RESPONSES OF SOIL MICROINVERTEBRATES AND THEIR ECOLOGICAL FUNCTIONS TO FOREST THINNING AND PRESCRIBED FIRE IN VALLES CALDERA NATIONAL PRESERVE, NEW MEXICO

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ABSTRACT

RESPONSES OF SOIL MICROINVERTEBRATES AND THEIR ECOLOGICAL FUNCTIONS TO FOREST THINNING AND PRESCRIBED FIRE IN VALLES CALDERA NATIONAL PRESERVE, NEW MEXICO

KARA SKYE GIBSON

Most multicellular animals in forests are nematodes, collembolans, and mites living within the soil and litter. Their abundance is staggering: millions of nematodes, and tens to hundreds of thousands of mites and collembolans, usually reside within a square meter of the forest floor. These animals consume a wide range of resources, including fungi, bacteria, plants, and other soil animals. Through their feeding activities, and via their dispersal of microbes, they are important contributors to nutrient cycling, decomposition, and other ecological processes affecting plant performance. However, these key components of soil food webs have been largely neglected in forest restoration research. This dissertation focuses on responses of nematodes, collembolans, and mites to forest restoration activities in New Mexico's Valles Caldera National Preserve. The first study examines how total abundance of these groups varies in untreated, thinned only, and thinned/burned ponderosa pine forest management units. We report that mites appear to be more sensitive to combined thinning and fire than nematodes or collembolans, and identify easily and inexpensively measured habitat and resource indicators which may aid land managers in assessing treatment implications for soil fauna. In the second study, we subjected volcanic loamy soils in a xeric mixed conifer forest to one, three, or nine passes from a feller buncher (a common type of tree harvester) to assess how disturbance from heavy logging machinery affects soil physical properties and nematode communities, with the

aim of determining thresholds for negative impacts. We found that substantial compaction occurred after a single pass, affecting soil to a depth of at least 23-27 cm. Nematode communities, however, appeared relatively resistant to disturbance: impacts on sensitive nematode taxa were apparent only after nine passes. Finally, in the third study, a field mesocosm experiment, we investigated the functional implications of faunal community shifts that occur with forest restoration treatments. Our manipulation of soil mesofauna communities indicated that mesofauna can influence decomposition indirectly by affecting the functional composition of fungal communities, but that this phenomenon may be dependent on ecological context. Together, these studies assist in evaluating how restoration treatments affect the structure and functions of soil food webs.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

PREFACE

Chapters II-IV of this dissertation were written to appear as articles in peer-reviewed journals. As such, some redundancy is unavoidable. Chapter II is formatted for, and was published in, the journal *Trees, Forests, and People* in January of 2022 with coauthors Nancy Collins Johnson, Channing Laturno, Robert Parmenter, and Anita Antoninka. Chapter III has been formatted for submission to the journal *Forest Ecology and Management*, and Chapter IV has been prepared for submission to *Ecological Monographs*.

CHAPTER I: INTRODUCTION

Animals in the phylum Nematoda (commonly referred to as roundworms or nematodes) and the arthropod subclasses Acari (mites) and Collembola (springtails or collembolans) are the most abundant metazoans in terrestrial ecosystems and have shaped soil processes for more than 400 million years (Dunlop and Garwood, 2018; Poinar, 2011). Their evolutionary histories are intricately entwined with those of plants and unicellular microorganisms. The first forests were rooted in soils already teeming with these microinvertebrates, which variously consumed plant tissue (living or dead), bacteria, fungi, other minute animals, or some combination of these resources (Schaefer and Caruso, 2019). Symbiotic associations between plants and ectomycorrhizal fungi, requisite for the nutrition of most tree species in modern temperate and boreal forests, arose in the context of grazing pressure from fungivorous fauna. As they do today, detritivorous mites and collembolans would have contributed to early nutrient economies by comminuting (or fragmenting) organic material, increasing the surface area available to microbial decomposers; meanwhile, microbivores in all three faunal groups would have mineralized nitrogen and phosphorous bound in fungal and bacterial biomass, enhancing the availability of these nutrients to plants. We can be certain that early nematodes, mites, and collembolans also dispersed otherwise immobile microbes throughout the soil matrix, regulated microbial communities, and opened niches for predatory macrofauna.

Modern soil food webs remain dominated by these microinvertebrate groups, which continue to provide key services. Because they are integral to the structure and function of terrestrial ecosystems, understanding how they are affected by forest management practices is important. This dissertation examines impacts of common forest restoration treatments on soil

fauna within Valles Caldera National Preserve, which protects a 21 km wide caldera formed following a volcanic eruption ~1.25 million years ago. The ponderosa pine, xeric mixed conifer, and mesic mixed conifer forests in this preserve face challenges emblematic of threats to forests across the Southwest United States. Overgrazing, logging, and fire suppression have dramatically altered their stand structure, disrupted natural fire regimes, and promoted the accumulation of heavy fuels, leaving these forests extremely vulnerable to high severity fire as the climate warms and dries (Allen et al., 2002). Within the past 15 years, more than half of the 90,000 acre preserve burned in two catastrophic fires, the Las Conchas Fire in 2011 and the Thompson Ridge Fire in 2013 (Valles Caldera Trust, 2014). Treatment of surviving forests with thinning and prescribed burning to recreate historic stand structure, reduce the risk of high severity fire, enhance biodiversity, and improve ecosystem functions (Covington et al., 1997; Reynolds et al., 2013) has become an urgent priority for managers of the preserve, as it has for managers of public lands across the Southwest.

Implementation of these restoration treatments provided us with the opportunity to study their effects on soil food webs, which are poorly characterized to date. In our first study, we take a broad view, examining how mite, collembolan, and nematode abundances vary across untreated, thinned, and thinned/burned ponderosa pine forest management units. We then turn to a xeric mixed conifer forest, where we investigate how traffic from heavy logging machinery affects the physical structure of soils and the nematode communities within them. Finally, we examine how forest restoration affects the functions provided by mites and collembolans in a field mesocosm experiment at the aforementioned ponderosa pine site.

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CHAPTER II: ABUNDANCE OF MITES, BUT NOT OF COLLEMBOLANS OR NEMATODES, IS REDUCED BY RESTORATION OF A PINUS PONDEROSA FOREST WITH THINNING AND PRESCRIBED FIRE

Abstract

Thinning, mastication, and prescribed fire are restoration treatments frequently employed in unnaturally dense second-growth *Pinus ponderosa* forests of the Western United States. Although a goal of these treatments is to restore ecosystem structure and function, little information is available regarding treatment effects on soil micro- and mesofauna, which comprise the overwhelming majority of metazoan forest inhabitants and occupy key positions in soil food webs. We quantified nematodes, mites, and collembolans in soil and litter habitats within untreated control, thinned (comprising thinning and masticating wood), and burned (comprising thinning and masticating, followed by broadcast burn) *P. ponderosa* forest management units at Valles Caldera National Preserve in New Mexico, USA. We linked patterns in animal abundance to resource and habitat characteristics, hypothesizing that resources and available habitat for many taxa would increase with thinning and decrease with burning. Two years after thinning, densities of collembolans and nematodes in the thinned unit were higher than in the untreated control unit, but one year post-fire, their densities in the burned unit were similar to those of the untreated control unit. Mite abundance, however, was not elevated in the thinned unit and was lower in the burned unit. Although faunal communities were highly heterogeneous, a significant proportion of the variance in faunal abundances was explained by easily and inexpensively measured habitat and resource characteristics: bulk density, soil organic matter (SOM), pH, grass cover, and litter cover and depth. These findings demonstrate the

abiotic and biotic factors that structure faunal habitats so that forest managers have a more complete understanding of the impacts of forest restoration treatments.

2.1 Introduction

Restoring frequent-fire-adapted *Pinus ponderosa* (ponderosa pine) forests is a high priority for forest managers in the western United States. Overharvesting, overgrazing, and fire suppression following Euro-American settlement have created dense stands of slow-growing, small-diameter trees with heavy litter accumulation and reduced understory vegetation, which are increasingly vulnerable to high-severity fire as the climate warms and dries (Allen et al., 2002). Mechanized thinning and prescribed or managed burning are restoration techniques employed to recreate historic stand structure, reduce the risk of stand-replacing wildfire, promote biological diversity, and improve ecosystem functions eroded by disruption of historic disturbance regimes (Covington et al., 1997; Reynolds et al., 2013).

While considerable research has tracked responses of aboveground organisms to these treatments, those of belowground biota have received little attention. Impacts on soil and litter dwelling micro-and mesofauna, including nematodes, mites, and collembolans, remain particularly understudied in xeric, fire-adapted forests of the Western United States. (An exception is Camann et al. (2012, 2008) who have reported a reduction in mite abundances following prescribed burning of a *P. ponderosa/P. jeffreyi* forest in the Pacific Northwest, with signs of continuing decline in oribatid mites two years post-fire.) Furthermore, the effects of mastication (an increasingly common fuels treatment) on these numerically dominant metazoa have not been investigated. Because nematode and microarthropod detritivores, microbivores, root herbivores, and predators influence microbial communities (Crowther and A'Bear, 2012),

carbon and nutrient cycling (Gan and Wickings, 2020), and pathogen populations (Sabatini and Innocenti, 2001), understanding how they are affected by forest treatments is crucial for evaluating restoration practices.

Both mechanized thinning and reintroduction of long-absent fire are likely to result in some immediate mortality of soil micro- and mesofauna. Animals may be crushed by heavy logging equipment. Litter-dwelling fauna are the most likely to experience lethal temperatures during burning, while those below the soil surface may or may not succumb depending on fire behavior, soil depth and moisture, and small-scale fuels characteristics. Although heat transfer attenuates dramatically with depth, significant mortality of soil mites, collembolans, and nematodes may occur at temperatures well below the oft-cited "biological effects threshold" of 60°C (Malmström, 2008; Pingree and Kobziar, 2019), depending on heating duration, soil moisture, and an animal's cuticular structure. Given dramatic variation in soil micro- and mesofauna generation times (from days to years) and reproductive output (from single offspring to hundreds), post-treatment community changes due to mortality alone could potentially persist for years.

Changes to habitat quality and resource availability with restoration could also have profound effects on micro- and mesofauna assemblages. Because soil micro- and mesofauna are too small to physically shift soil particles, pore size and connectivity are critical parameters governing habitat availability (Erktan et al., 2020). Compaction from logging machinery and combustion of organic matter should each be expected to decrease accessible pore space for many soil animals. On the other hand, deposition of thinning residues (i.e., slash or masticated wood) ought to increase habitat for litter-dwelling fauna. This influx of organic matter, along with root necromass from cut trees, also provides a slow resource pulse for saprotrophic

organisms (particularly fungi) and their consumers—at least until these residues are burned. Precipitous declines in microbial biomass, and especially of fungi, are well-documented after fire (Pressler et al., 2019). Primary and secondary consumers in the soil food web are also likely to respond to post-treatment shifts in understory plant diversity and abundance, which govern long-term carbon and nutrient inputs to the soil food web and shape microbial communities (Hättenschwiler et al., 2005). Finally, any changes in soil moisture due to altered canopy cover, ground cover, or water holding capacity should be of great consequence to soil fauna in xeric forests, and particularly to nematodes, which are aquatic organisms that depend on water films for movement.

We examined responses of soil mites, collembolans, and nematodes to thinning with mastication alone or with prescribed fire in a *P. ponderosa* forest within Valles Caldera National Preserve, New Mexico. Ponderosa pine forests in the region historically experienced low-severity surface fires with decadal to subdecadal return intervals (Touchan et al., 1994; Dewar et al. 2021). The native Jemez Pueblo people heavily influenced fire regimes from the pre-colonial era until the late 1600s, increasing ignitions and reducing fuel connectivity (Swetnam et al., 2016). Relative to the period following Jemez Pueblo population collapse, fires were more frequent but smaller in spatial extent, and were effectively decoupled from interannual climate variation (Roos et al., 2021). Depopulation resulted in more widespread, less frequent, more intense (although still low-severity) fires driven primarily by climate variability (Swetnam et al., 2016). This period of "free range" fires persisted until the late 1800s (Dewar et al. 2021), when intensive livestock grazing by Euro-American colonists eliminated fine fuels and inaugurated the current era of fire suppression (ibid.). Recruitment after clear-cut logging in the 1930s (Anschuetz and Merlan, 2007), and a federal policy of fire suppression, produced the thickets of

stunted trees that are now common in ponderosa pine forests across much of the American Southwest.

Our study took place within three adjacent management units at different treatment stages. Our objective was to link patterns in post-treatment abundance of these three faunal groups with relevant habitat and resource characteristics. We hypothesized that resources and available habitat for soil micro- and mesofauna increase following thinning and mastication and decrease with subsequent prescribed fire. We thus posited that nematodes and microarthropods would be more abundant (relative to an untreated control unit) within a thinned and masticated treatment unit due to an increase in masticated wood, soil organic matter, and herbaceous plants, and less abundant within an adjacent unit that had been thinned, masticated, and broadcast burned as a function of reduced litter cover and soil organic matter.

2.2 Methods

2.2.1 Study site and sample collection

Responses of nematodes and microarthropods to forest fuels treatments were assessed in three adjacent ponderosa pine-dominated management units (zones for planning and implementation of forest management and restoration treatments) at Valles Caldera National Preserve, New Mexico (**Fig. 2.1 A**). The study area was located on Banco Bonito, a rhyolite lava flow from ~68,000 years ago (Goff, 2009). Even aged stands are approximately 70-80 years old and most trees are ~20-40 cm in diameter at breast height (Parmenter, unpublished data). Annual precipitation averaged 590 mm from 1981–2010, and the mean annual temperature for this period was 6.6 °C, with monthly mean temperatures ranging from -2.3 °C in January to 17 °C in July (PRISM, 2021). Soils in the study area are rhyolite-derived sandy loams to loamy sands

belonging to the Totavi-Jemez-Rock Outcrop association (Hacker and Banet, 1987). Two management units—hereafter the "burned" (82 ha) and "thinned" (120 ha) units—were treated in 2012 and 2014, respectively, with mechanical thinning (and removal of harvested wood) followed by mastication of unmarketable timber and slash. These treatments resulted in an average tree density of 60 trees ha^{-1}. The burned unit received a low-intensity broadcast burn in October of 2015 after thinning as described above. An adjacent portion of an untreated control unit (encompassing approximately 90 ha) served as a control retaining ~300 trees ha^{-1}.

In late August and early September of 2016, we selected eight areas within each unit with approximately matching slope and aspect, then randomly selected origin points (by blindly throwing a pin flag backward) for arrays of four quadrats as depicted in **Fig. 2.1B** and **1C**. In order to assess ground cover changes with restoration treatments, we measured ground cover and litter depth at each quadrat. A 0.5 m x 0.5 m gridded frame was used to estimate percentage cover by grasses, forbs, litter, mosses, lichens, scat, rock, wood, mushrooms, bare ground, and tree seedlings or exposed roots. Litter depth was measured as near as possible to the center of the quadrat. Overall slope and aspect were also recorded for each quadrat.

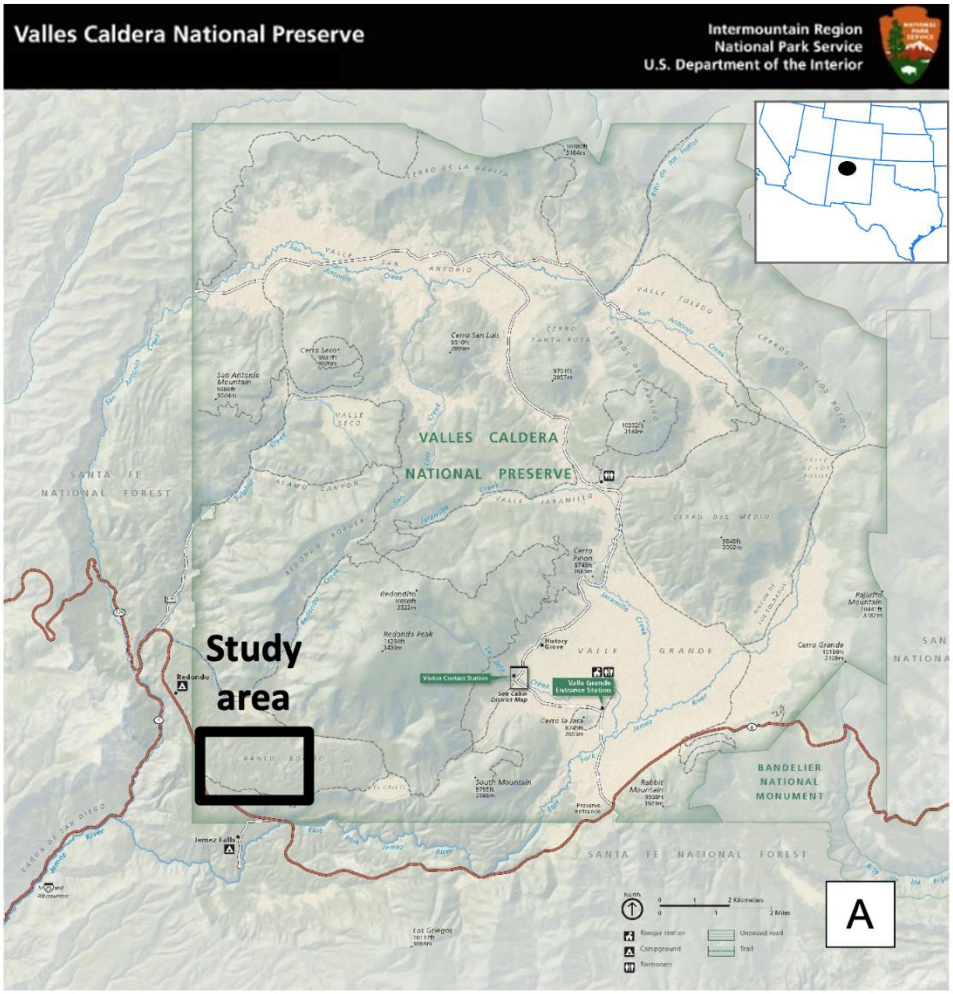

Fig. 2.1 (**A**) Location of study area within Valles Caldera National Preserve and the US state of New Mexico.

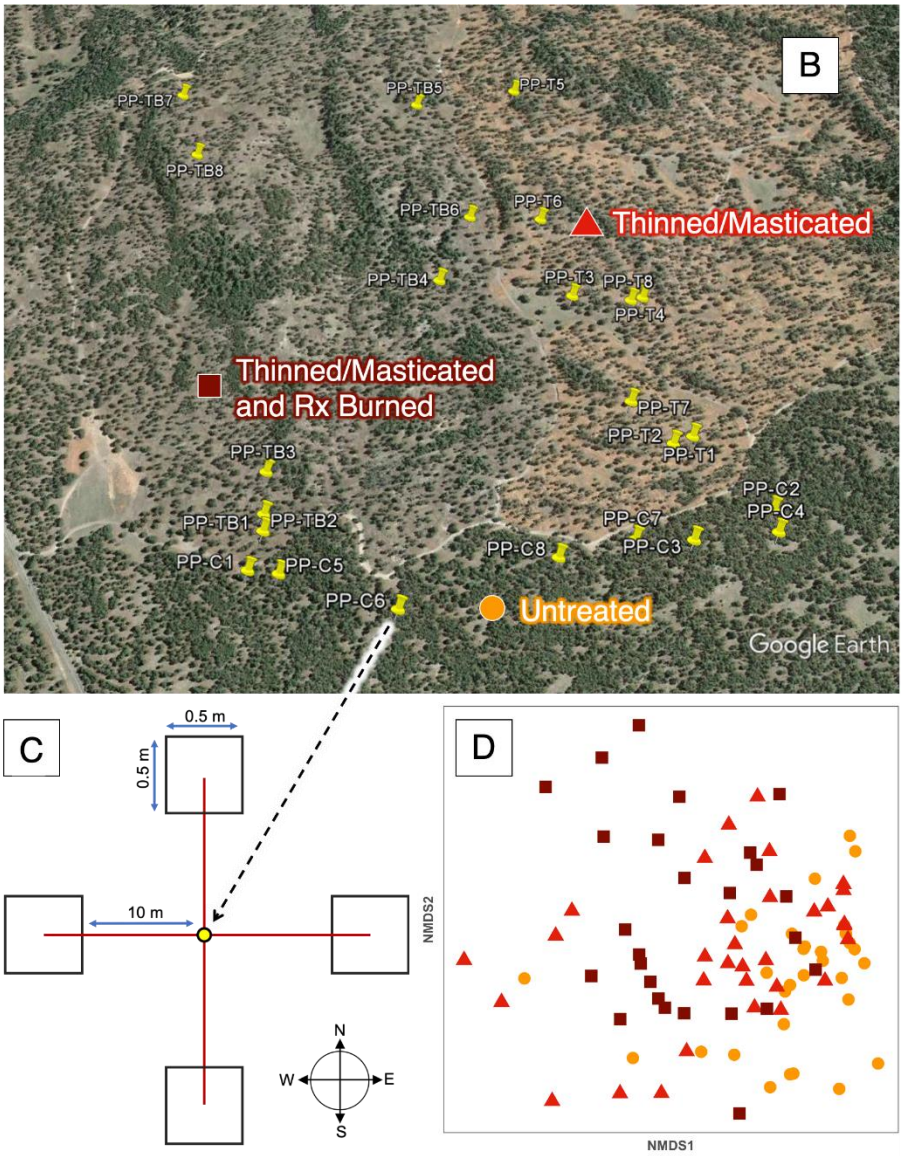

Fig. 2.1. (**B**) Sampling locations in thinned, burned, and untreated management units within the study area at Banco Bonito, Valles Caldera National Preserve, New Mexico, USA. Each yellow pin represents the origin point of a quadrat array as shown in (**C**) Ground cover and litter depth were measured at each quadrat, and soil and litter cores were collected from one randomly selected quadrat per array. (**D**) Non-metric multidimensional scaling ordination of ground cover in quadrats. Maroon squares represent quadrats in the thinned/masticated and burned management unit; red triangles represent quadrats in the thinned/masticated management unit; and orange circles represent quadrats in the untreated management unit.

One of the four quadrats in each array was randomly selected for collection of soil cores. Three 5.08 cm diameter soil cores were collected from the uppermost 10 cm of mineral soil and the O_a layer, if present. One core each was reserved for extraction of nematodes, microarthropods, and for abiotic analyses requiring dried soil, respectively. We used a 10.16 cm diameter circular corer to collect a litter sample (if litter cover was present) for extraction of microarthropods before sampling the underlying soil for these organisms. An additional smaller soil core (2.5 cm diameter, to a depth of 9.5 cm) was collected from each randomly selected quadrat for quantification of hyphal lengths. Microarthropod soil samples were transported intact in the PVC core samplers to reduce animal mortality. The other core samplers were rinsed with water and then cleaned with 90% isopropyl alcohol. Soil cores to be dried for abiotic analyses were stored in open air while in the field, then were dried at 47 °C upon return to Northern Arizona University. Nematode and microarthropod soil and litter cores were stored in coolers on ice, and soil samples for hyphae extraction were frozen on dry ice until arrival at NAU. Nematode and microarthropod core samples were then refrigerated at 4 °C until animals were extracted. Samples for hyphae extraction were stored at -20 °C.

2.2.2 Soil biota extraction

Microarthropods were extracted from soil and litter within two weeks of collection using high-gradient Tullgren funnels (similar to Crossley and Blair, 1991). Soil or litter samples were spread on cheesecloth within funnels which emptied into scintillation vials holding tap water. Insulated chambers housing the collection vials were cooled with ice bottles to maintain a strong temperature gradient as light was gradually intensified over 4 days, followed by a 2-day period of maximum illumination by 15W bulbs. Two microarthropod soil and litter samples—one from

the untreated control unit and one from the burned treatment unit—were excluded due to sample damage; final sample sizes for analyses of microarthropod responses were thus *n*=7 for the untreated control unit, *n*=8 for the thinned unit, and *n*=7 for the burned unit. Collected microarthropods were preserved in approximately 70% ethanol and refrigerated. Extracted animals were counted using a dissecting microscope at 20–63x magnification and sorted to mites, collembolans and other fauna (e.g., ants, macroarthropod larvae, and enchytraeids). We counted a total of 6,995 soil mite individuals, 1,468 soil collembolans, 35 other soil fauna, 9,139 litter mites, 1,463 litter collembolans, and 268 other litter fauna.

Nematodes were initially extracted from 30 g of soil using modified Baermann trays ("nematode rafts": Gibson, 2016), without a decanting and sieving pre-extraction step, and preserved in DESS solution (Yoder et al., 2006). To enable calculation of nematode densities per g dry soil, gravimetric soil moisture of the nematode core was determined from a separate 5 g subsample dried at 105°C. When samples were examined the following year, however, nematode abundances were improbably low (compared to abundances determined from preliminary sampling). Nematodes were thus re-extracted from archived refrigerated samples in random order by autumn of 2017 using decanting, sieving, and sucrose centrifugation (Ferris, 2012). Approximately 100 cc of soil (unless less than this amount remained from the previous extraction) was used for each extraction, and soil moisture was quantified again as described above. Two damaged samples were excluded from each of the thinned and burned treatments. Final sample sizes for analyses of nematode responses to restoration treatments were consequently *n*=8 for the untreated control management unit, *n*=6 for the thinned management unit, and *n*=6 for the burned management unit. Nematodes were enumerated using a dissecting microscope at 20x–63x magnification. A total of 4,690 nematodes were counted in samples

extracted by the sucrose centrifugation method (data presented in the main text), and 2,037 nematodes in samples extracted by the Baermann tray method (presented in **Fig. S2.1**.) Despite the likelihood that nematode densities were reduced by extended storage, we feel that the nematode abundance data obtained using the more efficient method are better suited to assessing differences across management treatments, therefore these data are presented in the main text.

Fungal hyphae were extracted from 4 g of soil according to Abbott et al. (1984) and classified as fine (<5 μm) and coarse (>5 μm) arbuscular mycorrhizal (AM) fungi, heavily melanized septate fungi, and other septate fungi using a compound microscope. Hyphae were examined under a compound microscope at 200x magnification and quantified using the gridline intersect method (Abbott et al., 1984).

2.2.3 Analysis of soil abiotic properties

Dried soil from the 203 cc abiotic core was sieved to 2 mm and the fine fractions were weighed to estimate bulk density. Most samples contained few particles > 2 mm. Dried soil was subsampled using a microsplitter to ensure representative fractions for analyses. Soil organic matter (SOM) was measured by loss on ignition after five hours at 550 °C (Heiri et al., 2001). Particle size distribution was analyzed at the Northern Arizona University Sedimentary Records of Environmental Change Laboratory with laser diffraction using a Beckman-Coulter LS-230 Particle Size Analyzer. We measured soil pH according to the method described in Grover et al. (2020). Available N and P were extracted using the methods of Keeney and Nelson (1982) and measured in the Colorado Plateau Analytical Laboratory. Nitrate and ammonium content was determined following Wendt (1999), and orthophosphate content was analyzed by the Olsen Method (Olsen et al., 1954).

2.2.4 Data analysis

All analyses were conducted in R (v.4.0.3; R Core Team, 2020). Where model assumptions of normality and homogeneity of variance could be met, we used ANOVA to detect treatment differences in soil abiotic properties and in densities of microarthropods, nematodes, and hyphae, and performed post-hoc comparisons with Tukey's honestly significant difference test ($\alpha \leq 0.1$ to account for heterogeneity and small sample size). Data were log transformed to meet assumptions of normality and homogeneity of variance. When assumptions for ANOVA could not be met, we used Kruskal-Wallis and performed post-hoc comparisons with pairwise Wilcoxon rank sum tests, using the Benjamini and Hochberg correction for multiple comparisons. *P*-values calculated with Wilcoxon rank sum tests are approximate where ties occurred.

Non-metric multidimensional scaling (NMDS) ordination was used to examine relationships among soil faunal assemblage composition (in terms of broad faunal groups), soil properties, hyphal densities, and ground cover (litter depth was omitted because of three missing values). The NMDS plots were based on total densities of nematodes, collembolans, mites, and other fauna (mainly ants, enchytraeids, and macroarthropod larvae) and were produced with the package "vegan" (Oksanen et al., 2020) using Bray-Curtis dissimilarity distance values. Habitat and resource variable vectors were overlaid using the function envfit. Figures were created using the package "ggplot2" (Wickham, 2011), with the exception of correlation matrices included in the supplementary information, which were constructed with the package "corrplot" (Wei and Simko, 2017).

We used multiple linear regression and an automated stepwise model selection procedure (based on ΔAIC_c <2.00) to explore the most important habitat and resource predictors for abundances of individual faunal groups in soil and (if applicable) litter habitats. We did not model abundance of animals in the "other fauna" category separately because these non-target arthropods were absent from most samples. Litter depth was excluded due to multiple missing observations, but values were imputed by using treatment averages for variables missing only one observation. After removing highly collinear predictor variables (R^2>0.6) and applying log transformations as needed to satisfy model assumptions of normality, linearity, and homogeneity of variance, we used the "step" function to search for the optimal model for each faunal group. We specified a lower scope limit of faunal group ~ 1 and an upper limit of faunal group ~ log.NO3 + log.PO4 + percent.Wood + percent.Litter + log.percent.Grasses + log.percent.Forbs + log.percent.Bare + log.SOM + BulkDensity + Clay + Fine.AM + Coarse.AM + Total.NonAM.

2.3 Results

2.3.1 Habitat and resource characteristics

Soil fauna resource and habitat characteristics within control, thinned, and burned management units are shown in **Table 2.1**. Soil organic matter in the thinned unit was 44.3% higher on average than in the control unit, and 58.6% higher than in the burned unit. The inverse trend was observed for bulk density, which was 34.5% higher on average within the burned unit than within the thinned unit, and intermediate within the control. Relative to the control unit, soils in the thinned unit were slightly more acidic and soils in the burned unit were marginally more alkaline. Phosphorus and nitrogen tended to be most available in the burned unit and lowest in the untreated control unit, but variance in PO_4, NH_4, and NO_3 was large, especially within the

burned unit (**Table 2.1**), and treatment differences were not statistically significant. Soil texture differences were detected with the control unit having higher fine soil fraction compared to the two treatment units. Of the fungal hyphae categories quantified, only abundance of coarse AM hyphae differed by treatment: it was 76% higher on average in the thinned unit than in the untreated control unit, and intermediate in the burned unit.

2.3.2 Meso- and microfauna abundance

The abundance of micro- and mesofaunal groups differed across restoration treatments. Lower densities of soil and litter mites were observed within the burned unit than within the thinned and control units, which had similar soil mite abundances (**Fig. 2.2**). Soil collembolans (**Fig. 2.2**) and nematodes (**Fig. 2.3**) showed similar patterns across treatment units, in that members of these three groups were most abundant in the thinned unit, while densities in control and burned units were similarly low. (Nematodes extracted immediately with the less-efficient Baermann tray method showed the same overall pattern as those extracted later with the more-efficient sucrose centrifugation method, although treatment differences for the Baermann tray data were not statistically significant (ANOVA: p=0.16; **Fig. S2.1**).) Litter collembolan abundances (**Fig. 2.2**) were quite variable, with few or no collembolans encountered in many of the litter samples, but collembolans tended to be more numerous in litter from the thinned unit. Most samples did not contain individuals in the "other soil fauna" and "other litter fauna" categories, and abundances of these groups did not differ across treatments (**Fig. S2.2**).

2.3.3 Habitat and resource predictors of soil faunal communities

Across faunal group subsets, grass and litter cover, bare ground, and nitrate consistently correlated with NMDS axis scores; ammonium was also strongly correlated in ordinations based on all fauna in all habitats, and on microarthropods alone, while fine sand and phosphate were correlated with soil fauna community NMDS axis scores (**Fig. 2.4**). Selected multiple regression models for nematodes and soil, litter, and total microarthropod densities are summarized in **Table 2.2**. In addition, nematodes were negatively correlated with pH (r^2=0.41, P<0.01 for the bivariate correlation), and litter mites were positively correlated with litter depth (r^2=0.40, P<0.01 for the bivariate correlation), two habitat variables that were excluded from the model selection procedure due to strong collinearity with SOM and missing values, respectively.

Table 2.1 Litter depth, soil abiotic properties, and lengths of arbuscular mycorrhizal (AM) and septate hyphae (m g^{-1}). Groups with different letters are significantly different at $P<0.1$ according to univariate ANOVA or Kruskal-Wallis (KW), after correction for multiple comparisons using Tukey's test of honestly significant differences for ANOVA or Benjamini Hochberg adjustment for KW.

	Test	*P*	*Control*			*Thinned*				*Burned*			
			n	Mean	SE		*n*	Mean	SE		*n*	Mean	SE	
Litter depth (cm)	KW	0.21	7	3.92	1.25	a	8	3.03	1.01	a	6	1.44	0.64	a
Bulk density (g/cm^3)	ANOVA	0.014	8	0.92	0.05	ab	8	0.77	0.04	b	7	1.02	0.07	a
pH	ANOVA	0.084	8	4.85	0.16	ab	8	4.56	0.22	b	8	5.25	0.23	a
% SOM	KW	0.047	8	6.00	0.77	ab	8	8.66	1.45	a	8	5.46	1.26	b
% C	KW	0.37	8	2.82	0.54	a	8	3.34	0.81	a	8	2.34	0.71	a
PO_4 μg/g	KW	0.26	7	3.44	0.69	a	8	3.73	0.75	a	8	6.43	1.57	a
NH_4 μg/g	KW	0.093	7	5.90	0.39	a	8	7.92	1.14	a	8	18.48	9.48	a
NO_3 μg/g	KW	0.37	7	0.21	0.02	a	8	0.33	0.10	a	8	0.59	0.21	a
% N	KW	0.37	8	0.12	0.02	a	8	0.13	0.02	a	8	0.11	0.04	a
% Clay	ANOVA	0.004	8	9.28	0.94	a	8	5.10	0.40	b	8	6.43	0.90	b
% Silt	ANOVA	0.008	8	43.71	4.18	a	8	25.78	2.24	b	8	32.06	4.31	b
% Very fine sand	ANOVA	0.006	8	19.60	1.39	a	8	12.50	0.89	b	8	16.08	1.71	ab
% Fine sand	ANOVA	0.070	8	14.32	2.02	b	8	20.17	1.56	a	8	19.33	1.86	ab
% Medium sand	ANOVA	0.008	8	7.67	2.28	b	8	18.91	1.61	a	8	13.92	2.78	ab
% Coarse sand	ANOVA	0.004	8	5.00	2.00	b	8	16.41	1.88	a	8	11.29	2.43	ab
Fine AM hyphae (m/g)	ANOVA	0.90	8	7.49	0.95	a	8	8.01	1.20	a	8	7.22	1.51	a
Coarse AM hyphae (m/g)	ANOVA	0.041	8	1.81	0.33	b	8	3.19	0.40	a	8	2.31	0.34	ab
Septate hyphae (m/g)	ANOVA	0.63	8	3.41	0.84	a	8	4.12	0.72	a	8	4.59	1.03	a

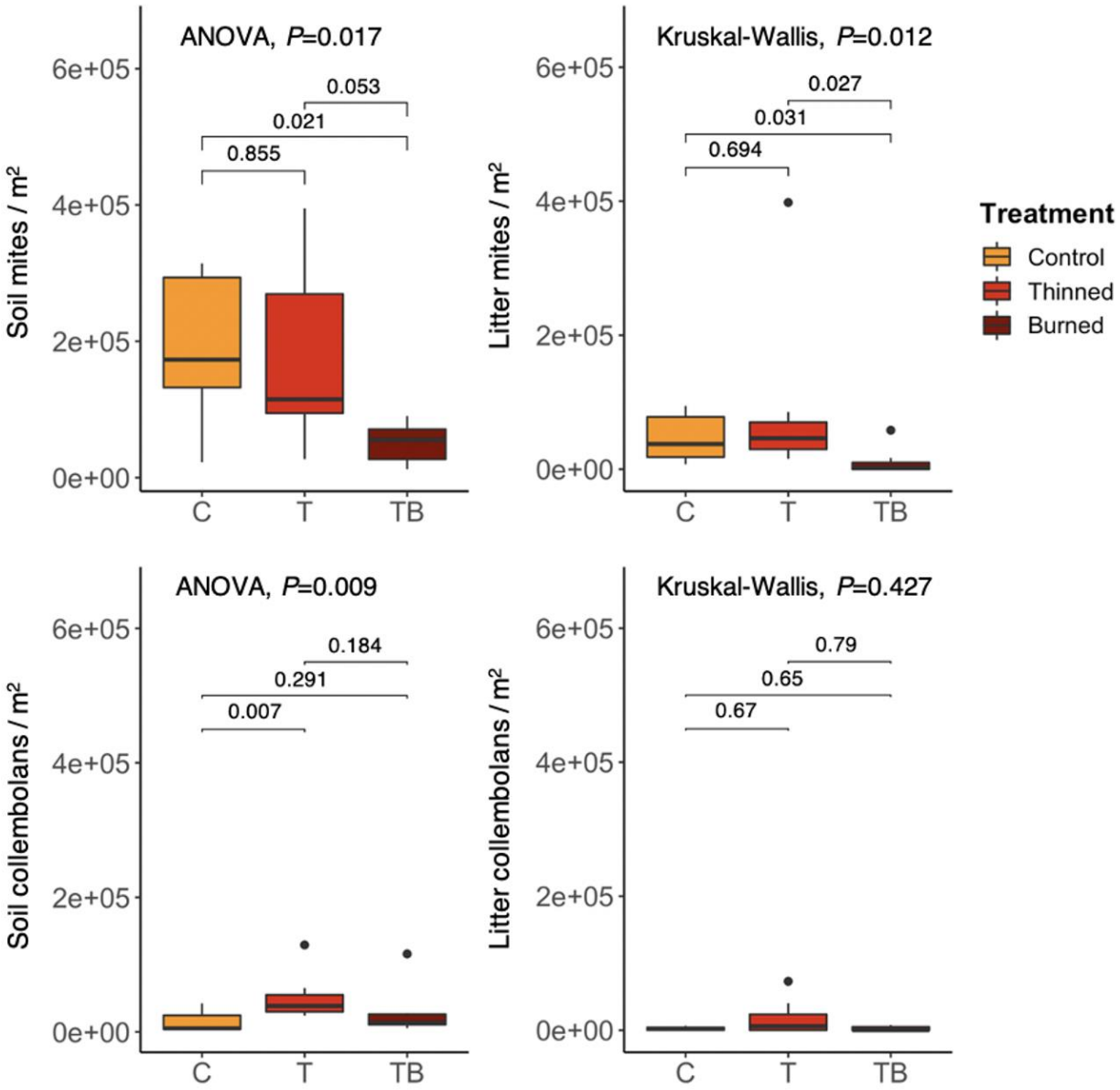

Fig. 2.2 Densities of mites and collembolans in soil and litter habitats within untreated control, thinned, and burned management units. The center line within each box represents the median for the treatment, and the lower and upper bounds of the box represent the first and third quartiles, respectively. The whiskers show any data points extending up to 1.5 times the interquartile range from the bounds of the box. Any dots are extreme values more than 1.5 times the interquartile range from the upper or lower box boundaries. Horizontal bars above the boxes show *P*-values for pairwise comparisons, adjusted for multiple comparisons by Tukey's test of honestly significant differences for ANOVA or Benjamini Hochberg adjustment for Kruskal-Wallis.

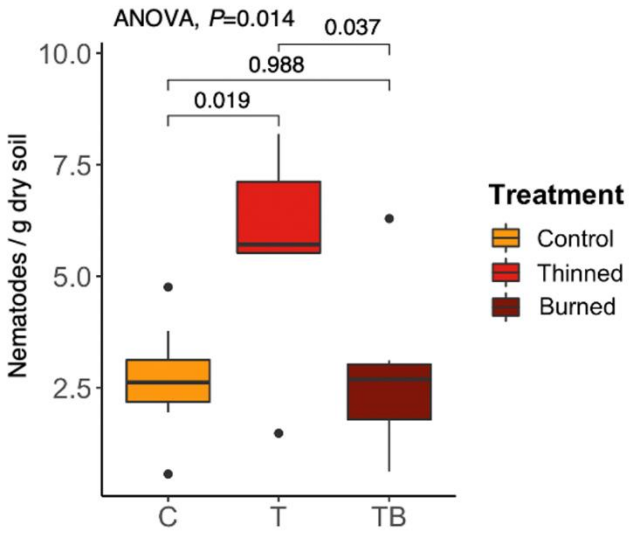

Fig. 2.3 Nematode abundance in untreated control, thinned, and burned treatment units. Horizontal bars show pairwise comparison *P*-values, adjusted for multiple comparisons by Tukey's test of honestly significant differences.

