

Beyond mountain pine beetle: soil carbon storage a decade after tree mortality and the possible influence of soil fungi

by

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## Abstract

Mountain pine beetle (MPB; *Dendroctonus ponderosae*) disturbances, amplified by climate change, have led to extensive tree mortality and ecosystem succession in boreal forests across western Canada. Often following attack, former ectomycorrhizal (EM) pine stands in Alberta are replaced by arbuscular (AM) mycorrhizal shrubs and forbs. There has been growing interest in the varying ways that EM versus AM fungi influence critical soil processes, particularly concerning carbon cycling. While our comprehension of the specific impacts that MPB-induced mycorrhizal community succession has on long-term soil carbon storage remains somewhat limited, emerging frameworks offer broad yet valuable initial insights into this complex dynamic. Specifically, given the functional differences between mycorrhizal fungal types, a shift from EM- to AM-dominance in affected stands may promote soil organic matter formation and carbon stabilization, potentially enhancing soil carbon stores. The objective of this study was to address the following questions: 1) Will the dominant mycorrhizal type change with disturbance? 2) Does extensive tree mortality change the amount of carbon and nitrogen stored in forest floors and mineral soils? I sampled soil and conducted vegetation surveys at 80 lodgepole pine-dominated sites across west-central Alberta, split by disturbance severity (forests with >70% lodgepole pine basal area killed by MPB versus intact forest) and soil texture (coarse versus fine). I used density fractionation to separate soils into mineral-associated organic matter (MAOM) and particulate organic matter (POM) pools. I explored whether disturbance, mycorrhizal type, soil texture, and sampling depth affected carbon and nitrogen concentrations in these pools. There was a pronounced shift in mycorrhizal community composition from EM to AM dominance following MPB-induced forest transformations. However, overall carbon and nitrogen concentrations in bulk mineral soil, and carbon and nitrogen stocks in forest floors, remained largely unaffected. In addition, I confirmed that carbon and nitrogen storage are strongly dependent on soil texture and depth. Though there were no changes in soil carbon concentrations in the bulk soil, carbon in the MAOM fraction was

relatively higher in the disturbed than intact sites. Greater carbon and nitrogen allocation into the MAOM pools is consistent with emerging hypotheses on the importance of AM vegetation to long-term carbon storage in soils. Taken together, these patterns in carbon storage may point to the resiliency of these soils, supported by soil organic matter interactions with the mineral matrix and potentially the buffering effects from the increase of AM fungi and their unique nutrient dynamics. The findings from this study may enhance our understanding of soil processes, offering opportunities to optimize soil carbon stocks and ecosystem services in recovering boreal forests.

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## 1. Introduction

Natural disturbances are integral to forest ecosystems, steering their life cycles and shaping ecological dynamics. In Alberta's boreal forests, wildfires play a critical role in the natural landscape, contributing to and maintaining biodiversity and ecosystem processes (Weber & Stocks, 1998). However, the emergence of novel disturbance regimes, driven by various global change factors, has the potential to disrupt the historical trajectories of these forests (Ratajczak et al., 2018; Rillig et al., 2019). Given the significant role of plants and microbes in regulating biogeochemical processes, the composition of vegetation and their mycorrhizal fungal symbionts in succeeding communities may have a profound influence on future soil carbon stores (Clemmensen et al., 2015; Mayer et al., 2022; Rodriguez-Ramos et al., 2021). Outside of the Rocky Mountains, mountain pine beetle (MPB) (*Dendrotonus ponderosae* Hopkins) has emerged as a novel disturbance agent in many parts of Alberta. The consequences of its transformations on aboveground forest structure and the implications for future community assemblages and primary processes in these landscapes are not well understood. By incorporating the evolving knowledge of forest carbon pathways, from litter inputs to stabilized soil carbon pools, we can better anticipate the potential long-term impacts of MPB-disturbance on key ecosystem processes through above and belowground forest succession.

### **1.1. Mountain pine beetle as a novel disturbance regime in Alberta**

In western Canadian forests, unprecedented levels of mountain pine beetle (MPB) attacks have resulted in widespread mortality of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm), damaging over 2.4 million hectares of Alberta's forests (C. Whitehouse, personal communications, May 24, 2023; Canadian Forest Service, 2022). Geographical distribution patterns for most insect species, including MPB, are primarily determined by climate tolerance (Cudmore et al., 2010). Over this century, boreal forests are projected to undergo the most rapid changes in climate conditions compared to all other biomes (Gauthier et al., 2015). Consequently, due to climate change factors such as warmer

minimum winter temperatures, increased summer heat accumulation, and increased water deficits, it is expected that the intensity and range suitable for MPBs will continue to expand beyond historical limits (Carroll et al., 2004; Safranyik et al., 2010). Endemic MPB populations in western North America, with satellite populations in other forests such as southwestern Saskatchewan, have historically played important roles in the natural disturbance regime of those areas (Nealis & Cooke, 2014; Taylor & Carroll, 2004). However, as a consequence of climate change, these populations are extending into forests further northward, eastward, and to higher elevations, including boreal forests east of the Canadian Rocky Mountains (Cullingham et al., 2011; Taylor & Carroll, 2004).

While all western North American pine species are suitable hosts for MPB, lodgepole pine is especially favoured and of particular concern given its extensive distribution (Carroll et al., 2004; Furniss & Carolin, 1977). With a broad ecological amplitude, lodgepole pines are native to regions spanning from the Yukon to southern California, and from the Pacific Ocean to South Dakota (Lotan & Critchfield, 1990). These pines are early seral species, shade-intolerant, and typically make up stands of even-aged trees (Axelson et al., 2009). They possess adaptations for fire, historically the chief factor influencing forest composition and succession in Alberta (Horton, 1956). Lodgepole pines can quickly regenerate through their serotinous cones, which open and release seeds when sufficient heat is present (Horton, 1956). Consequently, MPB attacks are typically associated with poor lodgepole pine regeneration, as the disturbance does not provide the necessary heat to open the serotinous cones (Lieffers et al., 2023).

Furthermore, since MPBs are not part of the natural disturbance regime in these forests, the trees of this species lack adequate adaptations, developed from evolutionary history, necessary to defend against attack or to persist following infestation (Safranyik et al., 2010). The beetles bore into the inner bark of mature host trees to mine for nutrients from the phloem tissue, effectively disrupting the flow of water and nutrients and ultimately killing the affected trees (Safranyik & Carroll, 2006). Tree species historically exposed to MPBs have evolved defence mechanisms, such as resin production, to physically

and chemically protect against attack (Safranyik et al., 2010; Zhao et al., 2019). Variations in genetic profile may also determine beetle resistance and survivorship from one tree to another (Six et al., 2018). Without adequate defence mechanisms or genetic advantages, as in the case of many lodgepole pine individuals in Alberta, MPB activity could drive substantial changes in vulnerable ecosystems. Extensive tree mortality affects various aspects of forest values, including timber supply and employment opportunities (Corbett et al., 2016), valuable wildlife habitats (Saab et al., 2014), and carbon storage (Kurz et al., 2008).

### ***1.2. Forest vegetation and carbon pools response to MPB- disturbance***

Following MPB attack in Alberta, former even-aged seral lodgepole pine stands often do not regenerate back with pine (Birch et al., 2019; Lieffers et al., 2023) but are instead replaced by diverse communities of shrubs and forbs (Pec et al., 2015; Steinke et al., 2020). The post-disturbance stand conditions are notably distinct from those resulting from wildfire. In MPB-affected areas, dead trees are left standing, serotinous cones remain unopened, understory vegetation is undisturbed, and forest floors experience no direct effects (Amiro et al., 2010; Axelson et al., 2010; Burton, 2008). It is expected that conditions created by MPB attacks do not encourage pine regeneration. Instead, MPB is considered a stand-releasing process that promotes the growth of existing suppressed plants and trees, such as outcompeted or shade-intolerant understory species (Astrup et al., 2008; Axelson et al., 2010). While canopy thinning by bark beetles does not directly impact ground vegetation, it triggers subsequent changes to regeneration microsites. These changes include alterations in soil properties, increased dead woody debris, decreased space competition, and increased light availability and soil moisture, all of which may indirectly encourage understory changes (Astrup et al., 2008; Cigan et al., 2015; Pec et al., 2015).

Exploring how these successional patterns affect carbon pools is crucial because boreal forests account for at least one-third of the global terrestrial carbon pool (Pan et al., 2011). Early model-based

projections predicted that MPB-affected areas in British Columbia would reach 270 Mt of carbon loss over 21 years (Kurz et al., 2008). This drop in net biome production was attributed to reduced photosynthesis capacity and increased heterotrophic respiration in dead forests (Kurz et al., 2008). However, empirical surveys have shown less drastic changes in carbon fluxes (Amiro et al., 2010; Bowler et al., 2012; Brown et al., 2012). In fact, following an initial dip in net ecosystem production (NEP) in the year of the disturbance, studies have consistently found rapid subsequent recovery marked by a surge in understory growth and photosynthetic productivity in MPB-attacked stands (Amiro et al., 2010; Bowler et al., 2012; Brown et al., 2012). By the fifth-year post-disturbance, these stands often reached carbon neutrality (Amiro et al., 2010; Bowler et al., 2012; Brown et al., 2012). Although the recovery speed may vary among stands, this pattern holds consistent across insect and pathogen-disturbed forests in the western United States and Canada (Hicke et al., 2012).

Along with live residual trees remaining post-disturbance, the forest growth release has been identified as a significant contributor to ecosystem productivity, offering considerable potential to compensate for the depleted canopy layer. This rebound in NEP after the year of disturbance from secondary growth has been observed in other insect-induced stand mortality events. Examples include severe defoliation by spongy moth (*Lymantria dispar*) in 2007 in New Jersey and Wisconsin's forest tent caterpillar (*Malacosoma disstria*) infestation in 2001 (Amiro et al., 2010). These patterns underscore the critical role played by residual vegetation in shaping the direction and magnitude of MPB-induced disturbances on carbon stores in boreal forests.

### ***1.3. Mycorrhizal fungal communities rearrange with changes in vegetation: implications on key soil processes***

**1.3.1. Mycorrhizal fungi play an important role in SOM formation and stabilization.** Since initial carbon fluxes models for forests affected by MPB, new concepts have emerged on how carbon and nitrogen move through and become stabilized in ecosystems (Cotrufo et al., 2013; Phillips et al., 2013).

In particular, there has been growing interest in how plants and their associated mycorrhizal fungi mediate nutrient dynamics (Averill et al., 2014; Clemmensen et al., 2015; Cornelissen et al., 2001; Craig et al., 2018; Phillips et al., 2013; Read & Perez-Moreno, 2003; Verbruggen et al., 2016). Nearly all terrestrial plant species engage in symbiosis with mycorrhizal fungi, and they are generally specific in the mycorrhizal group with which they associate, the two most common groups being ectomycorrhizal (EM) and arbuscular mycorrhizal (AM) (Smith & Read, 1997). Within these mycorrhizal associations, plants supply fungal partners with carbohydrates produced through photosynthesis, and in return, they benefit from improved access to soil resources facilitated by the fungal mycelium (Smith & Read, 1997). Considering the vast presence of mycorrhizae and their substantial role in promoting plant growth, their positive effects on the soil carbon balance are well recognized (Frey, 2019; Hawkins et al., 2023; Wu et al., 2023; Zak et al., 2019).

While EM and AM fungal types are structurally and physiologically distinct, both groups are capable of influencing soil organic matter (SOM) dynamics. Morphologically, EM fungi colonize extracellularly on host plant roots, while AM fungal hyphae penetrate directly into plant cells (Smith & Read, 1997). At these nutrient exchange sites, fungal partners receive carbon supplied by their plant hosts to build expansive hyphal networks, thereby transporting significant quantities of plant carbon down into the soil matrix (Hawkins et al., 2023). Beyond living hyphae and tissues, fungal necromass and exudates present reservoirs of significant plant-derived photosynthate that are instrumental in SOM formation and stabilization processes (Frey, 2019). As such, AM hyphal biomass, which is generally more labile with faster turnover rates than EM fungi, can contribute significantly to SOM pools through necromass accumulation. These residues are important products for soil aggregation, which provide nutrient capture, binding, and physical resistance through mineral-organic complexes (Rillig & Mummey, 2006). This stabilization process can increase soil carbon storage by physically protecting SOM from decomposition (Grandy & Neff, 2008; Keller et al., 2021; Lin et al., 2017; Morris et al., 2019; Verbruggen

et al., 2013). Together, belowground carbon allocation processes facilitated by mycorrhizal fungi have significant contributions to stable SOM pools.

### **1.3.2. Nutrient acquisition strategies by EM and AM fungi may stimulate soil carbon losses**

**differently.** Given that mycorrhizal fungi are a dominant component of forest soil communities, changes in community composition and abundance could hold major implications for long-term SOM pools.

Aboveground plant succession, triggered by MPB attack, affects belowground communities as the mycorrhizal fungal groups rearrange in response to changes in available plant hosts and altered environmental conditions (Pec et al., 2015; Rodriguez-Ramos et al., 2021). Specifically, following MPB-induced lodgepole pine mortality, EM fungi, which commonly associate with conifers, decrease and are instead replaced by a greater abundance of AM fungi, which commonly associate with most shrub and forb species (Mayer et al., 2022; Pec et al., 2015; Rodriguez-Ramos et al., 2021).

