta-amplicon sequencing to characterize fungal community structure from each soil sample.

Site Selection

The Utah Department of Natural Resources sourced Utah fire data for the previous 20 years. Three hundred GPS points 100 m inside of the burn boundaries were used to compile national GIS layers including topography, land use and cover, human impacts, and climate data. Habitats were dominated by pinyon pine and juniper, with common understory plant communities dominated by Asteraceae and Poaceae. Sites were spread across Utah from 38.5 to 41.6 degrees latitude and ranged in elevation between 1483 m and 2960 m, with a median elevation of 1660 m (Fig. 1). The annual mean temperature at sites ranged from −7.9 °C to −3.4 °C with a median of −5.0 °C. Soil types were predominantly a mixture of Nielsen, Sterling, and Sneed series.

Using these and other site characteristics (see Supplementary Material 1 [Table SM1]), we built a pairwise distance matrix for every possible combination of variables and selected a subset of the 300 sites that had minimal land variation but still maintained substantial ranges in burn chronology and annual mean temperature (see Supplementary Material 1 [Fig. SM1]). Effort was made to reduce site variability, especially in plant community structure, and this took precedence over chronosequence sampling density. All raw site data and full code for selecting study sites can be found in Supplementary Material 1.

Field Collection

Photography, site marking, and sample collection protocols were designed before fieldwork began. Three soil samples were collected with sterile utensils from each site at a depth of 5 to 10 cm, 0.5 m from the site center

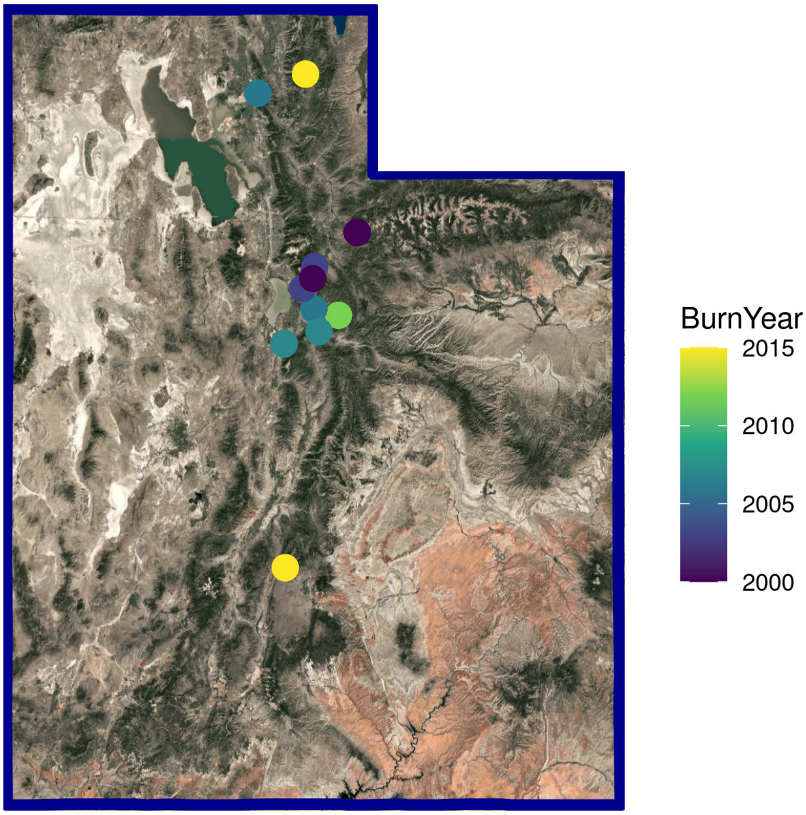

Fig. 1. Map of Utah showing fire sites considered in this study. Point color reflects the year that each site was bu

in the north, east, and west cardinal directions. Soils were frozen at −80 °C within 6 h of collection. Local plant cover was recorded and photographed, and representative plant samples were collected for later identification. International Field Collection Forms were filed for each plant collection, and all specimens are housed in the Utah Valley University Herbarium (UVSC).