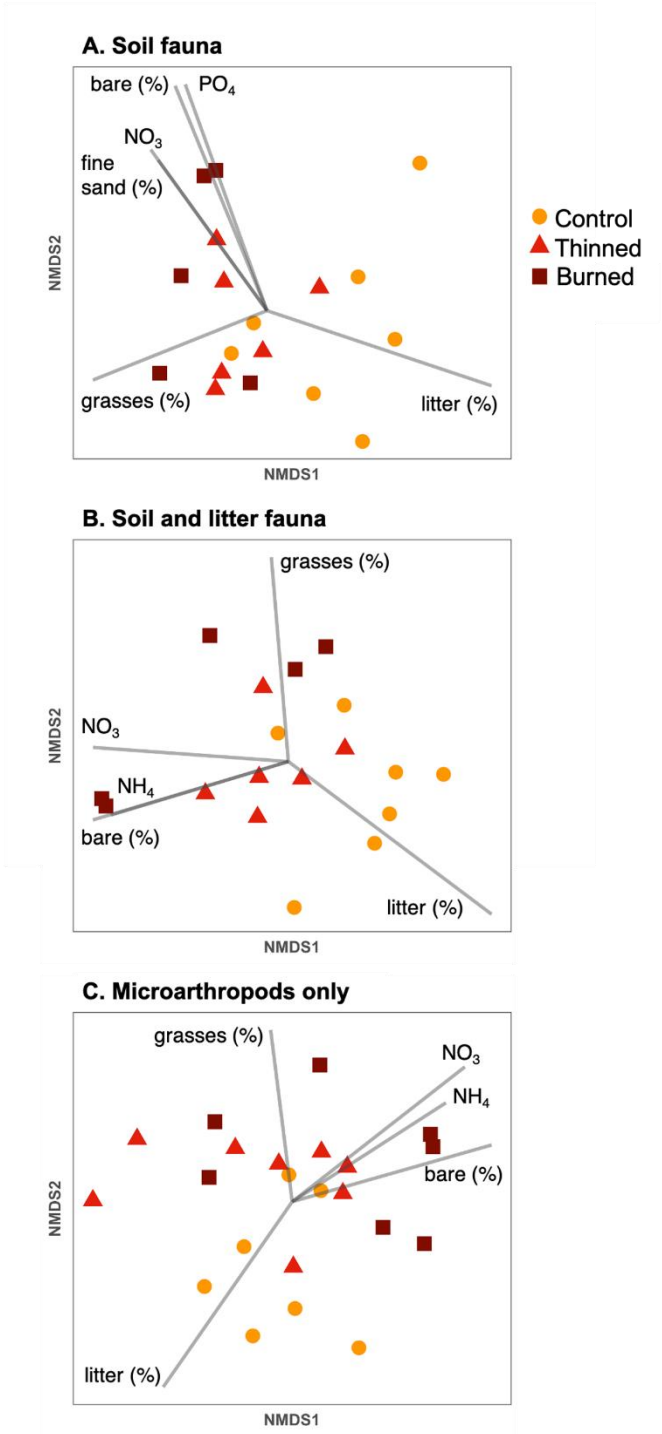

Fig. 2.4 Non-metric multidimensional scaling ordinations of (**A**) all soil fauna (including mites, collembolans, nematodes, and other taxa) (final stress= 0.089); (**B**) all litter and soil fauna, including soil nematodes and soil and litter mites, collembolans, and other taxa (final stress=0.134); and (**C**) soil and litter mites and collembolans only (final stress= 0.133). Displayed resource and habitat vectors have a correlation with community dissimilarity of $R^2 \geq 0.2$.

Table 2.2 Summaries of models predicting abundances of faunal groups. Optimal models were selected using an automated stepwise procedure based on Akaike information criterion (AIC) values.

	Parameter Estimate	Std. Error	*t* value	Parameter *P*-value	Adjusted R^2	Overall model *P*-value
ln (Soil mites / m^2)						
Intercept	8.52	0.91	9.404	<0.001		
% Litter cover	0.01	0.01	1.823	0.085		
Fine AM hyphae (m/g)	0.15	0.07	2.222	0.039		
ln (% SOM)	0.72	0.39	1.854	0.080		
					0.32	0.017
ln (Litter mites / m^2)						
Intercept	8.89	2.81	3.164	<0.01		
% Litter cover	0.02	0.01	1.804	0.092		
Bulk density	-5.96	1.29	-4.618	<0.001		
% Clay	-0.23	0.09	-2.695	0.017		
ln (% Bare ground)	-0.68	0.21	-3.275	<0.001		
ln (NO_3 μg/g)	-0.94	0.31	-3.000	<0.001		
% Wood cover	-0.03	0.01	-1.739	0.104		
ln (% Forb cover)	0.46	0.31	1.510	0.153		
					0.82	<0.001
ln (Total mites / m^2)						
Intercept	13.64	0.89	15.364	<0.001		
% Litter cover	0.02	0.01	4.012	<0.001		
Bulk density (g/cm^3)	-2.42	0.91	-2.645	0.016		
% Clay	-0.12	0.06	-1.891	0.074		
					0.50	<0.01
ln (Soil collembolans / m^2)						
Intercept	12.38	1.67	7.472	<0.001		
% Clay	-0.21	0.05	-3.936	<0.01		
ln (% Grass cover)	0.43	0.12	3.684	<0.01		
% Wood cover	0.03	0.01	2.997	<0.01		
ln (NO_3 μg/g)	0.27	0.19	1.449	0.165		
					0.67	<0.001
ln (Litter collembolans / m^2)						
Intercept	14.90	5.71	2.611	0.019		
Bulk density (g/cm^3)	-8.81	2.58	-3.419	<0.01		
ln (% Forb cover)	-1.97	0.61	-3.227	<0.01		

% Clay	-0.45	0.17	-2.694	0.016		
Fine AM hyphae (m/g)	-0.43	0.16	-2.672	0.017		
ln (% Bare ground)	-0.73	0.29	-2.527	0.023		
ln (NO_3 μg/g)	-0.87	0.60	-1.452	0.167		
					0.62	<0.01
ln (Total collembolans/ m^2)						
Intercept	11.62	0.88	13.236	<0.001		
% Litter cover	-0.02	0.01	-2.295	0.034		
% Clay	-0.23	0.06	-3.674	<0.01		
ln (% Bare ground)	-0.39	0.14	-2.820	0.011		
ln (% SOM)	0.80	0.32	2.518	0.022		
					0.62	<0.001
Nematodes / g dry soil						
Intercept	-1.31	1.82	-0.716	0.482		
ln (% SOM)	2.78	1.00	2.783	0.012		
					0.26	0.012

2.4 Discussion

2.4.1 Overall patterns

Soil faunal groups exhibited different associations with forest restoration treatments. Our hypotheses that resource and habitat availability would be enhanced by thinning and reduced by burning were partly supported. We observed that nematodes and collembolans were more abundant in the thinned unit (nematodes and soil collembolans strongly, litter collembolans weakly); however, mite abundances were similar in the thinned unit and in the control unit. As expected, nematode and mite densities were lower, and collembolans tended also to be reduced, in the burned unit relative to the thinned unit. Although the burned unit hosted the fewest mites, densities of nematodes and collembolans in this unit were similar to those in the untreated control, suggesting that, as broad groups, these taxa may be resilient or resistant to restoration treatment disturbances. It is possible, however, that with higher replication we would have detected differences in nematode and collembolan abundances between control and burned units.

As predicted, abundances of individual faunal groups were correlated with physicochemical and biological indicators of faunal habitat and resource availability that were likely impacted by the restoration treatments.

2.4.2 Physicochemical predictors of soil fauna responses

Because accessible pore space and water availability are two of the most important parameters governing soil faunal activity and trophic interactions (Erktan et al., 2020), modification of soil physical structure and water holding capacity are potentially the most consequential impacts of forest restoration treatments for these animals. Thinning and mastication were associated with reduced bulk density and increased SOM relative to the untreated control unit, while soils in the burned unit had less SOM and higher bulk density. Despite minor soil texture differences among treatment units, bulk density was not correlated with soil texture, but it was related to SOM (r^2=0.52, P<0.001 for the bivariate correlation of bulk density with ln % SOM), indicating restoration treatments were primarily responsible for bulk density changes. Logging machinery simultaneously compacts soil and churns fragmented organic material deeper into soil layers, so it is not possible to distinguish the effects of compaction versus bulk density changes due to organic matter addition (in the thinned unit) and combustion (in the burned unit); shallow surface soils are likely more subject to churning by equipment wheels, thereby reducing bulk density and increasing SOM, whereas deep soils would be more susceptible to compaction without increases in SOM.

Bulk density was selected as an important covariate in mite (litter and total) and collembolan (litter) abundance models. On average, collembolans and mites have much wider bodies than nematodes, and thus require larger pore sizes for movement. Although not quantified

here, pore size and connectivity changes following restoration treatments may be particularly important for microarthropods that "commute" from the litter layer to lower soil horizons to avoid desiccation (Siepel, 1996; Walter and Proctor, 2013). Selected models also indicated sensitivity of mites and especially collembolans to soil texture: coarse, sandy soils hosted larger microarthropod populations than fine, clay-rich soils. Because slightly coarser soils were present in the thinned unit and the correlation with collembolans was particularly strong (r^2=0.44, P<0.001 for the bivariate correlation), the patterns we observed in collembolan treatment responses may also be partly explainable by soil texture. Soil texture was also correlated with soil faunal communities, but not with litter and total faunal communities.

Soil organic matter was positively correlated with nematode abundance and was the only habitat variable determined by the model selection procedure to be an important predictor for this group. Organic carbon has been demonstrated to track strongly with nematode densities on a global scale (van den Hoogen et al., 2019). In addition to likely offering higher densities of microbial prey, the higher water holding capacity of more organic soils should extend periods of activity for nematodes in xeric ponderosa pine forests. Nematodes were also negatively correlated with pH, although collinearity of pH and SOM in this study makes it difficult to disentangle the effects of these two variables on nematode abundance. Global models also suggest that pH is also an important driver of nematode abundance (van den Hoogen et al., 2019). As pH strongly influences bacterial diversity and richness (Fierer and Jackson, 2006; Rousk et al., 2010), changes in nematode abundance with pH could be related to changes in basal food resources, or to direct physiological effects, or both. Correlations between nematode abundances and soil properties in our study should be interpreted with caution, however, as soil properties may also have affected nematode survival in archived samples.

Mineral N and P were correlated with NMDS axis scores. Each successive restoration treatment in this study tended to be associated with higher nutrient availability; thinning and mastication promote mineralization of organic nutrients previously bound up in living and dead plant material, and low intensity burning may increase mineral nutrients through several mechanisms, including direct conversion of organic to mineral N and P during combustion and changes to microbial communities (Certini, 2005; Covington and Sackett, 1986).

2.4.3 Biotic drivers: plant inputs are key

Soil fauna responded to changes in ground cover associated with restoration treatments. Litter cover, grass cover, and bare ground were orthogonal correlates in all three faunal community ordination sets, indicating that resources and habitat associated with these ground cover classes drove distinct changes in faunal communities. Sampling locations with more litter hosted more mites in the litter and below it, and with greater total abundance of collembolans, while absent or patchy ground cover reduced densities of microarthropods active above the soil surface. Grass cover was positively associated with soil collembolan abundance. Collembolans spanning a range of trophic niches might benefit from resources provided directly or indirectly by grass roots, litter, or arbuscular mycorrhizal fungi (Ngosong et al., 2014). Some herbo-fungivorous collembolans may prefer roots over fungal hyphae when given a choice (Endlweber et al., 2009), and grass roots, which tend to be poorly-defended in comparison to conifer roots, could be especially palatable. A meta-analysis of studies examining nematode trophic groups indicated that energy flow through the herbivory channel is greater in grassland than in forest soil food webs (Zhao and Neher, 2014).

Although declines of fungal biomass after fire have been widely reported (reviewed in Pressler et al., 2019), we did not observe a decrease in septate hyphae or fine AM hyphae with burning. Fine AM hyphae were positively correlated with soil mites, however, and the broad morphological categories we employed in quantification of hyphae do not allow us to discriminate taxa that may vary in their appeal to soil fauna, so it is possible that burning may have reduced fungi representing important food sources for mites. Alternatively, a decline in mite abundance in the burned unit and their failure to increase in the thinning and mastication unit may stem from predominant life history characteristics in this group rather than changes in resource availability. Mite assemblages in temperate forests often contain a high proportion of taxa which move and reproduce slowly, and these may be slower than most nematodes or collembolans to recolonize more severely burned patches from unimpacted refugia in a burn-severity mosaic.

2.4.5 Conclusions and next steps

Our findings indicate variable responses of broad soil fauna groups to restoration treatments. We observed total abundances of nematodes and collembolans to be relatively resilient to restoration treatments. Mite densities, in contrast, did not appear to have recovered one year after burning. Investigations in other systems have variably found rapid recovery of mite abundances (Hutchins et al., 2011; Jacobs et al., 2015) after low-intensity fire, or persistent depression of populations for at least several years (Malmström et al., 2008); further surveys are needed to assess the longevity of changes to mite communities after prescribed burning in ponderosa pine forests, as well as to illuminate how functional and taxonomic diversity of mite, collembolan, and nematode assemblages may be affected by restoration treatments. We also cannot definitively say that

patterns we observed reflect changes from pre-treatment abundances because we were unable to collect pre-treatment data. In the future, surveys should ideally include pre-treatment sampling.

Despite high heterogeneity in communities of soil and litter fauna, the treatment-related habitat variables we measured explained a relatively large proportion of the variation in nematode, collembolan, and mite abundances. These patterns suggest some potential indicators of restoration-related changes to soil meso- and microfauna communities: bulk density, SOM, pH, grass cover, and litter cover and depth. These variables are all easy and inexpensive for non-specialists to measure, offering potential utility to land managers who may not be equipped to directly quantify micro- and mesofauna responses to treatment decisions. Future studies are needed to test the generality of these indicators.

It is important to note that both the untreated control unit and the thinned and burned unit in our study represent departures from historic conditions for ponderosa pine forests in the region (Touchan and Swetnam, 1995), and unavailability of a true reference system complicates judgement of the "desirability" of observed changes in micro- and mesofauna communities. While we might expect a history of frequent fire in *P. ponderosa* forests to have selected for soil biota that are either resistant or resilient to fire—traits seen, for example, in Collembola of a fire-prone South African fynbos ecosystem (Janion-Scheepers et al., 2016)—long absence of fire disturbance may have altered the prevalence of these traits in contemporary faunal assemblages. Prescribed fires that follow more than a century of fire suppression likely burn hotter and longer than did historic fires in this area (Roos et al., 2020). Disturbance and mortality from high-severity wildfires should greatly surpass negative impacts from forest management treatments undertaken to reduce wildfire risk. However, we submit that if the goal is to restore forest communities (including soil faunal assemblages) and their ecological functions to putative pre-

Euro-American settlement conditions, managers should consider the ways in which restoration activities mirror or depart from historic disturbances to soil and litter habitats, and strive to minimize non-historic habitat modifications when crafting treatment plans.

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CHAPTER III: DETERMINING THRESHOLDS FOR IMPACTS OF LOGGING MACHINERY ON SOIL NEMATODES AND PHYSICAL PROPERTIES

Abstract

Mechanized tree thinning causes considerable soil disturbance, but little information is available regarding thresholds for impacts on the dominant multicellular animals in soils: nematodes. These trophically diverse microfauna perform important ecological functions (for example, nitrogen mineralization, dispersal of microbes, and regulation of lower trophic levels) and are widely consumed by predatory and omnivorous mesofauna. Because nematodes are too small to physically modify soil pore structure, their movement is restricted to pores of sufficient size to accommodate them. Compaction from heavy logging machinery may thus reduce nematode abundances by decreasing available pore space. Nematodes also exhibit a wide range of life history characteristics, and some taxa are slow to recover from disturbance due to relatively long generation times and low reproductive output. We examined responses of nematode assemblages and soil physical characteristics to increasing number of passes (one, three, or nine) by a tracked harvester (a feller buncher) during thinning of a xeric mixed conifer forest in New Mexico, USA. Within and between the harvester tracks, we measured soil surface penetration resistance and shear strength, quantified bulk density at four depth increments to a maximum depth of 27 cm, and characterized nematode assemblages in the upper 10 cm. We hypothesized that nematode responses to harvester traffic would vary according to their life history characteristics, and that compaction would disproportionately affect large bodied taxa. Eight months after treatment, we found that nematode communities were less impacted than soil physical properties by harvester passes. Soil compaction was evident with a single pass and extended deep into the soil profile to

at least 23-27 cm. Total nematode abundances were unaffected by any level of disturbance. However, densities of nematodes presumed to have longer generation times and lower reproductive output were reduced following nine harvester passes. Abundances of sensitive nematode groups were correlated weakly with bulk density at the 9-13 cm depth interval, but this relationship was stronger for slender compared to large-diameter taxa, suggesting that harvester disturbance did not limit pores accessible to nematodes. We note that the harvester produced complex soil disturbance, with surface soil mixing and subsurface compaction, which may have obscured relationships between bulk density and nematode abundances. Our results indicate that nematode communities are unlikely to be affected by low levels of soil disturbance from heavy logging machinery, but nevertheless emphasize the importance of minimizing areas subjected to logging machinery traffic, especially where sensitive soil types occur.

3.1 Introduction

Understanding how forest thinning affects soil biota is crucial for minimizing negative impacts on soil food webs and the ecosystem processes they mediate. However, little attention has been paid to how use of heavy logging machinery affects the most abundant animals in forest soils. Nematode assemblages often include millions of individuals per square meter (Yeates, 2007) and comprise bacterivorous, fungivorous, predatory, omnivorous, and herbivorous taxa, all of which perform important (and generally beneficial) functional roles (Neher, 2001). Microbivore nematodes enhance microbial activity, modulate the biomass and composition of microbial communities, and can contribute substantially to nutrient cycling (Ferris et al., 1997; Fu et al., 2005; Trap et al., 2016): in a meta-analysis of manipulative laboratory and greenhouse studies, Trap et al. (2016) found that N mineralization nearly doubled in the presence of bacterivore nematodes. Fungivore nematodes are probably less important than bacterivore nematodes for N

mineralization (Ferris et al., 2004; Okada and Ferris, 2001). Omnivorous and predatory nematodes can regulate densities of lower trophic levels (Steel and Ferris, 2016). Root herbivore nematodes can stimulate or suppress plant growth, depending on their densities and identities; their feeding can also influence plant community dynamics, although the ramifications of root herbivore activities in natural systems remain poorly characterized relative to agricultural systems (Wilschut and Geisen, 2021). Nematodes in all feeding groups can also disperse microbial propagules which adhere to their cuticles or survive passage through their intestines (with the latter dispersal mechanism more likely in microbivore nematodes) (Ingham et al., 1985). Finally, nematodes are important prey items for higher trophic levels in soil food webs: not only do many predatory microarthropods rely on them, but they also likely represent a key source of nutrition for many otherwise detritivorous or microbivorous microarthropods which consume nematodes in small quantities (Heidemann et al., 2014). Indeed, nematodes are suspected to be an important source of omega-3 fatty acids in terrestrial food webs (Menzel et al., 2018). Management impacts on nematodes can thus reverberate to affect larger organisms, which may also be directly affected by changes to soil physical properties.

Soil compression and shearing caused by logging equipment can both fatally injure nematodes and modify key aspects of their habitat. Nematodes are aquatic organisms, requiring water films for activity (although many species are capable of anhydrobiosis); they are also too small to alter soil pore structure by their own movements. Pore size, connectivity, and soil hydration status thus determine their ability to sense and access food (Erktan et al., 2020), and, for sexually reproducing species, to find mates. Soil disturbances from tracked harvesters alter all three of these habitat parameters. Compaction reduces pore volumes, pore connectivity, water infiltration, and gas exchange (Reicosky et al., 1981; Shestak and Busse, 2005). These changes

could restrict nematode movements and hamper their ability to detect chemical signals indicating the location of prey and conspecifics. Near the surface, however, harvester traffic can temporarily stimulate microbial prey for nematodes by severing roots and mixing organic and mineral soil layers. Topsoil mixing can potentially also decrease the bulk density of uppermost soil layers, but because aggregates are destroyed, a preponderance of the pores created may be small and inaccessible. Finally, harvesters can reduce vegetative ground cover, restricting the flow of matter and energy into soil food webs and altering microclimate.

The objective of this study was to determine how impacts to nematode communities and soil physical properties vary with number of passes by a tracked harvester. We subjected volcanic loamy soils to one, three, or nine passes from a feller buncher during thinning of a xeric mixed conifer forest in the Valles Caldera National Preserve in New Mexico, U.S.A. Within and between the feller buncher tracks, we characterized nematode assemblages in the uppermost 10 cm of soil (where they are most abundant), measured surface penetration resistance and shear stress, documented ground cover variability, and quantified bulk density changes at four depth increments up to a maximum of 27 cm after eight months. We hypothesized that nematode responses to disturbance from harvester traffic would vary by life history characteristics and feeding habits, as integrated in the functional guild classification system of Ferris (Ferris et al., 2001). Specifically, we predicted that *r*-selected bacterivore and fungivore taxa (with high reproductive output and generation times of days to weeks) would be relatively resilient to disturbance, possibly responding positively to topsoil mixing (*H1*), while *K*-selected species (with low reproductive output and generation times of months to years) would be most sensitive (*H2*). We also expected that compaction would reduce total habitable pore volume for nematodes, and that large-bodied *K*-selected taxa would be most negatively impacted, as these

nematodes require the largest pores for movement (*H3*). Finally, we anticipated that reduction of vegetative ground cover would decrease herbivorous nematodes because of direct food source loss (*H4*). Our data regarding compaction at depth are also relevant to a vertebrate, the endangered endemic Jemez Mountains Salamander (*Plethodon neomexicanus*), which spends most of the year belowground.

3.2 Materials and Methods

3.2.1 Study site, experimental design, field measurements, and sample collection

This study was performed at a study site located at 35.953 °N, 106.591 °W and ~2,700 m elevation in the Valles Caldera National Preserve, New Mexico, U.S.A. Soils at this site are volcanic loams to silt loams classified primarily as Vitrandic Hapludalfs, Vitrandic Hapludolls, and Vitrandic Argiudolls (Hibner et al., 2010). Overstory vegetation consists of mixed conifer forest including *Picea engelmannii* (Engelmann spruce), *Picea pungens* (blue spruce), *Abies concolor* (white fir), *Pseudotsuga menziesii* (Douglas-fir), and *Pinus ponderosa* (ponderosa pine), with occasional *Populus tremuloides* (quaking aspen). Mean temperatures range from ~15 °C in July to ~ -5 °C in December and January, and the area receives an average of ~690 mm of precipitation annually (PRISM Climate Group, 2021).

In November 2017, we established three experimental transects along natural corridors between trees to assess soil compaction and disturbance by logging machinery and impacts to soil nematode communities. Sections of each of the first three transects received treatments of one, three, and nine passes by a track feller buncher (TimberPro model TL735-B with a Quadco 22B saw attachment and 600 mm single grouser track shoes; total weight approximately 30,086 kg, distributed as 54.40 kPa). Trees surrounding the transects were left intact to isolate the effects of soil disturbance from those of light and temperature changes that occur with tree removal.

Three replicate treated and untreated sample pairs were collected the following July at evenly spaced points along the one, three, and nine pass sections of the three feller buncher transects, respectively. Treated samples were collected from the center of the machine track (subsequently termed "track samples"), and untreated samples (hereafter referred to as "intertrack samples") were collected from between the tracks (**Fig. 3.1**). Sampling and surface measurements occurred at three evenly spaced points per transect section. Prior to sampling, we characterized ground cover for 0.25 m^2 areas centered on each sample collection point, quantifying percent cover by grasses, shrubs, forbs, mosses, lichens, pine litter, spruce litter, forb litter, moss litter, thatch, woody debris, sticks, scat, and bare ground. All sampling and *in situ* soil measurements were performed at consistent points marked on our 0.25 m^2 cover frame. We measured soil surface resistance to penetration (three readings with a model FT 011 pocket penetrometer; QA supplies, Norfolk, VA), litter depth, shear strength using a TORVANE (Durham Geo Slope Indicator, Tucker, GA), and trench depth (the depth of the nearest indentation formed by feller buncher tracks). We collected soil cores for determination of bulk density at depth increments of approximately 2-6 cm, 9-13 cm, 16-20 cm, and 23-27 cm. Cores were retrieved using a bulk density sampling cup with liner ring (AMS, Inc., American Falls, ID) designed to minimize compaction during sampling. Because most soil fauna reside in the uppermost 0-10 cm, we sampled this interval for nematodes. Overlying litter, if present, was cleared away, and soil cores for nematode extraction were removed using pipe segments with an internal diameter of 5.08 cm.

Fig. 3.1 One of three experimental feller buncher disturbance transects. Flags represent sampling points within and between the tracks (each cluster of three flags represents one sampling location). Each of the three transect blocks included three sections treated with 1, 3, and 9 passes, respectively. Samples and measurements were taken at three points per track and intertrack transect section (N=54 sampling locations).

3.2.2 Sample processing

Bulk density soil samples were dried at 105 °C and weighed. Bulk density was calculated as soil sample dry weight divided by 90.59 cm^3, the internal volume of the sampling cup liner ring. Five out of 216 bulk density samples were excluded from analysis due to damage. To ensure that no confounding correlation with soil organic matter (SOM) and bulk density existed, and to examine relationships between SOM and nematode communities, we determined soil organic matter (SOM) content by loss on ignition for the 2-6 cm and 9-13 cm depth increments overlapping or partially overlapping the nematode sampling depth interval. We analyzed soil organic matter content only for feller buncher transect samples where nematode communities were also characterized. Samples were sieved to 2 mm and homogenized, then 5 g subsamples were dried at 105 °C, weighed, heated at 450 °C for 24 hours, and reweighed (Bisutti et al., 2004).

Nematode soil samples were kept on ice for transportation to Northern Arizona University and were stored at 4 °C until processing. Nematodes were extracted by centrifugal flotation with Ludox colloidal silica solution using a method modified from Griffiths et al. (1990). Soil samples were sieved gently to 6.3 mm and thoroughly homogenized, and a 5 g subsample was dried for 48 hours at 105 °C to determine gravimetric water content. An 80 cc soil subsample for nematode extraction was weighed and transferred to a 500 mL centrifuge tube, which was filled with tap water and shaken. Subsamples were then centrifuged at 2110 rpm (~700 g) for 12 minutes. Floating organic matter was removed from the centrifuge tubes with a spoon and the supernatant was decanted and discarded. Nematodes and soil particles in the remaining pellet were resuspended in 300 mL of Ludox (diluted to a specific gravity of 1.17 g/cm^3 with DI water) and centrifuged again at the same speed for 6 minutes. Nematodes were

retrieved from the Ludox supernatant by pouring it over a 20 μm sieve, then were backwashed into a beaker with tap water. The original Ludox solution which passed through the sieve was then returned to the centrifuge tube, and the Ludox centrifugation and sieving steps were repeated two times. Finally, the resulting nematode suspension was poured through an 850 μm sieve to remove organic debris. Collected animals were preserved in DESS solution (Yoder et al., 2006) and refrigerated at 4 °C until examination. Eight randomly selected track/intertrack sample pairs per disturbance level were included in nematode analyses (48 total samples).

As nematode yields were very high, we estimated total sample abundance based on ~10% subsamples. We used a Hensen-Stempel pipette, developed to avoid sampling fractionation of plankton suspensions, to obtain representative 4 mL subsamples of 40 mL nematode suspensions. Samples were mixed gently by repeated inversion prior to subsampling, and subsampled nematodes were examined using an inverted compound microscope at 100X-400X magnification. We validated the accuracy of this abundance estimation method for 11 samples by comparing abundances calculated by subsampling to those obtained by direct examination of all nematodes present in a sample. Enumeration of entire nematode samples was performed using a stereomicroscope at a magnification of 40X-78.8X. Correlation between these abundance estimation methods was deemed sufficient to justify subsampling (R^2=0.932).

The first 200 nematodes encountered in each subsample were identified to the taxonomic level necessary for classification to feeding group and position on the colonizer-persister scale (cp class; Bongers, 1990). This scale represents the continuum from *r*-strategists (cp1) to *K*-strategists (cp5). Nematodes in colonizer-persister classes cp1 and cp2 are considered indicators of organic enrichment and/or basal fauna (disturbance-tolerant nematodes occurring in virtually all soils), while nematodes in the maturity indicator classes cp3, cp4, and cp5 are associated with increasing food web stability, complexity, and connectance (Ferris et al., 2001). Assignments

were made according to the NEMAPLEX Nematode Ecophysiological Parameter database (Ferris, n.d.), with the exception of Monhysteridae, which we grouped with cp3 bacterivores because *Monhystera* was found by Fiscus and Neher (2002) to be sensitive to tillage effects. Because specimen condition sometimes made determination of family impossible, and this information is necessary for assignment of cp4 and cp5 Dorylaimida to both cp class and feeding group, all Dorylaimida were grouped together as cp4/cp5 omnivores, predators, and fungivores. We distinguished the groups cp1 bacterivores, cp2 bacterivores, cp3 bacterivores, cp4 bacterivores, cp2 fungivores, cp4/cp5 Dorylaimida, cp4 predators, cp2 plant associates (the ubiquitous and enigmatic Tylenchidae), and strict herbivores (which were not assigned to cp class, as plant parasitic taxa are not commonly used as indicators of disturbance). Group assignments for taxa are listed in **Table 3.1**. We refer to these groups as functional guilds (*sensu* Ferris et al., 2001), but it should be noted that the order Dorylaimida encompasses multiple functional guilds.

3.2.3 Statistical analyses

Treatment differences in soil physical properties and abundances of nematode groups were assessed by Wilcoxon rank sum tests, with the exception of soil organic matter content differences between track and intertrack samples, which were analyzed via *t*-test. We used bivariate regression to test whether abundances of total nematodes, and of sensitive groups, could be predicted from indicators of soil physical disturbance, and whether herbivorous nematodes were correlated with plant cover classes. For regressions of nematode groups and bulk density, we examined each of the bulk density sampling intervals that overlapped with our nematode sampling interval (2-6 cm and 9-13 cm) as well as their average. Predictor and response variables were log transformed where necessary to achieve normality and constant

variance. Wilcoxon rank sum tests and linear regressions were performed in R (R Core Team, 2020) and visualized with package *ggplot2* (Wickham, 2011). We tested multivariate treatment group differences using multi-response permutation procedure (MRPP) and visualized community distances with non-metric multidimensional scaling ordination (NMDS) in PC-ORD (McCune and Mefford, 2006). All NMDS and MRPP analyses were performed using Bray-Curtis distance.

Table 3.1 Feeding group, cp class, and functional guild assignments for nematode taxa at Seco 5.

Taxon	**Feeding group(s)**	**Colonizer-persister class(es)**	**Functional guild assigned**
Panagrolaimidae	Bacterivore	cp1	cp1 bacterivore
Rhabditidae	Bacterivore	cp1	cp1 bacterivore
Cephalobidae	Bacterivore	cp2	cp2 bacterivore
Plectidae	Bacterivore	cp2	cp2 bacterivore
Tylenchidae	Plant associate	cp2	cp2 plant associate
Criconematidae	Herbivore	NA	Herbivore
Hoplolaimidae	Herbivore	NA	Herbivore
Hemicyclophoridae	Herbivore	NA	Herbivore
Other Tylenchoidea (apart from Tylenchidae)	Herbivore	NA	Herbivore
Trichodoridae	Herbivore	NA	Herbivore
Aphelenchidae	Fungivore	cp2	cp2 fungivore
Aphelenchoididae	Fungivore	cp2	cp2 fungivore
Prismatolaimidae	Bacterivore	cp3	cp3 bacterivore
Teratocephalobidae	Bacterivore	cp3	cp3 bacterivore
Rhabdolaimidae	Bacterivore	cp3	cp3 bacterivore
Monhysteridae	Bacterivore	cp3*	cp3 bacterivore
Alaimidae	Bacterivore	cp4	cp4 bacterivores
Mononchidae	Predators	cp4	cp4 predators
Dorylaimida	Omnivores, predators, and fungivores	cp4/cp5	cp4/cp5 omnivores, predators, and fungivores

*Included with cp3 bacterivores based on Fiscus and Neher's (2002) finding that *Monhystera* was sensitive to indirect effects of tillage (but classified as cp2 according to Bongers et al. (1995)).

3.3 Results and Discussion

3.3.1 Soil physical properties

The tracked feller buncher altered surface resistance to penetration, shear stress, and bulk density. Feller buncher disturbance tended to reduce surface resistance to penetration. Penetration resistance differed most in track samples relative to intertrack samples at three passes; we observed a similar trend for nine passes but no difference with one feller buncher pass (**Fig. 3.2 A**). Effects of feller buncher traffic on surface resistance to penetration may have been more readily detectable at three than at nine passes because churned topsoil was compacted with repeated passes. Soil shear strength tended to be lower in track than in intertrack samples, although treatment differences were significant only for one feller buncher pass (**Fig. 3.2 B**). Effects of logging machinery on bulk density appeared negligible in the uppermost interval (**Fig. 3.3 A)**, likely due to topsoil mixing, but were discernible at lower depth intervals (**Fig. 3.3 B-D**). The magnitude of bulk density change did not appear to attenuate with depth. This result is contrary to most previous studies, which have generally found that compaction from heavy machinery is greatest near the surface (Cambi et al., 2015; Hwang et al., 2020) and decreases rapidly with depth. However, exceptions to this pattern have been reported, including for loam to silt loam forest soils (Jourgholami et al., 2014) such as occur at our study site. Volcanic parent material may also render soils more vulnerable to compaction (Cambi et al., 2015). Treated and control samples from the two uppermost sampling depths in the feller buncher transects did not differ in soil organic matter content (2-6 cm: t = -0.39312, df = 42.946, p-value = 0.696; 9-13 cm: t = -0.96179, df = 40.472, p-value = 0.341), indicating that treatments likely were not confounded with pre-existing bulk density differences. Mean SOM in intertrack samples collected from the 2-6 cm depth interval was 8.05% (std. err=0.418) compared to 8.27% in the

track samples (std. err=0.394); in the 9-13 cm depth interval, mean SOM in intertrack samples was 5.87% (std. err=0.166), compared to 6.13% for track samples (SE= 0.202).

3.3.2 Nematode community impacts

Total nematode abundance was unaffected by any level of feller buncher traffic (**Fig. 3.4**), and total nematodes were not correlated with bulk density of either the 2-6 cm interval, the 9-13 cm interval, or the mean of these two intervals (R^2<0.05, p>0.15 in all cases). There was no significant relationship between total nematode densities and penetration resistance (R^2=0.050, p=0.127) or shear strength (R^2=0.043, p=0.162). However, as we hypothesized, nematode functional groups differed in their responses to disturbance from the harvester.

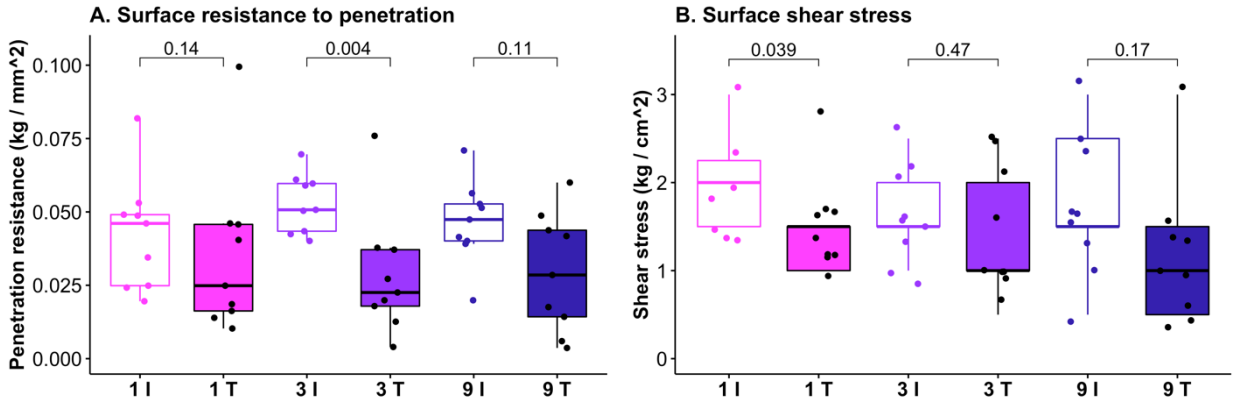

Fig. 3.2 (**A**) Soil surface resistance to penetration as measured with a pocket penetrometer. Each point represents the average of three readings. (**B**) Shear stress as measured by TORVANE. *P*-values above brackets are calculated from Wilcoxon rank sum tests and have not been corrected for multiple comparisons. Open boxplots show data from between the feller buncher tracks (I=intertrack), and filled boxplots show data from the tracks (T). Pink, purple, and blue represent one, three, and nine passes, respectively. The line within each box shows the median for that treatment, and the lower and upper bounds of the box indicate the 25th and 75th percentiles, respectively. Whiskers extend to 1.5 x the interquartile range from the lower and upper box bounds. Individual observations are plotted as dots.

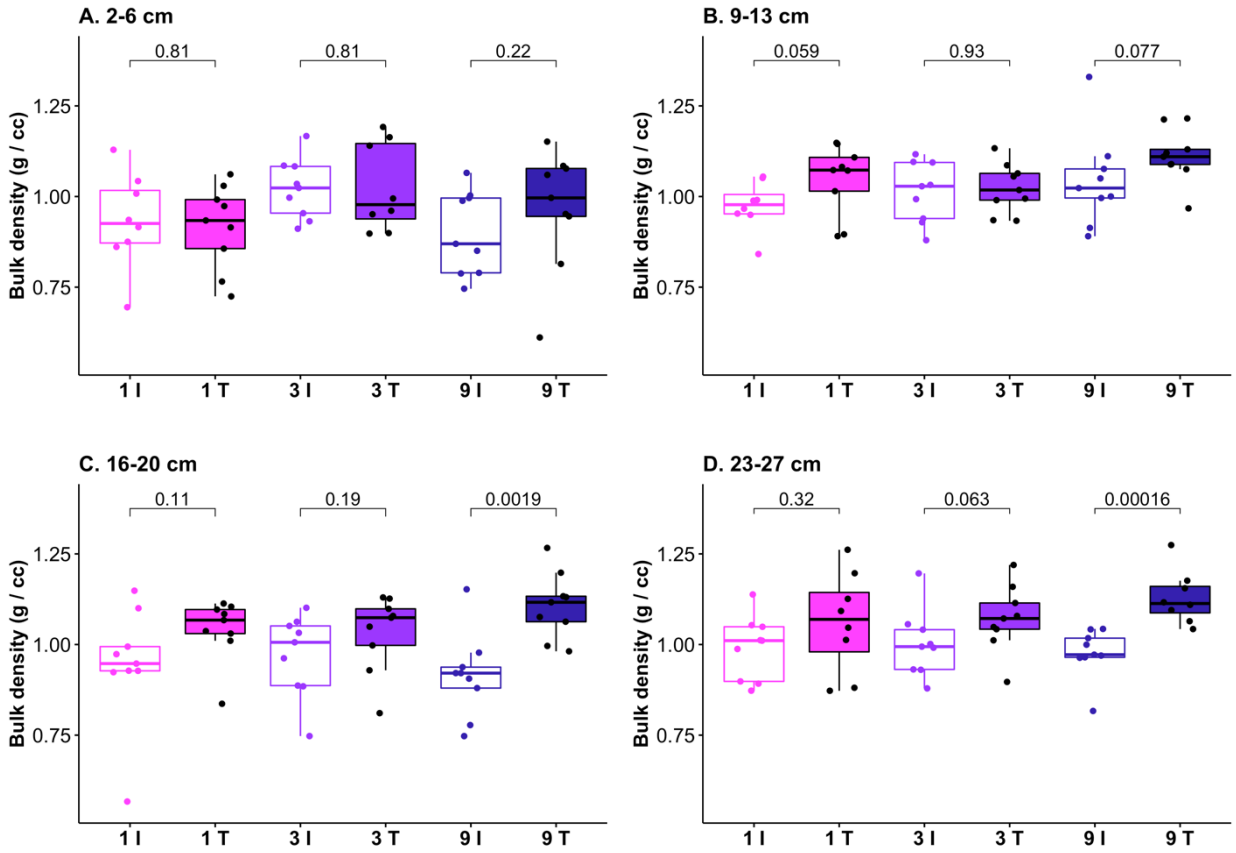

Fig. 3.3 Soil bulk densities (g/cm^3) from track (T) and intertrack (I) sampling locations that received 1, 3, or 9 passes from a feller buncher. (**A**) 2-6 cm sampling depth; (**B**) 9-13 cm sampling depth; (**C**) 16-20 cm sampling depth; (**D**) 23-27 cm sampling depth. *P*-values above brackets are calculated from Wilcoxon rank sum tests and have not been corrected for multiple comparisons. Open boxplots show data from between the feller buncher tracks, and filled boxplots show data from the tracks. Pink, purple, and blue represent one, three, and nine passes, respectively. The line within each box shows the median for that treatment, and the lower and upper bounds of the box indicate the 25th and 75th percentiles, respectively. Whiskers extend to 1.5 x the interquartile range from the lower and upper box bounds. Individual observations are plotted as dots.