Despite the notable effects of mycorrhizal fungi in SOM dynamics, variations in nutrient acquisition strategies between EM and AM groups, driven by their specific lifestyle requirements, can contribute to soil carbon loss. Mycorrhizae can destabilize and deplete soil carbon when mining for nutrients, such as nitrogen and phosphorus, locked within SOM. They employ mechanisms such as direct enzymatic breakdown and stimulating microbial activity, which negatively affect SOM storage (Frey, 2019). The genetic capacity to produce oxidative enzymes that decay complex organic matter has only been found in EM fungal species thus far (Read & Perez-Moreno, 2003; Zak et al., 2019). In nitrogen-limited systems, including northern boreal forests, this ability to tap into both inorganic and organic sources can be especially advantageous for EM fungi (Cornelissen et al., 2001).

Mycorrhizal fungal species that lack the genetic capacity to produce extracellular enzymes may employ alternate nutrient acquisition strategies (Frey, 2019). Without direct access to complex organic nutrient sources, they may scavenge for inorganic nutrients made available by saprotrophic microbes. AM fungi generally rely on this strategy to capture nutrients mobilized in bulk soil, especially as they are



usually found under plants with rapid decomposition rates (Brzostek et al., 2015; Cornelissen et al., 2001). Additionally, mycorrhizal fungi can further stimulate the activity of saprotrophic microbes by releasing plant carbon subsidies through hyphal exudates and necromass, thereby mobilizing nutrients (Frey, 2019). This process, known as the priming effect, involves using fresh carbon as a catalyst to destabilize old, recalcitrant SOM for nutrient acquisition (Kuzyakov, 2002). Since stimulating microbial activity leads to a spike in respiration and accelerated breakdown of stable SOM sources, this nutrient acquisition method can also result in soil carbon losses (Fontaine et al., 2011). Interestingly, while the priming effect would intuitively be more beneficial for AM fungi, which cannot produce enzymes, this phenomenon has been observed more frequently in EM-dominated stands (Brzostek et al., 2015; Sulman et al., 2017). This discrepancy could be due to slower decomposition rates and lower microbial biomass production in EM-dominated soils, potentially resulting in less physically protected SOM, which is thus more vulnerable to priming effects (Sulman et al., 2017). At the same time, it has also been hypothesized that competition between mycorrhizal fungi and free-living saprotrophs for shared limiting soil resources may impede litter and SOM decomposition (Gadgil & Gadgil, 1971). Some supporting evidence exists for this theory (Brzostek et al., 2015; Gadgil & Gadgil, 1971, 1975; Sterkenburg et al., 2018), though potential confounding variables make it challenging to confirm patterns conclusively.

There are species-specific variations within mycorrhizal groups in soil carbon cycling processes (Soudzilovskaia et al., 2015). Nonetheless, general differences between EM fungi, which employ mining strategies, and AM fungi, which employ scavenging strategies, suggest that the relative abundance of each group in forest soils can strongly impact principal carbon processes and pools. Thus, while mycorrhizal activities can contribute to SOM stabilization, distinct nutrient-acquisition strategies may also drive destabilization and carbon losses from long-term storage pools (Clemmensen et al., 2015; Frey, 2019).

#### **1.4. Current research in forest carbon dynamics now focuses belowground**

**1.4.1. Evolving understanding of the decomposition process on carbon storage.** Investigating how soil processes respond to these forest community changes holds importance because soils provide essential ecosystem services, storing up to 85% of all terrestrial carbon in boreal forests (Lal, 2005). While the death of EM trees removes a major aboveground carbon store, emerging research suggests that the unique biogeochemical processes associated with AM vegetation and their fungal partners, which are expected to thrive in post-disturbance communities, may buffer this loss (Cotrufo et al., 2013; Craig et al., 2018; Phillips et al., 2013). Traditionally, plant and fungal tissue recalcitrancy was thought to serve as the primary determinant of carbon retention. Slower to break down inputs, such as recalcitrant pine litter, were assumed to preserve nutrient compounds better than easily decomposing inputs, such as broadleaf vegetation litter (Langley & Hungate, 2003). However, these views are now increasingly considered outdated, with growing research adopting a more holistic perspective on the decomposition process. It is now recognized that stable organic matter arises not from the mere preservation of raw litter but, rather, through a continuum of microbial and biochemical transformations that convert organic biopolymers into novel stabilized compounds (von Lützow et al., 2006; Prescott, 2010; Sokol & Bradford, 2019). In fact, soil carbon levels in AM-dominated forests tend to be greater than in EM-dominated forests, although the underlying factors driving this pattern remain ambiguous (Craig et al., 2018).

**1.4.2. Mycorrhizal groups differ in contributions to soil carbon stores.** Differences in the quality and decomposition rates of AM versus EM litter may influence overall soil processes, including microbial production, nutrient ratios and ultimately the formation of stable SOM (Craig et al., 2018; Phillips et al., 2013; Prescott, 2010; Spohn & Stendahl, 2022). The mycorrhizal-associated nutrient economy (MANE) framework, developed by Phillips et al. (2013), conceptualizes how tree species in temperate forests and their mycorrhizal associates may contribute to nutrient cycling differently. The framework predicts that

systems dominated by EM trees, such as intact pine forests, will have an organic nutrient economy (Phillips et al., 2013). Litters from EM plants are generally low quality and difficult to break down, resulting in organic nutrients accumulating in the forest floor. Since EM fungi have the enzymatic capacity to tap into nutrients in the organic form, this direct nutrient pathway may limit the availability of nitrogen to ammonium oxidizers. As a result, these systems are expected to support smaller bacterial communities and slower carbon and nitrogen turnover rates (Phillips et al., 2013). Conversely, in AM-dominated forests with higher-quality litter, the framework predicts that an inorganic nutrient economy will occur (Phillips et al., 2013). High-quality litter allows microbial communities of free-living bacteria and fungi to rapidly cycle and transform plant-derived carbon and nitrogen into inorganic forms (Phillips et al., 2013). Given the differing modes of nutrient acquisition between AM- and EM-dominated communities, Phillips et al. (2013) suggest that the relative abundance of AM and EM vegetation could serve as a tool to predict nutrient dynamics in forests.

Furthermore, Cotrufo et al. (2013) introduced the Microbial Efficiency-Matrix Stabilization (MEMS) framework based on the hypothesis that plant litter quality can determine the rate of SOM stabilization by influencing microbial production. According to the MEMS framework, high-quality litter inputs from labile AM plants are utilized and decomposed more efficiently by microbes than recalcitrant inputs from EM trees. While stimulated decomposer activity was initially presumed to result in soil carbon losses, it is now recognized for its role in generating microbial by-products that are critical for aggregation, organo-mineral associations, and ultimately the formation of stable SOM (Frey, 2019; von Lützow et al., 2006). As such, the MEMS framework proposes that AM-dominated communities, which promote greater microbial products relative to the amount of litter metabolized, would result in larger stable SOM pools, relative to EM-dominated communities (Cotrufo et al., 2013). Building on this concept of microbial use efficiency of plant litter, the availability of other nutrients required by microbes in the soil,

such as nitrogen, would presumably also affect the rate at which litter transforms into SOM (Kirkby et al., 2013).

**1.4.3. AM-dominated forests may result in larger long-term carbon pools.** Soil organic matter encompasses mineral-associated organic matter (MAOM) and partially decomposed materials known as particulate organic matter (POM). These two pools have broad distinctions chemically and physically, in addition to ecological functioning and turnover times (Lavallee et al., 2020; von Lützow et al., 2007). The formation of MAOM involves organic materials such as root exudates, leachates from fresh surficial litter, and microbially-transformed organic matter, including fungal residues (Klink et al., 2022) and plant inputs in the rhizosphere (Sokol & Bradford, 2019). These organic materials become physically protected through adsorption to soil mineral surfaces or occlusion within aggregates (Samson et al., 2020). As a result, MAOM can persist on longer timescales compared to POM and is thus considered a more dominant determinant of soil carbon storage (Grandy & Neff, 2008).

Following MPB attack, formerly EM-dominated lodgepole pine forests are often replaced by AM-dominated succeeding communities. Considering the MANE (Phillips et al., 2013) and the MEMS (Cotrufo et al., 2013) frameworks together, it is expected that high-quality AM materials in disturbed forests can stimulate greater microbial production, are cycled more rapidly, and are more likely to become stabilized in the MAOM pools, compared to low-quality EM materials in intact forests. Carbon entering soils of these EM-dominated forests may be more likely to go into the POM pools, characterized by shorter residency times (Cotrufo et al., 2013; Craig et al., 2018a; Lang et al., 2023).

### ***1.5. Knowledge gaps in existing frameworks***

These conceptual frameworks offer valuable starting points for linking forest mycorrhizal community shifts with SOM responses. However, their application in empirical studies across ecosystems is limited due to the complex and multicausal nature of SOM formation. For instance, a

study along an ecosystem gradient in New Zealand found that litter quality had minimal impact on carbon accumulation in MAOM (Mikutta et al., 2019). Instead, the study underlined the prominent role of minerals and their carbon saturation levels, among other mechanisms and environmental conditions, in determining the quality and quantity of SOM (Mikutta et al., 2019). The carbon saturation concept also suggests that the conversion of litter to stable SOM may be more contingent on the available soil carbon storage capacity, with litter quality and microbial efficiency assuming a background role (Castellano et al., 2015). In addition, underlying these mycorrhizal plant and fungal community processes, soil nutrient dynamics are strongly influenced by soil mineralogy (Lang et al., 2023). Fine-textured soils, for example, provide more sites for the adsorption of organic compounds onto mineral surfaces, which protects them against microbial decomposition (von Lützow et al., 2006). Across diverse climates, soil orders, and forest species compositions, soil texture remains the strongest and most positive factor affecting MAOM carbon and nutrient concentrations (Lang et al., 2023).

Furthermore, there is concern regarding research and management strategies that place excessive emphasis on MAOM. Overly generalized formation pathways may overlook the nuances of different contexts and the role of POM, which can still provide important contributions to overall carbon dynamics over relatively shorter time scales (Angst et al., 2023). The significance of POM may be particularly pronounced in boreal forest systems with slower turnover rates overall, due to colder climates and acidic coniferous soils (Angst et al., 2023). This underscores the need to incorporate context specificity into soil carbon and nitrogen formation pathways (Lang et al., 2023), especially when applying frameworks developed in temperate systems (Cotrufo et al., 2013; Craig et al., 2018; Phillips et al., 2013). Ultimately, these models can serve as foundations as we further explore shifts in SOM processes that accompany the expected transition from forests dominated by EM pine trees to forests dominated by AM shrubs and forbs. Even in stands beyond recovery, there is still an opportunity to

enhance other ecosystem services and restore value back to these landscapes, such as through supporting soil carbon accrual processes.

### ***1.6. Research objectives***

Here, I investigated the effects of MPB-induced tree mortality on shifts in mycorrhizal types, through the recovery of vegetation, and on soil carbon storage. Specifically, I addressed the following questions:

1) Will the dominant mycorrhizal type change with disturbance? 2) Does extensive tree mortality change the amount of carbon and nitrogen stored in forest floors and mineral soils? I predicted that disturbed forests would succeed towards AM plant dominance and hold more soil carbon and nitrogen, especially in stable MAOM pools.