DNA Extraction and Library Preparation

Genomic DNA from 0.25 g of soil was extracted from each sample using DNeasy PowerSoil Kits (QIAGEN, Venlo, The Netherlands). Fungal DNA was amplified with the ITS1F (CTTGGTCATTTAGAGGAAGTAA; Gardes and Bruns 1993) and ITS2 (GCTGCGTTCTTCATCGATGC; White et al. 1990) primers modified with the addition of Illumina adaptors (Caporaso et al. 2011) using the following protocol: 98 °C 2 min; 22 cycles of 98 °C 15 s, 52 °C 30 s, 72 °C 30 s; 72 °C 2 min). After 22 cycles, the PCR product was diluted 1:12 and 1 μL of this was used as a template for 8 more rounds of PCR with a 60 °C annealing temperature in which bidirectional barcodes bound to reverse-complemented Illumina adaptors acted as primers. Resulting barcoded libraries were cleaned, normalized, and sequenced with the Illumina MiSeq platform (V3 chemistry, 2 × 300 bp).

Bioinformatics

Reads were demultiplexed and barcode sequences were removed by the sequencing center. Quality filtration and bioinformatics were performed in R. Briefly, we extracted the ITS1 region, filtered forward reads based on quality, utilized a clustering-free divisive amplicon denoising algorithm (DADA) to infer amplicon sequence variants (ASVs) (Callahan et al. 2016), removed chimeras and potential contaminants, and assigned taxonomy against a custom ITS1 database.

The ITS1 region of the rDNA was extracted from all raw reads using ITSxpress

(Rivers et al. 2018). Quality control on ITSxpress output consisted of removing reads with ambiguous base calls and those with a maxEE of >2, and truncating each read when quality scores dropped below 20. Due to lower quality, and to reduce false-positive detection, reverse reads were not used (Pauvert et al. 2019). Filtered forward reads were subjected to de novo chimera detection and removal in DADA2, and potential contaminants were inferred from extraction negatives and removed from all samples using the prevalence method in the decontam package (Davis et al. 2018). Cleaned and filtered ASVs were assigned taxonomy with the RDP Classifier algorithm against a custom database consisting of the UNITE database (v. 1.12.2017) and a custom set of outgroups including ITS1 sequences from metazoans and Viridiplantae taken from NCBI. The outgroups added to UNITE can be found in Supplementary Material 1. Any sequences matching nonfungal taxa were removed. The remaining ASVs that were unambiguously assigned to fungi were used in all downstream analyses within the '*phyloseq*' R package (McMurdie and Holmes 2013). All sequences have been deposited in the NCBI Sequence Read Archive under the accession PRJNA550446.

Statistical Analyses

All analyses were performed in R (Version 3.4.4). A PERMANOVA model of community composition as an interactive function of Burn Year, Fire Treatment, and Location was fit using the *adonis* function of the '*vegan*' package (Okansen et al. 2016). A Bray–Curtis community distance matrix was generated with the *vegdist* function of the '*vegan*' package. The community distance between paired burned and unburned sites at the same location was regressed against time since burn and decadal annual mean temperature in a linear mixed-effect model using the '*lme4*' package (Bates et al. 2015), with paired community distance as a response and annual mean temperature (random effect) and years since burn (fixed effect) as predictors. *P* values were obtained using the '*lmerTest*' package (Kuznetsova et al. 2017). Differential abundance of taxa between burn treatments was analyzed using a beta-binomial model with the '*corncob*' R package (Martin et al. 2020).

RESULTS

No fungal community of any burned site we observed had fully rebounded to the alpha diversity or community structure of its unburned counterpart within the 20-year time frame that was studied. All samples were dominated by Ascomycota and Basidiomycota, regardless of whether they were burned or not, but the relative dominance of these 2 main phyla decreased in older sites. In burned sites 14 years or older, Ascomycota and Basidiomycota still dominated in terms of relative abundance, but other phyla such as Mucoromycota and Olpidiomycota were also more common (Fig. 2, Supplementary Material 1 [Fig. SM4]). Relative abundance of taxonomic groups did not correlate significantly with annual mean temperature, elevation, latitude, or soil type.