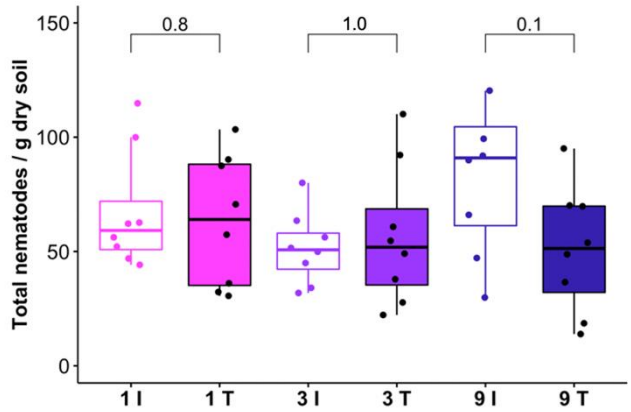

Fig. 3.4 Total nematode abundances in track (T) and intertrack (I) transect areas which received 1, 3, or 9 passes from the feller buncher. One outlier observation is not shown (276 nematodes / g dry soil in a 9 pass intertrack sample). *P*-values above brackets are calculated from Wilcoxon rank sum tests and have not been corrected for multiple comparisons.

Fungivore and bacterivore nematodes with colonizer-persister values of cp1 and cp2 appeared resilient to harvester traffic, as predicted (*H1*). Total abundances of nematodes in these relatively *r*-selected groups were similar in track and intertrack samples at all treatment levels ($p>0.5$ for track and intertrack comparisons at all pass levels). Cp2 bacterivores were similarly abundant in track and intertrack samples for one and three pass treatment levels (**Fig. 3.5 A**). Although this functional guild was less abundant in track than intertrack samples at nine passes, this pattern appears to have resulted from elevated densities in several of the nine pass intertrack samples. These patterns are consistent with the basal indicator designation applied to this group by Ferris (2001). Only about 20% of samples (eight samples from feller buncher tracks, and two intertrack samples) yielded any cp1 bacterivores at all; where they occurred, these nematodes usually were present in low numbers (< 1 nematode / g dry soil), and track and intertrack differences were not statistically detectable (one pass: $p=0.17$; three passes: $p=0.17$; nine passes: $p=0.37$). Cp2 fungivores likewise comprised a small fraction of the nematode communities in our samples. In keeping with their dual classification as enrichment opportunists and basal fauna, nematodes in this functional guild appeared unaffected by one pass, but tended to be more

abundant in track than intertrack samples at three and nine passes (**Fig. 3.5 B**). Fungi exploiting dead roots or organic material churned into the soil may have supported an increase in cp2 fungivores beneath the tracks.

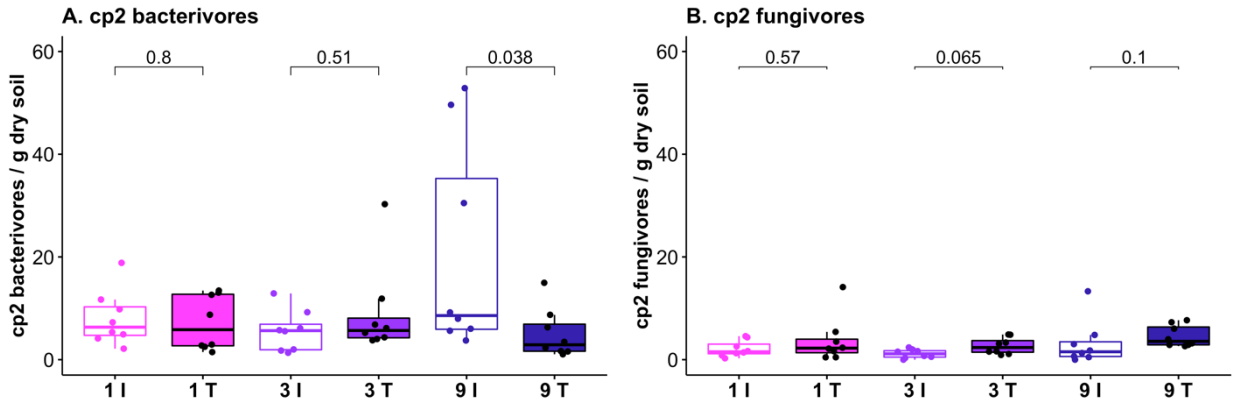

Fig. 3.5 Abundances of basal indicator cp2 bacterivores (**A**) and basal/enrichment indicator cp2 fungivores (**B**) in track (T) and intertrack (I) transect areas which received 1, 3, or 9 passes from the feller buncher. *P*-values above brackets are calculated from Wilcoxon rank sum tests and have not been corrected for multiple comparisons.

As hypothesized (*H2*), nematodes in colonizer-persister groups cp3 through cp5 appeared sensitive to soil disturbance from the feller buncher, but their numbers declined significantly only at nine passes (**Fig. 3.6 A**). Total cp3, cp4, and cp5 nematodes were correlated negatively with bulk density of the 9-13 cm sampling interval (**Fig. 3.6 B**), but not with the 2-6 cm interval (R^2=0.008, p=0.550) or the mean of the 2-6 cm and 9-13 cm intervals (R^2=0.049, p=0.131). Abundance of nematodes in these groups also correlated positively with penetration resistance (**Fig. 3.6 C**), but we did not detect a relationship between sensitive nematode groups and our soil shear strength measurements (**Fig. 3.6 D**). The dominant cp3, cp4, and cp5 groups, persister bacterivores (**Fig. 3.6 E**) and Dorylaimida (**Fig. 3.6 F**), exhibited similar patterns in their responses to the harvester disturbance treatment levels. Contrary to an expectation that larger taxa requiring larger pores would be most impacted by compaction (*H3*), slender cp3 and cp4 bacterivores correlated more positively with bulk density (R^2=0.070, p=0.073 for the 9-13 cm

bulk density sampling interval) than did large-bodied Dorylaimida (R^2=0.029, p=0.251 for bulk density at 9-13 cm). It is likely that topsoil mixing by the feller buncher obscured relationships between nematode body size and bulk density near the soil surface. Topsoil mixing destroys aggregates, which may have resulted in fewer macropores despite reducing bulk density. Quantification of pore volumes and connectivity, in conjunction with measurement of nematode body diameters, may be necessary to illuminate direct effects of soil compaction on nematode communities. Alternatively, it is also possible that there was no observable effect of bulk density on Dorylaimida because these cp4 and cp5 nematodes had not recovered sufficiently from the initial disturbance to be limited by soil pore sizes.

Neither herbivore nematodes (**Fig. 3.7 A**) nor plant associate nematodes in the family Tylenchidae (**Fig. 3.7 B**) were sensitive to measured levels of feller buncher traffic. However, herbivores appear to have been impacted negatively by harvester effects on vegetation, as anticipated (*H4*). Herbivorous nematodes corresponded with ground cover plot dissimilarity (**Fig. 3.7 C**, **Fig. 3.8**), and effects of feller buncher disturbance on ground cover were detectable with nine passes (**Table 3.2**). Herbivorous nematodes were more abundant in plots with greater grass and thatch cover, and less numerous in plots with more bare ground (**Fig. 3.7 C**). When examined as bivariate relationships, only the correlation between herbivorous nematodes and percent grass cover was significant (R^2=0.20, p=0.002). Tylenchidae comprised a median ~27% of nematode individuals across samples, in line with proportions frequently reported from natural systems (Ferris and Bongers, 2006), and were not correlated with grass or any other cover class (R^2<0.1, p>0.1 for all relationships). Feeding habits in this polyphyletic family remain poorly resolved; members have been variously reported to feed on plant roots, fungi, mosses, or algae

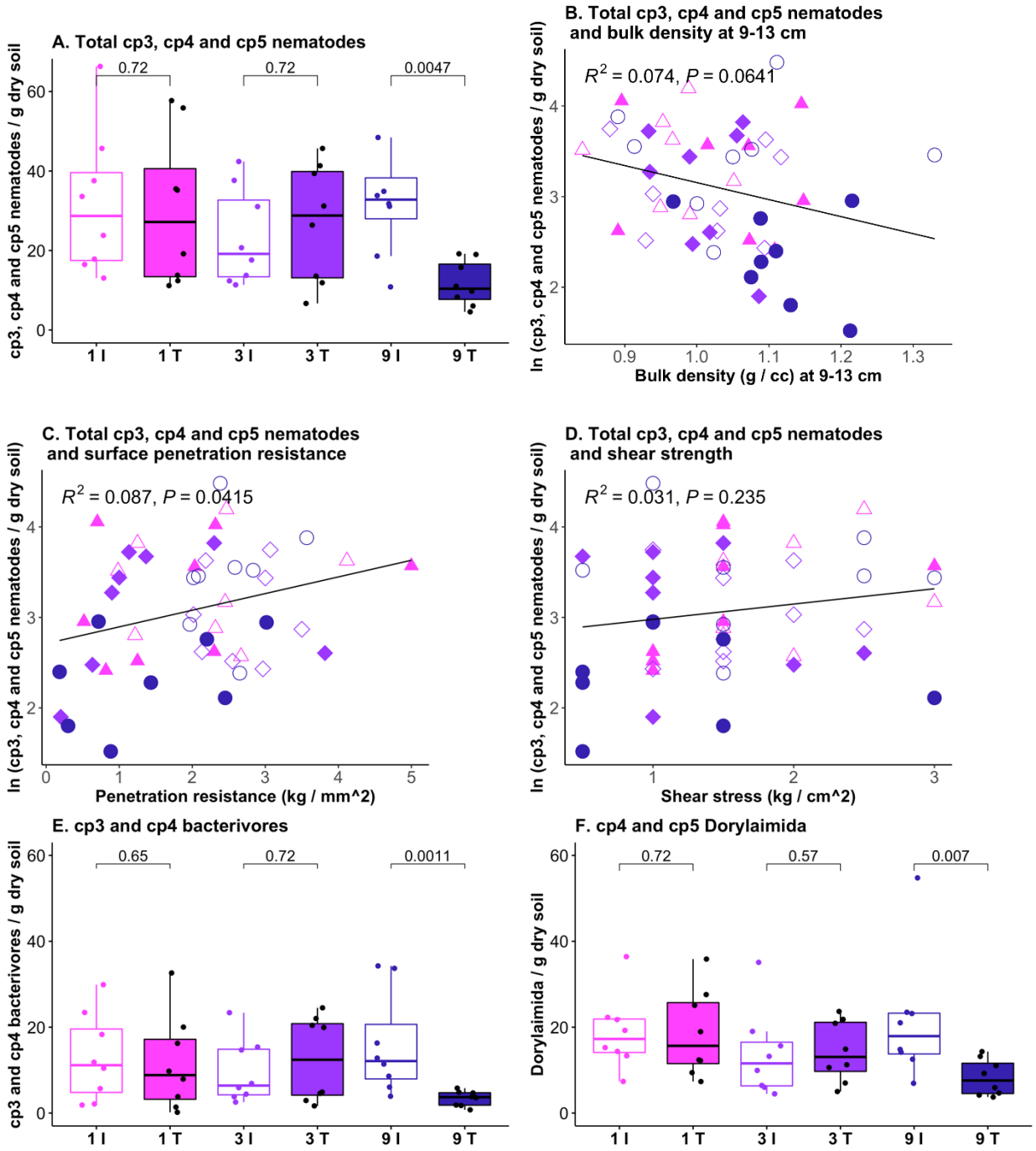

Fig. 3.6 Total abundances of cp3, cp4, and cp5 nematodes in feller buncher tracks (T) that received one, three, or nine passes, and matched intertrack (I) sampling locations (**A**); and correlations between total cp3, cp4, and cp5 nematodes and (**B**) bulk density at 9-12 cm, (**C**) surface penetration resistance, and (**D**) soil shear stress. (**E**) Harvester disturbance treatment responses of total cp3 and cp4 bacterivores. (**F**) Responses of Dorylaimida to harvester traffic. *P*-values above boxplots are from Wilcoxon rank-sum tests and have not been corrected for multiple comparisons. The line within each box shows the median for that treatment, and the lower and upper bounds of the box indicate the 25th and 75th percentiles, respectively. Whiskers extend to 1.5 x the interquartile range from the lower and upper box bounds. Individual observations are plotted as dots.

(Okada et al., 2005; Qing and Bert, 2019). Variability in food preferences within the Tylenchidae may explain why their densities were uncorrelated with ground cover; finer taxonomic resolution is likely necessary to uncover relationships between Tylenchidae and their food sources.

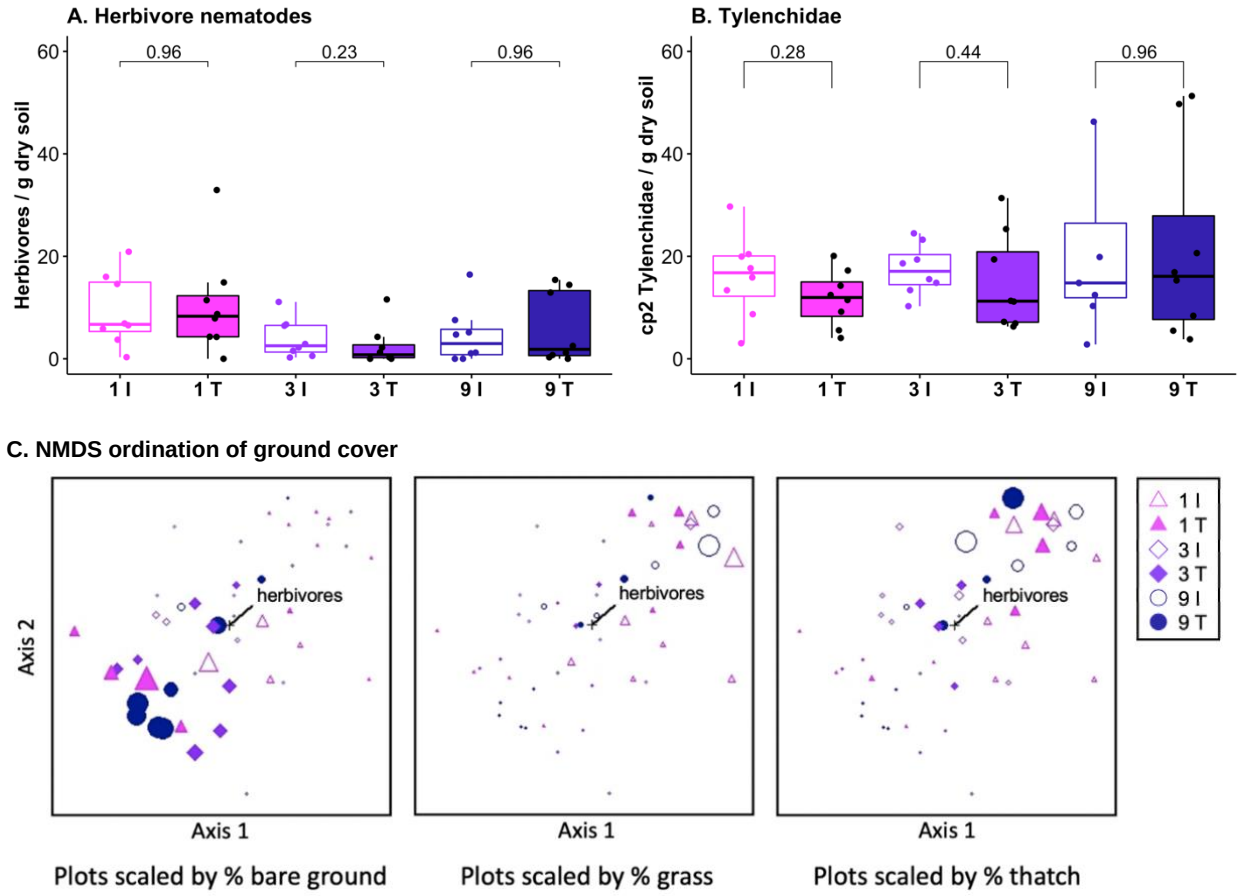

Fig. 3.7 Densities of (**A**) herbivore nematodes and (**B**) Tylenchidae (one observation of 174 Tylenchidae / g dry soil in a 9-intertrack treatment is not shown). *P*-values above boxplots are from Wilcoxon rank-sum tests. The line within each box shows the median for that treatment, and the lower and upper bounds of the box indicate the 25th and 75th percentiles, respectively. Whiskers extend to 1.5 x the interquartile range from the lower and upper box bounds. Individual observations are plotted as dots. (**C**) Correlation of herbivore abundance with plot ground cover dissimilarity along axes 1 and 2 of a three-dimensional non-metric multidimensional scaling (NMDS) ordination using Bray-Curtis distance. Points are scaled according to percent bare ground, grass cover, and thatch (senesced grass) cover, respectively. I=intertrack, T=track; 1, 3, and 9 refer to number of feller buncher passes received.

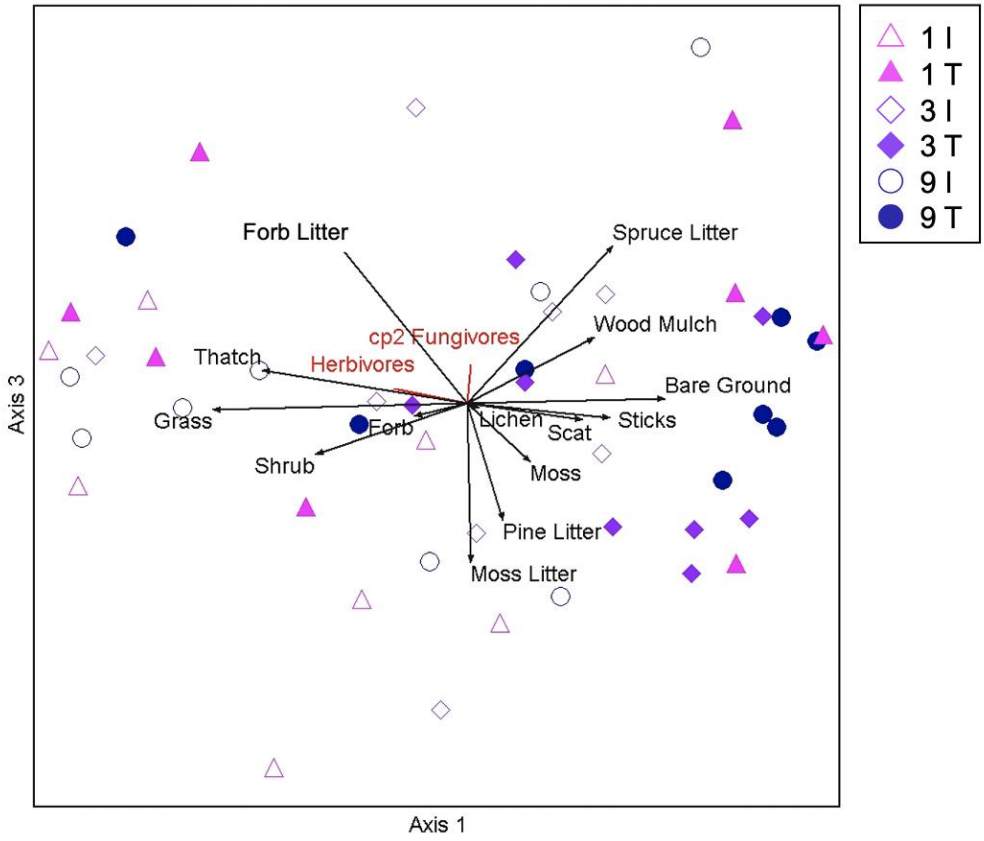

Fig. 3.8 Axes 1 and 3 of a three-dimensional non-metric multidimensional scaling ordination (stress=11.428) of plot ground cover. Cover classes are shown as black vectors, and nematode groups correlated with ground cover dissimilarity (R^2>0.1) are shown as red vectors. I=intertrack, T=track; 1, 3, and 9 refer to number of feller buncher passes received.

Table 3.2 Multi-response permutation procedure (MRPP) results for ground cover.

Ground cover		
	A	*p*
Overall group differences	0.0292	0.0521
1 pass (intertrack vs. treated)	-0.0306	0.9603
3 passes: intertrack vs. treated	0.0038	0.3708
9 passes: intertrack vs. treated	0.0524	0.0272*
1 pass intertrack vs. 9 pass treated	0.0629	0.0126*

Multi-response permutation procedure detected nematode community differences between track and intertrack locations only with nine passes (**Table 3.3**), and these differences were modest ($A < 0.08$). Ordination of nematode communities based on functional guilds

revealed correlations with ground cover, litter depth, and trench depth (**Fig. 3.9)**. Communities in nine pass track and nine pass intertrack samples were more variable than communities in one pass and three pass track and intertrack samples. The most pronounced difference in nematode communities was between the one pass intertrack samples and the nine pass track samples (**Table 3.3**), which might indicate effects of soil disturbance on adjacent "undisturbed" areas—for example, due to horizontal stress (Labelle and Jaeger, 2011) or to severed roots and hyphae. Similar patterns were evident in comparisons of ground cover across treatment levels (**Table 3.2**). However, these trends could also have resulted from spatial autocorrelation.

Table 3.3 Multi-response permutation procedure (MRPP) results for nematode communities from the compaction experiment. Overall group differences are for all treatment level comparisons (15 in total).

Functional guilds		
	A	*P*
Overall group differences	0.0292	0.0521
1 pass: intertrack vs. track	-0.0306	0.9603
3 passes: intertrack vs. track	0.0038	0.3708
9 passes: intertrack vs. track	0.0524	0.0272*
1 pass intertrack vs. 9 pass track	0.0629	0.0126*

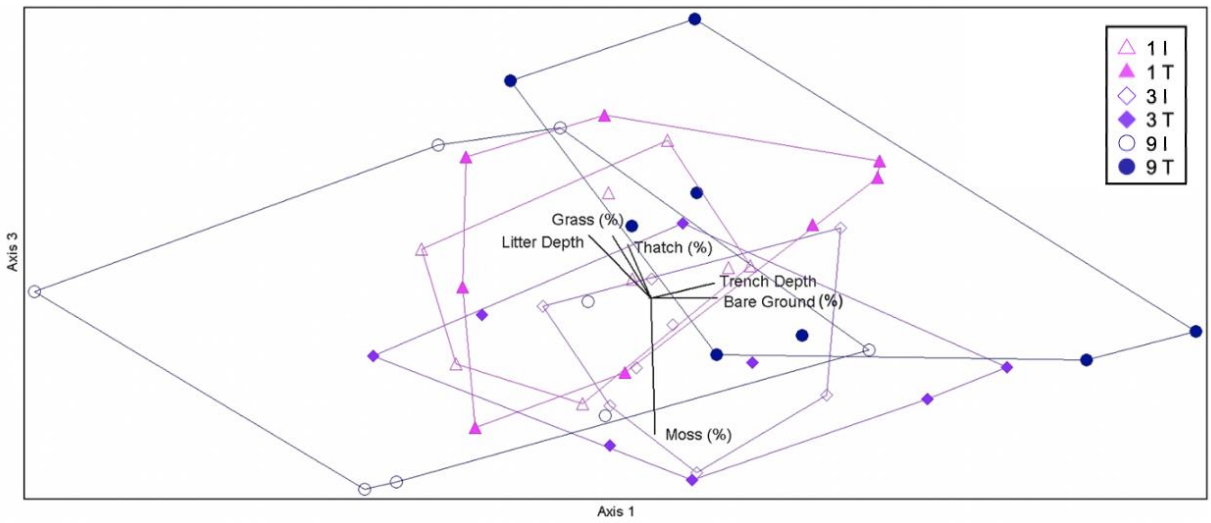

Fig. 3.9 Non-metric multidimensional scaling ordination based on nematode functional groups discriminated in this study. Axes 1 and 3 of a 3-dimensional solution (stress=10.870) are shown. R^2 cutoff for vectors is 0.1. I=intertrack, T=track; 1, 3, and 9 refer to number of feller buncher passes received.

3.4 Conclusions

Our study highlights the vulnerability of some soil types to deep compaction with even one pass from heavy logging machinery, emphasizing the importance of using the lightest effective equipment and minimizing the area it is driven upon. It is probable that compaction extended deeper into the soil profile than the maximum depth we measured (27 cm). This is concerning because recovery from compaction takes longer at depth: soils may recover within a few years from compaction near the surface, but compaction at 20-30 cm may persist for half a century or longer (Mohieddinne et al., 2019). At our study site, deep compaction also has implications for preservation of the endangered Jemez Mountains Salamander (*Plethodon neomexicanus*). These strictly terrestrial, lungless salamanders burrow below the surface to avoid desiccation during dry periods. Tree thinning in *P. neomexicanus* habitat is conducted only outside the seasonal window for surface salamander activity, but our findings question whether this precaution is adequate to avoid salamander mortality. We note, however, that our experimental transects were not covered with slash mats ahead of harvester passage, a common practice which provides some protection against soil compaction, especially when soils are wet (Han et al., 2006). On the other hand, the harvester in our study was not loaded with trees and the soil was partially frozen when treated, factors which likely mitigated compaction. We recommend that techniques for avoiding compaction (e.g., use of slash mats and thinning when soils are dry or frozen) should be evaluated *in situ* prior to treating large areas in *P. neomexicanus* habitat, especially where volcanic soils of moderate or fine texture occur.

In contrast to soil physical properties, nematode communities were not significantly impacted until soils had received nine passes from the feller buncher. Nematode responses to disturbance were predictable according to their life history characteristics, and only *K*-selected

taxa were negatively affected by soil disturbance. However, larger-bodied nematodes were not more sensitive than slender nematodes to changes in bulk density within the 0-10 cm interval we sampled, indicating that recovery of soil nematode communities may not depend on the recovery of soils from compaction. Our results suggest that nematode communities are relatively resilient to disturbance from heavy harvesters. If so, nutrient cycling, microorganism dispersal, and pest regulation services provided by nematode communities are unlikely to be impacted by moderate logging machinery traffic.

Acknowledgements

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CHAPTER IV: MODULATION OF THE GADGIL EFFECT BY SOIL MESOFAUNA IN THINNED/BURNED AND UNTREATED PONDEROSA PINE FORESTS

Abstract

Soil mesofauna likely influence the distribution and associated functions of fungal communities, but few manipulative studies have parsed the direct and indirect contributions of mesofauna to fungal-mediated ecosystem processes in the field. We used mesocosms of novel design to untangle relationships among microarthropods, fungal communities, and decomposition of labile (cellulose) and recalcitrant (wood) substrates in contrasting ecological contexts: thinned/burned and untreated ponderosa pine forest management units. Our mesocosms were engineered to manipulate microarthropod communities via mesh treatments while minimizing—and enabling measurement of—mesh treatment side effects. Because fungivorous microarthropods may preferentially graze saprotrophic hyphae over ectomycorrhizal hyphae, we hypothesized that they could influence decomposition indirectly by modulating the Gadgil effect (where ectomycorrhizal fungi decelerate decomposition by outcompeting saprotrophic fungi for nitrogen). This experiment also provided an opportunity to test the resource-ratio theory-based prediction of Smith and Wan (2019) that the Gadgil effect should occur in recalcitrant—but not labile—substrates. We anticipated, however, that decomposition of a labile substrate would be directly increased by comminuting (or fragmenting) microarthropods. We used multigroup structural equation modeling (SEM) to quantify direct and indirect effects of mesofauna on decomposition. After two growing seasons, our SEM indicated that medium and large mesofauna (> 150 µm) increased the ratio of ectomycorrhizal (EcM) fungi to litter and wood saprotrophic (LWS) fungi, but only in the thinned/burned management unit. This EcM:LWS ratio was the best

predictor of wood decomposition in the thinned/burned forest, where higher ratios were correlated with reduced decomposition, consistent with the Gadgil effect. However, we found no evidence of the Gadgil effect in the untreated forest, despite higher EcM:LWS ratios and higher densities of microarthropods there. Decomposition of the labile substrate was unaffected by the EcM:LWS ratio, as resource-ratio theory would predict. We also observed no effect of microarthropods on decomposition of the labile substrate, a result consistent with other reports from moisture-limited systems. Our findings suggest that the Gadgil effect may play out differently in contrasting ecological theaters, with decomposition rates determined by the stage (abiotic context and substrate recalcitrance) as well as the cast (communities of microarthropods and fungi).

4.1 Introduction

The tens to hundreds of thousands of collembolans and mites inhabiting a square meter of forest soil (Marra and Edmonds, 2005) contribute to ecosystem functions through direct and indirect mechanisms. Directly, comminution (fragmentation) of litter by some of these microarthropods (most of which are mesofauna: animals 0.1-2.0 mm in size) can accelerate decomposition and enhance leaching of low-molecular weight compounds into the soil, contributing to formation of stable soil organic matter (SOM) fractions (Soong, 2014). Indirect effects mediated by microbial communities, however, are theorized to be more important in many natural systems. Mesofauna are likely important dispersal vehicles for microbial propagules, and have been demonstrated to hasten recovery of microbial communities following disturbance (Maraun et al., 1998). Although mesofauna include representatives of many trophic groups, most taxa in forest soils are fungivores or fungivore/detritivores, and, thus, they have the potential to modulate ecological

processes by altering fungal abundance, community composition, and activity through grazing (A'Bear et al., 2014). "Choosy generalist" mesofauna may avoid unpalatable, poisonous, or structurally-protected fungal taxa (Böllmann et al., 2010; Klironomos and Kendrick, 1996; Maraun et al., 2003), potentially altering the enzymatic capabilities of fungal communities. For instance, fungivores may prefer saprotrophic hyphae over ectomycorrhizal hyphae (Pollierer and Scheu, 2021). Fungivore preferences thus have the potential to modulate the Gadgil effect (Gadgil and Gadgil, 1971): the oft-cited but highly variable depression of decomposition rates when ectomycorrhizal fungi are present (Fernandez and Kennedy, 2016). Whether fungivores suppress grazed fungi likely depends on grazing intensity and mycelial growth form (Crowther et al., 2011; Janoušková et al., 2018). Chemicals produced by some mesofauna may also reduce mycelial growth independently of grazing effects (A'Bear et al., 2010), although this phenomenon has been little investigated. Some ectomycorrhizal fungi, however, turn the tables by preying upon soil mesofauna, trading the nitrogen they acquire from their victims for carbon from their host plants (Klironomos and Hart, 2001).

Despite their presumed importance in regulating decomposition rates and structuring fungal communities, field measurements of the functional roles of soil mesofauna that can be causally dissected remain scarce because they are difficult to study and manipulate *in situ*. Microarthropod effects on fungal communities have most often been investigated in laboratory microcosm or greenhouse mesocosm studies featuring simplified faunal and fungal communities (A'Bear et al., 2014; Kampichler et al., 2001). These approaches provide only limited insight into complex natural systems, especially where processes may be strongly influenced by interactions between saprotrophic and mycorrhizal fungi. Meanwhile, the effects of microarthropods on decomposition have most commonly been investigated via litterbag

experiments. In a meta-analysis of 40 years of litterbag experiments testing microarthropod effects on decomposition, Kampichler and Bruckner (2009) made the disconcerting observation that none of the 101 experiments surveyed had accounted for the potential side effects of faunal exclusion treatments. Noting that the mean effect size estimate from studies employing insecticide treatments (most commonly naphthalene, which has substantial nontarget effects on microbial communities (Lan et al., 2019; Tan et al., 2019)) was approximately twice that of studies using mesh size differences (which alter microclimate), and that applying a correction factor for side effects could change the sign of microarthropod effects, they concluded that the real contribution of microarthropods to decomposition could not be assessed. More than a decade later, it appears that side effects remain largely unaccounted for in field studies examining mesofauna effects on decomposition.

Similarly, the context-dependency of ecological functions performed by mesofauna remains little explored. The magnitude, drivers, and even the direction (positive or negative) of faunal effects on soil processes are probably dependent on biotic and abiotic context (Briones, 2014). In fire-adapted dry forests of the Southwest, restoration of overcrowded second-growth stands with thinning followed by low-severity burning is likely to alter many biotic and abiotic characteristics relevant to food web function. Organic matter and litter are reduced by reintroduction of fire, while available N is increased ephemerally (Sánchez Meador et al., 2017). Thinning also alters soil moisture and increases soil temperature. Perhaps most importantly, both fungal (Reazin et al., 2016; Smith et al., 2005) and faunal (Camann et al., 2012; Gibson et al., 2022) communities are expected to shift following restoration treatments. Thinning should reduce the relative abundance of ectomycorrhizal fungi (EcM) and increase the relative abundance of litter and wood saprotrophs (LWS). Forest restoration treatments could thus reduce the strength of the Gadgil effect. Mesofauna communities in early-successional restored forests,

meanwhile, should be taxonomically simpler and include fewer individuals relative to untreated late-successional forests. These changes could alter interactions between mesofauna communities and fungal communities while reducing the direct contribution of mesofauna populations to decomposition. Propagule dispersal by soil fauna might, however, be especially important in recently burned soils if fungi are patchily distributed in the typical post-fire habitat mosaic.

Our objective was to address knowledge gaps regarding the functional importance of soil mesofauna in complex natural communities by examining their effects on fungal functional groups and decomposition in contrasting ecological contexts. Our hypotheses are graphically summarized in **Fig. 4.1**. We predicted that mesofauna would increase the ratio of EcM to LWS fungi because we expected them to exert stronger grazing pressure on the latter than the former (*H1*). Microarthropods were expected to directly increase decomposition of a labile substrate (cellulose) via comminution (*H2*), but to have negligible direct effects on decomposition of a recalcitrant substrate (wood) because comminuting microarthropod should prefer labile substrates (*H3*). However, we hypothesized that microarthropods would decrease decomposition of wood indirectly, by intensifying the Gadgil effect (*H4*). According to Smith and Wan (2019), resource-ratio theory (Tilman, 1982) predicts that the Gadgil effect should occur only in recalcitrant substrates, where EcM fungi can outcompete LWS for N. We, therefore, did not anticipate an effect of EcM:LWS ratios on cellulose decomposition (*H5*). Finally, we speculated that hypothesized microarthropod and Gadgil effects (*H1*, *H2*, and *H4*) would be weaker in thinned/burned than in untreated ponderosa pine forests (*H6*) given the ways restoration treatments were predicted to alter microarthropod communities (reducing abundances) and fungal communities (reducing EcM:LWS ratios).

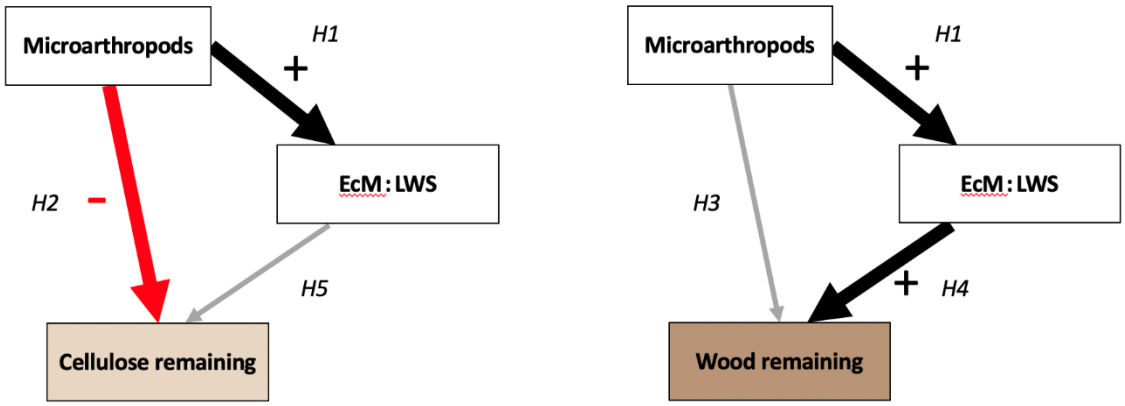

Fig. 4.1 Hypothesized effects (*H1-H5*, described in the main text) of microarthropods on decomposition of wood and cellulose substrates via direct and indirect pathways. EcM=ectomycorrhizal fungi; LWS=litter and wood saprotrophs. Important hypothesized positive pathways are shown in black, and important negative pathways are shown in red. Gray pathways were hypothesized to be unimportant.

We tested these hypotheses using field mesocosms of novel design, deployed for two growing seasons in thinned/burned and untreated ponderosa pine forests in the US state of New Mexico. We manipulated soil mesofauna communities in these mesocosms using three mesh treatments (21 µm, 41 µm, and 1000 µm mesh opening sizes) designed to restrict recolonization of defaunated soil and litter according to faunal size class, plus a fourth treatment of 1000 µm mesh with root severing to account for ingress of roots to 1000 µm mesh mesocosms (**Fig. 4.2**). We characterized soil fungal communities and microarthropod communities at the conclusion of our study and measured decomposition of cellulose and wood standard substrates. Our mesocosms were constructed to minimize mesh treatment side effects while also allowing quantification of interior soil moisture differences over time (details in methods).

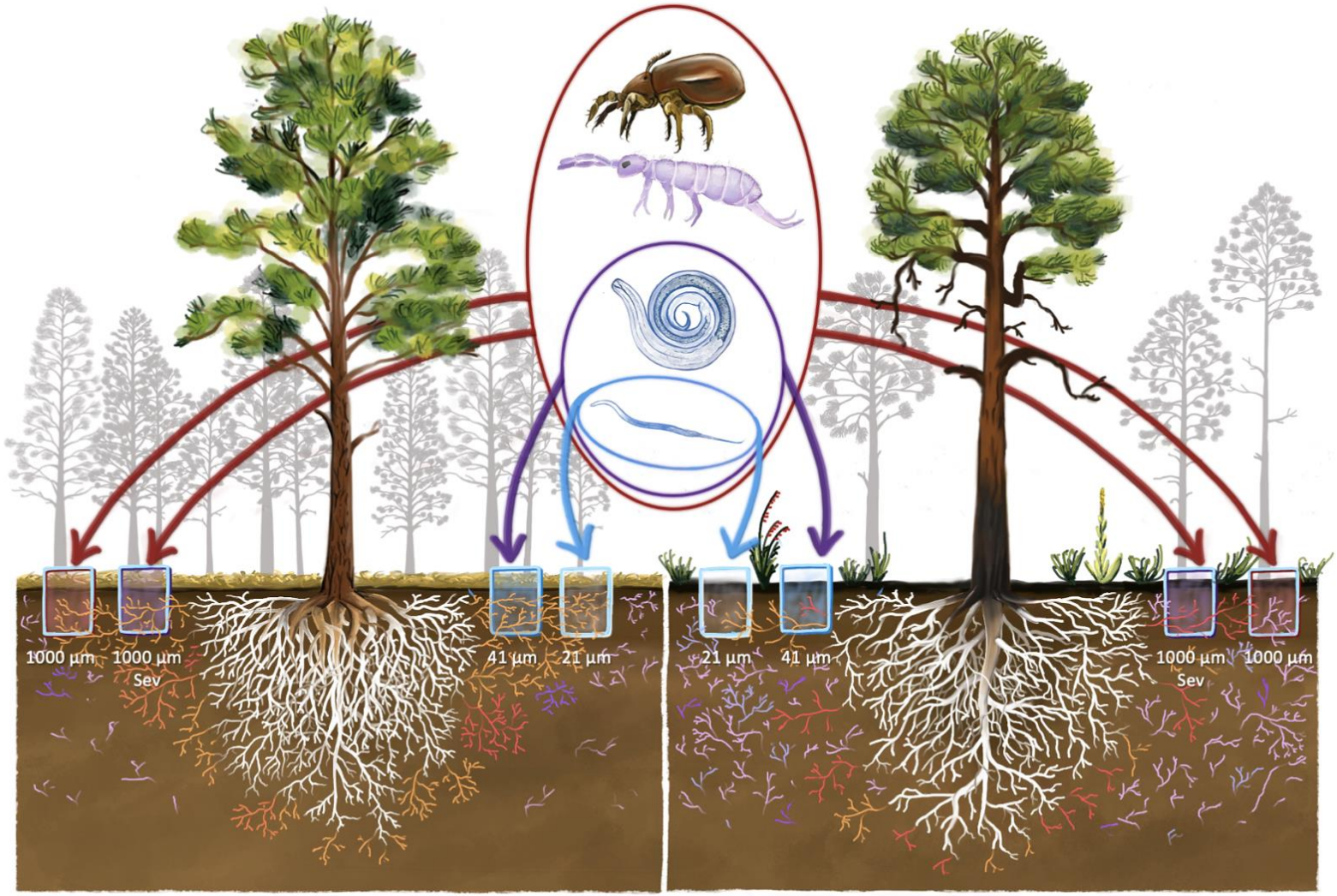

Fig. 4.2 Overview of our field mesocosm treatments. At ponderosa pine driplines in untreated (left) and thinned/burned (right) forest management units, we installed mesocosms designed to allow colonization by microfauna only (21 µm mesh and 41 µm mesh) or by microfauna and mesofauna (1000 µm mesh). Because roots could access the 1000 µm mesh mesocosms, we also included a fourth treatment of 1000 µm mesh treatment with root severing (1000 µm Sev).