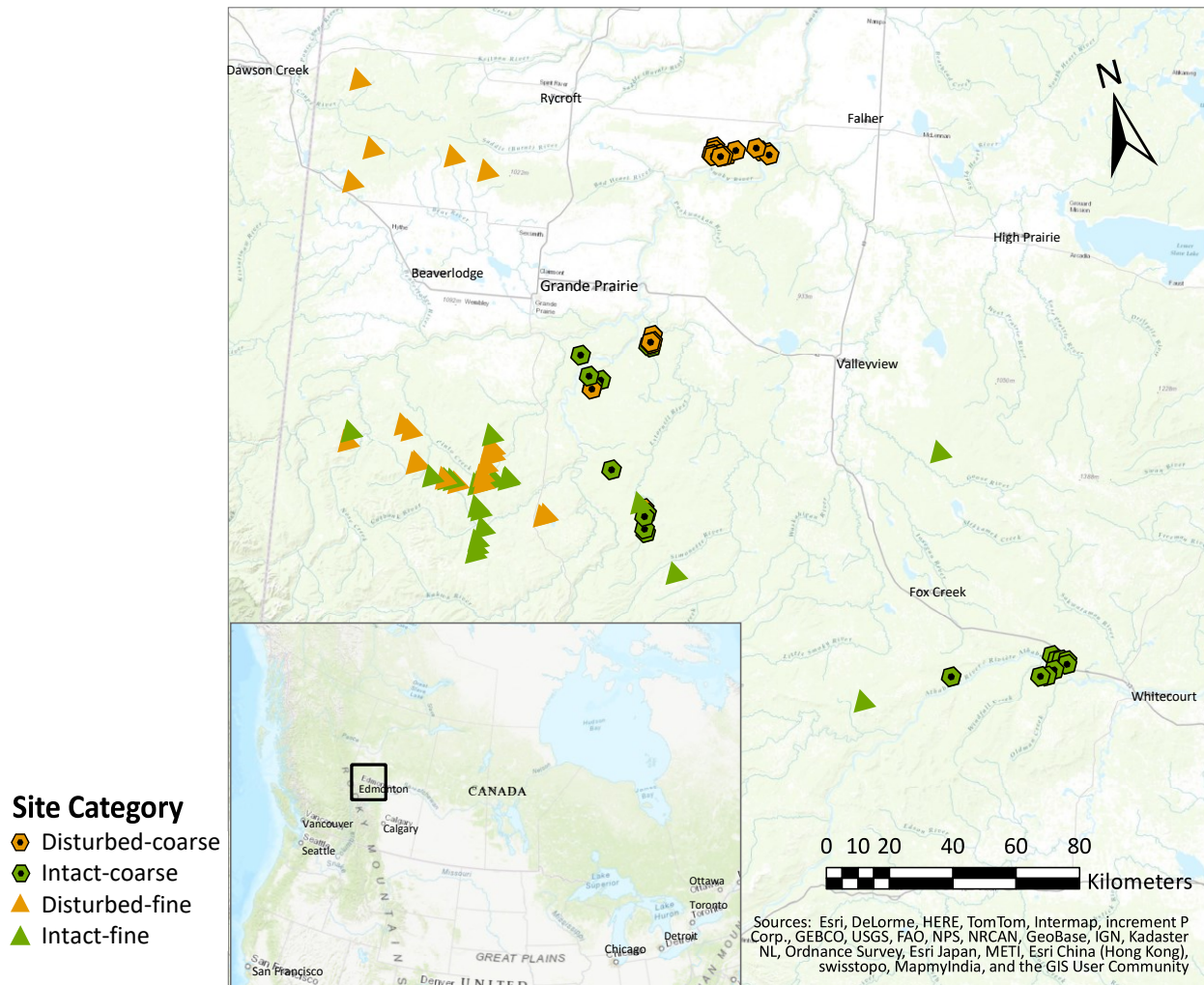
## 2. Methods

### 2.1. Study area

The study was conducted in west-central Alberta, Canada in the Lower Foothills (mean annual precipitation (MAP) of 464 mm; mean annual temperature (MAT) of 3.0 °C; 500 – 1150 m above sea level) and Boreal Mixedwood (MAP 389 mm; MAT 1.5 °C; 225 – 1225 m above sea level) ecological subregions, outside the nearest town of Grande Prairie (55.170834, -118.794724) (Beckingham et al., 1996; Beckingham & Archibald, 1996). These regions experience typical boreal climates of long cold winters and short mild summers (Beckingham et al., 1996; Beckingham & Archibald, 1996). Stand-replacing fires with short return intervals are common in the region, creating even-aged forests with simple stand structures that generally do not surpass 150 years of age (Baldwin et al., 2020). This portion of the province has also experienced periodic outbreaks of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) disturbance since the late 1990s, with a sharp increase in activity in 2006 (Alberta Sustainable Resource Development, 2007). Reference sites are characterized by the occurrence of lodgepole pine (*Pinus contorta* Dougl. Ex. Loud. Var. *latifolia* Engel.), white spruce (*Picea glauca* (Moench) Voss), balsam poplar (*Populus balsamifera* L.), and trembling aspen (*Populus tremuloides* Michaux), with other common tree species including balsam fir (*Abies balsamea* (Linnaeus) Miller var. *balsamea*), white birch (*Betula papyrifera* Marshall), and black spruce (*Picea mariana* (Miller) Britton, Sterns & Poggenburgh) (Beckingham et al., 1996; Beckingham & Archibald, 1996). Frequent species in the understory include prickly rose (*Rosa acicularis* Lindl.), low-bush cranberry (*Viburnum edule* (Michx.) Raf.), green alder (*Alnus viridis* var. *crispa* (Aiton) House), saskatoon berry (*Amelanchier alnifolia* (Nutt.) Nutt. ex M.Roem.), Canada buffalo-berry (*Shepherdia canadensis* (L.) Nutt.), twinflower (*Linnaea borealis* L.), bunchberry (*Cornus canadensis* L.), wild sarsaparilla (*Aralia nudicaulis* L.), and dewberry (*Rubus pubescens* Raf.) (Beckingham et al., 1996; Beckingham & Archibald, 1996). Predominate soils in this region are Gray Luvisols and Brunisols, developed in surficial glacial materials (Baldwin et al., 2020).

## 2.2. Site selection and experimental design

Eighty sites were surveyed, which included MPB-disturbed and intact forests on coarse- and fine-textured soils. There were 20 sites representing each of the following categories: 1) disturbed-coarse, 2) intact-coarse, 3) disturbed-fine, and 4) intact-fine (Fig. 1).



**Figure 1.** Location of the 80 field sites in west-central Alberta, Canada. Map inset shows extent of enlarged area.

Candidate sites were initially identified through available provincial databases of permanent sample plots established by the Government of Alberta’s Agriculture and Forestry division, as well as from past surveys by Steinke et al. (2019). Data from past surveys were collected between 2015 and 2017 and included stand characteristics such as forest structure, composition, disturbance type and



severity. In these initial surveys, MPB damage severity was determined by the abundance of MPB tubes, J-galleries and evidence of woodpecker activity. Using a combination of landscape maps and personal communications, I broadly categorized candidate sites into coarse or fine soil textures with 50% sand content as the cut-off. I confirmed the suitability and accessibility of each candidate site with field inspection, by ground-truthing the forest composition, live/dead status of the canopy trees, and soil textural class through hand-texturing. Sites required in addition to those previously surveyed ( $n = 28$ ) were scouted in appropriate areas on Crown land with the help of government foresters.

To test the influence of MPB-disturbance on soil carbon and nitrogen storage, I selected intact and disturbed mature lodgepole pine dominant stands (80% canopy composition). Stands chosen to represent disturbed sites had high levels of mortality, defined in this study as a minimum of 70% of canopy lodgepole pine trees killed by MPB, with no MPB-management in place since attack. Disturbance in these stands occurred between 2006 and 2010 (Alberta Sustainable Resource Development, 2007; Steinke et al., 2019). To test the influence of soil texture, stands belonging to the two disturbances were surveyed on both coarse and fine-textured soils. The average bulk density in the top 15 cm of the mineral soils was approximately  $1124.9 \text{ kg/m}^3 (\pm 83.1)$  and  $1197.3 \text{ kg/m}^3 (\pm 122.0)$ , in fine-textured and coarse-textured sites, respectively. For deeper horizons (15–45 cm depth), I relied on known approximations of boreal forest soil bulk densities (Shaw et al., 2005). Sites were a minimum of 1 km apart to ensure independence. Additionally, all the sites were at least 100 m from roads and cut block boundaries to minimize the edge effects. Site descriptions can be found in Table A1.

### **2.3. Forest surveys**

Sites were surveyed from June to August 2022. In each of the 80 sites, I established a 10 m radius circular plot ( $314 \text{ m}^2$ ) that was representative of the structure and composition of that particular forest stand, in which I conducted forest surveys and collected soils.

Standard forest mensuration data were collected for all trees within a 3.99 m radius fixed area subplot, embedded in the centre of each circular plot. I surveyed all trees (height  $\geq 1.3$  m and DBH  $> 7$  cm) for species, DBH, % mortality, calculated stems per hectare, and recorded seedling species and recruitment density (Table A1). I collected two tree cores from the two largest trees (in DBH) from each stand, to estimate stand age ( $\bar{x} = 76.6 \pm 27.2$  years old). Aging of the dead tree cores should be taken as rough approximations, as the samples do not reflect the years following attack and early stages of decay made it difficult to retain and identify all rings. The shrub layer was surveyed along a 20 m transect, following the plot diameter at a randomly selected orientation, using the line transect method to record species and abundance. Abundance was measured as the number of shrub stems intersecting the transect. I surveyed all forbs, herbs, and bryophytes within two randomly distributed 1 m x 1 m quadrats set within each plot (Table A2). Plant species richness in each quadrat was based on vascular plant species only. Bryophytes were present in all quadrats but were not included in plant richness calculations because they were not identified to species. To confirm the mycorrhizal identity of plant species, I excavated plant roots from soil depths of approximately 0–20 cm. Tracing the plant down to its fine roots, I carefully extracted the roots from the soil, rinsed them with water, and preserved them in separate containers of a 50% ethanol solution for transportation and storage. Across all sites, I collected a total of ten samples for each of the 20 most commonly recorded plant species ( $n=200$ ), which were later scored to determine the presence and identity (ecto-, arbuscular or ericoid mycorrhizal fungi) of mycorrhizal fungi colonizing roots (Table A3).

To determine the amounts and variability of carbon and nitrogen stored in soils, I collected samples from the forest floor and the upper mineral soil layers. In each plot, I sampled three random points representative of the stand. At each point, the live, above-ground plant material was gently removed to minimize soil compaction. To sample the forest floor, I cut along a square frame guide (20 cm x 20 cm) with a small saw to detach the organic layer from the adhering soil and took care to

maintain the square shape of the excavated volume. I measured and recorded the volume's thickness at all four corners. To sample the upper mineral layer, I used a 5.08 cm x 15.24 cm impact-driven soil core sampler (AMS, Inc., American Falls, USA) to extract approximately 310 cm<sup>3</sup> of fresh soil (to a depth of 15 cm), directly beneath the removed organic layer. The forest floor (n = 3) and mineral (n = 3) subsamples from each plot were transferred into separate bags, labelled, and air-dried. I calculated and recorded the volumes of all forest floor and bulk soil samples for subsequent bulk density calculations, a factor important in this study due to its known influence on soil carbon stocks (Périé & Ouimet, 2008). At one additional representative location within each plot, I excavated a soil pit to measure carbon concentrations and stocks of the deeper soil pools. The forest floor was sampled using the same method with the square frame. To sample the mineral layers, I dug a pit to a depth of 45 cm from the top of the mineral soil. Samples were collected at three depths (0–15, 15–30, and 30–45 cm), stored in separate labelled bags and air-dried.

## **2.4. Laboratory analyses**

**2.4.1. Root staining and microscopy.** Roots were cleared and stained using modified methods from Karst et al. (2021) and Neville et al. (2002). After rinsing with deionized water, fine roots (<1 mm in diameter) were cut into 1 cm segments and cleared in Eppendorf tubes with 10% KOH at 90 °C for 3 hours. I rinsed the roots with deionized water again and then soaked them in a 0.5% H<sub>2</sub>O<sub>2</sub> and 33.5% NH<sub>4</sub>OH solution (on a volume basis) at room temperature for 15–25 minutes, depending on the species, until transparent. The cleared roots were rinsed once more with deionized water and then stained with a 5% dark blue ink and vinegar solution at 90 °C for 3 minutes (Vierheilig et al., 1998). After cooling for 30 minutes, I destained the roots with an ink and vinegar solution. These roots were stored in deionized water at 4 °C until microscopy.

In this study, assigning plant species mycorrhizal type was a critical step for understanding the effects of the different groups, particularly AM versus EM, on soil processes. Arbuscular mycorrhizal and

EM fungi are structurally distinct. Arbuscular mycorrhizal fungi form structures which penetrate the host plant intracellularly, whereas EM fungi form structures that envelop fine roots externally (Smith & Read, 1997). Therefore, different methods were necessary to examine colonization for each group. To score the roots for AM colonization, thirty 1 cm long stained fine-root segments were randomly selected for each species and mounted horizontally across glass microscope slides. I examined the slides under a compound microscope at 400x magnification. Passes were made along the length of each root to record the number of fields of vision, the number of AM fungal structure intersections with the crosshairs on the ocular and the type of AM fungal structures (hyphae, arbuscules, vesicles) observed. I summed the number of observations across the 30 root fragments comprising each species' sample. Percent colonization of AM fungi was calculated as the total number of AM fungal structure intersections divided by the total number of fields of vision. To score roots for EM colonization, I examined 100 root tips for each species. I randomly dispersed stained root segments in Petri dishes covered in a film of water. Under a dissecting microscope at 20x magnification, I placed the petri dish over 1 cm grid paper and used the grid-line intersect method to estimate the proportion of EM fungi colonized roots. Roots were considered EM if a continuous mantle was present, which could be identified by dark and bulging tips, free of root hairs (Neville et al., 2002). Root scoring results were compared against mycorrhizal assignments of plant species available in European and North Asian databases (Akhmetzhanova et al., 2012; Bueno et al., 2017; Hempel et al., 2013) (Table A4). Using the root scoring results and databases, I determined the mycorrhizal type of all plant species identified in the forest surveys.