Alpha diversity was not significantly different overall between aggregated burned and unburned sites (Fig. 3), and there was no consistent pattern between burn status and Shannon diversity in between-site pairs. Beta diversity was significantly affected by burn status ($P = 0.041$), time since burn ($P = 0.001$), and annual mean temperature ($P = 0.001$) in an interactive PERMANOVA model (Supplementary Material 1 [Table SM1]). Further, there was a significant interaction term of time since burn and annual mean temperature ($P = 0.002$). Together, these model terms explained 16% of the variance in beta diversity, with the trend that older sites and burned subplots exhibited more dispersed communities than sites with more recent burns.

Mean community distance between paired burned and unburned sites showed a small but significant decrease over time since burn, congruent with previous research showing the decadal scale of recovery for fungi after fires. However, in this study, we also found that annual mean temperature was an important predictor of the rate of recovery (Fig. 4; linear mixed effects regression: $P < 0.0005$), and each temperature increase of 1 °C accounted for an additional 5% community similarity along our full chronoseries (Supplementary Material 1 [Table SM3]).

When location-specific plant community data were added to linear mixed-effect models, no significant correlation between plant cover or plant community and paired fungal

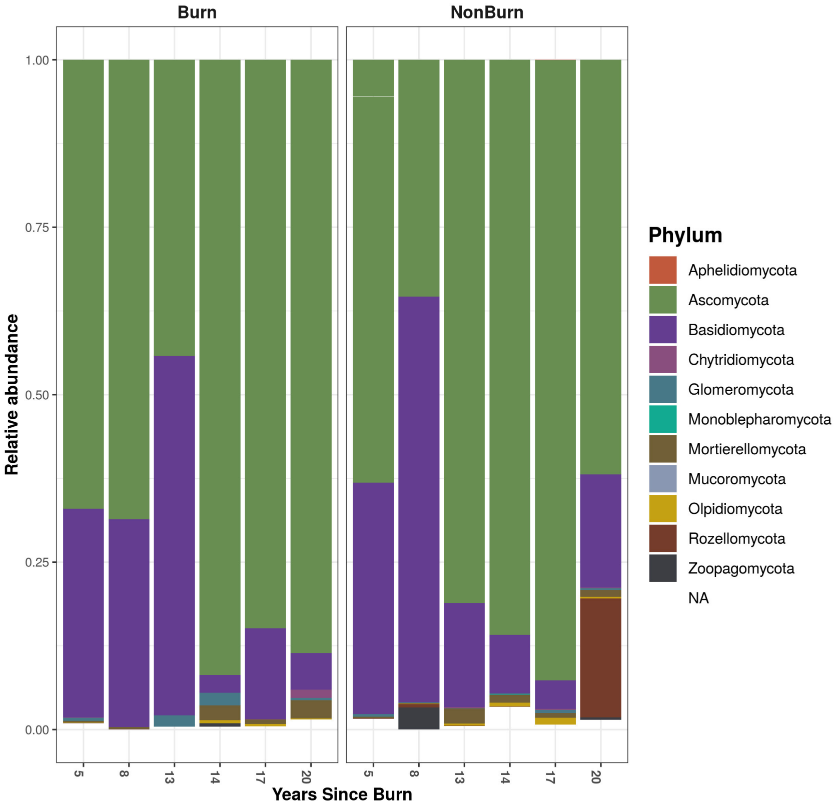

Fig. 2. Relative abundance of fungal phyla detected at each paired study location. Left panel shows the burned and right panel shows the unburned site for each pair. The *x*-axis reflects years since burn for the paired sites. Wh more than one location was represented by a given time point, the mean relative abundance was used.