4.2 Methods

4.2.1 Study sites

The study was conducted at Valles Caldera National Preserve in the US state of New Mexico within the Banco Bonito area (**Fig. 4.3**). Soils in this area are sandy loams to loamy sands (Gibson et al., 2022) formed by a rhyolite lava flow ~68,000 years ago (Goff, 2009) and belonging to the Totavi-Jemez-Rock Outcrop association (Hacker and Banet, 1987). Annual precipitation averaged 590 mm from 1981–2010, and the mean annual temperature for this period was 6.6 °C, with monthly mean temperatures ranging from -2.3 °C in January to 17 °C in July (PRISM, 2021). However, during the period encompassing our field experiment the area experienced abnormally low precipitation, receiving only ~60% of its average (PRISM, 2021). Mesocosms were installed within two adjacent ponderosa pine forest management units at different treatment stages, hereafter referred to as the thinned/burned unit and the untreated unit (characterized in Gibson et al., 2022). In 2012, the thinned/burned unit was thinned to a mean tree density of ~60 trees ha^{-1}, with larger trees retained. Marketable timber was removed, and remaining woody residues were masticated. A low-intensity broadcast burn was conducted in October of 2015. The untreated unit was separated from the thinned/burned unit by an old logging road and retained ~300 trees ha^{-1}. Mesocosm installation areas with similar topography and soil texture, each measuring approximately 1 ha, were established immediately across the logging road from one another in each of the management units.

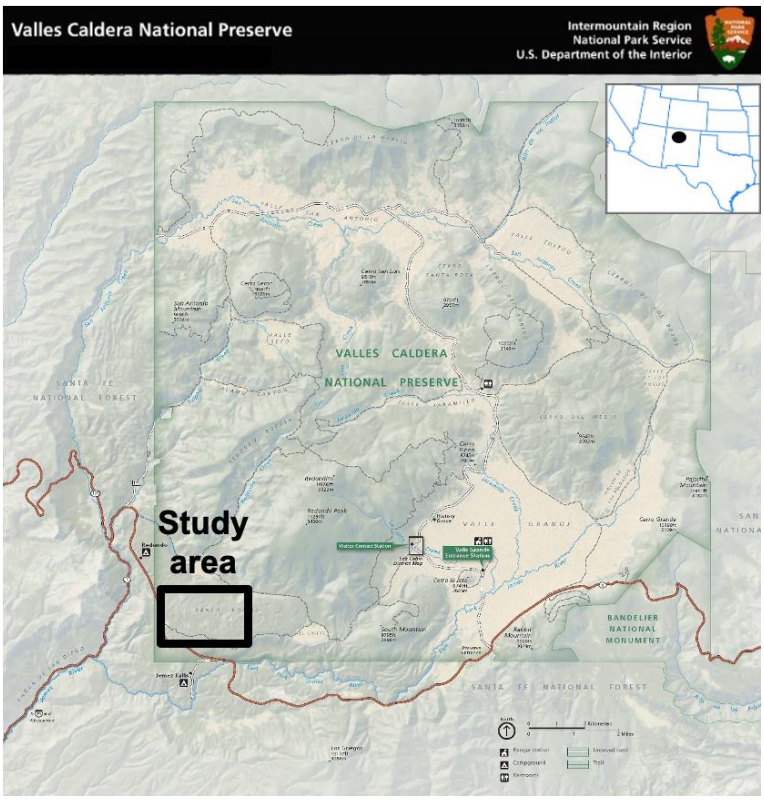

Fig. 4.3 Location of study area within Valles Caldera National Preserve and New Mexico.

4.2.2 Experimental design

Twelve trees per management unit with diameters at breast height between 34.4 - 55.4 cm were selected to serve as blocks. At each of these trees, we installed mesocosms filled with defaunated soil and litter. Mesocosm treatments were designed to permit recolonization by either small microfauna only (21 µm mesh); small and medium sized-microfauna including most nematodes, but not mites (41 µm mesh); all micro- and mesofauna but not roots (1000 µm mesh with monthly root severing, hereafter referred to as "1000 µm Sev"); or all micro- and mesofauna and roots (1000 µm mesh without root severing). One replicate of each mesocosm treatment was installed at each tree, in randomly assigned order, for a total of 96 experimental mesocosms. Six of these trees per study area were randomly selected to receive one additional replicate of each

mesocosm treatment for periodic destructive monitoring of recolonization by soil fauna (hereafter "sacrificial mesocosms", 48 in total). Four of the remaining trees in each study area were randomly selected for installation of three types of technical check units (24 technical check units in total) to quantify any side effects of mesocosm physical structure and root severing on soil properties and biota. "Severed disturbed technical checks" (DTC Sev) and "unsevered disturbed technical checks" (DTC) consisted of mesocosm-sized holes refilled with defaunated soil and covered with defaunated litter, with or without root severing, and "undisturbed technical checks" (UTC) consisted of intact forest floor equivalent in area to a mesocosm.

4.2.3 Mesocosm construction and installation

Five large windows were cut in the walls of 25 cm long sections of PVC sewer pipe with an internal diameter of 20.32 cm, then polyester mesh with hole sizes of either 21 µm, 41 µm, or 1000 µm was wrapped around the exterior of the mesocosms (**Fig. 4.4A**). We selected these mesh sizes because we originally aimed to manipulate nematode community complexity as well as microarthropod community complexity. Diameters of common small nematodes at this site range from 12.5-15 µm and most nematodes are at least 25 µm in diameter, while the smallest mites are approximately 46 µm in diameter. No mite or collembolan taxa measuring > 1 mm in diameter were encountered in the course of our earlier work at this site.

The bottoms and caps of all mesocosms were constructed identically to equalize drainage, infiltration, and albedo. Mesocosm bottoms were covered with 21 µm mesh and reinforced with PVC-coated fiberglass window screen to provide additional structural support (**Fig. 4.4B**). Tight-fitting removable caps (**Fig. 4.4C** and **Fig. 4.4D**) were assembled from vinyl

flashing and 41 µm mesh, chosen for its superior permeability to precipitation versus 21 µm mesh and because few soil microfauna were expected to colonize mesocosms from aboveground. Mesh was glued to surfaces with all-weather 100% silicone caulk. A ring of Fluon PTFE insect barrier (byFormica, Warner Robins, Georgia, USA) was applied above the windows to prevent climbing arthropods from entering the tops of the mesocosms.

Mesocosms were installed in June 2019 at tree driplines in semi-circular arrays centered on their southern aspects, at intervals of 50 cm, or greater if necessary to avoid understory vegetation (**Fig. 4.5**). If woody debris longer than mesocosm width but not covering more than half of the mesocosm footprint was present, the debris was moved. At each mesocosm location, litter and O horizon layers were collected separately using a segment of the sewer pipe with a sharpened end as a coring guide. Holes for the mesocosms were dug to 15 cm below the mineral soil surface with a 20.3 cm soil auger and the excavated soil was sieved to 5.6 mm and homogenized. Mineral and O horizon soil and litter were defaunated following a modified version of Franco et al.'s (2017) method for nematode exclusion. Briefly, soil and litter were placed in aluminum steam table pans, pre-wetted and allowed to incubate for 24 hours at ambient temperature, then heated at 65 °C for 3 days. Following this treatment, litter and O horizon soils were additionally frozen to -20 °C for at least 48 hours, because we expected fauna in these layers to be more resistant to heating than fauna in mineral soil. Mineral soil was sieved once more to 1.25 cm to break up hardened blocks that resulted from heating.

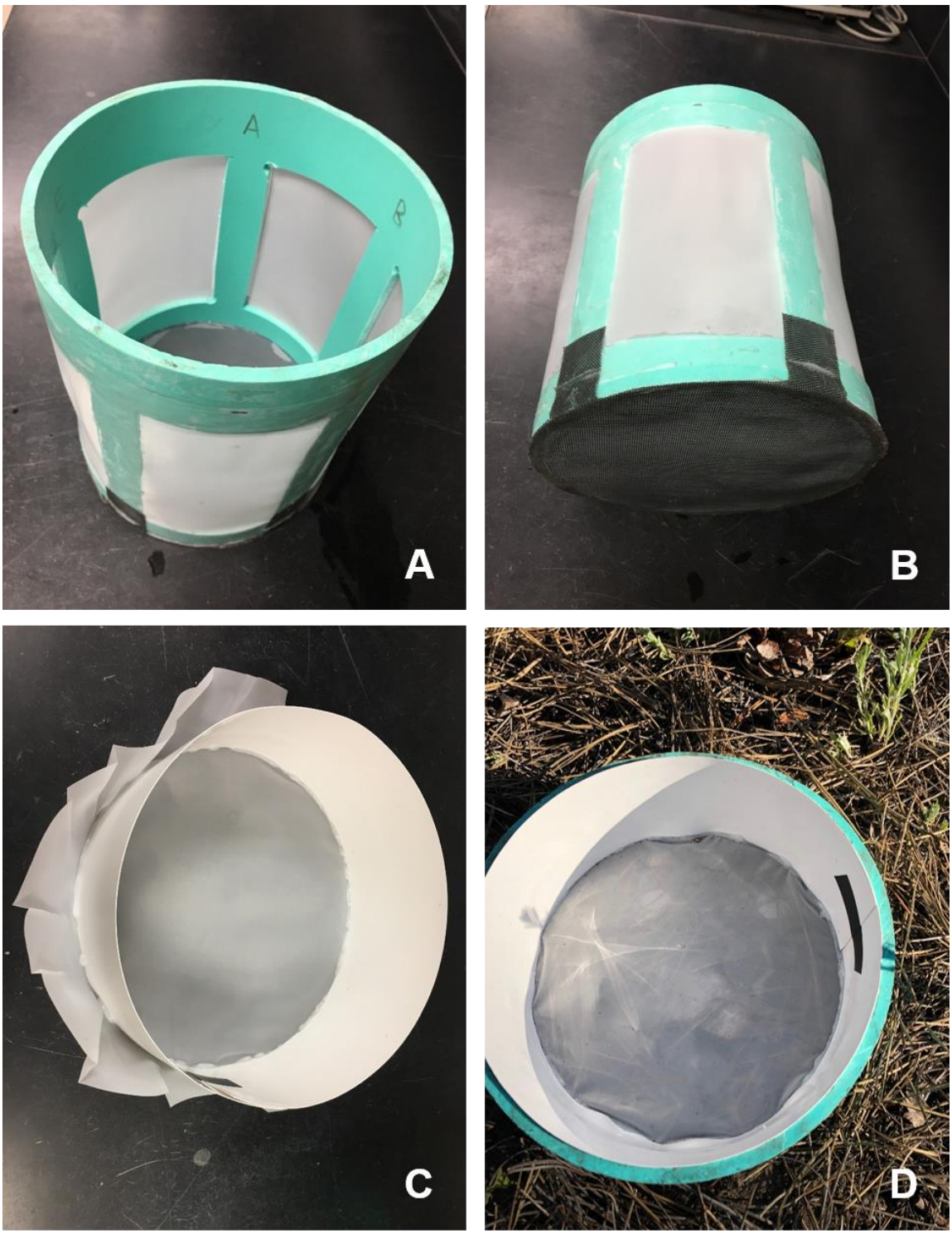

Fig. 4.4 Top (**A**) and bottom (**B**) views of mesocosms assembled from PVC sewer pipe, polyester mesh, and PVC-coated fiberglass window screen. Caps constructed from 40 µm mesh and vinyl flashing before (**C**) and after (**D**) installation of mesocosms.

Fig. 4.5 Experimental and sacrificial mesocosms at the dripline of a tree in the thinned/burned management unit. Other trees in the study, flagged with orange tape and marked with stars, are visible in the background.

Empty mesocosms were buried to a depth of 15 cm below the mineral soil surface and capped until defaunation of soil and litter was completed. Immediately prior to filling, the interiors of the mesocosms were sprayed with 70% ethanol to ensure no live fauna were present inside. Defaunated mineral soil, O horizon soil, and litter layers were returned to their trees of origin and used to fill mesocosms and the holes designated for disturbed technical checks. We leveled soil and distributed litter to maximize contact between interior and exterior soil and litter layers. Decomposition bags containing standard wood and cellulose substrates (described below) were placed between the litter and O horizon layers. Finally, the mesocosm caps were replaced, and petroleum jelly was applied between the flashing and the interior walls of each mesocosm to prevent fauna from entering through this crevice. During the growing season, we severed roots monthly to a depth of 20 cm around the root-exclusion treatment 1000 µm Sev mesocosms (smaller mesh sizes did not allow root entry) and around DTC Sev units.

4.2.4 Defaunation efficacy verification

We verified defaunation efficacy by extracting nematodes (which we presumed would be more resistant to the defaunation procedure than microarthropods) from subsamples of mineral soil retained from each tree during mesocosm installation. Subsamples were transported on ice to Northern Arizona University in Flagstaff, Arizona, and stored at 4 ℃ until extraction 10-19 days after mesocosms were filled. Nematodes were extracted from 100 cc soil using a combination of decanting and sieving and modified Baermann trays ("nematode rafts"; Gibson et al., 2019) and were retrieved from the trays after 48 and 72 hours. Extracted nematodes were refrigerated unpreserved and examined using a dissecting microscope at 40X magnification within one week of extraction. No nematodes were detected in 22 of the 24 samples, but the two remaining

samples each contained one nematode. The effects of sieving and defaunation on nitrogen availability were determined from analysis of three replicate samples of unsieved, sieved, and defaunated soil collected from each study site. Ammonium and nitrate were extracted according to Keeney and Nelson (1982) and analyzed via colorimetry (Wendt, 1999) using a Hach QuickChem 8500 analyzer with an ASX-500 series autosampler.

4.2.5 Decomposition disks

We used 100% cotton museum board (predominantly cellulose) and balsa wood as standard labile and recalcitrant substrates (Neher et al., 2003) to quantify the influence of faunal complexity on decomposition. Balsa wood (~1 mm thick) and museum board (~1.75 mm thick) disks with a diameter of 2.22 cm were dried at 60 °C, weighed, and placed in polyester mesh bags with openings of 1 mm. Each bag contained one disk of each type. We buried five decomposition bags in each mesocosm (except sacrificial units) beneath the litter layer. Decomposition bags were also placed at technical check units, over which we secured chicken wire to reduce disturbance of the bags.

4.2.6 Mesocosm monitoring and measurement of response variables

To prevent cross-contamination, all measurements and sampling activities were performed with tools and gloved hands that were sanitized with 70% ethanol between mesocosms. While their lids were removed at sampling timepoints, mesocosms were temporarily covered with sanitized plates that were removed only briefly to perform sampling activities. One replicate decomposition bag was collected from within each mesocosm and technical check unit in September 2019 (T1; the end of the monsoon season), April 2020 (T2; the end of winter), July

2020 (T3; the end of the dry season), August 2020 (T4; the height of the monsoon season), and September 2020 (T5; one year after the first sampling). We measured soil moisture at each timepoint using a portable probe (ML3 ThetaProbe with HH2 soil moisture meter; Delta-T Devices, Cambridge, UK), and soil temperature at the first timepoint, to quantify microclimate differences across mesocosm treatments. Temperature measurements were discontinued after the first timepoint because no temperature differences were detected across mesocosm treatments.

4.2.7 Colonization monitoring of sacrificial mesocosms

Sacrificial mesocosms were destructively sampled for nematodes and microarthropods at T1 and T3. Samples for nematode extraction were collected from the uppermost 10 cm of soil (including mineral and O horizons, but not litter) using a 2.54 cm diameter probe, and samples for microarthropod extraction (including the top 10 cm of soil and the overlying litter layer) were obtained using a 5.08 cm diameter corer. Microarthropod and nematode soil samples were transported on ice to Northern Arizona University and stored at 4°C until processing. Nematodes were extracted as described above and preserved in DESS solution (Yoder et al., 2006), then were enumerated under a dissecting microscope at 40X magnification. Microarthropods were extracted using high gradient Tullgren funnels with 15-watt bulbs over 7 days. Light intensity was gradually increased over 5 days, then held at maximum brightness for two days. Extracted animals were preserved in 70% ethanol. Microarthropods from sacrificial mesocosms were counted at 40-50X and categorized as mites, collembolans, or “others” (all other arthropods); additionally, we noted whether mites in the suborder Brachypylina (order Oribatida) were present (this is a diverse and often numerically dominant group of oribatids with adult body sizes typically >200 µm).

4.2.8 Final harvest

We destructively sampled all mesocosms and technical checks (with the exception of two mesocosms in the thinned/burned management unit which were compromised by mammal activity) at T5 to characterize final faunal and fungal communities and quantify ammonium, nitrate, and soil organic matter (SOM) content. Microarthropods were extracted and preserved as detailed previously, then were filtered using a 300 µm sieve. Microarthropods captured on this sieve were counted, and mites and collembolans were sorted to morphospecies. This size cutoff is used by the Alberta Biodiversity Monitoring Institute (2009) in their microarthropod inventories, and separates juveniles from identifiable adults for most taxa in the most speciose order of mites, the Oribatida. Microarthropods passing through the 300 µm sieve were separated into small (<150 µm) and medium (>150 µm and <300 µm) size classes by further filtration with a 150 µm sieve. The medium size class included several species belonging to the oribatid cohort Brachypylina, which were tallied separately; all other small and medium mites were enumerated but not identified. Collembolans in the small and medium size classes were classified as pigmented or non-pigmented. As for samples from sacrificial mesocosms, arthropods (proturans, thrips, spiders, enchytraeids, ants, termites, and insect larvae) not belonging to the Acari or Collembola were categorized as "others". Others were infrequently encountered: a total of 24 individuals were counted in mesocosms and technical checks in the thinned/burned management unit, and 94 individuals in the untreated management unit (with 33 of these individuals occurring in the same mesocosm). Because they were rare and comprised taxa with highly variable functional roles, others were not included in analyses except where otherwise noted.

Soil samples for determination of SOM, ammonium, and nitrate content were collected in envelopes and stored in closed containers with silica beads to air dry in the field, then were sieved to 2 mm prior to analysis. Ammonium and nitrate were extracted and quantified as described above. Soil organic matter was measured by loss on ignition from 5 g soil at 450 °C for 24 hours (Bisutti et al., 2004). Soil for fungal community analysis was transported from the field on dry ice and stored at -20 °C upon return to Northern Arizona University. We extracted DNA from these samples using Qiagen DNeasy PowerSoil kits (Germantown, MD USA).

Fungal community analysis was performed at the Arizona State University Genomics Core via next generation sequencing of the ITS region using the MiSeq Illumina platform. They used the barcoded primer set ITS1f-ITS2 (Smith and Peay, 2014) and followed the Earth Microbiome Project protocol (http://www.earthmicrobiome.org/emp-standard-protocols/) for library preparation. PCR amplifications for each sample were performed in duplicate, then pooled and quantified using Accublue® High sensitivity dsDNA Quantitation Kit (Biotium). A no-template sample was included during the library preparation as a control for extraneous nucleic acid contamination. 200 ng of DNA per sample was pooled and then cleaned using QIA quick PCR purification kit (QIAGEN). The pool was quantified by Illumina library Quantification Kit ABI Prism® (Kapa Biosystems), diluted to a final concentration of 4 nM, then denatured and diluted to a final concentration of 4 pM with a 25% of PhiX. Finally, the DNA library was loaded in the MiSeq Illumina and run using the version 2 module, 2x250 paired-end, following the directions of the manufacturer.

4.2.9 Fungal sequence data preparation

Microbiome bioinformatics were performed at the Arizona State University Biodesign Institute's Bioinformatics Core using QIIME 2 2020.8 (Bolyen et al., 2019). Raw sequence data were demultiplexed and quality filtered using the q2-demux plugin followed by denoising with DADA2 (Callahan et al., 2016) (via q2-dada2). All amplicon sequence variants (ASVs) were aligned with mafft (Katoh et al., 2002) (via q2-alignment) and used to construct a phylogeny with fasttree2 (Price et al., 2010) (via q2-phylogeny).

Taxonomic assignments were made by querying the 10,157 ASVs against GenBank's "internal transcribed spacer region (ITS) from Fungi type and reference material" database via basic local alignment sequence tool (BLAST) search using OmicsBox (Biobam Bioinformatics, 2019). We assigned sequences to the genus of the top BLAST match if both query cover and percent similarity were ≥ 90% (Nilsson et al., 2019). Sequences meeting match criteria for assignment to genus comprised an average of 52% of total sequences per sample (range: 2% - 96%); boxplots summarizing the percentage of classified sequences in each treatment combination are shown in **Fig. S4.1**. Lifestyle classifications for fungal genera were obtained from the FungalTraits database (Põlme et al., 2020). We classified genera as LWS that had primary or secondary lifestyles as litter or wood saprotrophs.

4.2.10 Statistical analyses

4.2.10.1 Mesh and forest management treatment effects and their interactions

Effects of mesh treatment, ponderosa forest restoration treatment, and mesh x ponderosa forest restoration treatment interactions on soil physical, chemical, and biotic response variables were assessed with two-way ANOVA. Where necessary, response variables were log transformed

(after adding 1 to all observations if there were 0 values) or transformed by arcsin of the square root (percent data) to meet model assumptions of normality and homogeneity of variance. We performed *F*-tests comparing main effects models (response variable ~ management treatment + mesh treatment) with interaction models (response variable ~ management treatment + mesh treatment + management treatment * mesh treatment) and included the interaction term when $p < 0.1$. *P*-values for post-hoc multiple pairwise comparisons were adjusted using Tukey's test of honestly significant differences. ANOVA analyses were conducted in R version 4.0.3 (R Core Team, 2020) and data were visualized as boxplots using ggplot2 (Wickham, 2011). We did not plot outliers if doing so would have required compression of the y-axis to an extent impeding visual discrimination of treatment patterns; figure captions note which plots omit one or more outliers.

4.2.10.2 Multivariate analyses of faunal and fungal communities

We used multi-response permutation procedure (MRPP) to assess faunal and fungal community differences between forest management units and mesh treatments. MRPP is a non-parametric test for differences among *a priori* groups and yields the statistic *A*, the chance-corrected proportion of between-sample distances explained by group identity (McCune and Mefford, 2011). *A* will equal 1 when all samples within groups are internally identical, but groups are distinct, and 0 if heterogeneity within groups is equal to the chance expectation. $A < 0$ indicates more within-group heterogeneity than should be expected to occur by chance, while $A > 0$ if there is more agreement within groups than should occur by chance (i.e., if differences between groups are likely to exist). MRPP tests were performed with total abundances of mite and collembolan morphospecies >300 µm; with abundances of oribatid mites > 150 µm; with fungal

reads assigned to genera as a percentage of total reads in each mesocosm (relative abundance of fungal reads by genus); and with relative abundance of fungal ASVs. All MRPP analyses were performed using Bray-Curtis as the distance measure.

We performed indicator species analyses (ISA) following the method of Dufrêne and Legendre (1997) to determine which taxa best explained treatment patterns. We conducted separate analyses of microarthropod morphospecies and size/broad group categories (as applicable for small, medium, and large size classes) and of fungal genera. Indicator species analyses of microarthropod groups were performed using total abundance, while relative abundance was used for fungal analyses. Indicator species analyses for mesh treatments (fine vs. coarse mesh, and all mesh treatments) were run separately for mesocosms in untreated and thinned/burned restoration treatments.

Microarthropod community differences were visualized using nonmetric multidimensional scaling (NMDS) ordination, performed using Bray-Curtis distance. Fungal community differences based on ASVs were visualized using principal coordinates analysis (PCoA) based on Bray-Curtis distance using q2-diversity after samples were rarefied (subsampled without replacement) to an average of 15,000 sequences per sample.

All multivariate analyses were conducted in PC-ORD (McCune and Mefford, 2011) with the exception of PCoA, which was performed using QIIME 2 (Bolyen et al. 2019). For MRPP and NMDS based on oribatids and microarthropods > 300 µm, we added a dummy variable column containing 1 for all rows to the main matrix prior to analysis since some samples contained no microarthropods > 300 µm.

4.2.10.3 Structural equation models

Because we hypothesized that forest restoration treatments would alter the influence of fauna on fungal communities and decomposition, we used multigroup structural equation models (SEMs (Grace, 2006; McCune et al., 2002)) to parse effects of mesh treatments, soil characteristics, and microarthropod abundances on fungal communities and decomposition within the thinned/burned and untreated management units. This approach enabled us to disentangle hypothesized direct and indirect effects, account for side effects of mesocosm mesh treatments on soil moisture, and compare effect sizes between forest management treatments. Effect sizes in SEMs are quantified as path coefficients, which when standardized are mathematically equivalent to either partial regression coefficients or correlation coefficients (Grace, 2006); the R^2 reflects the proportion of variance explained by upstream predictors. Structural equation models were constructed in AMOS (Arbuckle, 2019). Several goodness-of-fit tests are used to assess whether the covariance structure implied by the architecture of an SEM is consistent with the covariance structure of the data; unlike most hypothesis tests, high *P*-values for the maximum likelihood χ^2 goodness-of-fit test, adjusted goodness of fit index (AGFI), and Bollen-Stine bootstrap test (Bollen and Stine, 1992) are considered desirable (in other words, high *P*-values indicate that the hypothesized model structure fits the data well). Good model fit is indicated by low *P*-values for the root mean square error of approximation (RMSEA) index.

We fit separate multigroup models for cellulose decomposition and wood decomposition because we hypothesized that bacteria (unmeasured in this study) would be important drivers of cellulose decomposition, but not of wood decomposition. We did not include technical checks in the SEMs as they were replicated at only one quarter of trees (blocks). Prior to analysis, distributions were examined visually for normality, and bivariate relationships between modeled

variables were checked for linearity, very strong correlations, and influential outliers. Variables were log transformed when necessary to meet normality assumptions. Soil moisture was modeled as the mean Z score for each mesocosm over the five monitoring timepoints to account for seasonal variability in moisture values. One missing SOM value was imputed by averaging.

We used the mean proportion of wood and cellulose remaining from the final two monitoring timepoints (T4/day 426, and T5/day 458) as our measure of cumulative decomposition. One lignin observation from T4 and one cellulose observation from T5 that were extreme outliers were removed, and the observation from the remaining timepoint was used alone for that mesocosm. Similarly, the observation from the remaining timepoint was used when the other disk was damaged (one cellulose disk) or could not be located in the field (disks of both types from one missing decomposition bag). We are confident that these missing observations did not bias our model estimates because proportion mass remaining did not differ between T4 and T5 for either cellulose (Welch two-sample T-test: t = 0.824, df = 181.7, p = 0.411) or wood (t = 0.18995, df = 151.79, p = 0.850).

Our *a priori* SEM based on hypothesized relationships among mesocosm treatments, soil organic matter, soil moisture, microarthropod abundances, ratios of EcM to LWS fungi, and decomposition of wood and cellulose is shown in **Fig. 4.6**. We expected that fine mesh opening sizes would reduce colonization by microarthropods but increase soil moisture, and that soil organic matter would also increase soil moisture. We further anticipated that soil moisture and soil organic matter would influence microarthropod abundances, fungal communities, and decomposition.

Before building multigroup models, we fit separate models for wood and cellulose decomposition using data from the thinned/burned and untreated management units (four models

in total) to ensure that our *a priori* model fit the data well. We then repeated this process with two alternate versions of the *a priori* model (**Fig. S4.2**) that additionally included available nitrogen or small microarthropods to determine whether these variables should be added. After fitting all three *a priori* model configurations (resulting in 12 total models), we elected to exclude available nitrogen and small microarthropods because they did not increase the explanatory power of the models or, in most cases, improve model fit. The final multigroup models for wood and cellulose decomposition were built by beginning with an initial model in which all paths were constrained (paths in untreated and thinned/burned groups were not allowed to differ) and then incrementally unconstraining the paths with the largest standardized residual covariances until doing so reduced χ^2 by < 2.

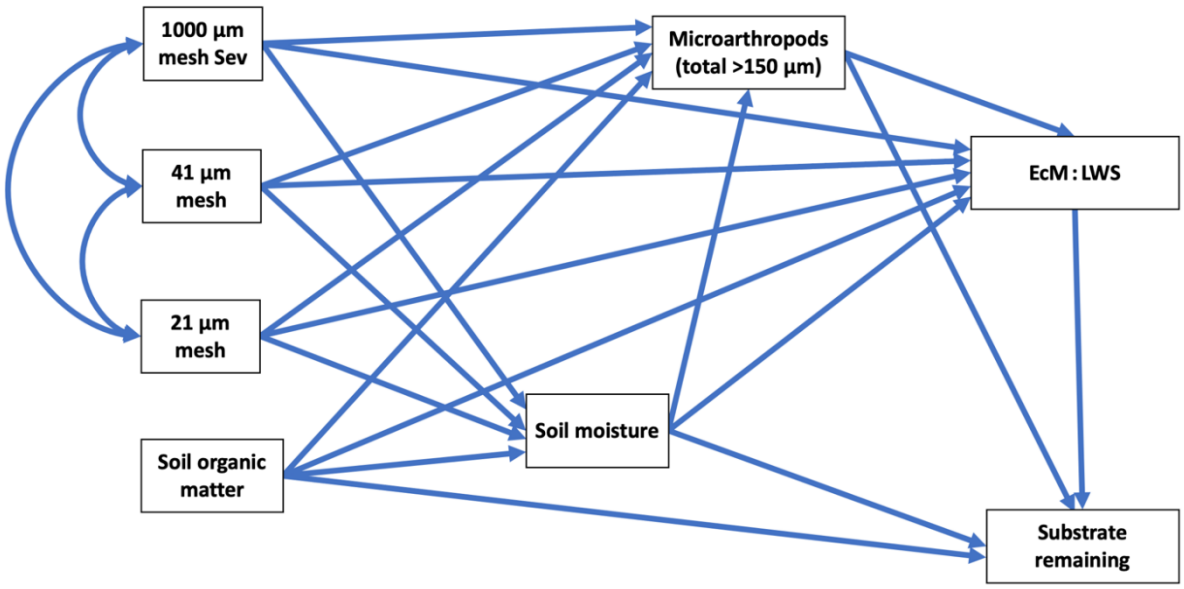

Fig. 4.6 *A priori* structural equation model. The unsevered 1000 µm mesh mesocosm treatment is the reference group for mesh treatments. EcM:LWS =ratio of ectomycorrhizal fungi to litter and wood saprotrophs.

4.3 Results

4.3.1 Manipulation of soil faunal complexity

4.3.1.1 Sacrificial mesocosms

Monitoring of sacrificial mesocosms at T1 and T3 showed some colonization of fine mesh mesocosms by very small microarthropods but indicated continued efficacy of mesh treatments at maintaining microarthropod community complexity differences (**Table 4.S1)**. Importantly, mites in the speciose, abundant, and generally large-bodied oribatid suborder Brachypylina were absent from all but one of the fine mesh sacrificial mesocosms. However, examination of nematodes collected at T1 revealed that 21 µm mesh mesocosms were already colonized by large nematode taxa (**Fig. S4.2**), and nematode community composition did not differ among mesocosm mesh treatments (MRPP based on morphospecies at T1: $A < 0.01$, $p > 0.3$ for pairwise comparisons of 21 µm vs. larger mesh sacrificial mesocosms in untreated control and thinned/burned units). We thus focus all further analyses on microarthropod community differences and not on nematode community differences.

4.3.1.2 Final faunal community complexity

Mesocosm mesh treatments maintained differences in microarthropod community complexity until final harvest at day 458 of our study. Two-way ANOVA results for animal abundances are listed in **Table 4.1**. Fine mesh mesocosms with 21 µm and 41 µm mesh hosted significantly fewer mites > 150 µm in both thinned/burned and untreated management units (**Fig. 4.7A**); abundance of collembolans > 150 µm was similar in 41 µm and 1000 µm mesocosms, especially within the untreated unit, but was greatly reduced in 21 µm mesh mesocosms within both management units (**Fig. 4.7B**). Fine mesh treatments were particularly effective in excluding

mites in the Oribatida (**Fig. 4.7C**). Mesh treatments were less successful, however, at manipulating small microarthropods. Abundance of mites < 150 µm (**Fig. 4.8A**) was similar across mesh treatments, and within the thinned/burned unit tended to be elevated in the 1000 µm mesocosms, indicating possible responsiveness of mites in this size class to roots or rhizosphere resources. Collembolans < 150 µm were significantly reduced (relative to other mesh treatments within the same forest management unit) only within 21 µm mesh mesocosms in the untreated management unit (**Fig. 4.8B**). In summary, mesh treatments effectively manipulated abundances of medium and large microarthropods > 150 µm, but not small microarthropods < 150 µm.

Morphospecies richness of microarthropods > 300 µm was also greater in coarse than in fine mesh mesocosms (**Fig. 4.8C**): a total of 37 morphospecies in this size class (excluding immatures) occurred within coarse mesh mesocosms, and 15 morphospecies within fine mesh mesocosms. Ten of the morphospecies encountered in the fine mesh mesocosms occurred as single instances of one to three individuals, and all but three were also present in coarse mesh mesocosms. Indicator species analysis (**Table 4.2**) showed only one significant indicator for a fine mesh mesocosm treatment (21 µm mesh mesocosms in the untreated unit). We suspect that this collembolan (an Entomobryidae sp.), which had a very large furcula (the appendage from which Collembola get their common name: springtails), was especially well equipped to colonize mesocosms through small tears in lids, or while lids were temporarily removed for soil moisture monitoring and collection of decomposition disks. Multi-response permutation procedure analyses based on morphospecies > 300 µm (**Table 4.3**) and on oribatid abundance (**Table 4.4**) confirmed that communities in fine and coarse mesh treatments differed within both management units, with the strongest differences usually observed between 21 µm mesh and 1000 µm mesh treatments. Community differences are visualized in **Fig. 4.9**

Table 4.1 Results of two-way ANOVA. Effects of mesh treatment, ponderosa restoration treatment, and mesh x ponderosa restoration treatment interactions on soil fauna, ratios of ectomycorrhizal to litter/wood saprotrophic fungal reads, ectomycorrhizal fungi and litter/wood saprotrophs as a proportion of total reads, proportion remaining of wood and cellulose standard substrates, and soil abiotic properties. Where *F*-tests justified the inclusion of an interaction term, the thinned/burned (TB) x mesh results are listed below the main effects results. EcM=ectomycorrhizal fungi; LWS=saprotrophic fungi capable of degrading litter and/or wood.

	Intercept		*Management treatment: TB*		*Mesh treatment: 21 µm*		*Mesh treatment: 41 µm*		*Mesh treatment: 1000 µm Sev*	
	Estimate (Std. err)	*t* *p(t)*	Estimate (Std. err)	*t* *p(t)*	Estimate (Std. err)	*t* *p(t)*	Estimate (Std. err)	*t* *p(t)*	Estimate (Std. err)	*t* *p(t)*
ln (Mites >150 µm)	4.772 (0.259)	18.424 *p*<0.001	**-1.846 (0.232)**	**-7.968 *p*<0.001**	**-1.879 (0.331)**	**-5.675 *p*<0.001**	**-1.319 (0.328)**	**-4.026 *p*<0.001**	-0.206 (0.328)	-0.630 *p*=0.530
Adj. R^2: 0.528 *F*=26.96 (4, 89); *P*<0.001										
ln (Collembolans >150 µm)	3.248 (0.287)	11.320 *p*<0.001	**-1.787 (0.257)**	**-6.961 *p*<0.001**	**-1.034 (0.367)**	**-2.818 *p*=0.006**	-0.314 (0.363)	-0.865 *p*=0.389	0.251 (0.363)	0.690 *p*=0.492
Adj. R^2: 0.384 *F*=15.47 (4, 89); *P*<0.001										
ln (Microarthropods >150 µm)	5.21 (0.25)	20.62 *p*<0.001	**-1.93 (0.23)**	**-8.54 *p*<0.001**	**-1.90 (0.32)**	**-5.90 *p*<0.001**	**-1.16 (0.32)**	**-3.61 *p*<0.001**	-0.16 (0.32)	-0.50 *p*=0.620
Adj. R^2: 0.553 *F*=29.74 (4, 89); *P*<0.001										
ln (Adult Oribatida)	3.82 (0.30)	12.73 *p*<0.001	**-2.23 (0.43)**	**-5.13 *p*<0.001**	**-3.41 (0.42)**	**-8.03 *p*<0.001**	**-2.12 (0.42)**	**-5.00 *p*<0.001**	0.02 (0.42)	0.04 *p*=0.964
Interaction (TB x mesh):					**1.81 (0.61)**	**2.96 *p*=0.004**	0.74 (0.61)	1.22 *p*=0.228	-0.23 (0.61)	-0.39 *p*=0.701
Adj. R^2: 0.643 *F*=24.9 (7, 86); *P*<0.001										
ln (Species richness of microarthropods > 300 µm)	1.698 (0.130)	13.077 *p*<0.001	**-0.676 (0.116)**	**-5.821 *p*<0.001**	**-0.875 (0.166)**	**-5.271 *p*<0.001**	**-0.867 (0.164)**	**-5.277 *p*<0.001**	-0.065 (0.164)	-0.397 *p*=0.692
Adj. R^2: 0.469 *F*=21.53 (4, 89); *P*<0.001										

Table 4.1 cont.

	Intercept		*Management treatment: TB*		*Mesh treatment: 21 µm*		*Mesh treatment: 41 µm*		*Mesh treatment: 1000 µm Sev*	
	Estimate (Std. err)	*t* *p(t)*	Estimate (Std. err)	*t* *p(t)*	Estimate (Std. err)	*t* *p(t)*	Estimate (Std. err)	*t* *p(t)*	Estimate (Std. err)	*t* *p(t)*
ln (Mites <150 µm)	5.343 (0.327)	16.335 *p*<0.001	0.410 (0.473)	0.867 *p*=0.388	0.041 (0.463)	0.090 *p*=0.929	0.092 (0.463)	0.200 *p*=0.842	-0.190 (0.463)	-0.410 *p*=0.682
Interaction (TB x mesh):					**-1.952 (0.669)**	**-2.918 *p*=0.004**	*-1.165 (0.662)*	*-1.760 p=0.082*	-0.566 (0.662)	-0.855 *p*=0.395
Adj. R^2: 0.133 *F*=3.042 (7, 86); *P*=0.007										
ln (Collembolans <150 µm)	2.387 (0.339)	7.044 *p*<0.001	**-1.122 (0.490)**	**-2.289 *p*=0.025**	**-2.061 (0.479)**	**-4.301 *p*<0.001**	-0.009 (0.479)	-0.019 *p*=0.985	0.112 (0.479)	0.233 *p*=0.816
Interaction (TB x mesh):					0.942 (0.693)	1.359 *p*=0.178	-0.248 (0.685)	-0.362 *p*=0.718	0.190 (0.685)	0.277 *p*=0.783
Adj. R^2: 0.323 *F*=7.339 (7, 86); *P*<0.001										
ln (Soil organic matter (%))	1.74 (0.08)	22.64 *p*<0.001	**-0.16 (0.07)**	**-2.27 *p*=0.026**	0.01 (0.10)	0.09 *p*=0.932	-0.03 (0.10)	-0.26 *p*=0.795	0.00 (0.10)	-0.04 *p*=0.967
Adj. R^2: 0.014 *F*=1.326 (4, 88); *P*=0.267										
Mean soil moisture Z score	-0.59 (0.18)	-3.32 *p*=0.001	0.04 (0.26)	0.14 *p*=0.886	**1.58 (0.25)**	**6.28 *p*<0.001**	**1.08 (0.25)**	**4.30 *p*<0.001**	**0.66 (0.25)**	**2.61 *p*=0.011**
Interaction (TB x mesh):					**-0.90 (0.36)**	**-2.47 *p*=0.016**	-0.21 (0.36)	-0.58 *p*=0.561	-0.30 (0.36)	-0.83 *p*=0.406
Adj. R^2: 0.370 *F*=8.804 (7, 86); *P*<0.001										
ln (EcM:LWS) Adj. R^2: 0.125 *F*=4.307 (4, 89); *P*=0.003	3.38 (0.37)	9.19 *p*<0.001	**-1.24 (0.33)**	**-3.77 *p*<0.001**	*-0.82 (0.47)*	*-1.74 p=0.085*	-0.37 (0.47)	-0.79 *p*=0.432	-0.37 (0.47)	-0.80 *p*=0.424

Table 4.1 cont.