**2.4.2. Soil processing and calculations.** The air-dried soil samples were homogenized and passed through a 2 mm sieve in preparation for subsequent analyses. The texture of the three mineral soil subsamples from each site (n=240) was measured with Laser Diffraction (LS 13320 Laser Particle Size Analyzer; Beckman Coulter, Indianapolis, USA) by the Natural Resources Analytical Lab at the University of Alberta, and reported as percent sand, silt and clay size fractions. Results from the Laser Diffraction

analysis were used to confirm soil texture categories assigned to sites in the field. The analysis flagged one coarse-textured site that was incorrectly categorized as fine-textured. With this correction, the study now includes 41 sites with coarse-textured soil and 39 sites with fine-textured soil (Fig. A3). I measured carbon and nitrogen content in unpooled subsamples to track within-site variations and in pooled composites to allow for greater consistency when investigating variation among sites (Cahill et al., 2017). To assess within-site spatial variations in carbon concentration occurring laterally across the soil surface, I measured the mineral subsamples collected from the three soil cores in each site (n=240) with the loss-on-ignition (LOI) method. Due to the known influence of soil texture on soil carbon, I evaluated coarse- and fine-textured soil sites separately. To assess spatial variability occurring with depth through the soil profile, I used LOI to measure the three mineral subsamples collected at three different depths from each soil pit (n= 240). According to established protocol (Sparks, 1996), I heated crucibles in a muffle furnace at 420 °C for 2 hours, cooled them in the desiccator, and then weighed them (+/- 0.1 mg). I added approximately 3 g of the hand-ground, sieved and air-dried soil samples to each crucible. The samples were oven-dried at 105°C for 4 hours, cooled, and weighed (+/- 0.1 mg). The oven-dried soil weight ( $Weight_{105\text{ }^{\circ}\text{C}}$ ) was calculated by subtracting the weight of the crucible from the oven-dried weight. Finally, I ignited the samples in the muffle furnace at 400°C for 16 hours, cooled, and weighed (+/- 0.1 mg). The ignited soil weight ( $Weight_{400\text{ }^{\circ}\text{C}}$ ) was calculated by subtracting the weight of the crucible from the ignition weight. The LOI (%) of the sample was then calculated as follows (1):

$$\text{LOI (\%)} = \frac{\text{Weight}_{105\text{ }^{\circ}\text{C}} - \text{Weight}_{400\text{ }^{\circ}\text{C}}}{\text{Weight}_{105\text{ }^{\circ}\text{C}}} * 100 \quad (1)$$

To calculate soil organic carbon content with the LOI values, I used the conventional (van Bemmelen) conversion factor, which assumes that 58% of soil organic matter is SOC.

To assess among-site carbon variations, the three soil core subsamples from each site were pooled (n = 80), and measured for total C and N content with dry combustion analysis (FLASH 2000

Organic Elemental Analyzer; Thermo Fisher Scientific, Bremen, Germany 2016) by the Natural Resources Analytical Lab. In addition, one forest floor sample from each site (n = 80) was measured for total C and N content by dry combustion. These samples were all ground using a TissueLyser (TissueLyser II; Qiagen, Hilden, Germany 2022) prior to analysis. Soil organic carbon (SOC) and total nitrogen (TN) stocks were determined by multiplying the percent concentration of carbon or nitrogen (%C or %N) with bulk density (BD) and the depth of the soil layer (SD) (2) (Bhatti et al., 2002):

$$\text{SOC or TN (kg/m}^2\text{)} = \text{C or N (\%)} * \text{BD (g/cm}^3\text{)} * \text{SD (cm)} * 0.1 \quad (2)$$

To explore the effects of MPB-disturbance on SOC pools of differing stabilities, I separated the soil samples into two fractions: particulate organic matter (POM; density less than  $\sim 1.7 \text{ g/cm}^3$ ) and mineral-associated organic matter (MAOM; density greater than  $\sim 1.7 \text{ g/cm}^3$ ). Particulate organic matter comprises younger, relatively less decomposed plant materials and is considered to be a more labile carbon store, whereas MAOM consists of more decomposed microbe-derived materials and is considered to be a more stable, mineral-protected carbon store (Grandy & Neff, 2008). By comparing the quantity of carbon residing in these physically and chemically contrasting forms, I could better determine carbon persistence across site categories. Pooled composites from each site (n = 80) were fractionated using a density-based technique (Maillard et al., 2015; Samson et al., 2020). I placed 15 g of each soil composite in separate 50 mL centrifuge vials with glass beads and dispersed soil aggregates using a reciprocating shaker. I then added 40 mL of a  $1.7 \text{ g/cm}^3$  standard-density sodium iodide (NaI) solution to each vial. The vials were shaken vigorously by hand to suspend the soil and then centrifuged (4400 RPM) for 120 minutes. The supernatant solution, which contained the suspended POM fractions, was then decanted and rinsed through a vacuum filtration system. The pelleted MAOM fractions remaining in the vial were resuspended in deionized water, centrifuged, and decanted for several cycles to remove the remaining NaI solution. After rinsing, the collected POM and MAOM fractions were dried

in an oven at 55 °C for 24 hours. I recorded the final dry weights to determine their relative contribution to the total soil mass. The average recovery rate of bulk soil, based on the whole soil after density fractionation into MAOM and POM, was 94% ( $SD = 5$ ). Sixty-six of the 80 sites had recovery rates greater than 90%. Incomplete rates could be attributed to dissolved organic carbon and colloidal particles lost during sensitive steps, such as sample filtration, rinsing, or recovery (Viret & Grand, 2019). The fractionated samples were ground using a Tissuelyser (TissueLyser II; Qiagen, Hilden, Germany 2022) and subjected to dry combustion analysis for total C and N content.

## **2.5. Statistical analyses**

Data were tested for normality and homogeneity of variances assumptions before analysis, according to Shapiro-Wilk's and Fligner-Killeen's tests, respectively. Continuous data, such as soil chemical variables, were transformed by their natural logarithm (ln-transformed) when necessary to fulfill normality requirements for parametric tests. Outliers were identified using boxplot methods and extreme outliers were removed prior to further calculations with the *rstatix* R package (Kassambara, 2023). Extreme outliers were defined as values above the third quartile plus three times the interquartile range or below the first quartile minus three times the interquartile range. Removed outliers are indicated in figure titles. For count data, including plant community surveys, I used nonparametric tests (Kruskal-Wallis rank sum test) to compare means, followed by Nemenyi's all-pairs test for significant models (*PMCMRplus* R package; Pohlert, 2022). I calculated the 95% confidence intervals for the means of count data using a Poisson distribution (*MASS* R package; Venables & Ripley, 2022). Following permutational multivariate analysis of variance using distance matrices in the *vegan* R package (Oksanen et al., 2022) to test if there were significant differences in vegetation communities between disturbance groups, I used indicator species analyses to determine which species could be indicative of each group. Using generalized linear models (GLMs) and two-way ANOVA tests, I investigated the potential main and interaction effects of soil texture, disturbance category, and soil

depth on the response variables, soil carbon and soil nitrogen. Significant models were followed by Tukey's post-hoc tests (*multcompView* R package; Graves et al., 2019) or Tukey's WSD post-hoc test of means for unequal variance (*semTools* R package; Jorgensen et al., 2022). Results were plotted with 95% confidence intervals for the means, using the *ggplot2* R package (Wickham, 2016). I calculated the power of the hypothesis tests using the *pwr* package in R (Cohen, 1998). For visualization in the figures, ln-transformed values were back-transformed using inverse ln. All statistical analysis and plotting were conducted with R (version 2022.12.0.353, Posit team, 2022). An alpha level of 0.05 was set to determine the significance for all statistical tests.

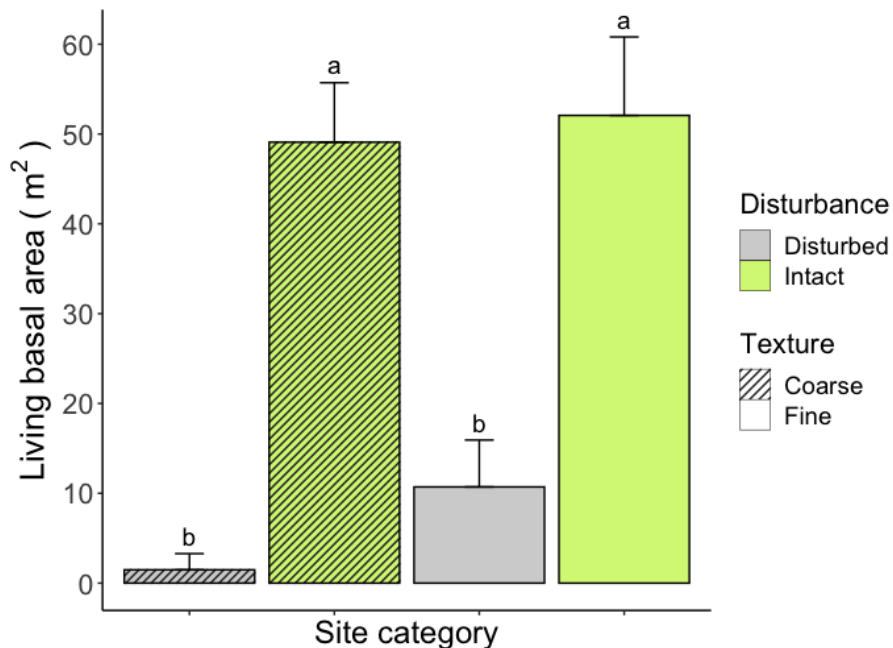


### 3. Results

#### 3.1. Mycorrhizal community composition

All plant species were assigned a mycorrhizal type (Table A3). Canopy trees were EM, while shrub and understory plants were mostly AM (Table A3). Root scoring results were largely consistent with the databases (Table A4). While there were some discrepancies with ericoid mycorrhizas, the relatively low abundance of plants associated with this mycorrhizal type is unlikely to affect overall results.

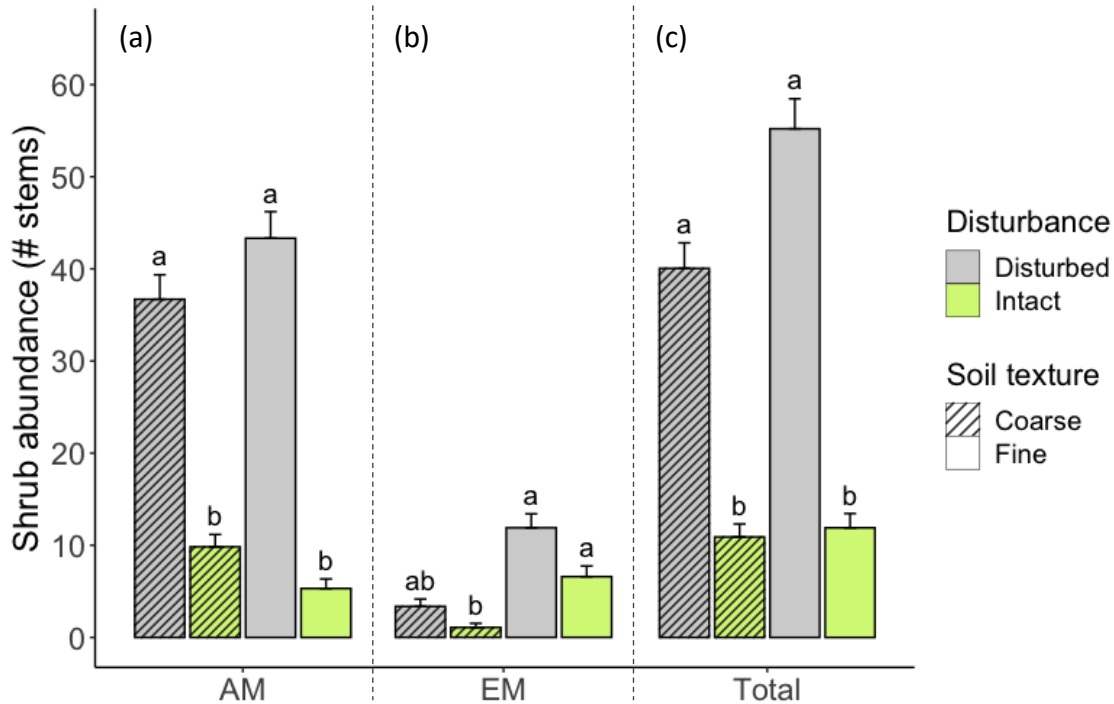
In the overstory, the living basal area was 79% and 97% less in disturbed versus intact sites, on fine- and coarse-textured soils, respectively (Fig. 2; Table A5). The mortality of lodgepole pine, the dominant canopy species, mostly accounted for these differences. All the trees observed in this study were EM species (Table A3), thus the mortality of trees in the canopy layer reflects the most consequential EM loss in disturbed sites.



**Figure 2.** Living basal area (mean  $\pm$  95% confidence interval for the means) of each site ( $n = 20$  for disturbed-coarse,  $n = 21$  for intact-coarse,  $n = 20$  for disturbed-fine, and  $n = 19$  for intact-fine sites). ‘Disturbed’= lodgepole

pine dominant sites with >70% basal area killed by mountain pine beetle; 'Intact'= lodgepole pine dominant sites free of mountain pine beetle activity. The Kruskal-Wallis rank sum test found significant differences between the four site categories ( $H(3) = 61.835, P < .001$ ). Means not sharing the same letter are significantly different (Nemeyi's All-Pairs Rank Comparison Test,  $P < .05$ ).