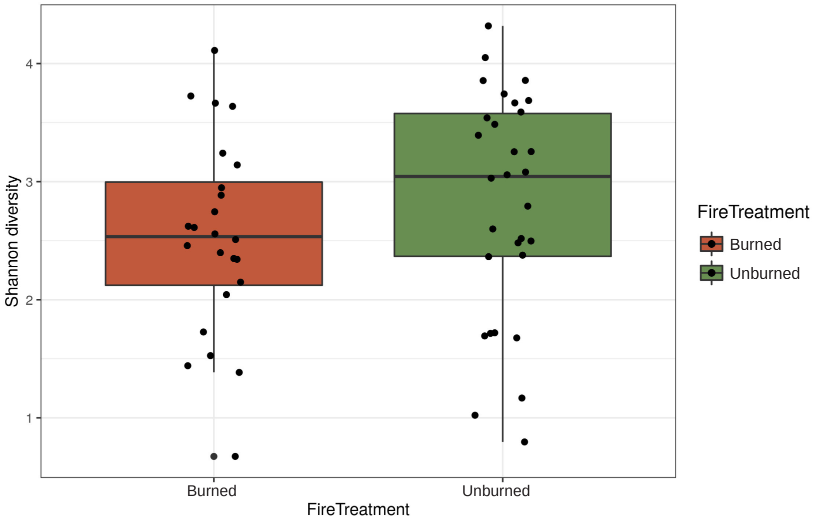

Fig. 3. Overall Shannon diversity values for all burned and unburned sites considered in this study.

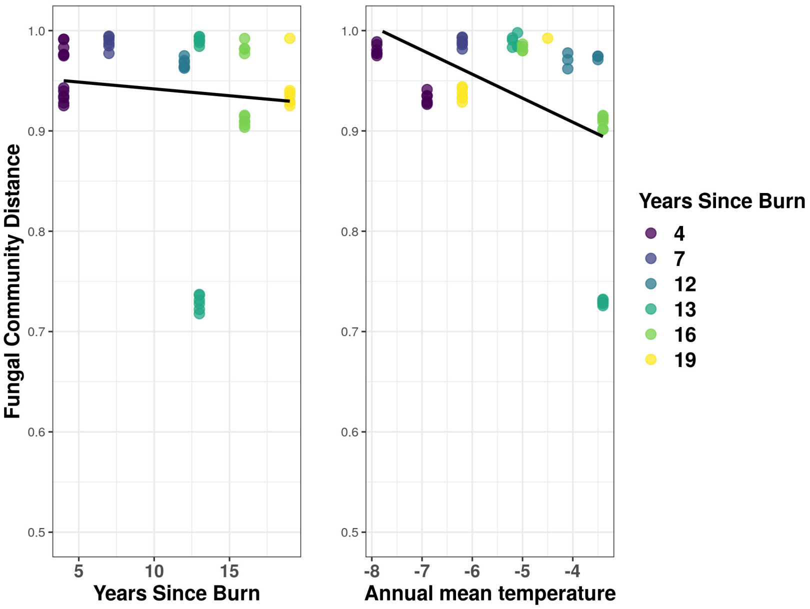

Fig. 4. Fungal community distance between the burned and unburned sites at each study location. Colors
years since burn. Left panel shows community distance as a function of years since burn. Right panel shows the sa
data as a function of mean annual temperature. Regression lines were calculated as ordinary least squares linear

community distance was found. Additionally, a Mantel test between plant and fungal community distances showed no significant correlation. These results likely stem from the high similarity in plant communities at each location.

Differential abundance analyses yielded 4 fungal families that were significantly enriched in either burned or unburned locations across all sites (Supplementary Material 1 [Fig. SM2]). The basidiomycetes Serendipitaceae and Thelophoraceae had greater abundance and variability in unburned sites, and the ascomycetes in Microascaceae and an unclassified family-level taxon in Dothidiales had greater abundance and variability in burned sites.

The broad diversity patterns we observed generally reflect those seen in related research. For example, our forest soils were dominated by the phyla Ascomycota and Basidiomycota, but this dominance was reduced over time since burn as other phyla such as Mucoromycota, Rozellomycota, and Olpidiomycota became detectably more abundant roughly 14 years after fire. However, where other work in boreal forests found that Basidiomycota was initially reduced after fire and recovered over time (Sun et al. 2015), our results from this montane biome show Ascomycota following that pattern instead.