	Intercept		*Management treatment: TB*		*Mesh treatment: 21 µm*		*Mesh treatment: 41 µm*		*Mesh treatment: 1000 µm Sev*	
	Estimate (Std. err)	*t* *p(t)*	Estimate (Std. err)	*t* *p(t)*	Estimate (Std. err)	*t* *p(t)*	Estimate (Std. err)	*t* *p(t)*	Estimate (Std. err)	*t* *p(t)*
arcsin (Proportion EcM) Adj. R^2: 0.064 F=2.595 (4, 89); P=0.042	0.63 (0.07)	8.55 p<0.001	**-0.17 (0.07)**	**-2.60 *p*=0.011**	-0.15 (0.09)	-1.60 p=0.114	-0.06 (0.09)	-0.69 p=0.495	0.01 (0.09)	0.10 p=0.921
arcsin (Proportion LWS) Adj. R^2: 0.121 F=4.196 (4, 89); P=0.004	0.107 (0.021)	5.170 p<0.001	**0.071 (0.018)**	**3.823 *p*<0.001**	0.022 (0.026)	0.819 p=0.415	0.001 (0.026)	0.043 p=0.965	0.031 (0.026)	1.196 p=0.235
Mean proportion wood remaining Adj. R^2: 0.030 F=1.72 (4, 89); P=0.153	0.9271 (0.0143)	64.7591 p<0.001	0.0207 (0.0128)	1.6159 p=0.110	-0.0206 (0.0183)	-1.1249 p=0.264	0.0128 (0.0181)	0.7082 p=0.481	0.0099 (0.0181)	0.5455 p=0.587
Mean proportion cellulose remaining	0.5643 (0.0533)	10.5847 p<0.001	*-0.0716 (0.0771)*	*-0.9292 p=0.355*	**-0.1761 (0.0754)**	**-2.3351 *p*=0.022**	-0.0465 (0.0754)	-0.6167 p=0.539	-0.0044 (0.0754)	-0.0582 p=0.953
Interaction (TB x mesh): Adj. R^2: 0.048 F=1.671 (7, 86); P=0.127					**0.3012 (0.1090)**	**2.7629 *p*=0.007**	0.0887 (0.1078)	0.82280 p=0.413	0.0925 (0.1078)	0.8580 p=0.393
ln (Available N (mg N g^{-1} dry soil)) Adj. R^2: 0.001 F=1.02 (4, 89); P=0.402	1.78 (0.19)	9.46 p<0.001	-0.16 (0.17)	-0.95 p=0.344	-0.04 (0.24)	-0.15 p=0.881	0.15 (0.24)	0.65 p=0.517	0.35 (0.24)	1.46 p=0.149
ln (Ammonium (mg N g^{-1} dry soil)) Adj. R^2: 0.000 F=1.011 (4, 89); P=0.406	1.73 (0.19)	8.96 p<0.001	-0.22 (0.17)	-1.25 p=0.214	0.00 (0.25)	0.02 p=0.985	0.18 (0.24)	0.76 p=0.452	0.33 (0.24)	1.35 p=0.179

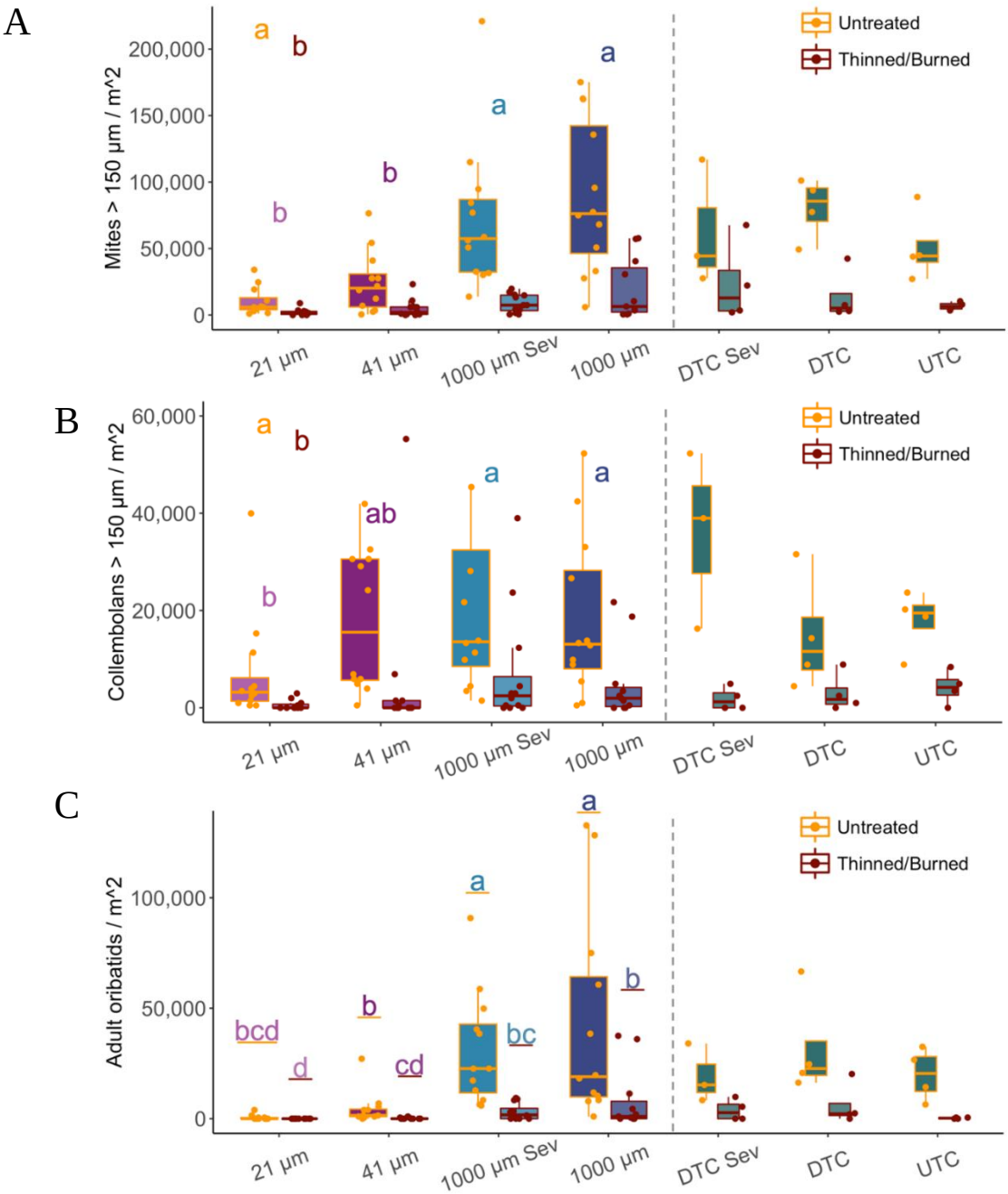

Fig. 4.7 Abundances in experimental mesocosms (left of dotted line) and technical checks (right of dotted line) of (**A**) all mites > 150 µm, (**B**) collembolans > 150 µm (two outliers are not shown), and (**C**) adult oribatid mites. The line within each box indicates the median, the lower and upper bounds of the box correspond to the 25th and 75th percentiles, and whiskers show the smallest and largest values that do not exceed 1.5 x the interquartile range from lower and upper box bounds. Boxplot widths are scaled by the number of individual observations, which are overlaid as dots. Letters indicate differences among either mesh and management treatment groups (for main effects two-way ANOVA models) or mesh x management treatment groups (for two-way ANOVA models including both main effects and interaction terms). Groups not sharing letters are significantly different at p<0.05 after adjustment for multiple pairwise comparisons using Tukey's method. ANOVA models are summarized in **Table 4.1**. 21 µm, 41 µm, and 1000 µm refer to mesocosm mesh window sizes. Sev=root severing; DTC=disturbed technical check; UTC=undisturbed technical check.

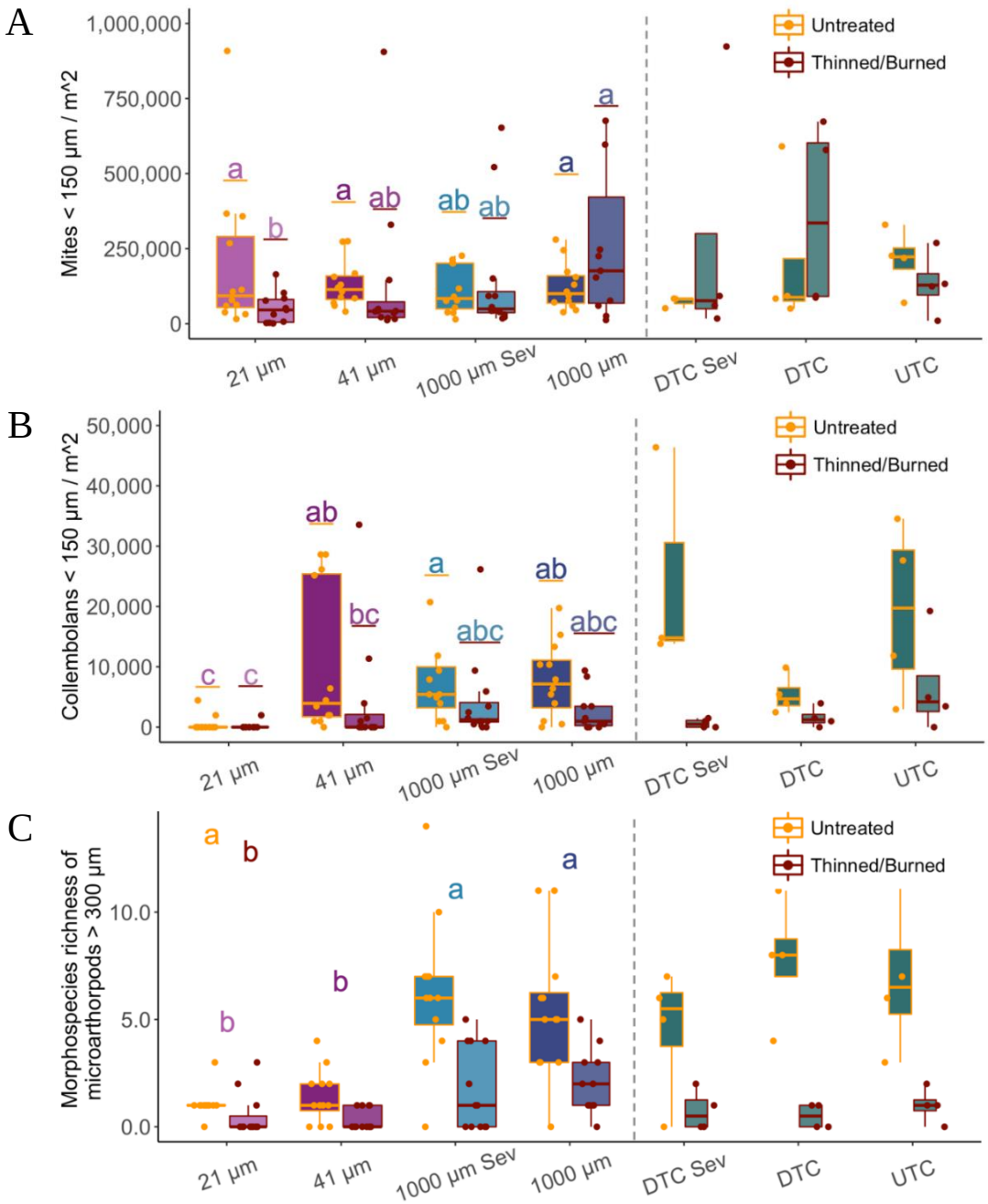

Fig. 4.8 Abundances in experimental mesocosms (left of dotted line) and technical checks (right of dotted line) of (**A**) small mites (< 150 µm) (one outlier removed from plot for visual clarity) and (**B**) small collembolans (one outlier not shown). (**C**) Morphospecies richness. The line within each box indicates the median, the lower and upper bounds of the box correspond to the 25th and 75th percentiles, and whiskers show the smallest and largest values that do not exceed 1.5 x the interquartile range from lower and upper box bounds. Boxplot widths are scaled by the number of individual observations, which are overlaid as dots. Groups not sharing letters are significantly different (p<0.05 after adjustment for multiple pairwise comparisons using Tukey's method) according to the ANOVA models summarized in **Table 4.1**. Differences between all treatment combinations are shown where an interaction term was included in the model; otherwise, letters indicate only mesh treatment and management unit treatment differences. 21 µm, 41 µm, and 1000 µm refer to mesocosm mesh window sizes. Sev=root severing; DTC=disturbed technical check; UTC=undisturbed technical check.

Table 4.2 Results of indicator species analyses for microarthropod taxa. We performed separate analyses for management unit (untreated=U, thinned/burned=TB) and for mesh treatments (coarse vs. fine, and all mesh treatments separately) within each management treatment, for a total of five indicator species analyses. L=size > 300 µm; M=size > 150 µm, < 300 µm; S=size < 150 µm. "Others"=microarthropods apart from Acari and Collembola. Taxa with observed indicator values (IV) >25 and $p<0.05$ from randomization tests with 9,999 permutations were considered significant indicators. Asterisks denote significance levels of observed IV: *=$p<0.05$, **=$p<0.01$, ***=$p<0.001$.

		Presence		Management		U fine/coarse		U mesh		TB fine/coarse		TB mesh	
Size	**Taxon**	**U**	**TB**	**Max Group**	**IV**	**Max Group**	**IV**	**Max Group**	**IV**	**Max Group**	**IV**	**Max Group**	**IV**
	Acari												
L	*Bdella* cf. *muscorum*	X	X										
L	Bdelloidea sp. 1	X											
L	cf. *Biscirus* sp.	X											
L	Cunaxidae sp. 1	X											
L	Cunaxidae sp. 2	X	X										
L	Cunaxidae sp. 3	X											
L	Cunaxidae sp. 4		X										
L	Damaeidae sp.	X				Coarse	33.3**						
L	*Eremaeus* cf. *boreomontanus*	X	X	U	28.4***	Coarse	58.3***	1000 µm	32.9*				
L	Euphthiracaroidea sp.	X											
L	Eupodidae sp.	X											
L	*Eupterotegaeus* sp.	X	X										
L	Gymnodamaeidae sp.	X											
L	Immature Mesostigmata	X	X	U	36.8*	Coarse	59.6***	1000 µm Sev	45**				
L	Immature Oribatida	X		U	35.4***	Coarse	65.5***	1000 µm	35*				
L	Mesostigmata sp. 1	X											
L	Mesostigmata sp. 2	X	X			Coarse	45.8***	1000 µm Sev	43.1**				
L	*Nothrus* sp.	X											

Table 4.2 cont.

		Presence		Management		U fine/coarse		U mesh		TB fine/coarse		TB mesh	
Size	**Taxon**	**U**	**TB**	**Max Group**	**IV**	**Max Group**	**IV**	**Max Group**	**IV**	**Max Group**	**IV**	**Max Group**	**IV**
	Acari												
L	*Odontodamaeus* sp.	X		U	25***	Coarse	50***	1000 µm	27.6*				
L	cf. Oribatulidae sp.	X	X										
L	Prostigmata sp. 1	X											
L	Prostigmata sp. 2	X											
L	Prostigmata sp. 3	X											
L	Prostigmata sp. 4	X	X										
L	Prostigmata sp. 5		X*										
L	Prostigmata sp. 6	X*											
L	Prostigmata sp. 7	X											
L	Prostigmata sp. 8	X											
L	Prostigmata sp. 9	X	X										
L	*Spinibdella* sp.	X	X										
L	Trhypochthoniidae sp.	X	X					1000 µm Sev	25*				
L	*Trichoribates* sp.	X											
M/L	Haplozetidae sp.	X	X			Coarse	30.6*						
M/L	*Propelops* cf. *canadensis*	X	X			Coarse	41.7***	1000 µm Sev	33.3*	Coarse	34.8**		
M/L	*Scheloribates* sp.	X	X	U	70.9***	Coarse	90.1***	1000 µm Sev	53.1**				
M	Brachypylina sp. 1	X											
M	Brachypylina sp. 2	X											
M	Opiidae sp.	X	X	U	56.2***	Coarse	81.8***	1000 µm	50*				
M	Other Acari > 150 µm, <300 µm	X	X	U	81.6***	Coarse	73.6***	1000 µm	39.6*	Coarse	70.3**	1000 µm	46.2*
M	*Tectocepheus velatus*	X	X			Coarse	78.7***	1000 µm	43.6**	Coarse	47.5***		

Table 4.2 cont.

		Presence		Management		U fine/coarse		U mesh		TB fine/coarse		TB mesh	
Size	**Taxon**	**U**	**TB**	**Max Group**	**IV**	**Max Group**	**IV**	**Max Group**	**IV**	**Max Group**	**IV**	**Max Group**	**IV**
S	Acari < 150 µm	X	X										
	Collembola												
L	Entomobryidae sp.	X	X	U	47.7***			21 µm	43.5*				
L	Entomobryomorpha sp. 1	X											
L	Entomobryomorpha sp. 2	X											
L	Entomobryomorpha sp. 3	X											
L	Entomobryomorpha sp. 4	X	X										
L	Hypogastruridae sp. 1	X	X										
L	Hypogastruridae sp. 2		X										
L	Isotomidae sp.	X		U	29.2***	Coarse	35*						
L	Onychiuridae sp.	X											
L	Tullbergiidae sp.	X	X										
M	Pigmented Collembola > 150 µm, <300 µm	X	X	U	28.6*	Coarse	48.6**						
M	Unpigmented Collembola > 150 µm, <300 µm	X	X	U	62***	Coarse	63*	1000 µm Sev	44.9*				
S	Collembola	X	X	U	54.4**	Coarse	61.5*						
	Others												
L	Others > 300 µm	X	X	U	33.2**	Coarse	48.4*	1000 µm Sev	43.9*	Coarse	28.4*		
M	Others > 150 µm, <300 µm	X	X										

Table 4.3 Post-hoc comparisons from multi-response permutation procedure (MRPP) analyses of microarthropod morphospecies >300 µm across mesocosm mesh treatments in untreated (overall group differences: A=0.094, p<0.001) and thinned/burned (overall group differences: A=0.071, p=0.004) forest management units. Note that p-values are not corrected for multiple comparisons.

Untreated

	41 µm		1000 µm Sev		1000 µm	
	A	*p*	*A*	*p*	*A*	*p*
21 µm	0.035	0.065	**0.117**	**<0.001**	**0.086**	**<0.001**
41 µm			**0.086**	**0.001**	**0.071**	**0.002**
1000 µm Sev					-0.003	0.566

Thinned/burned

	41 µm		1000 µm Sev		1000 µm	
	A	*p*	*A*	*p*	*A*	*p*
21 µm	-0.010	0.536	**0.053**	**0.049**	**0.101**	**0.003**
41 µm			**0.055**	**0.035**	**0.104**	**0.001**
1000 µm Sev					-0.015	0.788

Table 4.4 Post-hoc comparisons from multi-response permutation procedure (MRPP) analyses of oribatid assemblage differences across mesocosm mesh treatments in untreated (overall group differences: A=0.217, p<0.001) and thinned/burned (overall group differences: A=0.144, p<0.001) forest management units. Note that p-values are not corrected for multiple comparisons.

Untreated

	41 µm		1000 µm Sev		1000 µm	
	A	*p*	*A*	*p*	*A*	*p*
21 µm	**0.132**	**0.002**	**0.340**	**<0.001**	**0.265**	**<0.001**
41 µm			**0.129**	**<0.001**	**0.083**	**<0.001**
1000 µm Sev					-0.009	0.626

Thinned/burned

	41 µm		1000 µm Sev		1000 µm	
	A	*p*	*A*	*p*	*A*	*p*
21 µm	0.025	0.064	**0.210**	**<0.001**	**0.189**	**0.001**
41 µm			**0.115**	**0.006**	**0.095**	**0.012**
1000 µm Sev					-0.009	0.519

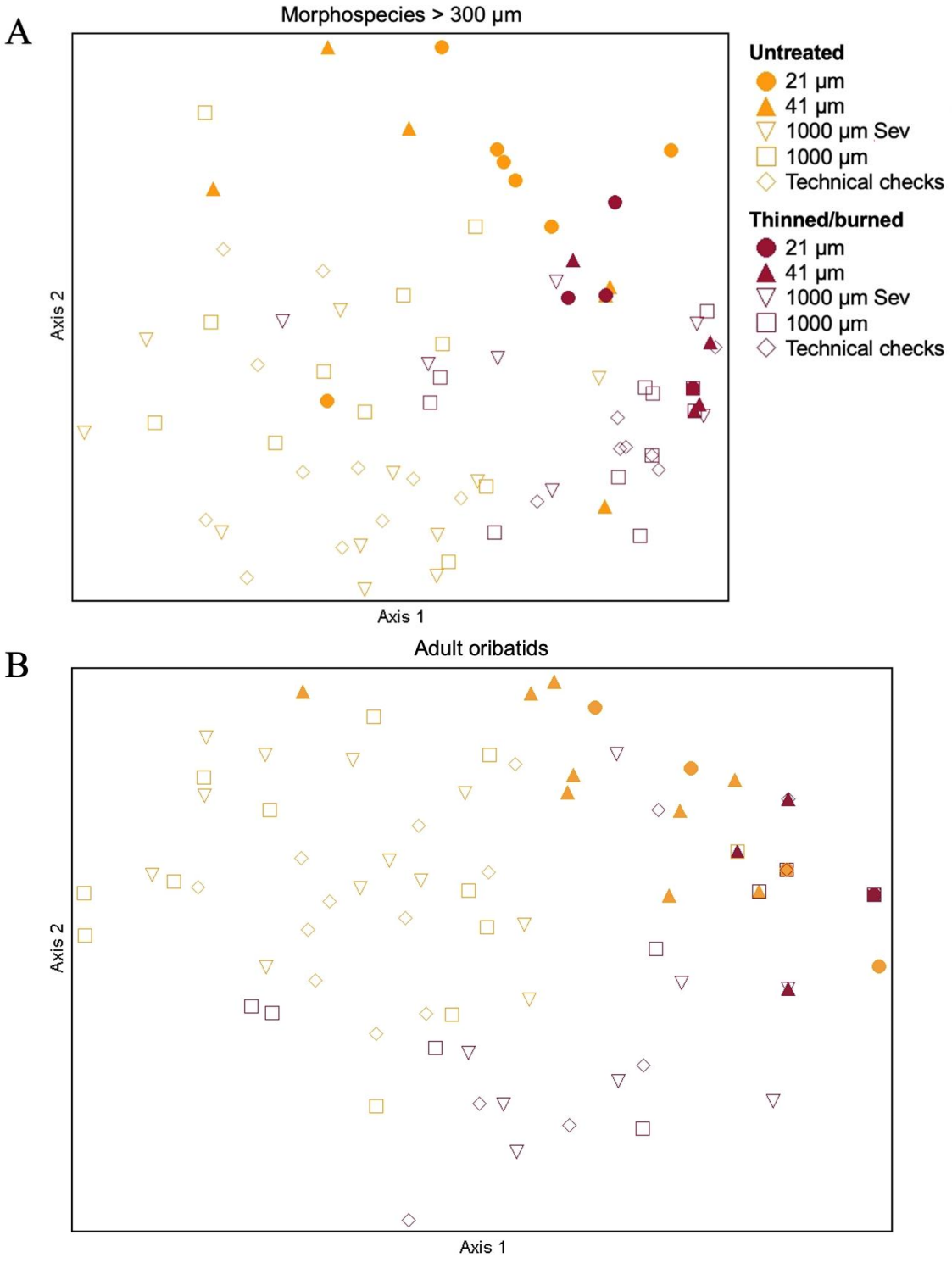

Fig. 4.9 Nonmetric multidimensional scaling (NMDS) ordinations of (**A**) abundances of morphospecies > 300 µm (final stress=12.21; axes 1 and 2 shown of three-dimensional ordination); (**B**) adult oribatids (final stress= 9.37; two-dimensional ordination). Note that mesh treatments are equally replicated (N=12), but many of the fine mesh mesocosms with few or no large fauna or oribatids are plotted atop one another.

4.3.1.3 Non-target mesocosm treatment effects

Defaunation, but not sieving, increased soil ammonium concentrations immediately after treatment, especially in soil from the untreated management unit (**Fig. S4.4 A**). Nitrate was below detectable levels in all but two defaunated samples from the thinned/burned unit. This pulse in available nitrogen had dissipated by the end of the study, at which time ammonium concentrations were very similar in mesocosm technical checks with and without defaunated soil (**Fig. S4.4 B**). Mesocosm mesh size and root severing influenced moisture retention, with 21 µm mesh mesocosms retaining the most, and 1 mm unsevered mesocosms the least, soil moisture on average (**Table 4.1; Fig. 4.10**). Median soil moisture differences between 21 µm and 1 mm unsevered mesocosms ranged from 1.2% at T3 to 6.2% at T5. We accounted for these moisture differences in our SEM as described below.

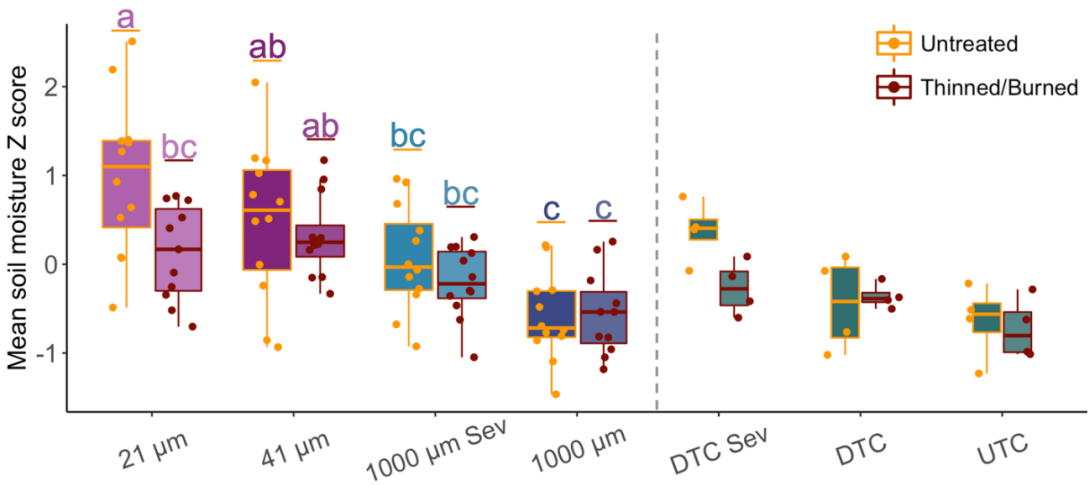

Fig. 4.10 Soil moisture differences across mesh treatments. Mean Z scores are the average of Z scores calculated from moisture measurements taken at each of 5 monitoring timepoints. The line within each box indicates the median, the lower and upper bounds of the box correspond to the 25th and 75th percentiles, and whiskers show the smallest and largest values that do not exceed 1.5 x the interquartile range from lower and upper box bounds. Boxplot widths are scaled by the number of individual observations, which are overlaid as dots. Letters indicate differences among either mesh and management treatment groups (for main effects two-way ANOVA models) or mesh x management treatment groups (for two-way ANOVA models including both main effects and interaction terms). Groups not sharing letters are significantly different at p<0.05 after adjustment for multiple pairwise comparisons using Tukey's method. ANOVA models are summarized in **Table 4.1**. 21 µm, 41 µm, and 1000 µm refer to mesocosm mesh window sizes. Sev=root severing; DTC=disturbed technical check; UTC=undisturbed technical check.

4.3.2 Forest management effects on soil fauna communities

Five years after restoration treatments were completed, microarthropod communities differed in the two management units (**Fig. 4.9**), with fewer animals and less complex communities in the thinned/burned unit mesocosms relative to the untreated unit mesocosms. Densities of mites and collembolans > 150 µm (including oribatid mites), and of collembolans < 150 µm, were lower in the thinned/burned unit than in the untreated unit (**Table 4.1; Fig. 4.7, Fig. 4.8B**). Coarse mesh mesocosms within the thinned/burned unit had oribatid abundances similar to fine mesh mesocosms within the untreated unit. Only mites < 150 µm were similarly abundant in thinned/burned and untreated management units (**Table 4.1; Fig. 4.8A**). Mesocosms in the thinned/burned unit also had lower species richness of microarthropods > 300 µm (**Fig. 4.8C**); just 20 large morphospecies were encountered within thinned/burned mesocosms and technical checks, compared to 41 morphospecies observed within untreated unit mesocosms and technical checks (**Table 4.2**). All but two of the large morphospecies in the thinned/burned unit also occurred within the untreated unit, and none were significant indicator species for the thinned/burned unit. Multi-response permutation procedure indicated that assemblage differences between management treatments were stronger for oribatid mites (A=0.093, $p < 0.001$) than for large morphospecies (A=0.065, $p < 0.001$).

4.3.3 Forest management and mesh effects on fungi and soil properties

4.3.3.1 Soil fungi

Fungal communities differed between the thinned/burned and untreated forest management units (**Fig. 4.11**). Multi-response permutation procedure detected a stronger management unit effect when based on fungal genera (A=0.046, $p < 0.001$) than on ASVs (A=0.024, $p < 0.001$), although

in both cases group dissimilarities were relatively modest ($A < 0.08$). Genera present in the two forest management units and their indicator values (if significant) are listed in **Table 4.S2**. Classification of genera to lifestyle groups revealed functional differences between communities in the management units. Untreated unit mesocosms included a higher percentage of ectomycorrhizal reads, and a lower percentage of litter/wood saprotroph reads, than did communities in thinned/burned unit mesocosms (**Fig. 4.12**). A similar number of ectomycorrhizal genera (thinned/burned: three genera; untreated: four genera) were indicators for both management units, but thrice as many genera with primary or secondary lifestyles as LWS were indicators for the thinned/burned unit (nine genera, among them three soft rot fungi) as were indictors for the untreated unit (three genera, including one soft rot fungus).

Multi-response permutation procedure revealed no fungal community differences among mesh treatments in either management unit, whether analyses were performed using genera (untreated unit: A=-0.015, p=0.952; thinned/burned unit: A=0.006, p=0.23) or ASVs (untreated unit: A=-0.006, p=0.916; thinned/burned unit: A=-0.015, p=0.998), and there were few strong indicator genera for mesh treatments. We note, however, that variability among tree blocks in each unit was very high (MRPP based on relative abundance of fungal genera for thinned/burned blocks: A=0.160, $p < 0.001$; for the untreated blocks: A=0.155, $p < 0.001$). Mesh treatments also did not differ significantly in the functional composition of their fungal communities, although relative abundance of ectomycorrhizal reads tended to be lower in fine mesh mesocosms than coarse mesh mesocosms within the thinned/burned unit (**Fig. 4.12A**) (inclusion of an interaction term in the ANOVA model was not justified). Neither relative abundance of LWS reads, nor EcM:LWS ratios, differed significantly across mesh treatments (**Fig. 4.12B, Fig. 4.12C**).

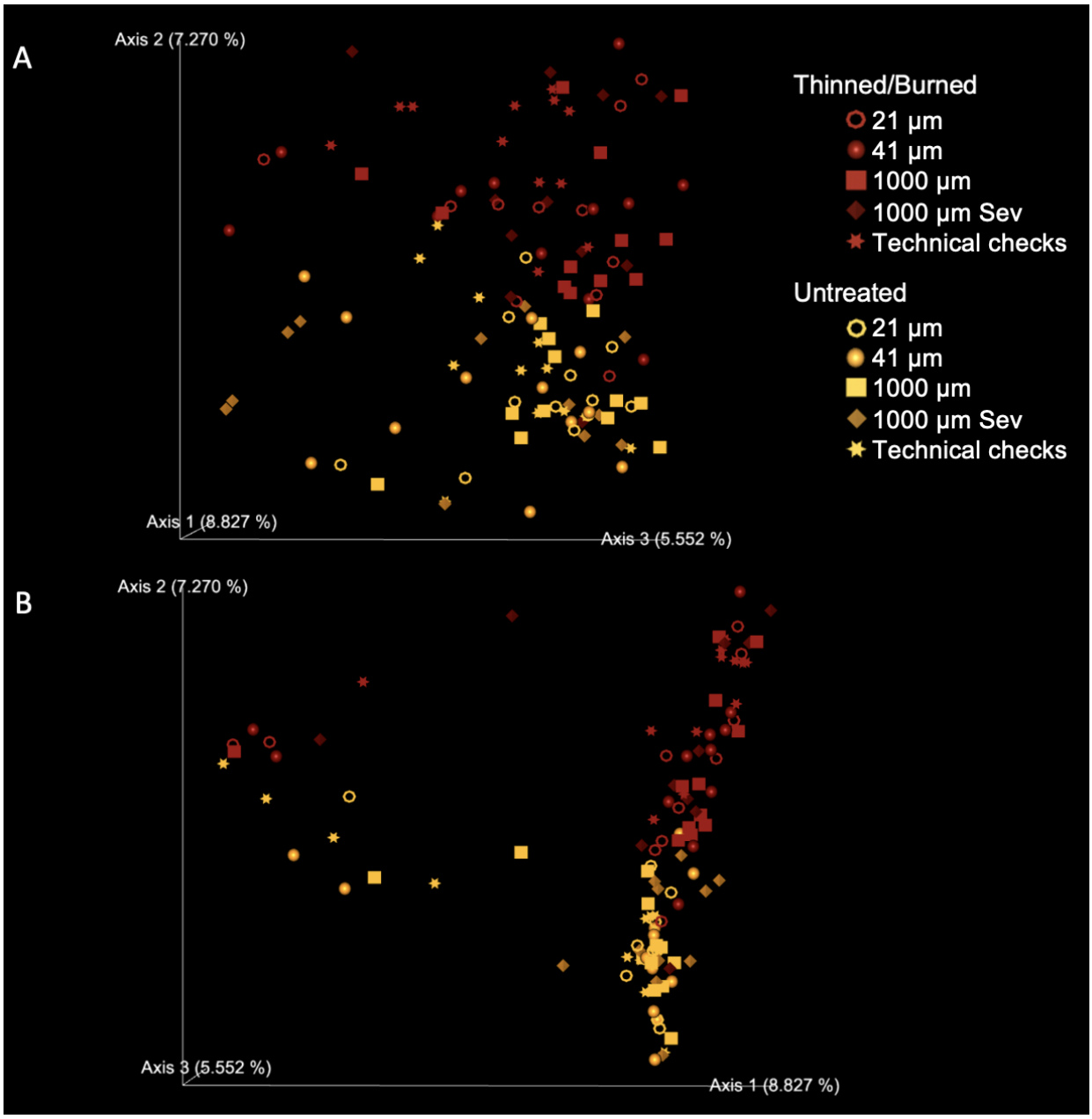

Fig. 4.11 Three-dimensional principal coordinates analysis (PCoA) ordination of fungal communities based on weighted Bray-Curtis distance, visualized with Emperor QIIME2View. Colors correspond to ponderosa restoration treatments, and shapes designate mesh treatments: 21 µm, 41 µm, 1 mm with root severing (1 mm Sev), 1 mm without root severing (1 mm), and technical checks without mesh or pipe. (**A)** Variation along PCoA axes 2 and 3. (**B)** Variation along PCoA axes 1 and 2.

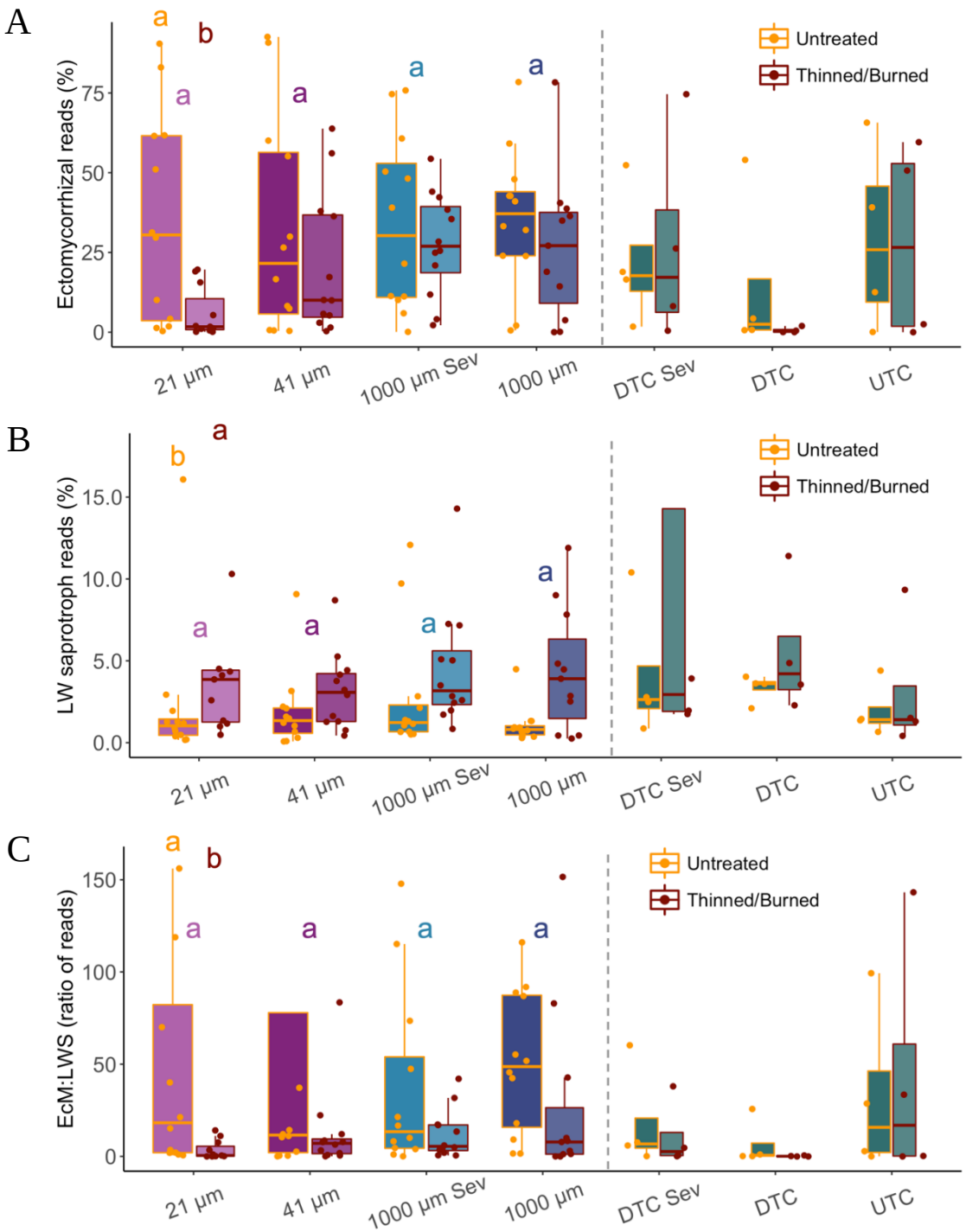

Fig. 4.12 (**A**) Ectomycorrhizal reads as a percentage of all reads, (**B**) litter and wood saprotroph reads as a percentage of all reads (two outliers from thinned/burned unit not shown), and (**C**) ratio of ectomycorrhizal (EcM) to litter/wood saprotroph (LWS) reads (three outliers from untreated unit not shown) in experimental mesocosms (left of dotted line) and technical checks (right of dotted line). The line within each box indicates the median, the lower and upper bounds of the box correspond to the 25th and 75th percentiles, and whiskers show the smallest and largest values that do not exceed 1.5 x the interquartile range from lower and upper box bounds. Boxplot widths are scaled by the number of individual observations, which are overlaid as dots. Letters indicate differences among either mesh and

management treatment groups (for main effects two-way ANOVA models) or mesh x management treatment groups (for two-way ANOVA models including both main effects and interaction terms). Groups not sharing letters are significantly different at $p<0.05$ after adjustment for multiple pairwise comparisons using Tukey's method. ANOVA models are summarized in **Table 4.1**. 21 µm, 41 µm, and 1000 µm refer to mesocosm mesh window sizes. Sev=root severing; DTC=disturbed technical check; UTC=undisturbed technical check.