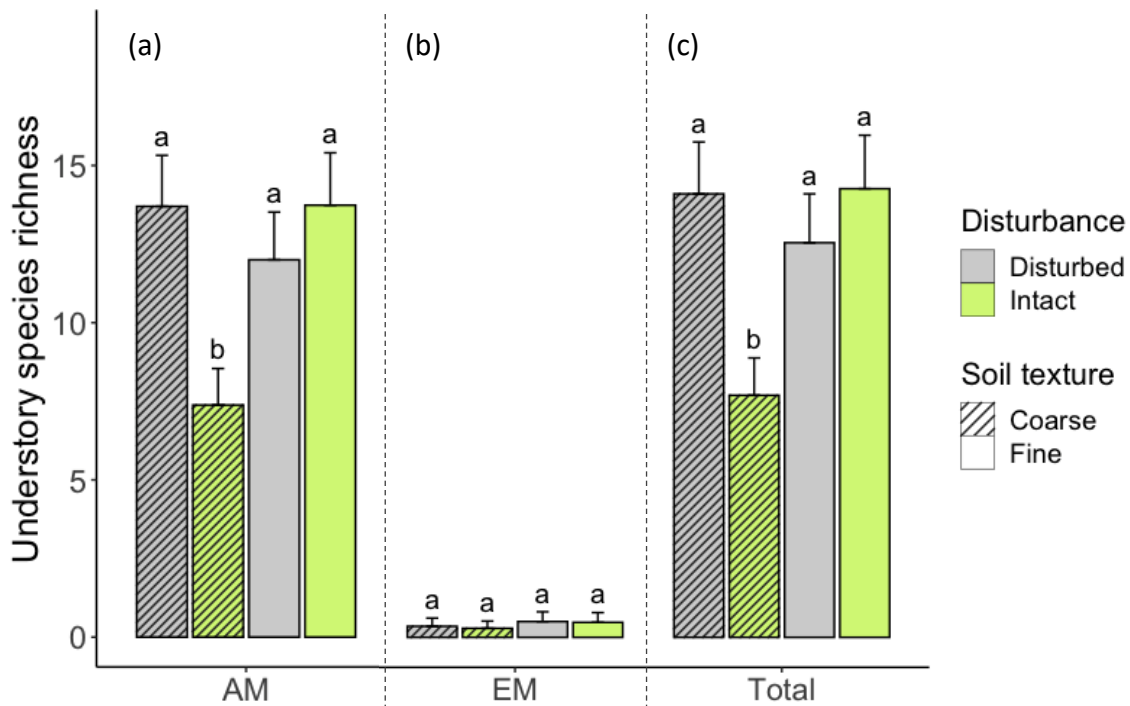
Shrub abundance, measured as the number of stems intersecting the 20 m line transect in each site, significantly differed between MPB-disturbed and intact stands, on coarse- and fine-textured soils (Table A6). Average shrub abundance in disturbed stands was greater than in intact stands by 364% on fine-textured soils and 267% on coarse-textured soils (Fig. 3c). This was mainly due to increases in shrubs that are AM species. On average, AM shrub abundance was greater in disturbed versus intact stands by 715% on fine-textured soils and 273% on coarse-textured soils (Fig. 3a; Table A6). Ectomycorrhizal shrub abundance, however, did not differ between intact and disturbed forests across either soil texture category (Fig. 3b; Table A6). Disturbance explained a small but significant amount of shrub abundance variation on both fine- ( $R^2 = .058, P = .018$ ) and coarse-textured sites ( $R^2 = .071, P = .006$ ) (Fig. A1). On fine-textured soils, the abundance of *Rosa acicularis*, *Oplopanax horridus*, *Streptopus amplexifolius*, and *Rubus idaeus* were all indicators of disturbed forests, but no significant species were identified for intact forests. On coarse-textured soils, *Amelanchier alnifolia* abundance was indicative of disturbed forests and *Ledum groenlandicum* abundance was representative of intact forests.



**Figure 3.** Abundance (mean  $\pm$  95% confidence interval for the means using Poisson distribution) of (a) arbuscular mycorrhizal (AM) shrubs, (b) ectomycorrhizal (EM) shrubs, and (c) total shrubs, recorded as the average number of stems intersecting the 20 m line transect in each site ( $n = 20$  for disturbed-coarse,  $n = 21$  for intact-coarse,  $n = 20$  for disturbed-fine, and  $n = 19$  for intact-fine sites). ‘Disturbed’= lodgepole pine dominant sites with >70% basal area killed by mountain pine beetle; ‘Intact’= lodgepole pine dominant sites free of mountain pine beetle activity. Kruskal-Wallis tests found significant differences between the four site categories in AM ( $H(3) = 26.593$ ,  $P < .001$ ), EM ( $H(3) = 20.491$ ,  $P < .001$ ), and total shrub abundance ( $H(3) = 24.677$ ,  $P < .001$ ). Means not sharing the same letter are significantly different (Nemeyi’s All-Pairs Rank Comparison Test,  $P < .05$ ).

Understory plant species richness, which included forbs and herbs, was 83% higher in disturbed stands compared to intact stands, on coarse-textured soils (Fig. 4c; Table A7). AM plant species richness, which was 86% greater in disturbed stands, accounted for most of the changes (Fig. 4a; Table A7). No significant differences in EM plant species richness were found between disturbances (Fig. 4b; Table A7). On coarse-textured soils, disturbance explained a small but significant amount of species composition variation ( $R^2 = .133$ ,  $P = .001$ ). *Lathyrus ochrus*, *Rubus idaeus*., and *Fragaria virginiana* represented

disturbed forests and *Vaccinium vitis-idaea* and *Ledum groenlandicum* represented intact forests (Fig. A2). On fine-textured soils, no significant differences were found in understory plant richness due to disturbance, where neither AM nor EM plant species differed between intact and disturbed forests (Fig. 4; Table A7). The disturbance category explained a small but significant amount of species composition variation ( $R^2 = .111$ ,  $P = .021$ ) in fine-textured soil sites, with *Equisetum sylvaticum* and *Lycopodium annotinum* representing disturbed forests and *Arnica cordifolia*, *Petasites frigidus*, and *Maianthemum canadense* representing intact forests (Fig. A2). While there were some changes in understory species composition, the communities remained dominated by AM species.



**Figure 4.** Understory species richness (mean  $\pm$  95% confidence interval for the means using Poisson distribution) of (a) arbuscular mycorrhizal (AM), (b) ectomycorrhizal (EM), and (c) total plants, recorded as the number of species observed within two 1 m<sup>2</sup> quadrats per site ( $n = 20$  for disturbed-coarse,  $n = 21$  for intact-coarse,  $n = 20$  for disturbed-fine, and  $n = 19$  for intact-fine sites). ‘Disturbed’= lodgepole pine dominant sites with >70% basal area killed by mountain pine beetle; ‘Intact’= lodgepole pine dominant sites free of mountain pine beetle activity. Kruskal-Wallis tests found significant differences between the site categories in AM ( $H(3) = 12.665$ ,  $P = .005$ ) and

total understory richness ( $H(3) = 25.877, P < .001$ ), but no differences in EM richness ( $H(3) = 1.4063, P = .704$ ).

Means not sharing the same letter are significantly different (Nemeyi's All-Pairs Rank Comparison Test,  $P < .05$ ).

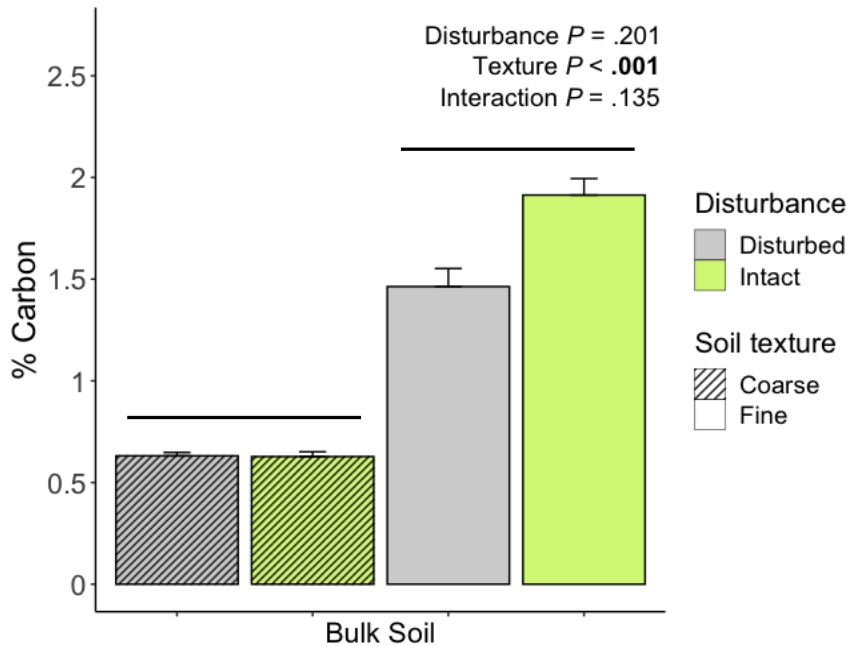
### **3.2. Soil texture and forest floor**

There was a clear distinction in soil particle size distribution between sites categorized as fine- or coarse-textured (Fig. A3). Soils of fine-textured sites had an average of 220% more silt and 275% more clay content than soils of coarse-textured sites (Fig. A3). Sites categorized as coarse-textured had soils with approximately 266% more sand than sites categorized as fine-textured (Fig. A3).

The main effects of soil texture were significant in explaining the thickness of the forest floors (Table A8). Forest floors were thicker in sites with fine-textured soils compared to coarse-textured soils (Fig. A4). No significant main effects from disturbance or interaction effects between disturbance and soil texture were detected on forest floor thickness (Table A8).

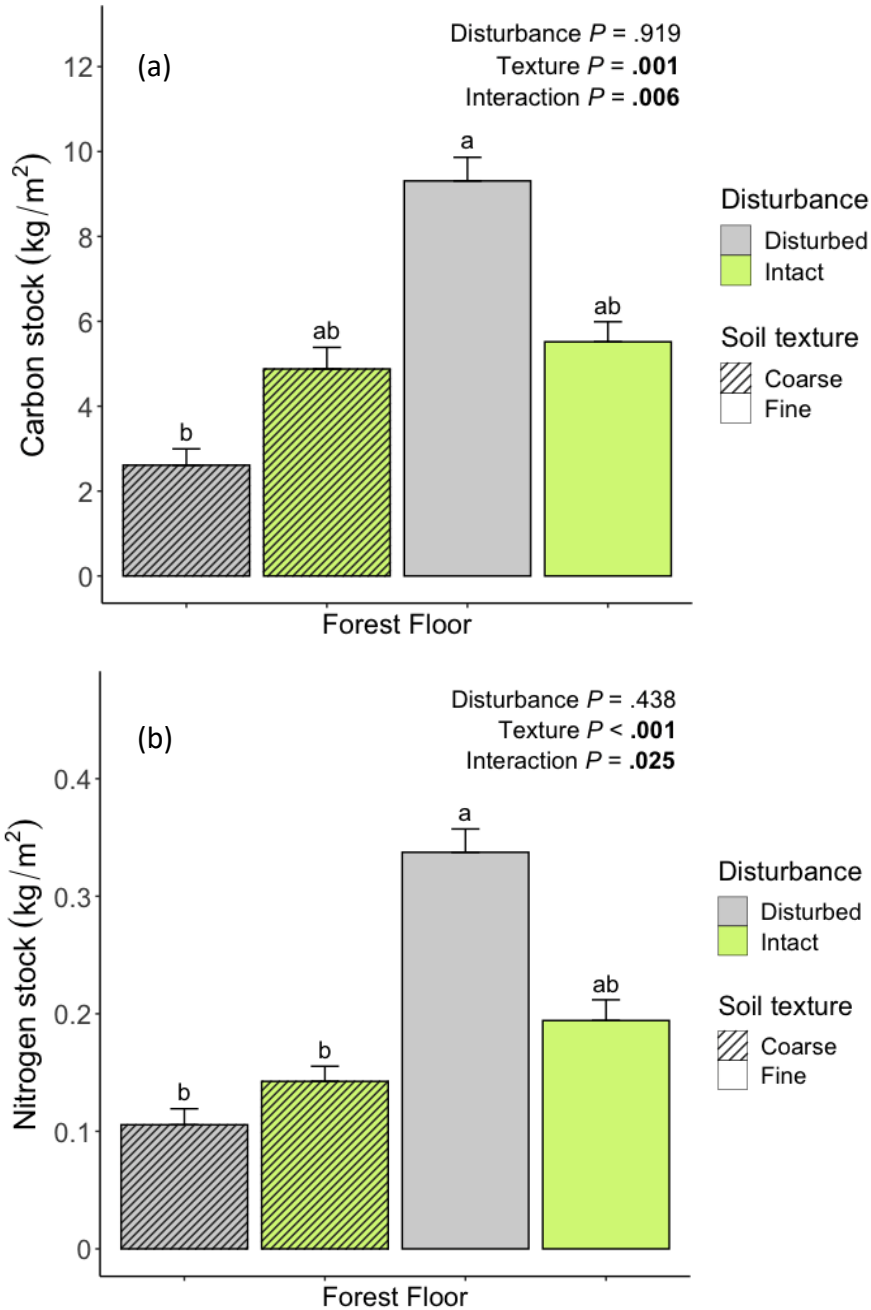
### **3.3. Soil carbon and nitrogen**

In bulk mineral soils, only the main effects of soil texture were significant in explaining the percent soil carbon (Table A9). Neither disturbance nor its interaction with soil texture had significant effects on soil carbon concentrations (Table A9). Carbon concentrations in fine-textured soils were 1.7-fold higher than in coarse-textured soils (Fig. 5). In addition, bulk mineral soil nitrogen concentrations followed similar patterns to carbon (Fig. A5). Only the main effects from texture were significant, while disturbance and interaction effects were not significant in explaining the percent soil nitrogen (Table A10). The carbon-to-nitrogen ratio in bulk mineral soil was significantly different between all stand categories, where intact-coarse sites held the highest average C/N ratio while the disturbed-fine sites held the lowest average C/N ratio (Fig. A6).