DISCUSSION

Though most studies on fungal recovery after fires have taken place in a single biome and focused on chronology as the main predictor, Dove and Hart (2017) showed via meta-analysis that the magnitude of at least the initial fungal community responses to fire can vary based on fire frequency and biome type. These are important observations because they suggest hypotheses to help explain observed discrepancies in fungal recovery trajectories between studies.

Here, we tested whether large-scale climatic factors could also help explain variance within a single biome. Comparing nearby pairs of burned and unburned sites along a forest fire chronosequence showed that climatic conditions can have a role in soil fungal community recovery trajectories. In particular, our observation that annual mean temperature of a site has a small but significant effect on recovery speed is a possible example of how local environmental variation can help explain discrepancies in fungal recovery times after fires.

Temperature directly affects microbial activity but can also influence microbial community composition, competition, and secondary metabolite production (Bárcenas-Moreno and Bååth 2009, Yogabaanu et al. 2017). Warming temperatures also affect plant succession trajectories (Prach et al. 2007), and plant succession is an important covariate for understanding fungal succession (Rudgers et al. 2007, Davey et al. 2015, Zhang et al. 2018). Taken together, the linkages between plant and fungal succession dynamics and temperature are difficult to uncouple. By limiting our study to a single biome and to sites with very similar plant communities, we were able to isolate, to some degree, the effect of temperature on fungal recovery from fire. Other factors besides plant community have been directly linked to fungal community dynamics, however. For instance, it has been shown that soil pH and nutrient content are strong drivers of fungal community structure (Glassman et al. 2017). Since fire can have a strong impact on soil properties such as pH, C:N ratio, and soil organic carbon (SOC) content (Boerner et al. 2009), it is possible that these edaphic characters varied between burned and unburned paired sites, though these variables were not measured in this study. Additionally, one of the site pairs in this study, burned 13 years prior to observation, had highly similar fungal communities (Fig. 3). Removing this site did not affect the significance of mean annual temperature in our model but did reduce the effect size. It seems clear that local stochastic processes in community assembly can reduce our ability to detect broader patterns.

In this montane biome, with mean annual temperatures below freezing, liquid water can be a limiting resource for plant and fungal growth (Monson et al. 2002, 2006). An increase in mean annual temperature at these sites likely means more days when fungi can be metabolically active. Our results support this assumption, in that warmer temperatures led to quicker recovery times.

Due to ongoing recent climate change, any chronosequence studies must inevitably deal with the potential covariance of time since burn and mean annual temperature. There was some correlation between these 2 variables in the present study, with older sites tending toward lower mean annual temperatures, which could be an effect of climate change (Supplementary Material 1 [Fig. SM2]). We were unable, however, to acquire site-specific environmental variables from 20 years prior to test this, due to lower resolution of observations from that time period.

Additionally, climate warming is inextricably linked to other variables that have been shown to affect fire severity and fire frequency such as reduced soil moisture and increased fuel load (Harvey 2016). These factors could also be important drivers of fungal recovery trajectories. These legacy factors were not considered in the present study since none of our selected sites had burned in the previous 75 years and all sites were from very similar biomes. Legacy sites may be important to consider in work of this nature.

Our results indicate that even within a single biome, slight alterations to climatic variables like mean annual temperature can affect the rate of fungal recovery from fires. This has implications for broader disturbance modeling efforts. For example, the reduction and rebounding of soil fungal communities is important for dynamic vegetation models, but many disturbance models use predictors that are simulated in isolation, neglecting any potential interaction effects (Seidl et al. 2017). As climate warms and fires in these biomes increase in intensity and frequency, the loss of fungal diversity and ecosystem services could be, to some small degree, mitigated by increased recovery rates due to warming in these often-frozen montane soils.

Supplementary Material

One online-only supplementary file accompanies this article (https://scholarsarchive.byu.edu/wnan/vol82/iss3/3).

Supplementary Material 1. Various data plots and statistical analyses (6 figures, 2 tables).

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