4.3.3.2. Soil properties and decomposition

Soil organic matter was higher in untreated than in thinned/burned mesocosms (**Table 4.1; Fig. 4.13A**), but mesh treatments did not affect SOM within either management unit. We found no effect of restoration treatments on soil moisture, except when comparing thinned/burned to untreated 21 µm mesh mesocosms (**Table 4.1, Fig. 4.10**). Available N was highly variable and showed no pattern with respect to forest management unit or mesh treatment. We also detected no differences between management units or mesh treatments in total decomposition of wood or cellulose at the final (T5) and penultimate (T4) monitoring timepoints (**Fig. 4.14**), although we observed faster decomposition of both substrates in the untreated unit at earlier timepoints (**Fig. S4.5)**.

4.3.4 Structural equation models

Our final multigroup models of cellulose and wood decomposition (**Fig. 4.15** and **Fig. 4.16**) fit the data well (cellulose decomposition: χ^2=34.388; *P*=0.545; Bollen-Stine Bootstrap *P*=0.652; AGFI=0.845; RMSEA=0.000; wood decomposition: χ^2=14.943, *P*=0.993; Bollen-Stine Bootstrap *P*=0.995; AGFI=0.914; RMSEA=0.000). Despite high variability in microarthropod communities between tree blocks, our mesh treatments explained a relatively high proportion of the variance in medium and large microarthropod abundances within both thinned/burned and untreated management units. Side effects of mesh treatments on soil moisture were also evident,

however, and influenced decomposition. Soil organic matter unexpectedly reduced soil moisture, possibly due to hydrophobicity of the pine needle duff, which we observed resisted wetting during brief rainfall events.

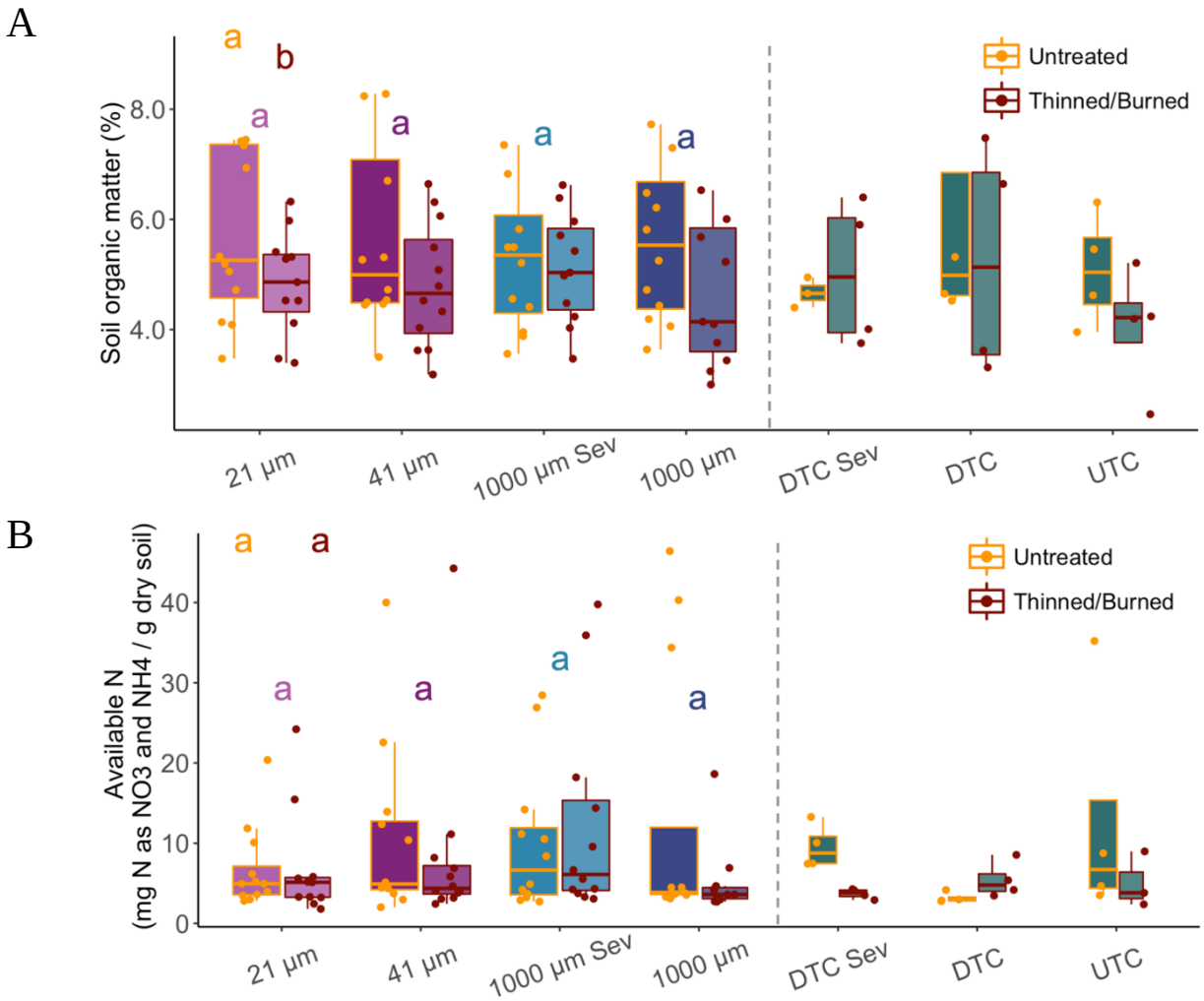

Fig. 4.13 (**A**) Soil organic matter (%) (six outliers not shown) and (**B**) available N in experimental mesocosms (left of dotted line) and technical checks (right of dotted line). The line within each box indicates the median, the lower and upper bounds of the box correspond to the 25th and 75th percentiles, and whiskers show the smallest and largest values that do not exceed 1.5 x the interquartile range from lower and upper box bounds. Boxplot widths are scaled by the number of individual observations, which are overlaid as dots. Letters indicate differences among either mesh and management treatment groups (for main effects two-way ANOVA models) or mesh x management treatment groups (for two-way ANOVA models including both main effects and interaction terms). Groups not sharing letters are significantly different at $p<0.05$ after adjustment for multiple pairwise comparisons using Tukey's method. ANOVA models are summarized in **Table 4.1**. 21 µm, 41 µm, and 1000 µm refer to mesocosm mesh window sizes. Sev=root severing; DTC=disturbed technical check; UTC=undisturbed technical check.

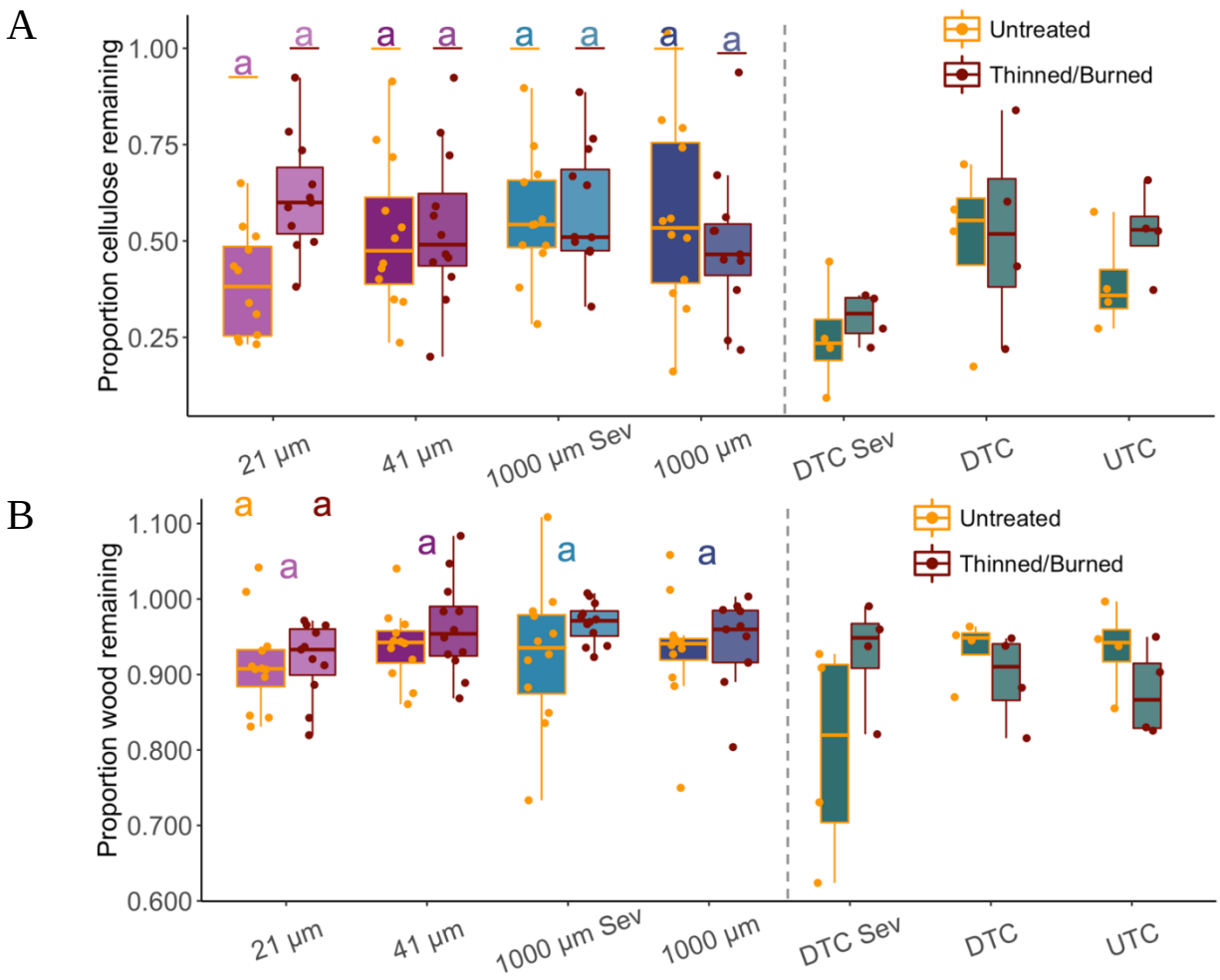

Fig. 4.14 Average proportion of initial cellulose (**A**) and wood (**B**) mass remaining in experimental mesocosms (left of dotted line) and technical checks (right of dotted line) at the final two decomposition disk harvests. The line within each box indicates the median, the lower and upper bounds of the box correspond to the 25th and 75th percentiles, and whiskers show the smallest and largest values that do not exceed 1.5 x the interquartile range from lower and upper box bounds. Boxplot widths are scaled by the number of individual observations, which are overlaid as dots. Letters indicate differences among either mesh and management treatment groups (for main effects two-way ANOVA models) or mesh x management treatment groups (for two-way ANOVA models including both main effects and interaction terms). Groups not sharing letters are significantly different at p<0.05 after adjustment for multiple pairwise comparisons using Tukey's method. ANOVA models are summarized in **Table 4.1**. 21 µm, 41 µm, and 1000 µm refer to mesocosm mesh window sizes. Sev=root severing; DTC=disturbed technical check; UTC=undisturbed technical check.

Medium and large microarthropods had a positive effect on the ratio of ectomycorrhizal fungi to litter/wood saprotrophs in the thinned/burned unit, but a weak (and statistically insignificant) negative effect in the untreated unit for both substrates. Mesh treatments had only weak direct effects on EcM:LWS. Total direct and indirect effects of each variable are listed in **Table 4.5** (cellulose decomposition) and **Table 4.6** (wood decomposition). The importance of abiotic and biotic predictors of decomposition differed for wood and cellulose substrates, and also between thinned/burned and untreated units.

The multigroup model of cellulose decomposition explained only 11% (thinned/burned unit) and 18% (untreated unit) of the variance in decomposition. Microarthropods did not affect cellulose decomposition directly in either unit. Although the ratio of ectomycorrhizal fungi to litter and wood saprotrophs tended to decrease cellulose mass loss in the untreated unit, soil moisture and SOM were the most important contributors to cellulose decomposition. In both management units, soil moisture significantly accelerated decomposition of our labile substrate, while SOM retarded it.

Our multigroup model of wood decomposition explained nearly 30% of the variance in mass loss within the thinned/burned unit (R^2=0.29), but did very poorly at predicting variability in wood decomposition within the untreated unit (R^2=0.04). Microarthropods had no direct influence on wood mass loss in either forest management context. However, our SEM illuminated an indirect effect of microarthropods on wood decomposition within the thinned/burned unit via their influence on fungal communities. Microarthropod abundance was the strongest predictor of EcM:LWS in this management unit, and the ratio of these fungal groups in turn explained the majority of the variation in wood decomposition captured by our model. Soil moisture and SOM had only very weak effects on wood decomposition in either unit.

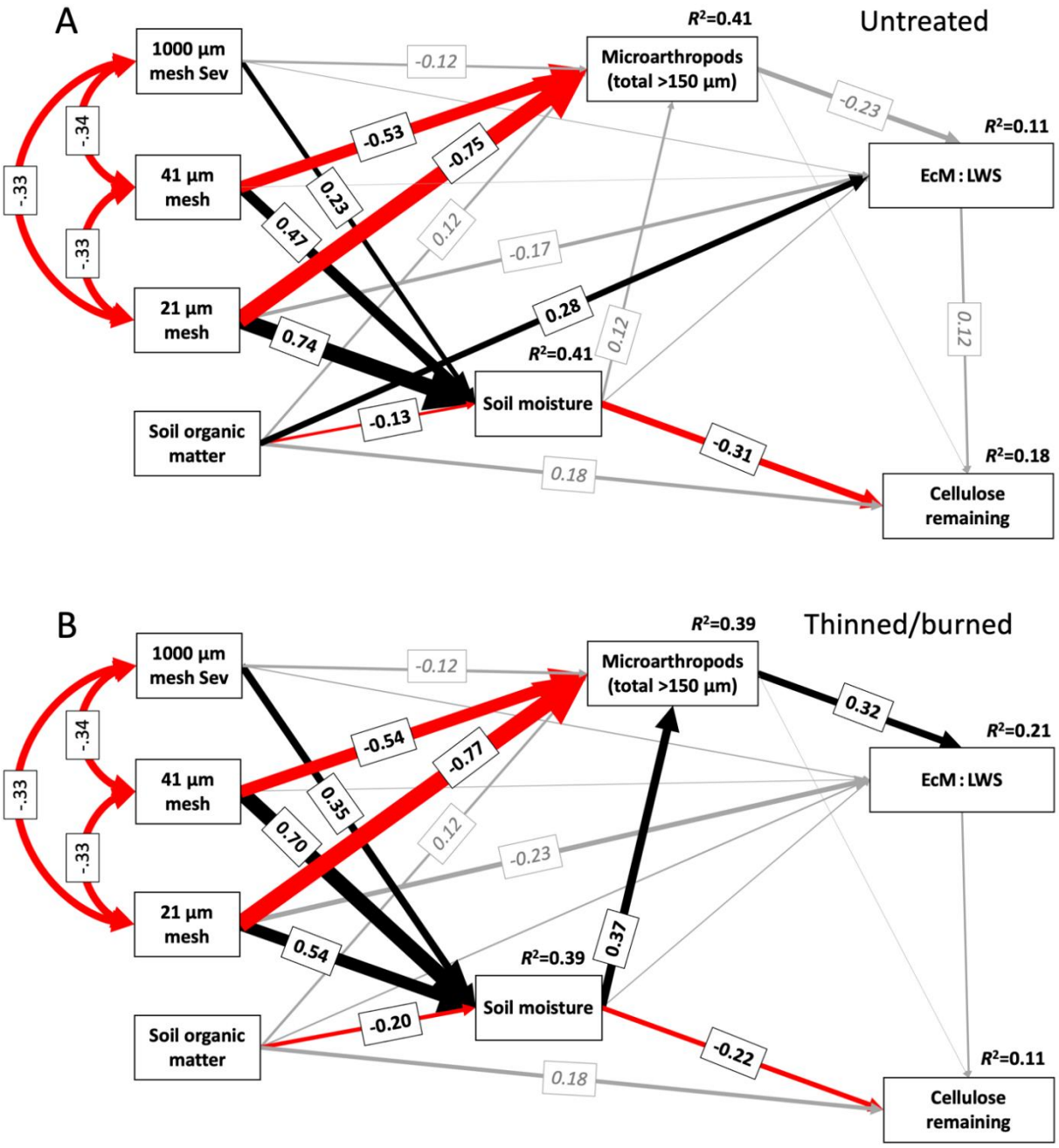

Fig. 4.15 Multigroup structural equation model of cellulose decomposition. (**A**) Untreated management unit. (**B**) Thinned/burned management unit. Soil moisture=mean Z scores of soil moisture measurements taken at five timepoints. Significant standardized path coefficients (λ) with $p < 0.05$ are shown in bolded black text; all other path coefficients are shown in gray italics where $\lambda \geq 0.1$ or are omitted if $\lambda < 0.1$. Black arrows indicate significant positive paths, red arrows represent significant negative paths. Arrow widths are scaled according to the standardized path coefficients. EcM:LWS =ratio of ectomycorrhizal reads to litter and wood saprotroph reads. Percent soil organic matter, microarthropod abundances, and EcM:LWS were log transformed prior to analysis.

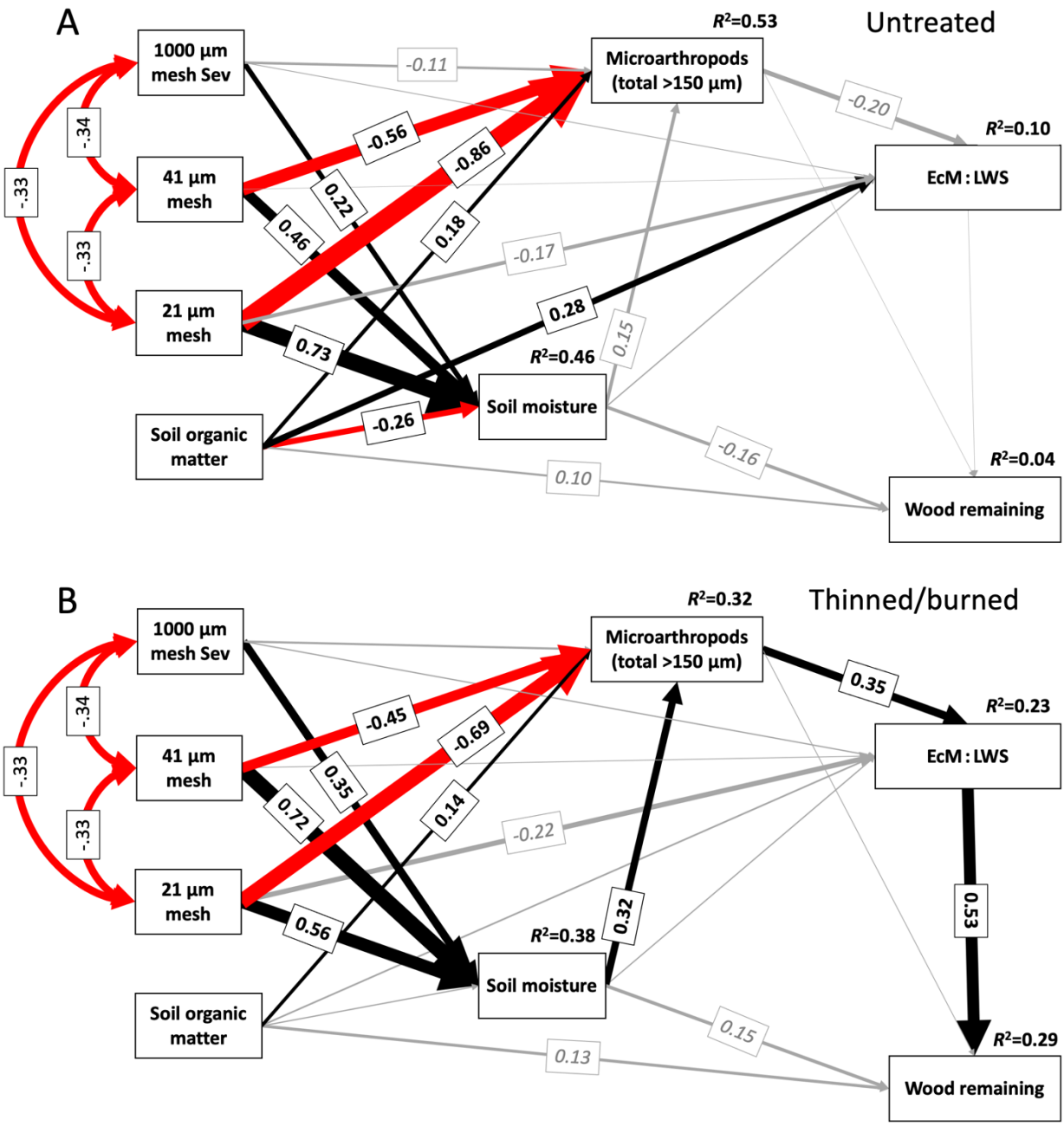

Fig. 4.16 Multigroup structural equation model of wood decomposition. (**A**) Untreated management unit. (**B**) Thinned/burned management unit. Soil moisture=mean Z scores of soil moisture measurements taken at five timepoints. Significant standardized path coefficients (λ) with $p < 0.05$ are shown in bolded black text; all other path coefficients are shown in gray italics where $\lambda \geq 0.1$ or are omitted if $\lambda < 0.1$. Black arrows indicate significant positive paths, red arrows represent significant negative paths. Arrow widths are scaled according to the standardized path coefficients. EcM:LWS =ratio of ectomycorrhizal reads to litter and wood saprotroph reads. Percent soil organic matter, microarthropod abundances, and EcM:LWS were log transformed prior to analysis.

Table 4.5 Hypothesized direct effects (H.D.E.) and observed direct, indirect, and total effects from the multigroup structural equation model of cellulose decomposition. Values are standardized path coefficients (*p*-values are in parentheses for direct effects). Bolded direct effects had path coefficients of the opposite sign hypothesized and $p<0.05$. Microarthropods=total microarthropods > 150 µm; EcM:LWS=ratio of ectomycorrhizal to litter/wood saprotrophic fungal reads; SOM=soil organic matter (%). Microarthropod abundances, EcM:LWS, and SOM were log transformed prior to analysis.

			Untreated			*Thinned/burned*		
Predictor variable	**H.D.E.**	**Response variable**	**Direct (*p*)**	**Indirect**	**Total**	**Direct (*p*)**	**Indirect**	**Total**
1000 µm mesh Sev	decrease	Microarthropods	-0.119 (0.246)	0.028	-0.092	-0.122 (0.246)	0.129	0.007
1000 µm mesh Sev	increase	Soil moisture	0.233 (0.003)	NA	0.233	0.345 (0.003)	NA	0.345
1000 µm mesh Sev	affect	EcM:LWS	-0.038 (0.712)	0.008	-0.03	-0.052 (0.712)	-0.015	-0.067
1000 µm mesh Sev	NA	Cellulose remaining	NA	-0.077	-0.077	NA	-0.082	-0.082
41 µm mesh	decrease	Microarthropods	-0.525 (<0.001)	0.056	-0.469	-0.537 (<0.001)	0.26	-0.276
41 µm mesh	increase	Soil moisture	0.47 (<0.001)	NA	0.47	0.697 (<0.001)	NA	0.697
41 µm mesh	affect	EcM:LWS	-0.025 (0.842)	0.081	0.056	-0.034 (0.842)	-0.122	-0.156
41 µm mesh	NA	Cellulose remaining	NA	-0.145	-0.145	NA	-0.17	-0.17
21 µm mesh	decrease	Microarthropods	-0.754 (<0.001)	0.088	-0.666	-0.771 (<0.001)	0.201	-0.57
21 µm mesh	increase	Soil moisture	0.735 (<0.001)	NA	0.735	0.538 (<0.001)	NA	0.538
21 µm mesh	affect	EcM:LWS	-0.165 (0.228)	0.111	-0.054	-0.226 (0.228)	-0.206	-0.432
21 µm mesh	NA	Cellulose remaining	NA	-0.243	-0.243	NA	-0.162	-0.162
SOM	increase	Microarthropods	0.119 (0.145)	-0.016	0.103	0.121 (0.145)	-0.073	0.048
SOM	increase	Soil moisture	**-0.132 (0.04)**	NA	-0.132	**-0.196 (0.04)**	NA	-0.196
SOM	affect	EcM:LWS	0.282 (0.043)	-0.016	0.265	-0.071 (0.601)	0.025	-0.046
SOM	affect	Cellulose remaining	0.177 (0.066)	0.073	0.25	0.184 (0.066)	0.04	0.224
Soil moisture	increase	Microarthropods	0.12 (0.353)	NA	0.12	0.374 (0.005)	NA	0.374
Soil moisture	affect	EcM:LWS	-0.055 (0.674)	-0.027	-0.082	-0.05 (0.674)	0.118	0.067
Soil moisture	decrease	Cellulose remaining	-0.314 (0.006)	-0.008	-0.323	-0.221 (0.006)	0.009	-0.212
Microarthropods	increase	EcM:LWS	-0.228 (0.132)	NA	-0.228	0.315 (0.047)	NA	0.315
Microarthropods	increase	Cellulose remaining	0.008 (0.931)	-0.026	-0.018	0.009 (0.931)	0.028	0.036
EcM:LWS	increase	Cellulose remaining	0.115 (0.291)	NA	0.115	0.088 (0.291)	NA	0.088

Table 4.6 Hypothesized direct effects and observed direct, indirect, and total effects from the multigroup structural equation model of wood decomposition. Values are standardized path coefficients (*p*-values are in parentheses for direct effects). Bolded direct effects had path coefficients of the opposite sign hypothesized and $p<0.05$. Microarthropods=total microarthropods > 150 µm; EcM:LWS=ratio of ectomycorrhizal to litter/wood saprotrophic fungal reads; SOM=soil organic matter (%). Microarthropod abundances, EcM:LWS, and SOM were log transformed prior to analysis.

			Untreated			*Thinned/burned*		
Predictor variable	**H.D.E.**	**Response variable**	**Direct (*p*)**	**Indirect**	**Total**	**Direct (*p*)**	**Indirect**	**Total**
1000 µm mesh Sev	decrease	Microarthropods	-0.111 (0.298)	0.034	-0.078	-0.089 (0.298)	0.111	0.021
1000 µm mesh Sev	increase	Soil moisture	0.224 (0.003)	NA	0.224	0.347 (0.003)	NA	0.347
1000 µm mesh Sev	affect	EcM:LWS	-0.038 (0.711)	0.003	-0.035	-0.051 (0.711)	-0.009	-0.06
1000 µm mesh Sev	NA	Wood remaining	NA	-0.033	-0.033	NA	0.02	0.02
41 µm mesh	decrease	Microarthropods	-0.561 (<0.001)	0.069	-0.492	-0.449 (<0.001)	0.229	-0.22
41 µm mesh	increase	Soil moisture	0.464 (<0.001)	NA	0.464	0.719 (<0.001)	NA	0.719
41 µm mesh	affect	EcM:LWS	-0.025 (0.84)	0.073	0.049	-0.033 (0.84)	-0.112	-0.145
41 µm mesh	NA	Wood remaining	NA	-0.064	-0.064	NA	0.04	0.04
21 µm mesh	decrease	Microarthropods	-0.86 (<0.001)	0.109	-0.751	-0.688 (<0.001)	0.177	-0.511
21 µm mesh	increase	Soil moisture	0.73 (<0.001)	NA	0.73	0.556 (<0.001)	NA	0.556
21 µm mesh	affect	EcM:LWS	-0.166 (0.222)	0.111	-0.056	-0.223 (0.222)	-0.206	-0.429
21 µm mesh	NA	Wood remaining	NA	-0.099	-0.099	NA	-0.126	-0.126
SOM	increase	Microarthropods	0.178 (0.04)	-0.039	0.14	0.142 (0.04)	-0.015	0.127
SOM	increase	Soil moisture	**-0.257 (0.017)**	NA	-0.257	-0.048 (0.682)	NA	-0.048
SOM	affect	EcM:LWS	0.283 (0.049)	-0.014	0.269	-0.07 (0.599)	0.047	-0.023
SOM	affect	Wood remaining	0.103 (0.217)	0.033	0.136	0.132 (0.217)	-0.024	0.108
Soil moisture	increase	Microarthropods	0.15 (0.226)	NA	0.15	0.319 (0.016)	NA	0.319
Soil moisture	affect	EcM:LWS	-0.056 (0.674)	-0.03	-0.086	-0.049 (0.674)	0.112	0.063
Soil moisture	decrease	Wood remaining	-0.159 (0.282)	-0.002	-0.161	0.153 (0.228)	0.023	0.175
Microarthropods	increase	EcM:LWS	-0.202 (0.195)	NA	-0.202	0.35 (0.022)	NA	0.35
Microarthropods	increase	Wood remaining	-0.022 (0.779)	0.004	-0.018	-0.034 (0.779)	0.187	0.152
EcM:LWS	increase	Wood remaining	-0.019 (0.899)	NA	-0.019	0.533 (<0.001)	NA	0.533

4.4 Discussion

We successfully manipulated soil mesofauna communities in thinned/burned and untreated ponderosa pine stands for two growing seasons, illuminating how interactions between mesofauna and complex fungal communities can influence ecological functions in a widespread forest type. Our study demonstrates that soil mesofauna can have significant impacts on the functional composition of fungal communities, with implications for decomposition. However, our findings also indicate that these effects are context and substrate dependent.

4.4.1 Direct effects of microarthropods on ectomycorrhizal fungi, litter/wood saprotrophs, and decomposition

Our hypothesis that microarthropod abundances increase EcM:LWS ratios (*H1*) was partially supported: we observed patterns consistent with this phenomenon only within the thinned/burned forest. There, abundance of microarthropods > 150 µm (the size class best manipulated by our mesh treatments, and that which we considered most likely to affect fungal communities through grazing and dispersal) was the strongest direct predictor of EcM:LWS in our multigroup SEM, explaining approximately 10% (cellulose model) to 12% (wood model) of the variance in this ratio. Microarthropods had no significant effect on EcM:LWS within the untreated unit. This finding is surprising, because microarthropod abundances were much higher in that management unit, and we had anticipated that more microarthropods would produce stronger grazing pressure on LWS (*H6*).

We may not have observed a relationship between microarthropods and EcM:LWS in the untreated unit for three reasons. First, our sampling methodology, combined with the fact that litter and organic layers were deep in the untreated unit but had mostly been combusted in the

thinned/burned unit, could have led to this outcome. The sample capacity of our Tullgren funnel extractors prevented us from separately extracting litter and soil fauna, and molecular characterization of fungi in the litter layer was beyond the scope of this study. These constraints likely had a negligible impact on our ability to resolve faunal/fungal interactions in the thinned/burned unit, where litter was sparse, but in the untreated unit, sampling in this way unfortunately excluded a large component of the fungal community. This may have hampered our ability to detect the influence of fauna on fungal groups, as litter-dwelling fungi were undoubtedly a significant food source for microarthropods in the untreated unit.

Second, microarthropod-facilitated dispersal of fungal propagules may have been important in affecting EcM:LWS ratios within the thinned/burned unit. We would expect dispersal services to be especially valuable where fungal communities are recovering from disturbance. Transport of ectomycorrhizal propagules by soil mesofauna remains an understudied topic, but endo- and especially ectozoochory by medium to large mites and collembolans are plausible dispersal mechanisms for EcM (Lilleskov and Bruns, 2005; Vašutová et al., 2019). Of course, in order for dispersal to increase EcM:LWS ratios, EcM would have to benefit disproportionately from the availability of microarthropod taxis.

A third possibility is that trophic interactions between mesofauna and fungi differed in the two management units. Five years after fire, and eight years after thinning, faunal and fungal communities in our treated and untreated sites remained profoundly different (**Fig. 4.9** and **Fig. 4.11**). Fungivorous mesofauna are often described as "choosy generalists"; restoration treatments certainly altered the menu choices, and perhaps also the predominant tastes of the diners. In the only published study analyzing the relative importance of ectomycorrhizal vs. saprotrophic fungi in microarthropod diets, Pollierer and Scheu (2021) reported that, while the vast majority of

examined collembolan and oribatid taxa consumed mainly saprotrophic fungi (as indicated by amino acid stable isotope signatures), ectomycorrhizal fungi appeared to be the primary food source for a few taxa. Consumption of EcM might be more common among the microarthropod taxa present in the untreated than in the thinned/burned unit; higher availability of EcM, and higher densities of microarthropods, could also make a given microarthropod taxon less selective. For example, Pollierer and Scheu (ibid.) reported that the isotopic signatures of some microarthropod taxa were shifted more toward ectomycorrhizal food sources in spruce than in beech forests. Communities in the two management units could also have different overall effects on growth of grazed fungi depending on the prevalence of feeding styles (e.g., browsing vs. grazing (Siepel and Ruiter-Dijkman, 1993)) or on feeding intensity, which should depend on the relative abundances of fauna and fungi.

As hypothesized (*H3*), we observed no direct effect of microarthropods on decomposition of our recalcitrant substrate (wood), but contrary to our expectations (*H2*), microarthropods did not directly increase decomposition of our labile substrate (cellulose) either. Instead, soil moisture emerged as the most important driver of cellulose mass loss in both thinned/burned and untreated forests. In a global decomposition study, Wall et al. (2008) found that mesofauna enhanced decomposition of grass litter (high in cellulose) at warm and mesic sites, but had no effect at sites where temperature or moisture limited microbial activity. Our dry ponderosa pine forests fall into the latter category for much of the year, and moisture limitations were especially acute during the period of our study.

4.4.2 Context-dependency of the Gadgil effect

Our multigroup SEM of wood decomposition in the thinned/burned unit supported our hypothesis (*H4*) that microarthropods can indirectly decelerate wood decomposition via intensification of the Gadgil effect. In the untreated unit, however, we found no evidence that EcM:LWS ratios influenced wood decomposition. This was in contrast to our expectations regarding the relative strength of the Gadgil effect in the two management units (*H6*): we had hypothesized that higher ratios of EcM:LWS fungi in the untreated unit (which we did observe) would increase the likelihood of observing increased decomposition when EcM were reduced. It is possible that we were unable to observe an effect of EcM:LWS on wood decomposition in the untreated unit because this ratio was unaffected by microarthropods there (in other words, because we did not in fact manipulate EcM:LWS ratios), or because we did not characterize fungal communities in the well-developed litter layer within that unit.

However, the Gadgil effect may also be contingent on the identities of interacting ectomycorrhizal and saprotrophic taxa. In a reciprocal litter transplant study manipulating fungal communities by trenching, Fernandez et al. (2020) found evidence for the Gadgil effect in a pine forest, but not in an oak forest (both tree genera form ectomycorrhizal associations). This variability was suggested to stem from functional differences between divergent EcM communities at the two sites. In our own study, management treatments appear to have dramatically altered fungal communities. Communities in the thinned/burned unit might include more EcM taxa that are superior competitors for N bound in highly recalcitrant substrates. Restoration treatments could potentially favor EcM taxa that efficiently exploit recalcitrant N in wood: combustion of material that is more labile than wood (i.e., pine needles) on the forest floor

could increase the importance of organic N bound in the belowground necromass of harvested trees.

Thinning should also lessen water limitation for remaining trees, potentially increasing the trade value of N for ectomycorrhizal fungi. Smith and Wan (2019) have theorized that the ability of an EcM fungus to restrict carbon acquisition by a saprotroph hinges on a lower R^* (*sensu* Tilman, 1982) of the EcM competitor than the saprotrophic competitor for recalcitrant N. Obtaining recalcitrant N (e.g., by oxidizing lignin) exacts a C cost not incurred when taking up labile N. This cost is subsidized for EcM fungi that degrade recalcitrant substrates, but in return some of the N obtained must be surrendered to the host plant. The value of the payment to the EcM fungus in photosynthetically fixed C, as well as the proportion of obtained N allocated to the host, can, according to this framework, alter competitive outcomes between EcM and saprotrophic fungi.

A final possibility is that burning, and perhaps also soil disturbance from mechanical thinning, intensified the Gadgil effect by increasing inter-guild fungal interactions. The presence of organic soil layers may allow vertical niche partitioning between saprotrophic fungi (colonizing upper organic layers) and EcM fungi (colonizing lower mineral layers) (Fernandez et al., ibid.), as demonstrated by Bödeker et al. (2016) in a boreal spruce forest. EcM fungi and saprotrophs in the thinned/burned unit, where organic layers are poorly developed, could share realized niche space to a greater extent than in the untreated unit. However, Peršoh et al. (2018) found no vertical stratification of EcM and saprotrophic functional guilds in the organic and mineral soil layers of another boreal spruce forest, so this phenomenon may not be universal within—let alone across—forest types.

4.4.3 Substrate dependency of the Gadgil effect

As Smith and Wan's (ibid.) models would predict, we observed no effect of EcM:LWS ratios on cellulose decomposition in either management treatment unit (*H5*). Our results support the theory that saprotrophic fungi (and probably bacteria, which are also important players in cellulose decomposition) have a lower R^* for labile N than do EcM fungi. In this scenario, EcM are inferior competitors for labile N, and EcM cannot suppress the growth of saprotrophs on a substrate so long as that substrate contains sufficient labile N to support saprotroph utilization of available carbon. Few studies have tested for the Gadgil effect in decomposition of labile and recalcitrant substrates within the same ecological setting. Our findings accord with those of Fernandez et al. (ibid.), who observed the Gadgil effect in decomposition of pine litter, but not oak litter (and only in a pine forest, as mentioned above).

4.4.4 Methods development

Our novel mesocosm design enabled us to perform repeated measurements within mesocosms while maintaining differences in faunal complexity for fifteen months. Although side effects were not eliminated, they were quantified, and we are confident that they were lower than would have occurred in this system with other faunal exclusion mesocosm designs (e.g., Vedder et al., 1996). These include: 1) altered infiltration, leaching, and UV penetration (addressed by using the same mesh size for lids and bottoms); 2) relatedly, differences in microclimate between substrates with and without focal fauna (addressed by repeatedly measuring soil moisture); and 3) the increased loss of litter fragments through coarse mesh (addressed by controlling the presence or absence of fauna in an entire soil/litter system, not just on the substrate). We also note that our mesocosms are inexpensive to construct and are compatible with LI-COR

chambers, facilitating measurement of gas fluxes. We are hopeful that the method we developed can aid in resolving links between soil fauna and fungi-mediated ecological functions across forest types and management treatments. Field data on the causality of these relationships are scarce, but critical for informing soil biogeochemical models (Grandy et al., 2016).

4.5 Conclusions

In an observational field study of faunal communities and ecosystem services, Neher et al. (2012) found that the majority of microarthropod groups correlated negatively with mass loss of wood (a substrate used infrequently in microarthropod decomposition studies), but the mechanistic underpinnings of this phenomenon have remained elusive. Our data reveal that microarthropod communities can alter the ratio of ectomycorrhizal fungi to saprotrophic fungi capable of degrading wood and litter, altering decomposition of recalcitrant substrates and suggesting a heretofore unexplored linkage between soil mesofauna and tree nutrition. To our knowledge, ours is the first experiment evidencing microarthropod contributions to the Gadgil effect. However, contrasting patterns in thinned/burned and untreated ponderosa pine forests highlight that the functional importance of soil fauna is context dependent: forest restoration treatments paradoxically increased the importance of soil fauna despite reducing their abundance. Our findings also support recent theoretical work by Smith and Wan (2019): we observed the Gadgil effect in a recalcitrant substrate, but not in a labile substrate, as predicted by their models based on resource-ratio theory. Much additional work is needed to unravel the abiotic and biotic parameters governing relationships between fauna, fungal communities, and decomposition across forest types and management treatments. Our work emphasizes the utility

of field mesocosm experiments to elucidate the real-world functional roles of mesofauna: the relationships we unearthed could not have been detected in simplified laboratory microcosms.