**Figure 5.** Carbon concentration measured in bulk soil (back-transformed ln-mean  $\pm$  95% confidence interval), to a depth of 15 cm. Surveys included 20 disturbed-coarse, 21 intact-coarse, 20 disturbed-fine, and 19 intact-fine sites. ‘Disturbed’= lodgepole pine dominant sites with >70% basal area killed by mountain pine beetle; ‘Intact’= lodgepole pine dominant sites free of mountain pine beetle activity. Statistically significant main effect from texture in bulk soil ( $F(1, 75) = 116.346, P < .001$ ), tested with two-way ANOVA. Removed extreme outlier: 1 intact-coarse. Means not sharing a horizontal line are significantly different (Tukey HSD Test,  $P < .05$ ).

For forest floors, the main effects of soil texture and its interaction with disturbance were significant in explaining both carbon and nitrogen stocks (Table A11). There were no main effects from disturbance (Table A11). In the absence of disturbance, carbon and nitrogen stocks in fine- versus coarse-textured soils were not significantly different (Fig. 6). However, with disturbance, carbon and nitrogen stocks in fine-textured soils were significantly greater than in coarse-textured soils (Fig. 6). On average, the forest floors of fine-textured sites contained 54% more carbon stocks than coarse-textured sites (Fig. 6a). Nitrogen stocks of forest floors were an average of 75% greater in fine-textured compared to coarse-textured sites (Fig. 6b).



**Figure 6.** Forest floor (a) carbon, and (b) nitrogen stocks (back-transformed  $\ln$ -mean  $\pm$  95% confidence interval). Surveys included 20 disturbed-coarse, 21 intact-coarse, 20 disturbed-fine, and 19 intact-fine sites. ‘Disturbed’= lodgepole pine dominant sites with >70% basal area killed by mountain pine beetle; ‘Intact’= lodgepole pine dominant sites free of mountain pine beetle activity. Statistically significant main effects of texture and interaction effects of texture with disturbance on carbon (texture:  $F(1, 76) = 10.886, P = .001$ ; interaction:  $F(1, 76) = 8.093, P =$

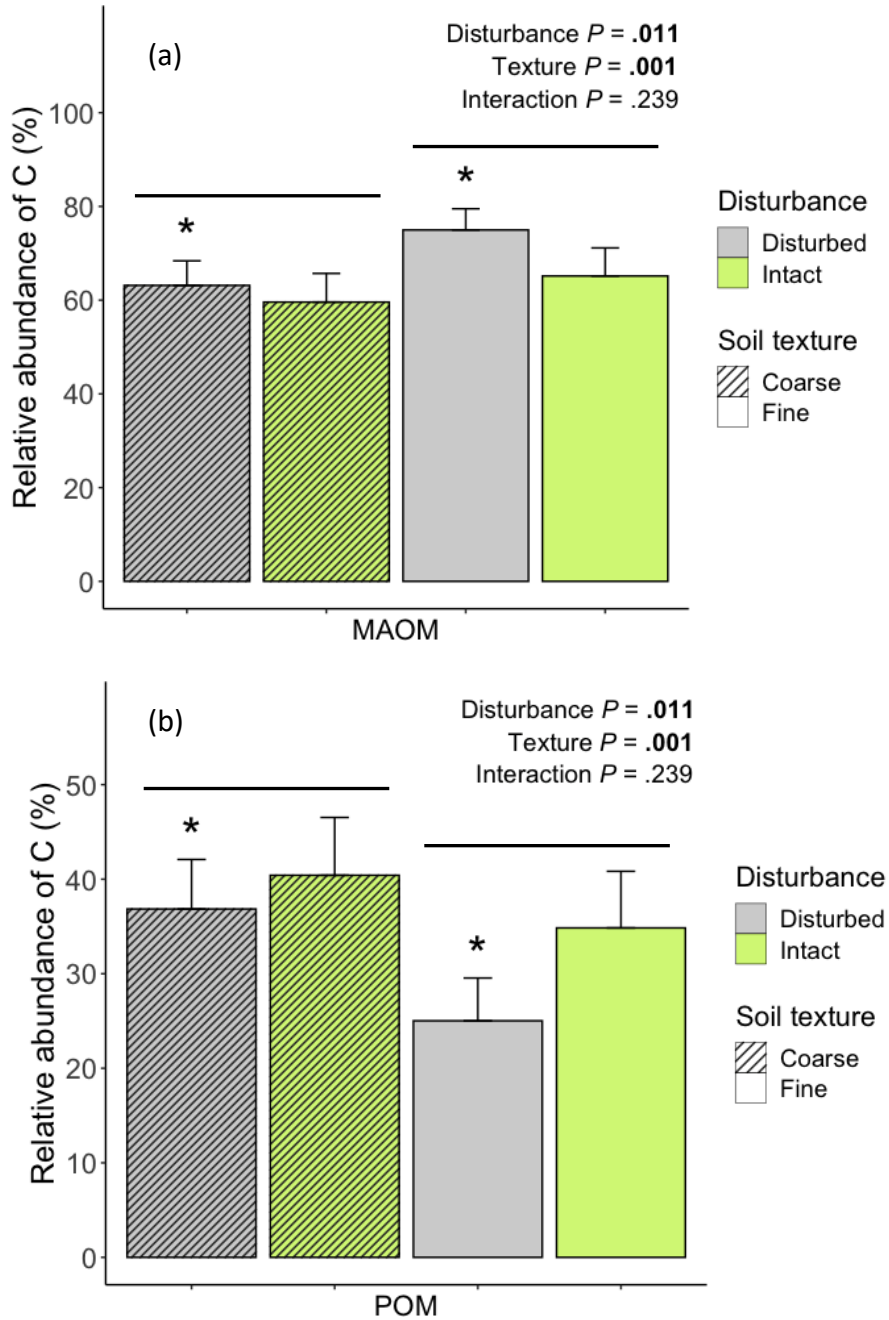
.006) and nitrogen stocks (texture:  $F(1, 76) = 14.396, P < .001$ ; interaction:  $F(1, 76) = 5.258, P = .025$ ), tested with two-way ANOVA. Means not sharing the same letter are significantly different (Tukey HSD Test,  $P < .05$ ).

When considering forest floor carbon concentrations, the interaction effects between soil texture and disturbance were significant, but there were no significant main effects from disturbance or texture alone (Table A9). On coarse soils, forest floors of intact stands held significantly greater carbon concentrations than disturbed stands (Fig. A7). Yet, on fine soils, there were no significant differences between disturbances (Fig. A7). There were no main effects from disturbance or texture on forest floor nitrogen concentrations, but interaction effects were significant, though weak (Table A10).

Mineral-associated organic matter fractions held considerably more soil carbon compared to the POM fractions across all sites, on average containing more than 60% of the total soil carbon (Fig. 7). For each soil fraction—MAOM or POM—soil texture had the most pronounced effect on the amount of carbon present (Table A12). There were also significant main effects from disturbance but no significant interactions between texture and disturbance (Table A12). On average, the relative abundance of carbon in the MAOM fractions was greater in fine-textured soils than coarse by 0.14-fold and greater in disturbed stands than intact by 0.11-fold (Fig. 7a). Patterns were reversed in POM, where the relative abundance of carbon in this fraction was higher in intact versus disturbed stands, and coarse-textured versus fine-textured soils (Fig. 7b). Likewise, the relative abundance of nitrogen followed a similar pattern as carbon. The relative abundance of nitrogen contained in MAOM fractions was greater in disturbed stands compared to intact stands, while the relative abundance of nitrogen contained in POM fractions was greater in intact stands compared to disturbed stands, though the differences were not statistically significant (Fig. A8). There were also differences in C/N ratios between stand categories in both fractions (Fig. A9). In POM, significant main effects came from disturbance, while in MAOM, significant main effects came from disturbance and texture, along with significant interaction effects.



Average C/N ratios were significantly greater in the intact stands compared to the disturbed stands, by 60% in MAOM and 14% in POM (Fig. A9).

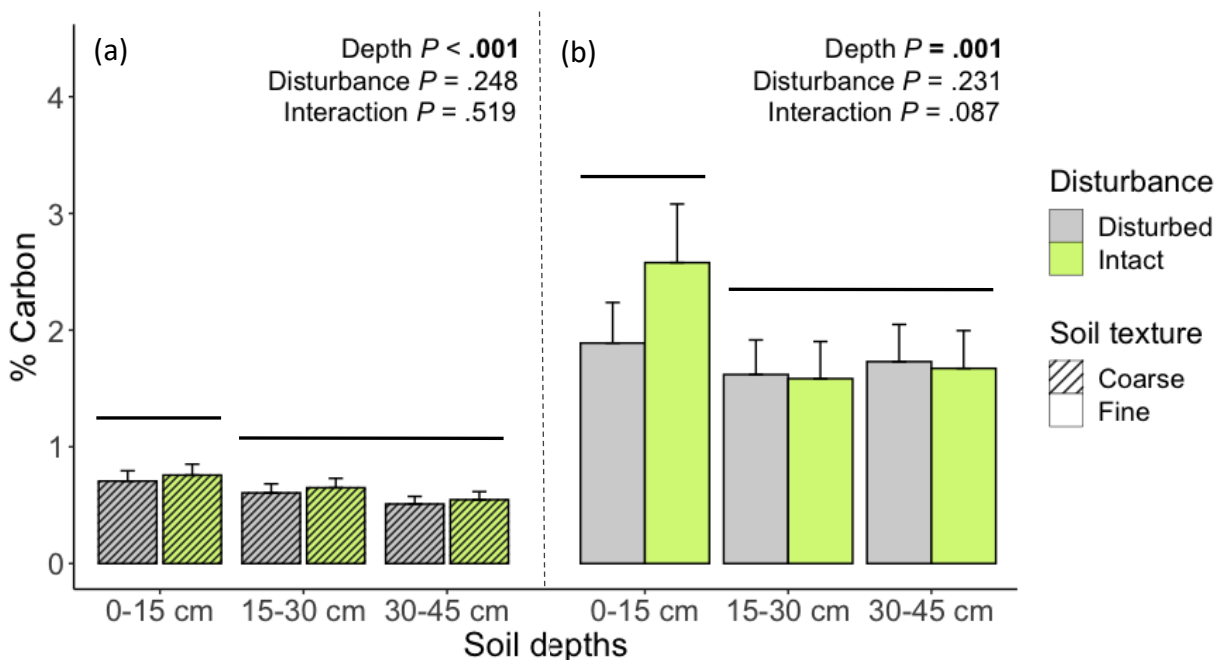


**Figure 7.** Relative abundance of carbon in (a) mineral-associated organic matter (MAOM), and (b) particulate organic matter (POM) fractions (mean  $\pm$  95% confidence interval), where 100% represents the sum of carbon in

both fractions. Surveys included 20 disturbed-coarse, 21 intact-coarse, 20 disturbed-fine, and 19 intact-fine sites. ‘Disturbed’= lodgepole pine dominant sites with >70% basal area killed by mountain pine beetle; ‘Intact’= lodgepole pine dominant sites free of mountain pine beetle activity. Statistically significant main effects of disturbance ( $F(1, 76) = 6.729, P = .011$ ) and soil texture ( $F(1, 76) = 10.899, P = .001$ ) in the relative abundance of carbon in both fractions, tested with two-way ANOVA. Asterisks denote significantly different means. Means not sharing a horizontal line are significantly different (Tukey HSD Test,  $P < .05$ ).

### 3.4. Confirming spatial variability of carbon with depth

In both coarse- and fine-textured sites, only the main effects of soil depth were significant in explaining soil carbon concentration (Table A13). There were no statistically significant main effects from disturbance type nor its interaction with soil depth (Table A13). Carbon concentrations at 0–15 cm differed from the deeper layers, at 15–30 cm and 30–45 cm (Fig. 8). On average, the percent carbon in coarse-textured sites was 0.79% in soils at 0–15 cm depth and 0.65% in soils at depths below (Fig. 8a). A similar pattern was found in soils of fine-textured sites. On average, the percent carbon in fine-textured sites was 2.53% in soils at 0–15 cm depth and 1.87% for depths below (Fig. 8b).



**Figure 8.** Carbon concentration (back-transformed ln-mean  $\pm$  95% confidence interval) at three different bulk mineral soil depths, in (a) coarse-, and (b) fine-textured soils. Surveys included 20 disturbed-coarse, 21 intact-coarse, 20 disturbed-fine, and 19 intact-fine sites. 'Disturbed'= lodgepole pine dominant sites with >70% basal area killed by mountain pine beetle; 'Intact'= lodgepole pine dominant sites free of mountain pine beetle activity. Two-way ANOVA found significant main effects of soil depth on % carbon, but no significant main effects from disturbance nor interactions. Removed extreme outliers: one 15-30 cm disturbed-coarse, one 30-45 cm disturbed-coarse, one 15-30 cm intact-fine, one 30-45 cm intact-coarse. Means not sharing a horizontal line are significantly different (Tukey HSD Test,  $P < .05$ ).

## 4. Discussion

### 4.1. Forest succession from EM to AM dominance

The disturbance caused by MPB drastically influenced aboveground community composition within the boreal forests investigated in this study. This shift was primarily due to the large-scale mortality of lodgepole pine trees, coupled with the subsequent growth release of vegetation in the forest understory. As anticipated, the living basal area significantly decreased as a result of disturbance (Fig. 2). Simultaneously, understory vascular species abundances in the disturbed stands were at least double that of intact stands (Fig. 3). This surge of understory vegetation can likely be attributed to reduced competition with canopy trees for resources, improved light access, and greater soil moisture levels.

The replacement of former pine stands by shrubs and forbs following disturbance is consistent with findings from previous studies. Without management interventions, pine regeneration is greatly limited in Alberta's MPB-disturbed forests and often results in shifts in species composition (Lieffers et al., 2023). For example, Pec et al. (2015) determined that the productivity of understory plant communities in MPB-disturbed stands exceeded pre-disturbance levels within the four years following the outbreak. Similar understory vegetation response patterns were found in beetle-attacked forests in eastern Colorado (Kovacic et al., 1985) and northern Utah (Stone & Wolfe, 1996). In fact, Kovacic et al. (1985) reported that five years after beetle attack, understory biomass was up to 100 times greater than intact reference stands. Stone & Wolfe (1996) also noted a significant increase in understory biomass, with an average tenfold increase in stands that experienced 50–70% overstory tree mortality. While the direction of forest succession is consistent across these studies, the magnitude of change depends on the extent of tree mortality (Pec et al., 2015; Steinke et al., 2020; Stone & Wolfe, 1996). Cases of high tree mortality, such as the disturbed sites examined in this study (>70% lodgepole pine basal area killed by MPB), had pronounced surges in understory plant species richness.

As confirmed with available databases and root-scoring results, this pattern of forest succession shifted mycorrhizal fungal communities from EM to AM dominance (Table A3; Table A4). Following the death of the primary EM hosts in the stands, there were significant increases in the relative abundance of AM shrubs. This pattern aligns with previous research showing declines in EM richness in MPB-disturbed forests driven by the loss of the dominant host tree species (Pec et al., 2017; Treu et al., 2014). Similarly, Štursová et al. (2014) found that the EM fungal symbionts of beetle-attacked Norway spruce trees disappeared within the first couple of years of their hosts' death, resulting in an estimated 12-fold decrease in soil fungal biomass during this period. The increase in AM abundance in the current study is also consistent with Kovacic et al.'s (1984) field study in Colorado, which determined significantly higher abundances of AM hosts and fungi in MPB-killed ponderosa pine compared to intact reference stands. However, such pronounced successional patterns could be due to the highly contrasting intact and severely disturbed stands included in the study.

In contrast, Rodriguez-Ramos et al. (2021) demonstrated that while fungal biomass was significantly higher and EM abundance was slightly lower in moderately attacked stands (70% lodgepole pine basal area killed) compared to paired controls, there were only minimal changes in AM abundance and diversity. Instead, the proportion of saprotrophic fungi, a guild not explored in my current study, exhibited the greatest increases in response to MPB-disturbance (Rodriguez-Ramos et al., 2021). Additionally, I utilized the mycorrhizal status of tree and plant hosts as a proxy for changes in the mycorrhizal fungal community. That is, the relative abundance of EM versus AM fungi was based on the composition of the vegetative community. This approach has been used in previous studies (Brzostek et al., 2015; Cheeke et al., 2017; Lin et al., 2017) but does not necessarily represent the fungal biomass contributions of each guild (Lang et al., 2020; Soudzilovskaia et al., 2015). Consequently, further investigation is necessary to comprehensively understand the effects of tree mortality on EM and AM fungal abundance and the timescale in which AM fungal dominance will endure.

## **4.2. The influence of MPB-disturbance on soil carbon storage**

### **4.2.1. Soil organic matter storage patterns differ according to dominant mycorrhizal group.**

Shifts in the relative abundance of EM and AM fungi can influence soil organic matter storage and cycling patterns. Building from frameworks by Cotrufo et al. (2013) and Phillips et al. (2013), I had initially predicted that disturbed, AM-dominated forests would exhibit higher soil carbon concentrations and greater carbon allocations to the MAOM fractions, compared to intact, EM-dominated forests. While some studies have suggested the potential for greater overall SOC stocks in EM-dominated systems compared to AM-dominated systems (Averill et al., 2014; Cotrufo et al., 2019), there is also compelling evidence demonstrating that AM-dominated systems may store more SOC, especially at depth (Craig et al., 2018; Fraterrigo et al., 2018). Succession toward more labile AM vegetation, as observed in the current study, has been linked to stimulated microbial activity, accelerated nutrient cycling belowground, and overall increases in carbon and nitrogen mineralization rates (Kristensen et al., 2020). However, the results of my study indicated similar levels of soil carbon and nitrogen concentrations in bulk mineral soil between MPB-disturbed and intact stands (Fig. 5; Fig. A5). The overall constancies were unexpected, as they were in spite of the major transformations in forest structure and mycorrhizal communities following large-scale tree mortality.

Where mycorrhizal group dominance did have significant effects was in the distribution of soil carbon between MAOM and POM pools. There was evidence for the predicted shift in belowground storage pools with disturbance. The role of MAOM has been highlighted for its importance in organic matter storage and preservation. Even though the MAOM fraction typically contains low carbon concentrations, it can still account for a substantial proportion of total soil carbon overall, with variations ranging from a quarter to over 90% across different soil ecosystems (Kleber et al., 2015). Global estimates indicate that, on average, MAOM constitutes approximately 65% of total SOC (Georgiou, 2022). Consistent with this estimate, the mean distributions of total carbon in MAOM in the

current study were 62% and 69% for intact and disturbed stands, respectively (Fig. 7). Total carbon stored in the MAOM fraction was significantly greater in the AM-dominated disturbed stands compared to the EM-dominated intact stands (Fig. 7). This suggests that changes in mycorrhizal community and litter quality may influence the distribution of carbon between long and short-term pools. The results are consistent with the hypothesis that AM-dominated systems, characterized by faster decomposition rates and higher microbial production, may better facilitate the formation of stable MAOM than EM-dominated systems, as previously proposed by Cotrufo et al. (2013).

While my results are consistent with the hypothesis that AM-dominated systems promote carbon storage in MAOM, it is important to acknowledge alternative explanations for my results. One possible explanation is that changes in the proportion of carbon stored in each pool may be attributed to relative reductions in the POM fraction size, due to the death of the POM-promoting EM trees following disturbance, while the absolute amount of MAOM remains the same. With the methods used in this study, it was not possible to confirm which pool changed and drove the observed patterns. However, when examining the carbon concentration values in the bulk mineral soils, there may be indirect evidence supporting this explanation. The mean percentage of carbon in soils of disturbed stands was slightly lower than in intact stands, though not significantly so. It may be that even this small difference in carbon concentration could be attributed to losses of POM in the disturbed stands, as POM decomposes more rapidly than MAOM, with no accompanying gains in MAOM carbon. Another explanation for my results is that the environmental conditions in disturbed stands, and not necessarily changes in mycorrhizal dominance, increased decomposition of organic matter (see **4.4.2 Other environmental factors to consider**). Further investigation is necessary to accurately isolate these processes.

In both MAOM and POM fractions, the carbon to nitrogen ratios were higher in the intact stands compared to the disturbed stands (Fig. A8). These findings were consistent with other studies that have

identified higher soil C/N ratios in forests dominated by coniferous species versus deciduous species (Cools et al., 2014; Vesterdal et al., 2007). Soil stoichiometric patterns largely reflect the tree species present (Lovett et al., 2004; Ross et al., 2011), driven by variations in litter quality and associated microbial substrate use efficiencies (Cools et al., 2014; Vesterdal et al., 2007). Plant inputs typically feature high C/N ratios, whereas microbial biomass generally contains low C/N ratios (Cools et al., 2014). As such, large accumulations of recalcitrant plant litter and POM products in EM-dominated intact stands contribute to higher C/N ratios (Ross et al., 2011). In contrast, AM-dominated disturbed stands may support larger soil microbial communities and higher nitrogen mineralization rates, resulting in lower C/N ratios (Ross et al., 2011). The stoichiometric balances of elements in forests help regulate plant and microbial community composition and productivity (Ågren & Weih, 2012), and the carbon turnover rate (Hartman et al., 2017). Nitrogen is often the limiting nutrient for growth in terrestrial systems (LeBauer & Treseder, 2008). Thus, environments with lower C/N ratios, such as the disturbed stands of this study, are more likely to support greater productivity above- and belowground.

**4.2.2. Disturbed stands may recover into net carbon stores.** The findings presented here suggest that MPB-disturbed forests may not always represent net carbon losses, contrary to predictions from past models. Results from the current study highlight that beyond the decreased carbon uptake by targeted trees and increased heterotrophic respiration, factors identified by Kurz et al. (2008), other significant ecosystem factors are at play. While most disturbances initially shift ecosystems to carbon sources, the subsequent recovery phase is typically linked to greater ecosystem carbon storage over time (Hillstrom et al., 2010; Magnani et al., 2007). Prior studies have documented minimal net changes in carbon flux at an ecosystem level following MPB-disturbance, both on a decadal scale (Moore et al., 2013) and 25 years post-outbreak (Pfeifer et al., 2011). Using an insect invasion simulation model, Crowley et al. (2016) similarly projected a pattern of net carbon loss transitioning into storage, albeit with an estimated recovery timeline of up to 300 years. In these scenarios, short-term increases in



heterotrophic respiration may be largely offset by the reduction of autotrophic respiration, due to the death of canopy trees and the loss of active root tissues (Matthes et al., 2018). These trends have been evident in past studies, including in Colorado subalpine forests (Moore et al., 2013) and Swedish subarctic forests (Parker et al., 2017). In addition, substantial growth release of surviving trees and understory vegetation may have significant compensating effects on stand productivity and ecosystem carbon storage post-outbreak (Landry et al., 2016; McEwen et al., 2020), although this vegetation growth release is not observed universally (Pfeifer et al., 2011). Still, the underestimation of stand release in Kurz et al.'s (2008) estimates may have contributed to the discrepancies found.

The assessment of the specific contributions of these processes to overall carbon and nitrogen fluxes is challenging with the methods used in the current study, especially if certain factors mask or amplify others. While the current study quantified belowground storage, it did not measure aboveground changes. However, given that soils store the majority of carbon in northern boreal forests, the influence of forest succession on belowground pools may be of greater relative significance than aboveground pools when considering overall ecosystem carbon storage.

Evaluating the full influence of MPB-disturbance on ecosystem carbon may also be limited by other factors. For example, it has been suggested that even a 50-year timeframe may fall short of capturing the full extent of carbon fluxes in higher-density fractions, such as MAOM (Lajtha et al., 2014). Furthermore, stand legacy might contribute to these gradual changes. For example, AM vegetation succeeding on soils historically dominated by EM species might be influenced by larger pools of unprotected POM fractions and reduced nitrogen availability stemming from recalcitrant EM litter legacy (Sulman et al., 2017). Moreover, in carbon-saturated soils, higher quantities or qualities of litter inputs may not necessarily elicit detectable responses (Castellano et al., 2015; Lajtha et al., 2014). While the findings in this study offer evidence for the influence of mycorrhizal community succession on soil

carbon stores, legacy effects may have contributed to the SOM patterns observed. Hence, it is evident that there are critical considerations that have yet to be integrated into existing carbon models.

**4.2.3. Responses in the organic forest floor.** Contrary to initial expectations, disturbance alone had no significant effects on carbon and nitrogen stocks in the forest floor (Fig. 6). Instead, there were interaction effects from soil texture and disturbance (Fig. 6). Multiple factors, including carbon or nitrogen concentration, bulk density, and layer depth, influence these forest floor stocks. Nonetheless, given that mean carbon and nitrogen stock values in this study closely mirrored the forest floor thickness trends, this variable is likely responsible for the patterns found. Litters may accumulate in the years immediately following disturbance as dead needles move from the canopy to the forest floor (Cigan et al., 2015; Klutsch et al., 2009). However, this increase is not universal. Other studies have found no significant differences in the thickness of the organic forest floor between intact and disturbed stands in the year following attack (McIntosh & Macdonald, 2013) and have even observed declines in depth after 2 to 35 years (Simard et al., 2011). In the current study, forest floor thickness did not significantly differ with disturbance 16 years later (Fig. A4). This could be due to the disturbed stands succeeding towards labile AM inputs, potentially mitigating the effects of recalcitrant EM input buildup from the decade prior. Additionally, surveys in the current study showed slightly higher shrub abundance on fine soils than on coarse soils. Although the differences were not statistically significant, even minor variations in stand release, and thus litter inputs, could contribute to the thicker forest floors on fine soils.

Furthermore, the mean percent carbon values in the forest floors for all site categories were lower than the expected 58% van Bemmelen factor for pure soil organic matter. This suggests the possible inclusion of some mineral materials into the forest floor during sampling. The likelihood of picking up underlying mineral materials may have been greater with moister or finer soils, or when sampling thin forest floors. The potential sampling errors could have introduced biases in the calculated

stock values. Overall, the specific factors driving the patterns observed here remain ambiguous, and there are opportunities for further investigations within this belowground carbon pool.

#### **4.3. *The influence of soil texture on carbon storage***

Across the study sites, soil texture emerged as the primary factor influencing soil carbon and nitrogen concentrations in the bulk mineral soils (Fig. 5; Fig. A5). As predicted, fine-textured soils consistently held significantly more carbon and nitrogen than coarse-textured soils, regardless of the dominant mycorrhizal type in the sites. The higher charge density of the fine mineral materials could have contributed to this pattern. By facilitating better sorption of organic compounds onto charged mineral surfaces, this, in turn, offers protection against microbial decomposition (von Lützow et al., 2006). These results align with previous studies establishing soil texture as the main influence on soil nutrient stores, with underlying effects from forest mycorrhizae (Lang et al., 2023; Spohn & Stendahl, 2022).