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CHAPTER V: OVERALL DISCUSSION OF RESULTS AND CONCLUSIONS

The studies presented in this dissertation indicate that forest restoration treatments impact microinvertebrate groups to differing degrees, with potential consequences for ecosystem functioning and higher trophic levels. The observational study (Chapter II) and the logging machinery soil disturbance experiment (Chapter III) both suggest that nematode communities are relatively resistant or resilient to low-intensity disturbances caused by thinning and prescribed fire. However, microarthropod communities appear to be more sensitive to restoration treatments. One year after prescribed fire, we observed lower abundances of mites in a thinned/burned management unit relative to an untreated management unit, while collembolans were similarly abundant in thinned/burned and untreated units (Chapter II). Five years later, field mesocosms in the thinned/burned management unit were colonized by fewer large mites, and by fewer collembolans of all sizes, than were mesocosms in the untreated unit (Chapter IV). It is possible that by situating our mesocosms at tree driplines, and excluding understory vegetation from the mesocosms, we were unable to observe overall neutral effects of combined restoration treatments on collembolans which were evident when sampling across the landscape. Nevertheless, our data suggest that negative effects of restoration treatments on large-bodied mites (notably mites in the order Oribatida) were persistent. This finding accords with those of Camann et al. (2012), who reported that oribatid mites showed signs of continuing decline two years after low intensity fire in a *P. ponderosa/P. jeffreyi* system in the Pacific Northwest. Mites in the Oribatida tend to be slow-moving, traversing less than five centimeters per day on average (Berthet, 1964). As oribatids are generally not phoretic, their recolonization of large burned areas could proceed quite slowly. Oribatids also have *K*-style life history traits, with low reproductive

output and generation times often exceeding a year, which should slow their recovery relative to more *r*-selected microarthropod taxa. Finally, it is possible that food and/or habitat resources favored by oribatids are negatively impacted by restoration treatments. Future studies are needed to parse the relative importance of dispersal limitations, life history traits, and habitat modifications in the depression of oribatid mite populations after restoration treatments. If dispersal proves to be a limiting factor, litter transplantation could prove a useful strategy in facilitating recovery of mite communities after prescribed burning and wildfires. This may be worthwhile as our field mesocosm study suggests that large microarthropods impacted by restoration treatments may be of greater functional importance in treated than in untreated forests and could possibly enhance recovery of ectomycorrhizal fungi. In Valles Caldera National Preserve, recovery of oribatid mite populations is also relevant to conservation of the endangered endemic salamander *Plethodon neomexicanus*, for whom oribatids are one of three main prey items (staphylinid beetles, which themselves consume oribatid mites, are another) (Cummer, 2005).

However, is also critical to remember that the reduced complexity of faunal communities in the thinned/burned management unit may or may not be representative of pre-fire-exclusion conditions. Impacts of thinning and prescribed fire on soil fauna are likely more extreme than those of historic low-intensity burns (e.g., due to disturbance from logging machinery and increased heat transfer to soil from higher fuel loads), but the untreated control unit in our study was undeniably also a very unnatural ecological stage for microarthropod communities. It is thus difficult to gauge the "desirability" of microarthropod community changes from a management perspective.

Our findings in Chapter IV must also be interpreted in the context of historically anomalous climate behavior in the region. While our mesocosms were deployed, the area received only an estimated ~60% of its average precipitation, and only ~50% of its average precipitation during the growing season (PRISM Climate Group, 2021). In an already xeric ecosystem type, these precipitation deficits likely had profound implications for soil food webs and their performance of ecological functions. However, increasing aridity is expected in the region due to anthropogenic climate change, so our findings may be more representative of future than of past conditions.

To the best of our knowledge, the experiment detailed in Chapter IV is the first to demonstrate modulation of the Gadgil effect by microarthropods. Much work remains to elucidate the mechanisms underlying the patterns we observed and to determine their importance in other systems. In particular, research is sparse regarding the role of microarthropods in dispersal of ectomycorrhizal fungi (Vašutová et al., 2019), the traits determining palatability of ectomycorrhizal and saprotrophic fungi to microarthropods (Pollierer and Scheu, 2021), and the significance of microarthropod/fungal interactions for nutrient and carbon cycling across forest types. Further studies concerning effects on fungal communities of the chemical arsenals possessed by some oribatid mites (A'Bear et al., 2010), and the phenomenon of ectomycorrhizal fungi preying upon microarthropods (Klironomos and Hart, 2001), may also help to resolve relationships between mesofauna and fungal community functioning. We are hopeful that the novel field mesocosm method presented in this dissertation will facilitate future investigations of soil fauna communities and their functional importance.

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Vašutová, M., Mleczko, P., López-García, A., Maček, I., Boros, G., Ševčík, J., Fujii, S., Hackenberger, D., Tuf, I.H., Hornung, E., Páll-Gergely, B., Kjøller, R., 2019. Taxi drivers: the role of animals in transporting mycorrhizal fungi. Mycorrhiza 29, 413–434.

APPENDIX I: SUPPLEMENTARY INFORMATION FOR CHAPTER II

Supplementary Information

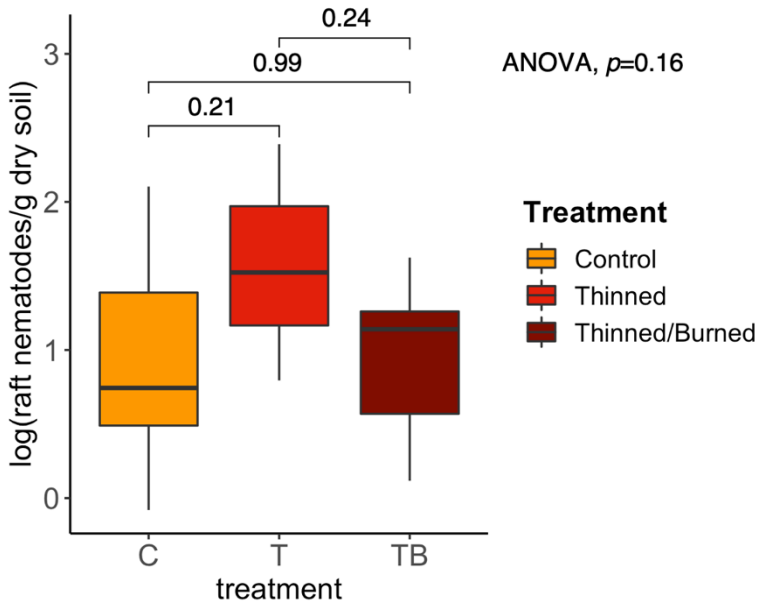


Fig. S2.1 Densities of nematodes extracted with modified floating Baermann trays ("nematode rafts"), without preliminary decanting and sieving. Nematodes extracted with this less-efficient method showed the same overall pattern in restoration treatment responses as did those re-extracted later with the more efficient sucrose centrifugation method, although the variance was higher and treatment effects were not significant. Despite the likelihood that nematode densities were reduced by extended storage, we feel that the nematode abundance data obtained using the more efficient method are better suited to assessing differences across management treatments, so these data are presented in the main text.

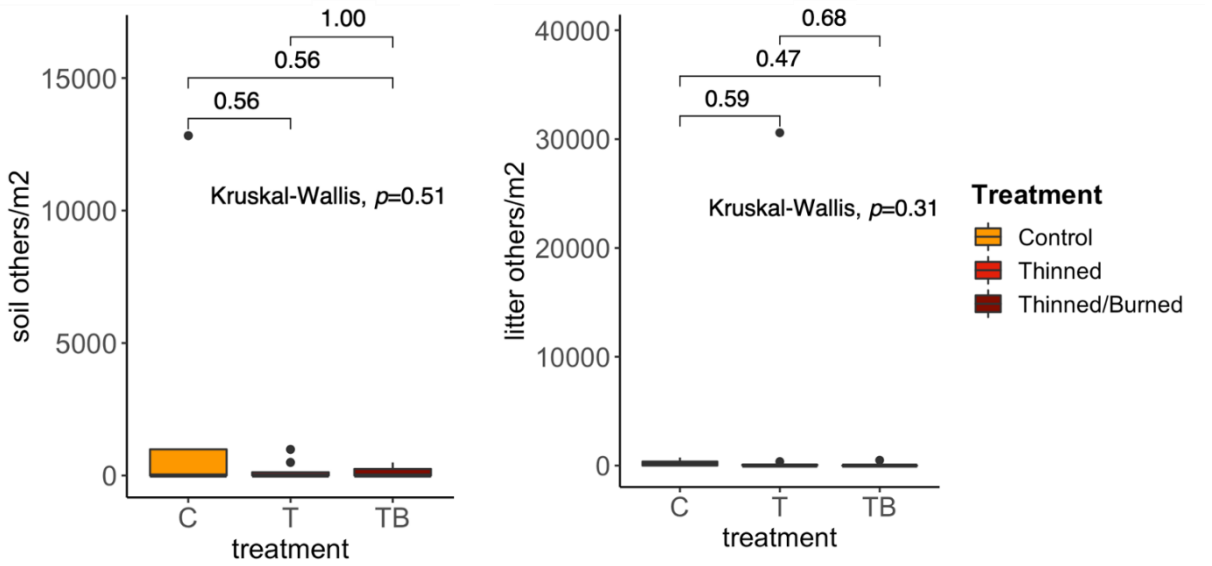
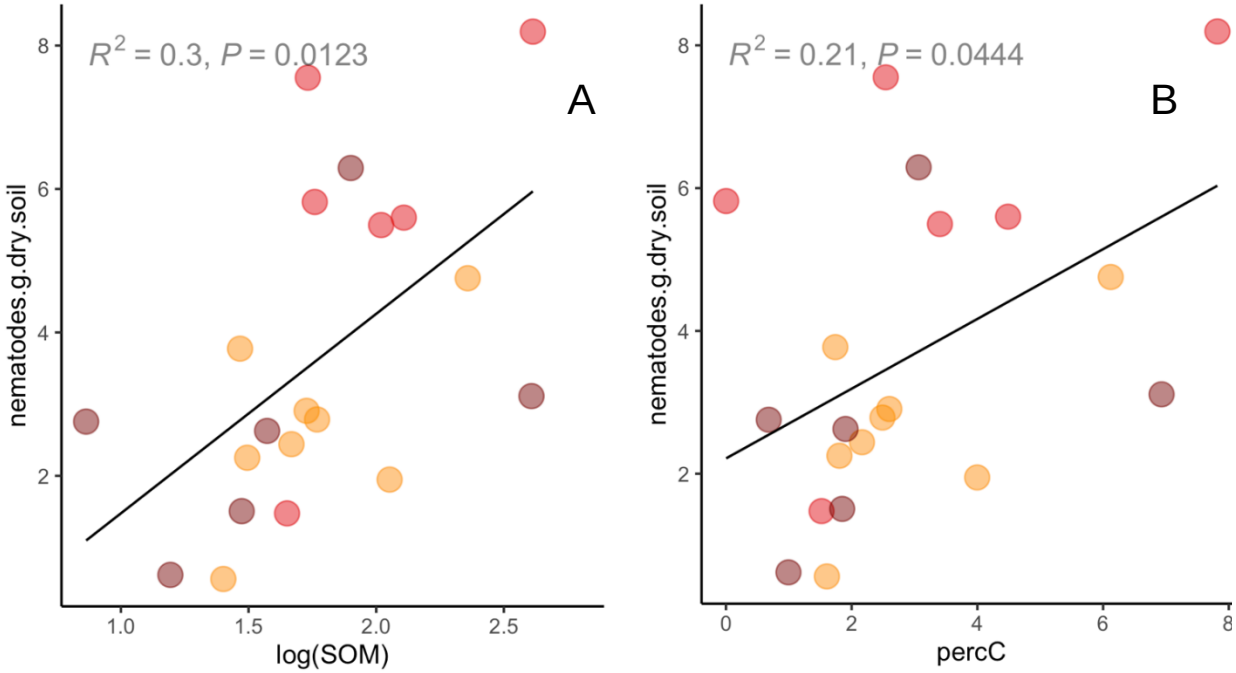
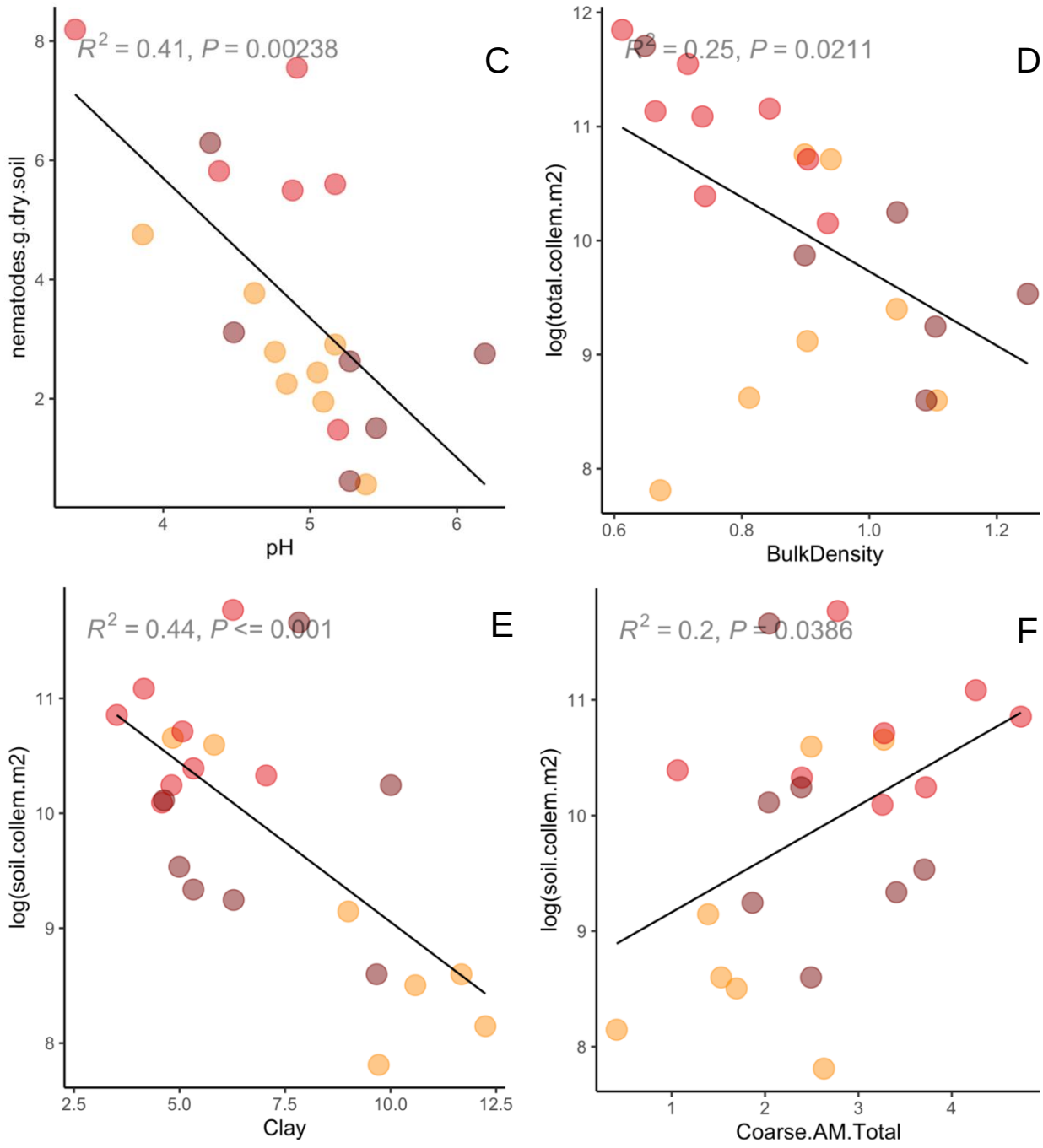


Fig. S2.2 Abundance of arthropods other than mites and collembolans (chiefly ants, macroarthropod larvae, and enchytraeids) extracted from soil and litter samples with Tullgren funnels.




C
R^2 = 0.41, P = 0.00238
nematodes.g.dry.soil
pH
D
R^2 = 0.25, P = 0.0211
log(total.collem.m2)
BulkDensity
E
R^2 = 0.44, P <= 0.001
log(soil.collem.m2)
Clay
F
R^2 = 0.2, P = 0.0386
log(soil.collem.m2)
Coarse.AM.Total

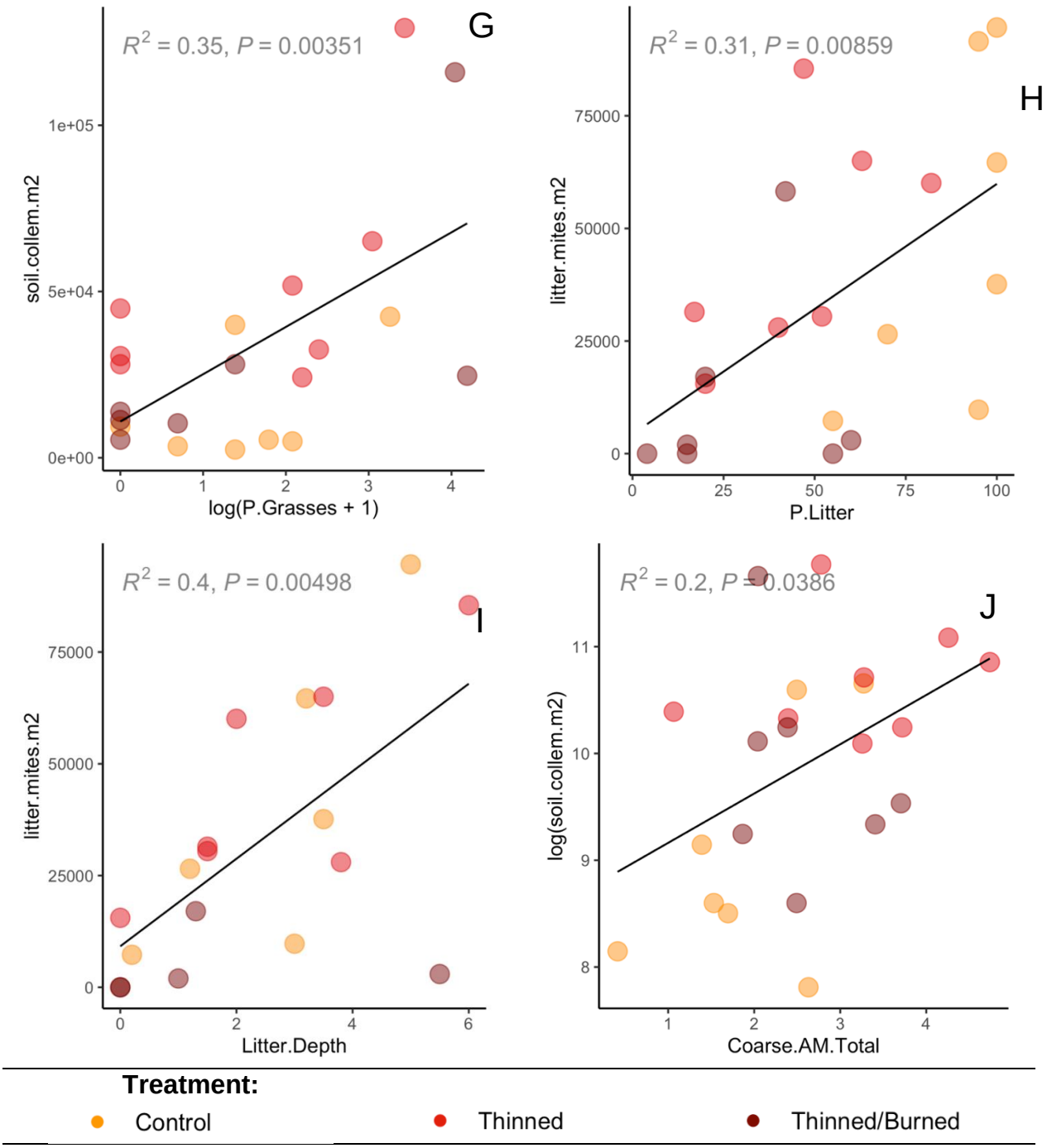


Fig. S2.3 Correlations between micro- and mesofauna groups and the habitat characteristics which best predicted their abundance. (**A**) Nematodes per g dry soil and percent soil organic matter. (**B**) Nematodes per g dry soil and percent soil carbon. (**C**) Nematodes per g dry soil and pH. (**D**) Total collembolans per m^2 and soil bulk density. (**E**) Soil collembolans per m^2 and percent clay. (**F**) Soil collembolans per m^2 and lengths of coarse arbuscular mycorrhizal hyphae (m per g dry soil). (**G**) Soil collembolans per m^2 and percent grass cover. H. Litter mites per m^2 and percent litter cover, after removing an outlier sample with both extremely high litter depth and extremely high mite abundances. I. Litter mites per m^2 and litter depth (cm), after removal of the same outlier.

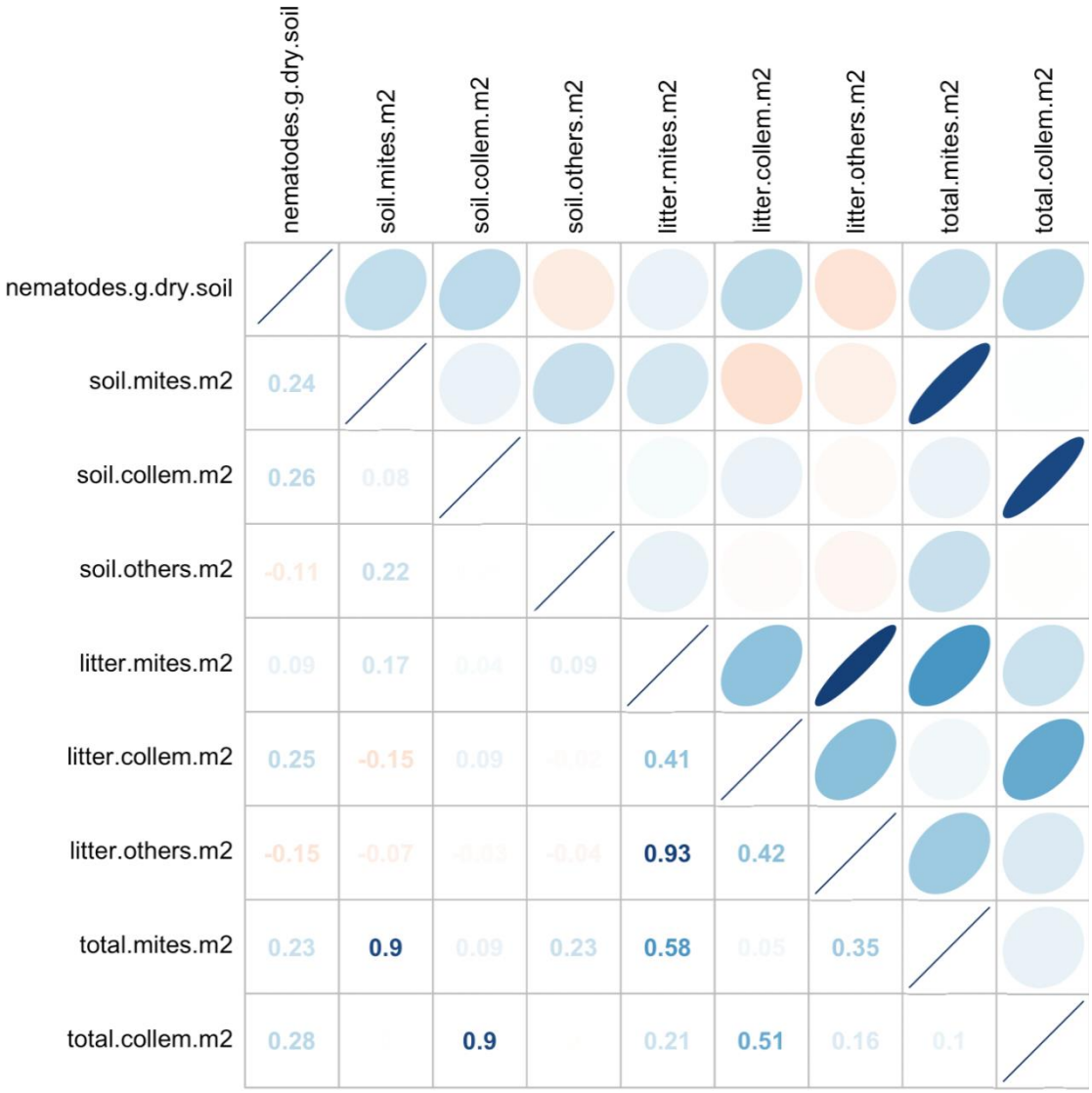


Fig. S2.4 Matrix of Pearson correlations between abundances of micro- and mesofauna groups. Correlation coefficients are color coded by strength and direction (relationships colored in blue are positive, and those shown in red are negative).

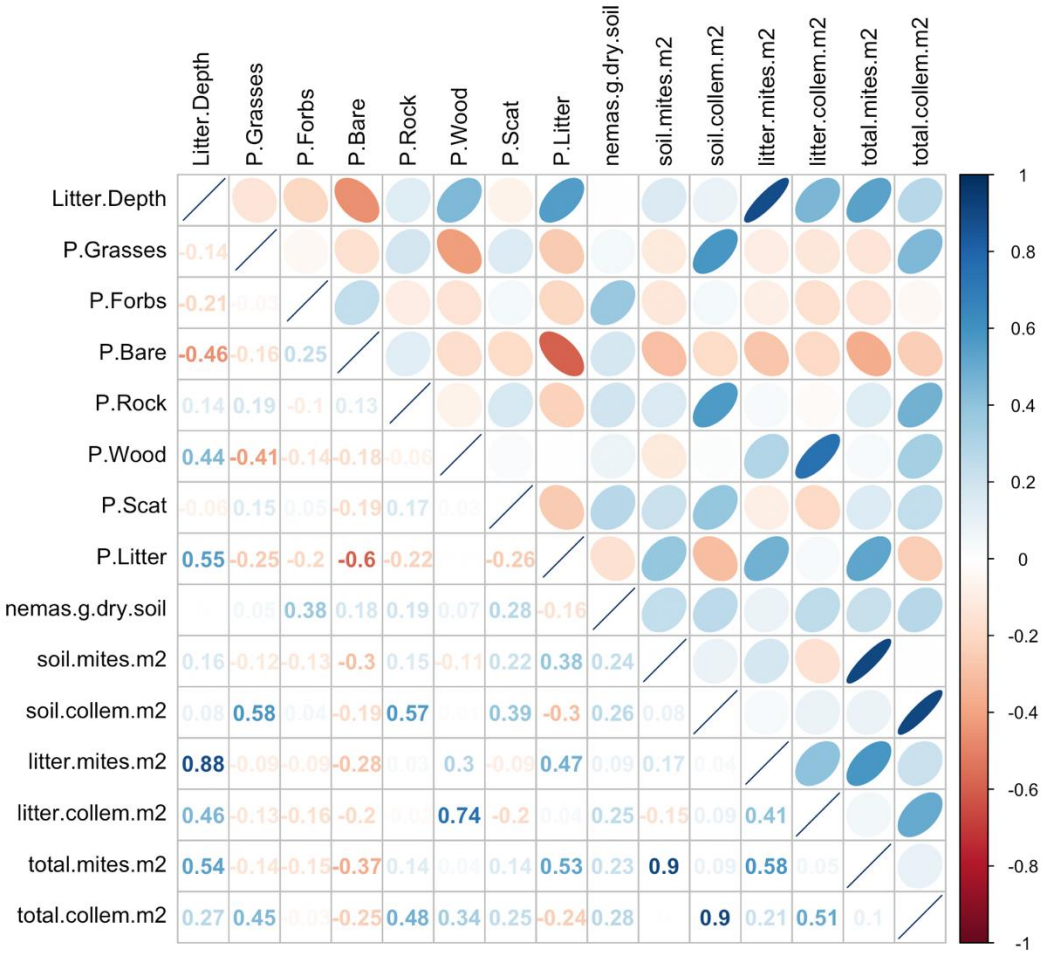


Fig. S2.5 Matrix of Pearson correlations between micro- and mesofauna groups and ground cover, color coded by strength and direction.

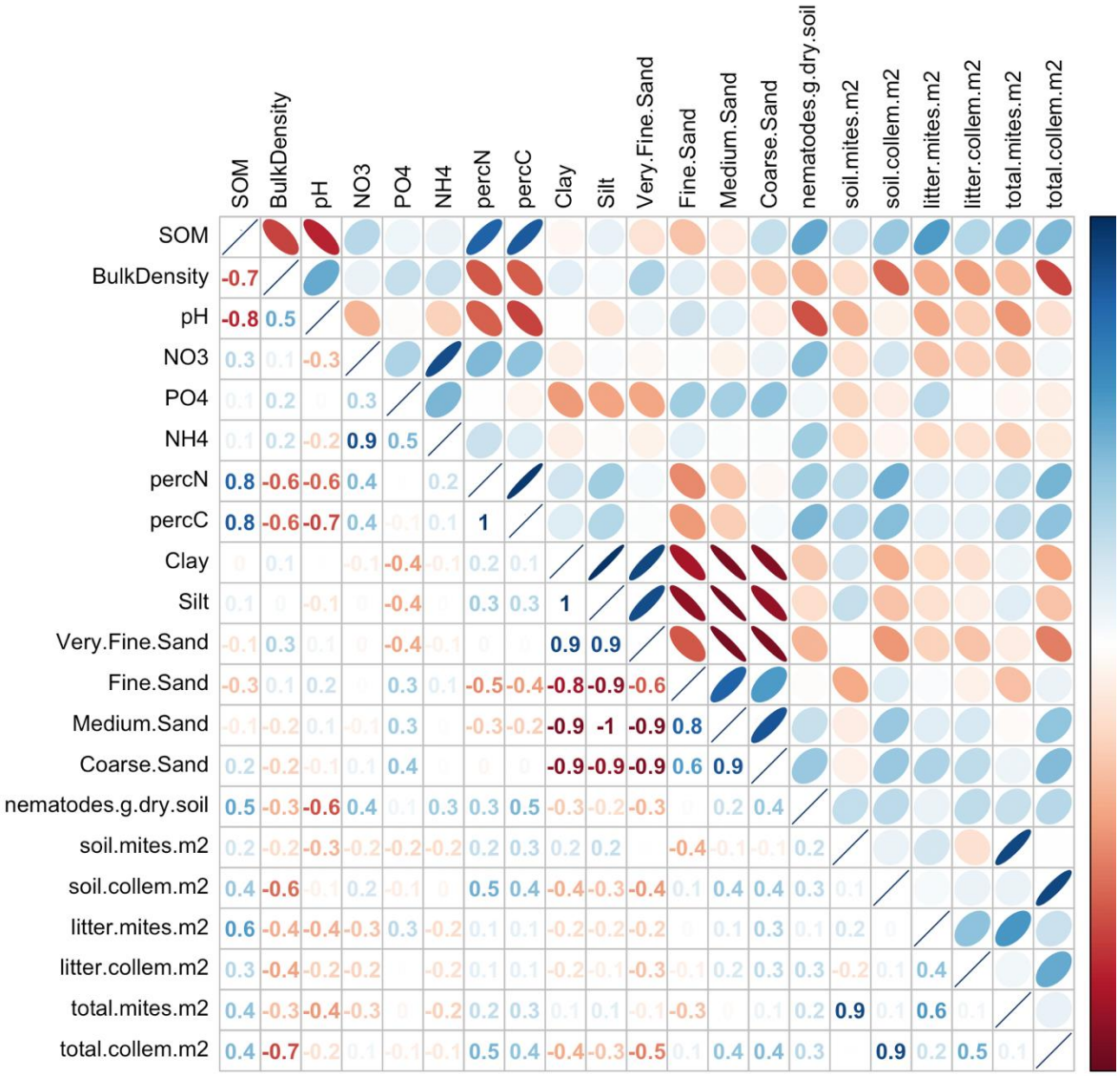


Fig. S2.6 Matrix of Pearson correlations between micro- and mesofauna groups and soil abiotic properties, color coded by strength and direction.

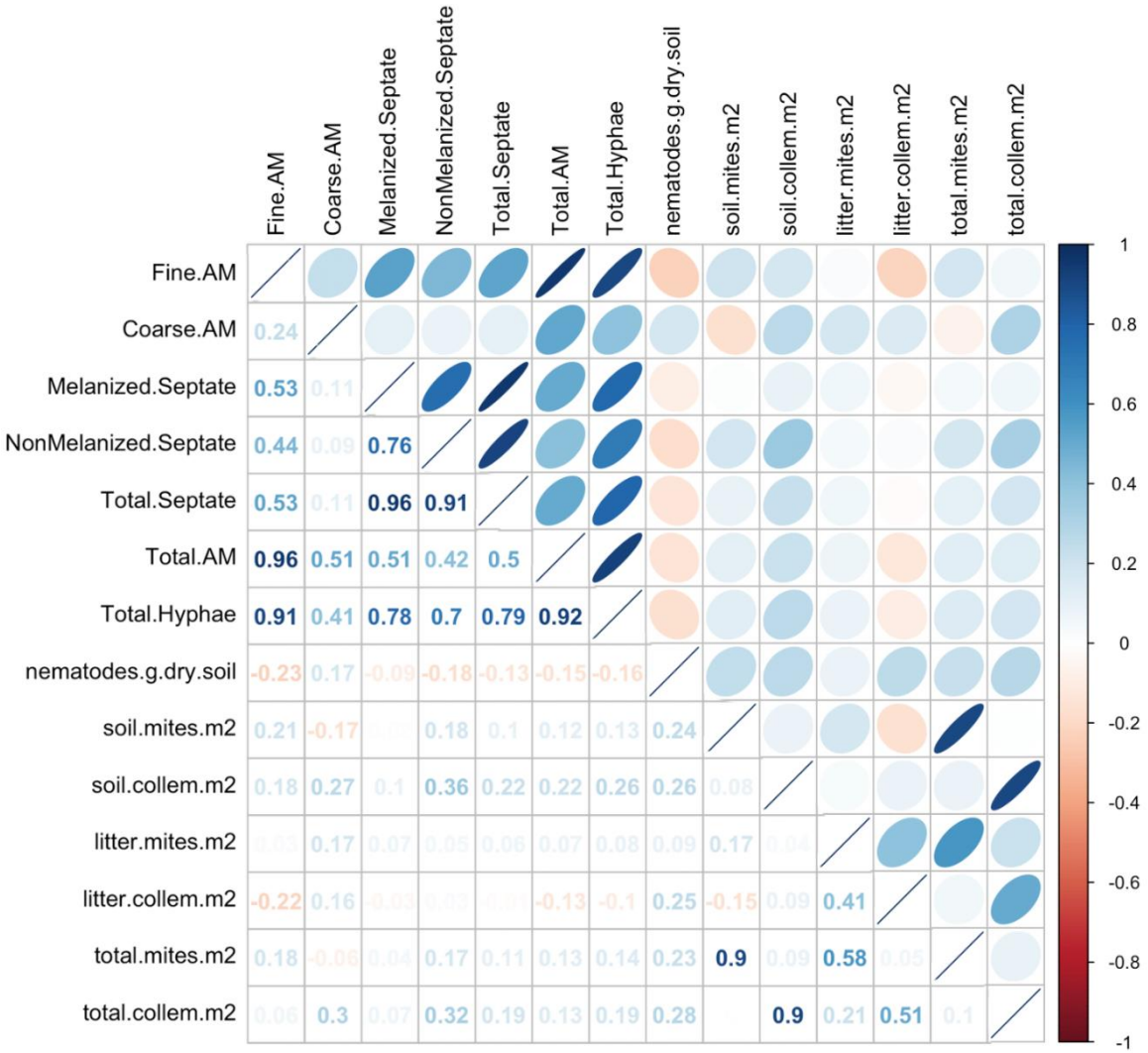


Fig. S2.7 Matrix of Pearson correlations between micro- and mesofauna groups and hyphal lengths (m per g dry soil), color coded by strength and direction

Table S4.1 Abundances of microarthropods in all size classes and presence of adult higher oribatids (number of units in which Brachypylina occurred/total units sampled) in sacrificial mesocosms sampled in September 2019 (T1) and July 2020 (T3). N=3 per restoration treatment unit.

	T1 Microarthropods			*T3 Microarthropods*		
	Mean mites	Mean collembolans	Presence of Brachypylina	Mean mites	Mean collembolans	Presence of Brachypylina
21 µm	84.3	11.2	0/6	51.2	6.8	0/6
41 µm	225.8	0.5	0/6	220.3	16	1/6
1 mm Sev	239.2	56.2	6/6	139.8	9.2	6/6
1 mm	310.8	79.2	6/6	208.3	8.8	5/6

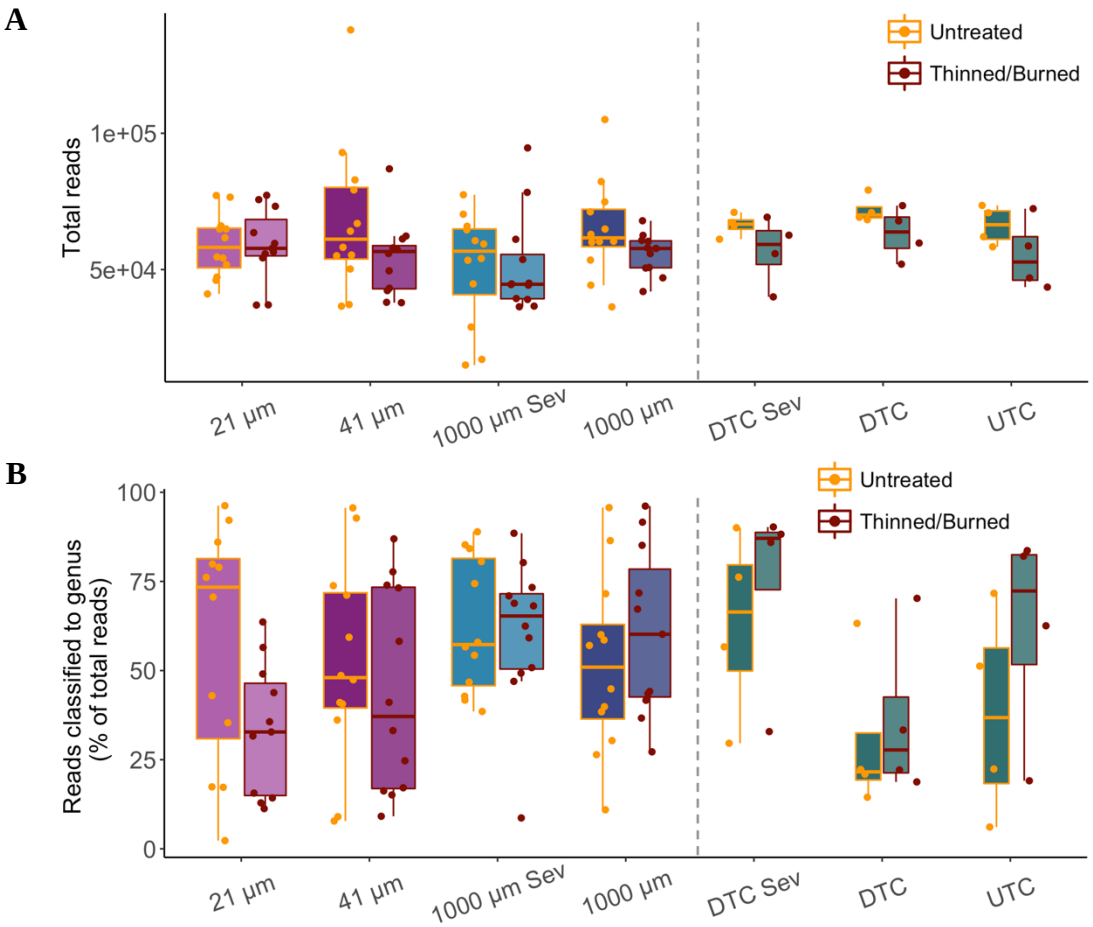


Fig. S4.1 Total reads (**A**) and percentage of total reads classifiable to genus (**B**) for mesh treatments and technical checks in each management unit.

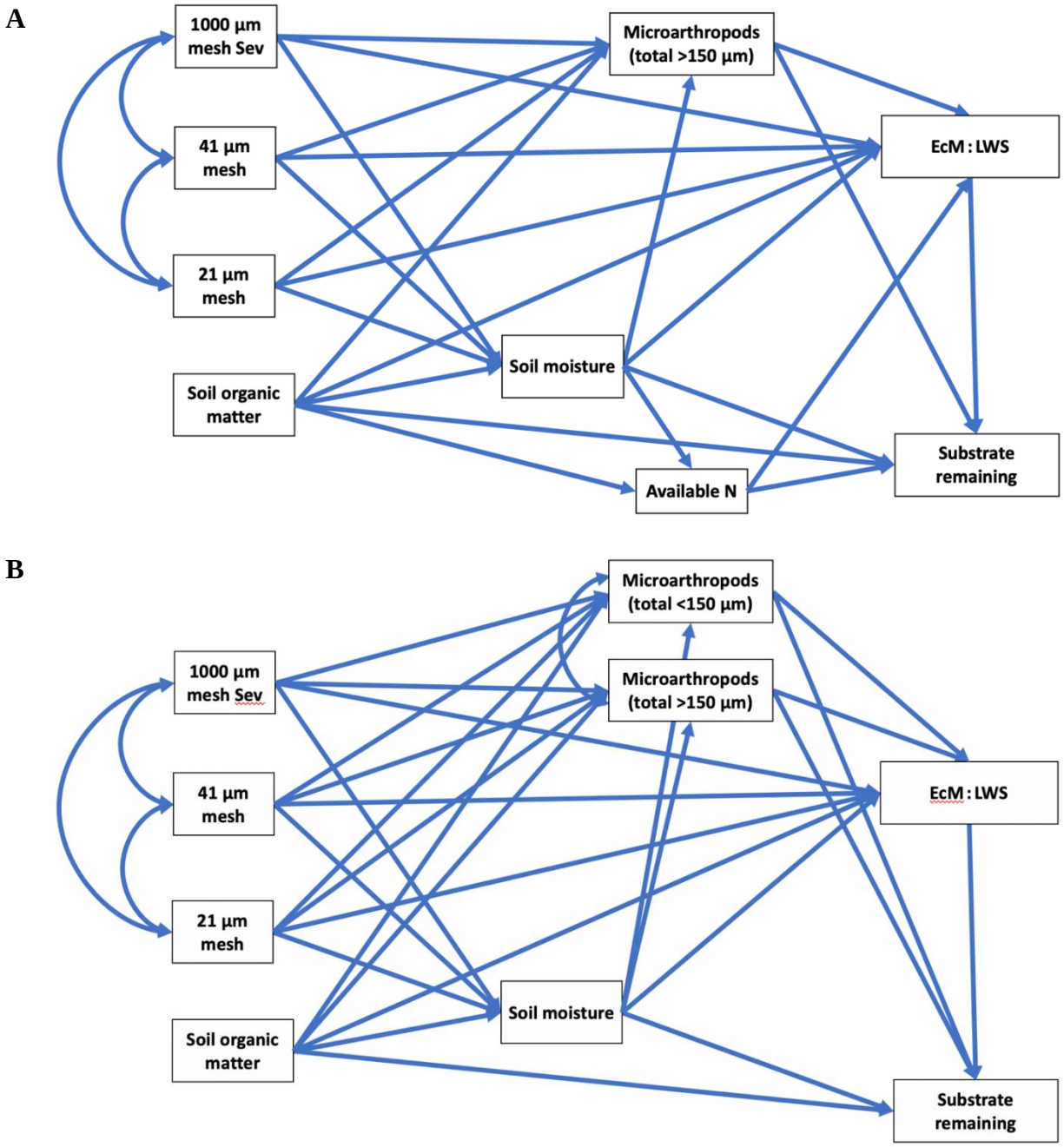


Fig. S4.2 Alternate a *priori* structural equation models compared to determine whether available nitrogen (**A**) or small microarthropods (**B**) should be included.

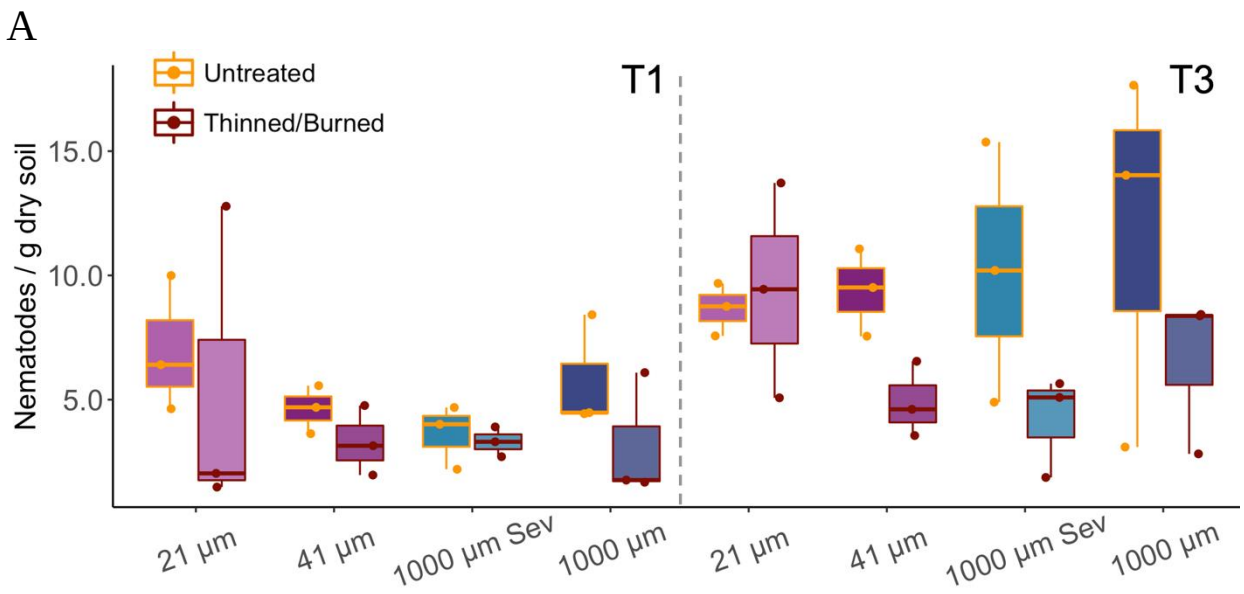


Fig. S4.3 Abundance of nematodes in sacrificial mesocosms.

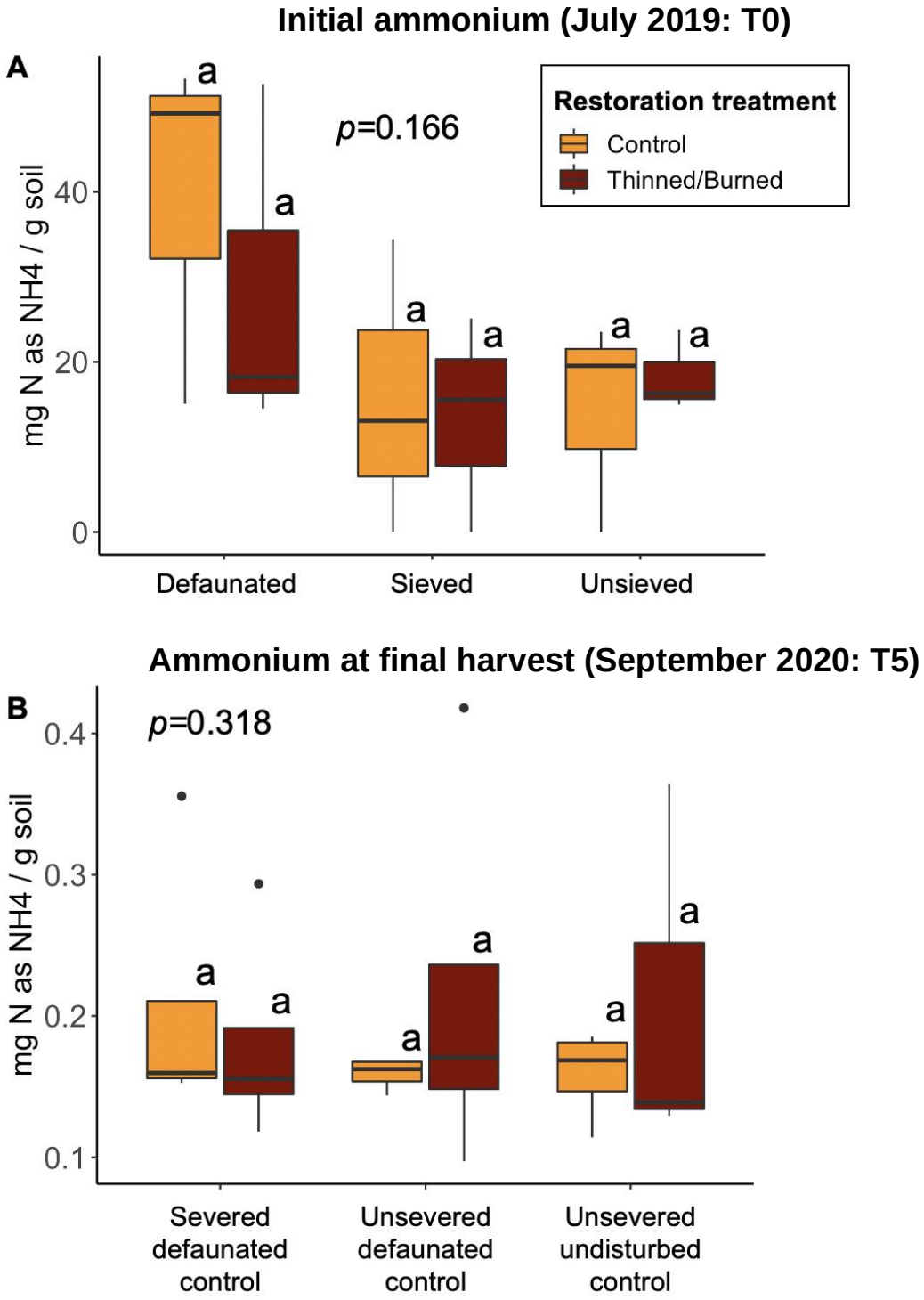


Fig. S4.4 Effects of soil defaunation and sieving treatments on ammonium content. (**A**) Ammonium content of defaunated (sieved and heated wet), sieved only, and unsieved (and unheated) soil collected from three trees per forest management unit prior to installation of mesocosms. Model *p*-value was calculated by Kruskal-Wallis H test. (**B**) Ammonium content of soil in the three types of mesocosm controls at the end of the study. Model P-value was calculated by ANOVA on log transformed values.

Table S4.2 Results of indicator species analyses for fungal genera. We performed separate analyses for management unit (untreated=U, thinned/burned=TB) and for mesh treatments (coarse vs. fine (CF), and all mesh treatments separately) within each management treatment, for a total of five indicator species analyses. Taxa with observed indicator values (IV) >25 and $p<0.05$ from randomization tests with 9,999 permutations were considered significant indicators. Asterisks denote significance levels of observed IV: *=$p<0.05$, **=$p<0.01$, ***=$p<0.001$. EcM=ectomycorrhizal; sapro=saprotroph; unsp=unspecified; path=pathogen; para=parasite; DSE=dark septate root endophyte; endo=endophyte; invert=invertebrate; mycopara=mycoparasite.

			Presence		**Max Group (IV)**		**Lifestyle**		
Order	**Family**	**Genus**	**U**	**TB**	**Management**	**Mesh/CF**	**Primary**	**Secondary**	**Notes**
Helotiales	Vibrisseaceae	*Acephala*	X	X			soil sapro	DSE	
Hypocreales	Bionectriaceae	*Acremonium*	X	X	U (86.6***)		unsp sapro	foliar endo	soft rot
Sordariales	Chaetomiaceae	*Acrophialophora*	X	X			plant path		
Phaeomoniellales	Celotheliaceae	*Aequabiliella*	X	X			plant path		
Pleosporales	Melanommataceae	*Alpinaria*		X			plant path	wood sapro	
Pleosporales	Pleosporaceae	*Alternaria*	X	X	TB (68.2***)		plant path	litter sapro	soft rot
Agaricales	Amanitaceae	*Amanita*	X	X	TB (65.1***)	U 1000 µm Sev (46.6*)	EcM		
Xylariales	Xylariales family incertae sedis	*Anungitea*		X			plant path		
Leotiales	Tympanidaceae	*Aotearoamyces*	X	X			wood sapro		
Chaetothyriales	Trichomeriaceae	*Arthrocladium*	X*				soil sapro	animal para	
Sordariales	Chaetomiaceae	*Arxotrichum*	X	X	TB (25.6**)		soil sapro		
Pleosporales	Didymellaceae	*Ascochyta*		X			plant path		
Eurotiales	Aspergillaceae	*Aspergillus*	X	X	TB (63**)	TB fine (68.6*)	unsp sapro	foliar endo	mold
Agaricales	Lyophyllaceae	*Asterophora*	X	X			mycopara	fungal sapro	
Dothideales	Saccotheciaceae	*Aureobasidium*	X	X	TB (87.7***)		sooty mold	litter sapro	
Onygenales	Onygenaceae	*Auxarthron*	X				soil sapro	animal sapro	
Geminibasidiales	Geminibasidiaceae	*Basidioascus*	X	X			soil sapro		
Basidiobolales	Basidiobolaceae	*Basidiobolus*	X				unsp sapro		
Hypocreales	Cordycipitaceae	*Beauveria*	X	X			animal para	animal sapro	invert para
Cantharellales	Hydnaceae	*Bergerella*	X	X			lichen para	fungal sapro	

Table S4.2 cont.

			Presence		Max Group (IV)		Lifestyle		
Order	**Family**	**Genus**	**U**	**TB**	**Management**	**Mesh/CF**	**Primary**	**Secondary**	**Notes**
Tubeufiales	Bezerromycetaceae	*Bezerromyces*		X			foliar endo	litter sapro	
Mucoromycota order incertae sedis	Mucoromycota family incertae sedis	*Bifiguratus*	X				soil sapro		mold
Helotiales	Sclerotiniaceae	*Botryotinia*		X*			plant path		
Helotiales	Sclerotiniaceae	*Botrytis*		X			plant path	litter sapro	
Buckleyzymales	Buckleyzymaceae	*Buckleyzyma*		X			epiphyte	litter sapro	
Helotiales	Ploettnerulaceae	*Cadophora*	X	X			litter sapro	plant path	
Helotiales	Pezizellaceae	*Calycina*		X			wood sapro	foliar endo	
Leotiales	Tympanidaceae	*Calyptrozyma*	X	X	TB (99***)		unsp sapro		
Microascales	Microascaceae	*Canariomyces*		X			soil sapro	litter sapro	
Saccharomycetales	Saccharomycetales family incertae sedis	*Candida*		X			nectar/sap sapro		
Chaetothyriales	Herpotrichiellaceae	*Capronia*	X	X			soil sapro	DSE	
Sordariales	Chaetomiaceae	*Chaetomium*	X	X			litter sapro	foliar endo	soft rot
Boletales	Gomphidiaceae	*Chroogomphus*	X				EcM		
Hypocreales	Hypocreaceae	*Cladobotryum*		X*			mycopara	fungal sapro	
Lecanorales	Cladoniaceae	*Cladonia*	X*				lichenized		
Chaetothyriales	Herpotrichiellaceae	*Cladophialophora*	X	X	TB (58.4*)		soil sapro	DSE	
Capnodiales	Cladosporiaceae	*Cladosporium*	X	X	TB (33*)		litter sapro	plant path	
Helotiales	Sclerotiniaceae	*Clarireedia*	X	X			plant path		
Agaricales	Entolomataceae	*Clitopilopsis*	X	X	TB (33.1*)		soil sapro		
Agaricales	Entolomataceae	*Clitopilus*	X	X	TB (50.5*)		litter sapro		
Hypocreales	Bionectriaceae	*Clonostachys*	X	X			wood sapro	plant path	nemato-phagous

Table S4.2 cont.

			Presence		Max Group (IV)		Lifestyle		
Order	**Family**	**Genus**	**U**	**TB**	**Management**	**Mesh/CF**	**Primary**	**Secondary**	**Notes**
Leotiales	Cochlearomycetaceae	*Cochlearomyces*	X	X			litter sapro		
Microbotryomycetes order incertae sedis	Colacogloeaceae	*Colacogloea*	X				mycopara	fungal sapro	
Helotiales	Dermateaceae	*Coleophoma*	X	X	U (69.7***)		plant path	foliar endo	
Helotiales	Ploettnerulaceae	*Collembolispora*	X*				litter sapro		
Pleosporales	Pleosporaceae	*Comoclathris*		X*			wood sapro		
Coniochaetales	Coniochaetaceae	*Coniochaeta*	X	X			unsp sapro	foliar endo	
Pleosporales	Coniothyriaceae	*Coniothyrium*	X	X	TB (31.8***)		plant path	litter sapro	soft rot
Agaricales	Psathyrellaceae	*Coprinellus*		X			soil sapro		
Agaricales	Cortinariaceae	*Cortinarius*	X	X	U (39.4**)		EcM		
Hypocreales	Nectriaceae	*Cosmospora*	X	X			mycopara	fungal sapro	
Agaricales	Hygrophoraceae	*Cuphophyllus*	X	X			soil sapro	unsp symbio	
Microbotryomycetes order incertae sedis	Microbotryomycetes family incertae sedis	*Curvibasidium*	X	X	U (40.7**)	U coarse (61.1***); U 1000 µm Sev (51.1**)	wood sapro	litter sapro	
Helotiales	Pezizellaceae	*Curviclavula*	X	X			unsp sapro		
Pleosporales	Pleosporaceae	*Curvularia*	X	X			plant path	litter sapro	
Cystobasidiales	Cystobasidiaceae	*Cystobasidium*		X			mycopara	fungal sapro	
Diaporthales	Cytosporaceae	*Cytospora*	X	X			plant path	litter sapro	soft rot
Helotiales	Helotiales family incertae sedis	*Dactylaria*		X			animal para	wood sapro	nematophagous
Helotiales	Dermateaceae	*Davidhawksworthia*	X	X			litter sapro		
Pleosporales	Didymellaceae	*Didymella*		X			plant path	litter sapro	
Dothideales	Dothideaceae	*Dothidea*	X				litter sapro	wood sapro	
Dothideales	Dothideaceae	*Dothiora*	X				wood sapro		

Table S4.2 cont.

			Presence		Max Group (IV)		Lifestyle		
Order	**Family**	**Genus**	**U**	**TB**	**Management**	**Mesh/CF**	**Primary**	**Secondary**	**Notes**
Agaricales	Entolomataceae	*Entoloma*	X				soil sapro	unsp symbio	
Mortierellales	Mortierellaceae	*Entomortierella*	X	X			unsp sapro*		
Pleosporales	Didymellaceae	*Epicoccum*	X	X			plant path	litter sapro	
Chaetothyriales	Herpotrichiellaceae	*Exophiala*	X	X	TB (83***)		animal para	litter sapro	
Microbotryomycetes order incertae sedis	Chrysozymaceae	*Fellozyma*		X			soil sapro		
Filobasidiales	Filobasidiaceae	*Filobasidium*		X			unsp sapro		
Pleosporales	Periconiaceae	*Flavomyces*	X*				root endo	soil sapro	
Hypocreales	Nectriaceae	*Fusarium*	X	X	TB (83.3***)	U 1000 µm Sev (34.2*)	plant path	litter sapro	soft rot
Hypocreales	Nectriaceae	*Fusicolla*	X*				mycopara	fungal sapro	
Geastrales	Geastraceae	*Geastrum*	X	X			litter sapro		
Sordariales	Sordariaceae	*Gelasinospora*	X	X			unsp sapro		
Geminibasidiales	Geminibasidiaceae	*Geminibasidium*	X	X			soil sapro		
Geoglossales	Geoglossaceae	*Geoglossum*		X			soil sapro	unsp symbio	
Thelebolales	Pseudeurotiaceae	*Geomyces*	X	X			soil sapro		
Pezizales	Pyronemataceae	*Geopora*	X	X			EcM		
Glomerellales	Plectosphaerellaceae	*Gibellulopsis*	X	X			plant path	litter sapro	
Helotiales	Helotiaceae	*Glarea*	X	X			soil sapro		
Filobasidiales	Filobasidiaceae	*Goffeauzyma*	X	X			soil sapro	litter sapro	
Erysiphales	Erysiphaceae	*Golovinomyces*	X				plant path		
Helotiales	Hamatocanthoscyphaceae	*Hamatocanthoscypha*	X	X			wood sapro	litter sapro	
Eurotiales	Aspergillaceae	*Hamigera*	X*				unsp sapro		
Agaricales	Hymenogastraceae	*Hebeloma*		X*			EcM		
Orbiliales	Orbiliaceae	*Helicoon*	X	X	U (83***)		wood sapro	litter sapro	

Table S4.2 cont.

			Presence		Max Group (IV)		Lifestyle		
Order	**Family**	**Genus**	**U**	**TB**	**Management**	**Mesh/CF**	**Primary**	**Secondary**	**Notes**
Pezizales	Helvellaceae	*Helvella*		X*			EcM		
Russulales	Bondarzewiaceae	*Heterobasidion*	X	X			plant path	wood sapro	white rot
Amphisphaeriales	Sporocadaceae	*Heterotruncatella*		X			plant path		
Hypocreales	Ophiocordycipitaceae	*Hirsutella*	X				animal para	animal sapro	invert para
Dothideales	Dothideales family incertae sedis	*Hormonema*	X	X	TB (70.2***)		unsp sapro	animal sapro	
Sordariales	Chaetomiaceae	*Humicola*	X	X			wood sapro		soft rot
Helotiales	Helotiales family incertae sedis	*Humicolopsis*		X			soil sapro		
Helotiales	Pezizellaceae	*Hyalodendriella*		X*			wood sapro		
Helotiales	Hyaloscyphaceae	*Hyaloscypha*	X	X			litter sapro	wood sapro	
Pezizales	Pezizaceae	*Hydnobolites*		X			EcM		
Helotiales	Helotiaceae	*Hymenoscyphus*	X	X			litter sapro	plant path	
Helotiales	Helotiaceae	*Hymenotorrendiella*		X			litter sapro		
Helotiales	Hyaloscyphaceae	*Hyphodiscus*	X	X			mycopara		
Helotiales	Hamatocanthoscyphaceae	*Infundichalara*	X	X	U (55.7*)		litter sapro		
Agaricales	Inocybaceae	*Inocybe*	X	X	TB (51.1*)	TB 1000 µm (80.6*)	EcM		
Chaetothyriales	Trichomeriaceae	*Knufia*	X	X			soil sapro	rock-inhabiting	
Saccharomycetales	Debaryomycetaceae	*Kurtzmaniella*	X				nectar/tap sapro		arthropod-assoc.
Agaricostilbales	Chionosphaeraceae	*Kurtzmanomyces*		X*			unsp sapro		
Tremellales	Cryptococcaceae	*Kwoniella*	X	X			unsp sapro		
Helotiales	Lachnaceae	*Lachnellula*	X	X			wood sapro		

Table S4.2 cont.

			Presence		Max Group (IV)		Lifestyle		
Order	**Family**	**Genus**	**U**	**TB**	**Management**	**Mesh/CF**	**Primary**	**Secondary**	**Notes**
Russulales	Russulaceae	*Lactarius*	X*				EcM		
Capnodiales	Teratosphaeriaceae	*Lapidomyces*	X	X			unsp sapro	rock-inhabiting	
Helotiales	Neolauriomycetaceae	*Lareunionomyces*	X	X			litter sapro		
Pezizales	Pseudombrophilaceae	*Lasiobolidium*	X				dung sapro	foliar endo	
Hypocreales	Cordycipitaceae	*Lecanicillium*	X				animal para	animal sapro	invert para
Glomerellales	Plectosphaerellaceae	*Lectera*	X	X			plant path		
Helotiales	Helotiales family incertae sedis	*Leohumicola*	X	X			soil sapro	ericoid mycorrhizal	
Hypocreales	Cordycipitaceae	*Leptobacillium*	X				animal para	fungal sapro	invert para
Microbotryales	Leucosporidiaceae	*Leucosporidium*	X	X			soil sapro		
Hypocreales	Cordycipitaceae	*Liangia*	X	X		TB coarse (37.1*)	unsp sapro*		
Mortierellales	Mortierellaceae	*Linnemannia*	X	X	U (58.6***)		unsp sapro*		
Pleosporales	Lophiostomataceae	*Lophiostoma*		X			wood sapro	litter sapro	
Mytilinidiales	Mytilinidiaceae	*Lophium*		X			litter sapro		
Agaricales	Lyophyllaceae	*Lyophyllum*	X	X	TB (51.9**)		EcM		
Agaricales	Inocybaceae	*Mallocybe*	X				EcM		
Capnodiales	Teratosphaeriaceae	*Meristemomyces*	X	X	TB (59.2***)		litter sapro	rock-inhabiting	
Hypocreales	Clavicipitaceae	*Metapochonia*	X	X	U (27.6**)		animal para	animal sapro	nemato phagous
Coronophorales	Ceratostomataceae	*Microthecium*	X	X			mycopara	dung sapro	
Pleosporales	Testudinaceae	*Montanitestudina*	X	X			unsp sapro*		

Table S4.2 cont.

			Presence		Max Group (IV)		Lifestyle		
Order	**Family**	**Genus**	**U**	**TB**	**Management**	**Mesh/CF**	**Primary**	**Secondary**	**Notes**
Pezizales	Morchellaceae	*Morchella*	X	X			soil sapro	root-assoc.	
Mortierellales	Mortierellaceae	*Mortierella*	X	X	TB (84.8***)		soil sapro	root-assoc.	chitinolytic
Cystofilobasidiales	Mrakiaceae	*Mrakia*	X	X	TB (52.4*)		unsp sapro		
Mucorales	Mucoraceae	*Mucor*	X	X			soil sapro		mold
Pleosporales	Amniculicolaceae	*Murispora*	X*				wood sapro		
Hypocreales	Clavicipitaceae	*Mycophilomyces*	X*				mycopara	fungal sapro	
Rhytismatales	Rhytismatales family incertae sedis	*Mycosymbioces*	X	X			mycopara	fungal sapro	
Hypocreales	Stachybotryaceae	*Myrothecium*	X*				litter sapro		
Helotiales	Amorphothecaceae	*Myxotrichum*	X*				soil sapro	foliar endo	
Filobasidiales	Filobasidiaceae	*Naganishia*	X	X	TB (97.3***)		unsp sapro		
Cantharellales	Botryobasidiaceae	*Neoacladium*	X				wood sapro		
Pleosporales	Neocamarosporiaceae	*Neocamarosporium*	X				wood sapro	plant path	
Helotiales	Dermateaceae	*Neofabraea*		X			plant path	litter sapro	
Phaeomoniellales	Celotheliaceae	*Neophaeomoniella*		X			plant path		
Chaetothyriales	Herpotrichiellaceae	*Neosorocybe*	X	X			unsp sapro*		
Pleosporales	Phaeosphaeriaceae	*Neostagonospora*	X	X			litter sapro	wood sapro	
Sordariales	Sordariaceae	*Neurospora*	X	X			unsp sapro		
Hypocreales	Niessliaceae	*Niesslia*		X			litter sapro	dung sapro	
Amphisphaeriales	Apiosporaceae	*Nigrospora*		X			litter sapro		
Pleosporales	Didymellaceae	*Nothophoma*	X*				litter sapro		
Pleosporales	Coniothyriaceae	*Ochrocladosporium*	X	X			wood sapro		
Helotiales	Amorphothecaceae	*Oidiodendron*	X	X	U (72.9***)	U 1000 µm Sev (53.0*)	soil sapro	root endo	

Table S4.2 cont.

			Presence		Max Group (IV)		Lifestyle		
Order	**Family**	**Genus**	**U**	**TB**	**Management**	**Mesh/CF**	**Primary**	**Secondary**	**Notes**
Hypocreales	Ophiocordycipitaceae	*Ophiocordyceps*	X	X			animal para	animal sapro	
Orbiliales	Orbiliaceae	*Orbilia*	X	X			wood sapro	animal para	nematophagous
Pezizales	Pyronemataceae	*Otidea*	X				EcM		
Capnodiales	Extremaceae	*Paradevriesia*	X				unsp sapro*		
Pleosporales	Cucurbitariaceae	*Parafenestella*	X	X			unsp sapro	fungal sapro	
Pleosporales	Phaeosphaeriaceae	*Paraphoma*		X			plant path	wood sapro	
Pezizales	Pyronemataceae	*Paratricharina*		X			soil sapro		
Tritirachiales	Tritirachiaceae	*Paratritirachium*	X				soil sapro		
Eurotiales	Aspergillaceae	*Penicillium*	X	X	U (69.8**)		unsp sapro	foliar endo	mold
Capnodiales	Teratosphaeriaceae	*Penidiella*	X	X			plant path	litter sapro	
Pleosporales	Periconiaceae	*Periconia*		X			plant path	foliar endo	soft rot
Capnodiales	Capnodiales family incertae sedis	*Perusta*	X	X			unsp sapro	rock-inhabiting	
Pezizales	Pezizaceae	*Peziza*	X*				soil sapro	foliar endo	
Phacidiales	Phacidiaceae	*Phacidium*	X				plant path	foliar endo	
Lichenostigmatales	Phaeococcomycetaceae	*Phaeococcomyces*	X	X			unsp sapro		
Dothideomycetes order incertae sedis	Dothideomycetes family incertae sedis	*Phaeosclera*	X*				litter sapro		
Polyporales	Phanerochaetaceae	*Phanerochaete*	X				wood sapro		white rot
Kriegeriales	Kriegeriaceae	*Phenoliferia*	X	X			unsp sapro		
Helotiales	Mollisiaceae	*Phialocephala*	X	X	U (45.9***)		soil sapro	root endo	
Eurotiales	Aspergillaceae	*Phialomyces*	X	X	U (49.2***)		mycopara	soil sapro	mold
Chaetothyriales	Herpotrichiellaceae	*Phialophora*	X	X			litter sapro	plant path	

Table S4.2 cont.

			Presence		Max Group (IV)		Lifestyle		
Order	**Family**	**Genus**	**U**	**TB**	**Management**	**Mesh/CF**	**Primary**	**Secondary**	**Notes**
Agaricales	Strophariaceae	*Pholiota*	X	X		TB 1000 µm (32.2**)	wood sapro	litter sapro	white rot
Filobasidiales	Piskurozymaceae	*Piskurozyma*	X	X			soil sapro		
Pleosporales	Melanommataceae	*Pleotrichocladium*	X	X			wood sapro	soil sapro	
Agaricales	Pluteaceae	*Pluteus*		X			litter sapro		white rot
Mortierellales	Mortierellaceae	*Podila*	X	X		U coarse (74.6**); U 1000 µm Sev (47.0*)	unsp sapro*		
Sordariales	Podosporaceae	*Podospora*	X	X			dung sapro	foliar endo	
Hypocreales	Ophiocordycipitaceae	*Polycephalomyces*	X	X			animal para	animal sapro	invert para
Pleosporales	Sporormiaceae	*Preussia*	X	X			dung sapro		
Taphrinales	Protomycetaceae	*Protomyces*		X*			plant path		
Agaricales	Psathyrellaceae	*Psathyrella*	X	X			wood sapro	litter sapro	
Gloniales	Gloniaceae	*Pseudocenococcum*		X			soil sapro		
Thelebolales	Pseudeurotiaceae	*Pseudogymnoascus*	X	X	U (62.4*)		soil sapro		
Microbotryomycetes order incertae sedis	Microbotryomycetes family incertae sedis	*Pseudoleucosporidium*	X	X			unsp sapro		
Pleosporales	Phaeosphaeriaceae	*Pseudoophiobolus*		X			litter sapro	wood sapro	
Helotiales	Drepanopezizaceae	*Pseudopezicula*	X	X	U (84.3***)		plant path		
Pleosporales	Didymosphaeriaceae	*Pseudopithomyces*		X			plant path	litter sapro	
Venturiales	Sympoventuriaceae	*Pseudosigmoidea*	X	X			soil sapro	DSE	

Table S4.2 cont.

			Presence		Max Group (IV)		Lifestyle		
Order	**Family**	**Genus**	**U**	**TB**	**Management**	**Mesh/CF**	**Primary**	**Secondary**	**Notes**
Capnodiales	Cladosporiaceae	*Rachicladosporium*		X*			litter sapro		
Thelebolales	Thelebolaceae	*Ramgea*	X	X			dung sapro		
Helotiales	Dermateaceae	*Rhizodermea*	X				root endo	soil sapro	
Boletales	Rhizopogonaceae	*Rhizopogon*	X	X	U (79.4***)		EcM		
Mucorales	Rhizopodaceae	*Rhizopus*		X			soil sapro	plant path	mold
Agaricales	Entolomataceae	*Rhodocybe*	X				litter sapro		
Sporidiobolales	Sporidiobolaceae	*Rhodosporidiobolus*	X	X		TB 1000 µm Sev (36.5*)	unsp sapro		
Sporidiobolales	Sporidiobolaceae	*Rhodotorula*	X	X	TB (71.8***)		unsp sapro	foliar endo	
Russulales	Russulaceae	*Russula*	X	X	U (76.6*)		EcM		
Eurotiales	Trichocomaceae	*Sagenomella*	X	X			unsp sapro		mold
Dothideales	Dothideales family incertae sedis	*Scleroconidioma*	X	X			plant path	litter sapro	
Sebacinales	Sebacinaceae	*Sebacina*	X	X			EcM		
Pleosporales	Phaeosphaeriaceae	*Septoriella*		X*			litter sapro		
Hypocreales	Cordycipitaceae	*Simplicillium*	X	X			animal para	animal sapro	invert para
Microbotryomycetes order incertae sedis	Microbotryomycetes family incertae sedis	*Slooffia*	X	X			unsp sapro		
Filobasidiales	Piskurozymaceae	*Solicoccozyma*	X	X	TB (81.7***)		soil sapro	epiphyte	
Pleosporales	Didymosphaeriaceae	*Spegazzinia*		X			wood sapro		
Hypocreales	Stachybotryaceae	*Stachybotrys*	X	X			wood sapro	litter sapro	soft rot
Pleosporales	Coniothyriaceae	*Staurosphaeria*	X				unsp sapro		
Boletales	Suillaceae	*Suillus*	X	X			EcM		
Symbiotaphrinales	Symbiotaphrinaceae	*Symbiotaphrina*	X	X			animal endosymbiont	litter sapro	

Table S4.2 cont.

			Presence		Max Group (IV)		Lifestyle		
Order	**Family**	**Genus**	**U**	**TB**	**Management**	**Mesh/CF**	**Primary**	**Secondary**	**Notes**
Eurotiales	Trichocomaceae	*Talaromyces*	X	X	U (81.8***)		unsp sapro		mold
Taphrinales	Taphrinaceae	*Taphrina*		X			plant path		
Capnodiales	Teratosphaeriaceae	*Teratosphaericola*	X	X			plant path		
Agaricales	Marasmiaceae	*Tetrapyrgos*		X*			litter sapro		
Tremellales	Cryptococcaceae	*Teunia*	X	X			soil sapro	epiphyte	
Thelebolales	Thelebolaceae	*Thelebolus*	X	X			dung sapro	foliar endo	
Hypocreales	Nectriaceae	*Thelonectria*		X			litter sapro		
Hypocreales	Nectriaceae	*Thyronectria*		X			plant path		
Pleosporales	Dothidotthiaceae	*Thyrostroma*	X				plant path	litter sapro	
Hypocreales	Ophiocordycipitaceae	*Tolypocladium*	X	X			animal para	foliar endo	
Thelephorales	Thelephoraceae	*Tomentella*	X	X	U (82.6***)		EcM		
Pezizales	Pyronemataceae	*Tricharina*		X			soil sapro	foliar endo	
Hypocreales	Hypocreaceae	*Trichoderma*	X	X			mycopara	foliar endo	soft rot
Agaricales	Tricholomataceae	*Tricholoma*	X	X			EcM		
Pezizales	Pyronemataceae	*Trichophaea*	X				EcM		
Amphisphaeriales	Sporocadaceae	*Truncatella*		X			plant path		
Agaricales	Psathyrellaceae	*Tulosesus*		X			unsp sapro*		
Pleosporales	Melanommataceae	*Tumularia*	X				litter sapro		
Leotiales	Tympanidaceae	*Tympanis*	X	X	TB (51.7*)		plant path	wood sapro	
Venturiales	Venturiaceae	*Tyrannosorus*	X	X			wood sapro		
Umbelopsidales	Umbelopsidaceae	*Umbelopsis*	X	X	U (80.3***)	U 1000 µm Sev (45.3*)	soil sapro	root-assoc.	mold
Leotiales	Tympanidaceae	*Vexillomyces*		X			unsp sapro*		
Pleosporales	Sporormiaceae	*Westerdykella*		X			dung sapro		
Capnodiales	Xenodevriesiaceae	*Xenodevriesia*	X	X			plant path		
Capnodiales	Teratosphaeriaceae	*Xenopenidiella*	X	X			litter sapro		

Table S4.2 cont.

			Presence		Max Group (IV)		Lifestyle		
Order	**Family**	**Genus**	**U**	**TB**	**Management**	**Mesh/CF**	**Primary**	**Secondary**	**Notes**
Helotiales	Hamatocanthoscyphaceae	*Xenopolyscytalum*	X	X			litter sapro	foliar endo	
Agaricales	Mycenaceae	*Xeromphalina*	X				wood sapro		white rot
Helotiales	Helotiaceae	*Xylogone*	X	X			mycopara	fungal sapro	
Saccharomycetales	Debaryomycetaceae	*Yamadazyma*		X			nectar/tap sapro		arthropod-assoc.

*=Not in FungalTraits, information inferred from family data

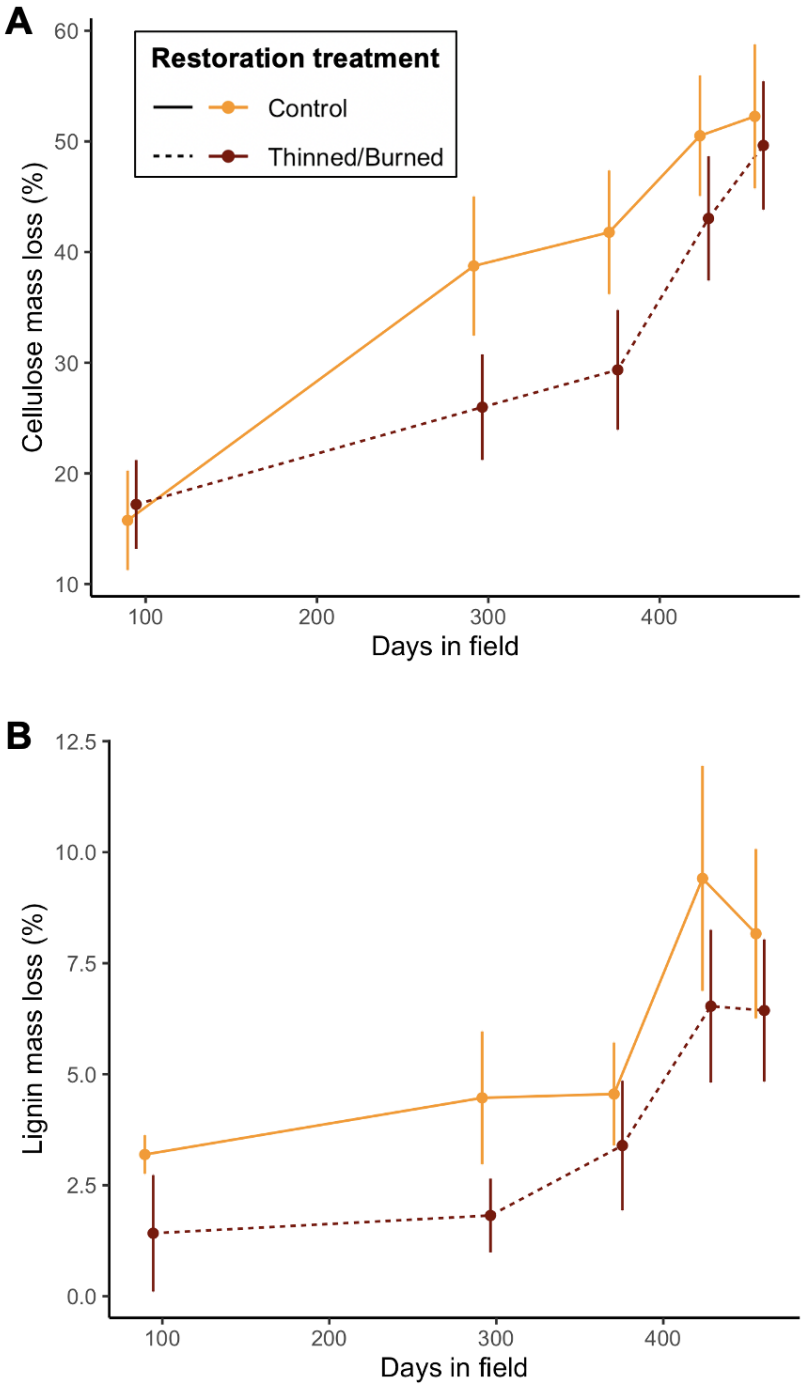


Fig. S4.5 Decomposition of recalcitrant and labile standard substrates in thinned/burned and untreated control ponderosa pine forest management units. (**A)** Mass loss of museum board over time. (**B)** Mass loss of balsa wood over time. Error bars represent 95% confidence intervals.