Soil texture's influence on carbon and nitrogen concentrations extended to the MAOM and POM fractions. The formation of MAOM and POM results from multiple cross-scale interactions between factors, including microbial community size and composition, quality and quantity of organic matter, and soil mineralogy (Lang et al., 2023). In this study, the effect of soil texture appeared to be relatively greater than disturbance category on carbon storage. While past research has indicated the differing influences of soil texture on each soil organic matter pool (Plante et al., 2006), this study found that fine-textured soils consistently held greater carbon concentrations in both the POM and MAOM fractions, as well as greater distribution of total soil carbon in MAOM, compared to coarse-textured soils. Fine-textured soils provide more opportunities for organic matter adsorption to mineral surfaces. In addition, it is possible that with the fractionation methods used in this study, some POM may have remained occluded within microaggregates, resulting in an overestimation of the MAOM fraction. This is more

likely to occur in fine-textured soils, where soil clay content positively correlates with the amount of POM carbon occluded within aggregates (Kölbl & Kögel-Knabner, 2004).

Despite the trending focus on MAOM in management, both POM and MAOM pools offer significant contributions. Factors that promote each should be examined to maximize forest soil carbon stocks (Angst et al., 2023). While the saturation effect limits carbon storage in MAOM, organic matter accumulation in POM is theoretically infinite (Sokol et al., 2022). As a result, in forests that provide continuous organic matter inputs, unstabilized POM pools could be of just as much relevancy and represent a major opportunity for soil carbon accrual (Cotrufo et al., 2019). The POM pools may be particularly important when managing forests on coarser-textured soils possessing lower sorption capacities.

Beyond the direct impact of soil texture on nutrient retention in these pools, indirect effects may also reinforce these findings. For example, soil communities differ in composition and distribution in relation to habitat conditions, where larger and more diverse bacterial communities may be found in finer soils that offer greater nutrient availability and surface area for activity (Kögel-Knabner et al., 2008). Greater bacterial abundance can accelerate organic matter cycling, a precursor to MAOM formation. Conversely, in coarse-textured soils, limited mineral surface area availability may constrain opportunities for organo-mineral binding and, thus, MAOM formation. At the same time, decomposition rates are closely linked to soil moisture, where fine soils with higher moisture retention typically exhibit slower organic matter decomposition rates (Zajícová & Chuman, 2021). This, in combination with greater productivity associated with wetter soils, identifies soil moisture as a key control of carbon storage in northern boreal soil (Harden et al., 1997). Although the current study did not test soil moisture, these processes offer plausible explanations for the greater POM and MAOM pool sizes found in sites with fine soils.

While particle size undoubtedly plays a central role in determining the interaction between organic matter and minerals, exploring specific mineral properties can provide deeper insights into SOM stabilization. Clay minerals, for example, encompass a broad spectrum of properties, including nutrient preservation strength (Rasmussen et al., 2018). Even among fine-sized fractions, different clay types have demonstrated significant variations in soil carbon retention (Feng et al., 2013; Jones & Singh, 2014; Six et al., 2002). Thus, the soil carbon saturation concept, which considers the finite capacity for stabilizing SOC, hinges on both the quantity and quality of soil minerals (Six et al., 2002). As such, although the primary direction of effect appears evident based on this study's findings, it is important to acknowledge that various underlying factors may work in tandem with soil texture, affecting the magnitude of the observed effect.

#### ***4.4. The influence of other abiotic factors on carbon storage***

**4.4.1. Organic matter processes vary with depth.** Belowground organic matter storage can vary depending on depth in boreal forests due to dynamic interactions among factors such as vegetation, climate, and geological influences (Lorenz & Lal, 2005). At the soil surface, high concentrations of SOC are typical in most temperate and boreal forests, as the forest floor layer accumulates substantial organic litter inputs from needles, roots, and other decaying plant materials (Baritz et al., 2010; Wiesmeier et al., 2013). Below the organic forest floor, soil carbon content generally decreases with depth (Rasmussen et al., 2018). My results confirmed the depth-dependent nature of soil carbon in the boreal forest (Fig. 8). In fact, some studies have emphasized that soil depth can be the strongest predictor of SOM, at times, even surpassing the effects of clay (Kögel-Knabner et al., 2008; Rasmussen et al., 2018). In the current study, carbon concentrations were indeed the highest in the top 15 cm of the mineral soil profile across all sites, but there were no significant differences between depths of 15-30 cm and 30-45 cm (Fig. 8). It is worth noting that the depth measurements in this study extended only to 45 cm in depth, so the influence of SOC depth patterns may become more pronounced at greater depths.

Additionally, due to differences in root and fungal hyphae traits between EM and AM, the dominant mycorrhizal type may further influence storage patterns with depth. Soils in AM-dominated forests may store a larger proportion of nutrients, including carbon and nitrogen, at depth, whereas EM-dominated forests may store more nutrients in upper soil layers (Craig et al., 2018). A study in Bavaria found such a pattern, with coniferous forest types storing more carbon in the organic layer and broadleaf forest types storing more in the mineral soil layers (Wiesmeier et al., 2013). However, my results did not reveal these differences, owing to various potential factors. For instance, Lajtha et al. (2014) suggested that minimal SOC response in surface mineral carbon pools would likely be detected even with changes in litter input quality and quantity. Building on the carbon saturation concept, Lajtha et al. (2014) expected that if comparing EM- and AM-dominated forests with the same soil texture, carbon concentrations in the upper soil layers would be similar. Indeed, my results supported this hypothesis, exhibiting no difference in SOC in the top 15 cm of soil between EM-dominated disturbed and AM-dominated intact stands.

Greater potential for soil carbon storage may lie in deeper layers that have not yet reached carbon saturation. Moreover, deeper soil organic carbon pools tend to have longer-term stability, with slower turnover times, due to reduced organic matter inputs limiting microbial activity (Fontaine et al., 2007; Lorenz & Lal, 2005). Deeper layers are generally less susceptible to climate-driven influences, such as temperature and precipitation fluctuations, and disturbance regimes. They are, therefore, less vulnerable to the periodic wildfires characteristic of boreal forests, thus preserving carbon stocks better than surface organic layers that may be easily burned (Cheng et al., 2023). These factors may collectively contribute to greater carbon stability found in deeper soil layers. The characteristics of pools at different depths emphasize the importance of considering the entire soil profile when managing to maximize carbon storage opportunities.

**4.4.2. Other environmental factors to consider.** In addition to the observed shift from EM to AM dominance, there are likely other changes in the environment following MPB-disturbance. Forest succession and structural transformations may influence abiotic mechanisms that control organic matter processes. For example, soil moisture may increase with overstorey tree mortality due to reduced precipitation interception and evapotranspiration (Cigan et al., 2015; Dhar and Hawkins, 2011; Hélie et al., 2005), though compensating responses by the understory vegetation may buffer the extent of this pattern (Steinke et al., 2020). Additional factors such as drainage patterns, slope position, and soil mineralogy may also influence soil moisture levels (Jakšić et al., 2021; Jia et al., 2016; Qu et al., 2021). While the sites included in this study were all on level slope positions with no distinctive aspect, there were clear differences in forest structure and soil texture between sites, promoting variations in soil moisture conditions.

Soil temperatures may also increase following disturbance due to increased light penetration as the attacked trees lose their needles (Kosunen et al., 2019). Additionally, studies have found increases in soil pH with tree mortality, which can be explained by reduced acidic rhizodeposition and reduced cation uptake by live trees (Cigan et al., 2015; Custer et al., 2020). Although the current study did not test soil moisture, temperature, and pH, these variables have known effects on decomposition, mineralization, and nitrification rates (Basile-Doelsch et al., 2020; Kovacic et al., 1985). They all play important roles in governing microbial activity (Basile-Doelsch et al., 2020; Custer et al., 2020). Furthermore, soil pH significantly affects the adsorption capacities of soil minerals (Basile-Doelsch et al., 2020; Custer et al., 2020). Therefore, changes in these abiotic factors after MPB-attack are directly linked to soil organic matter processes and stabilization. Environmental variables likely contributed to the outcomes found, alongside notable effects identified from dominant mycorrhizal type and soil texture. Since this study did not collect data for these variables, their potential underlying influences can not yet be excluded.

#### **4.5. Future direction**

Various interconnected factors shape boreal forest processes, many of which have yet to be addressed in past carbon budget models. To incorporate contemporary disturbance regimes into these models, it is necessary to enhance our understanding of how forests recover following novel MPB events. This particular study investigated mycorrhizal communities and soil carbon storage in response to MPB-disturbance. It would be valuable to delve deeper into the emerging patterns by addressing potential limitations and collecting data on other explanatory variables.

One area for further exploration is the assessment method of mycorrhizal group dominance. While the current study relied on the relative abundance of plant species to determine mycorrhizal groups, additional metrics such as fungal biomass, rooting depth, and fungal species composition could provide a more comprehensive understanding of how mycorrhizal fungi influence soil carbon dynamics. Moreover, extending soil data beyond the 45 cm profile depth used in this study may be beneficial in better capturing depth-driven changes in SOC, as well as MAOM and POM pool sizes. Additionally, given the study's focus on a small geographic area in west-central Alberta, there are potential limitations in terms of the broader applicability of the findings. Conducting similar field studies in MPB-disturbed stands of other boreal forest regions can help to enhance the understanding of region-specific patterns. For example, comparing the power analysis of MPB-disturbance on soil carbon between the current study and future studies in different regions may reveal whether its marginal effects detected here are universal or due to potential localized factors (Appendix B). Replicating this field study can be critical to identify region-specific trends for future forest models and management strategies.

The results from this study extend 16 years post-disturbance, but re-evaluating these ecosystems over an even longer timeframe could reveal how carbon pools fluctuate throughout ongoing mycorrhizal community shifts as disturbed forests continue to recover naturally. Future studies could also focus on how to investigate the short- and long-term impacts of altered soil fungal communities on



stable SOM pools. This extended analysis could improve guidance for the benefits and costs of different forest management strategies aimed at enhancing stable soil carbon stores, in addition to a more comprehensive understanding of forest recovery dynamics. Management strategies might involve allowing disturbed forests to recover naturally or implementing amendments to promote specific mycorrhizal fungal groups and their unique traits. Conducting further research to address these gaps can enhance the applicability of the study's findings in both the context of boreal forest management and carbon budget modelling.

While the MPB-disturbance event central to this study has passed its peak in Alberta, the legacy of modified ecosystem structure and composition will persist for decades to come. Considering climate change projections, disturbance regimes are expected to increase in frequency and intensity in boreal forests across the province and beyond. Consequently, gaining a deeper understanding of the implications of the MPB-disturbance on forest carbon pathways and pools can provide important information to guide the future management of these landscapes. The findings from this study may also hold relevance for other scenarios where dominant mycorrhizal types shift in response to forest disturbances, offering valuable insights for sustainable forest management practices in an ever-changing environment.

## 5. Conclusion

Shifts in mycorrhizal communities owing to altered disturbance regimes may have significant implications for SOM dynamics in western boreal forests. Drawing upon relevant frameworks, this study aimed to enrich our understanding of forest nutrient pathways and dynamics. I investigated variations in soil carbon and pool sizes following MPB-disturbance in west-central Alberta. The results revealed that stands with extensive lodgepole pine mortality have different mycorrhizal fungal community compositions than intact stands, suggesting a shift from EM- to AM-dominance with disturbance. This shift confirms the initial hypothesis and is in accordance with earlier literature, which have documented declines in EM guilds as mature tree hosts die, accompanied by increases in AM fungi due to upsurges in understory growth (Mayer et al., 2022; Rodriguez-Ramos et al., 2021; Treu et al., 2014).

Despite substantial changes in forest structure and composition aboveground, this study demonstrated that belowground carbon and nitrogen concentrations have remained virtually unchanged for over a decade since initial attack. The results confirmed soil texture and depth as important factors in determining soil carbon and nitrogen concentrations. The soils' resilience can be partially attributed to the strong nutrient retention capacity of the fine mineral particles. Moreover, the differing contributions of EM and AM guilds to nutrient cycling likely played a crucial role in buffering the impacts of stand death on carbon stores.

In addition, the results revealed significant differences in the distribution of soil carbon in MAOM and POM between EM-dominated intact stands and AM-dominated disturbed stands. The distribution patterns align with initial hypotheses that there is a greater tendency for carbon to enter stable MAOM pools in AM-dominated forests due to higher quality of litter and enhanced microbial production (Cotrufo et al., 2013; Craig et al., 2018; Phillips et al., 2013). The shift in carbon storage patterns suggests that forest succession in these MPB-disturbed forests may result in larger long-term carbon pools. The results here are consistent with predictions based on the MANE (Phillips et al., 2013)

and the MEMS (Cotrufo et al., 2013) frameworks, but possible alternative explanations and underlying environmental influences cannot yet be eliminated.

This study underscores the enduring value of stands with high levels of MPB-induced tree mortality as robust carbon sinks. If rehabilitating MPB-disturbed stands, the focus should be to balance silvicultural objectives with conserving critical carbon sinks, such as soils and existing AM vegetation. As AM-dominated attacked forests gradually transition back towards EM dominance in the future, it may be worthwhile to explore the possibility of identifying a tipping point in carbon dynamics, shifting from accrual to loss. Longer-term studies would be valuable in examining whether these patterns hold true in recovering forests beyond the timeframe of the current study. Considering the projected increase in the scale and severity of MPB events due to changing climatic conditions, ongoing investigation of forest carbon pathways and dynamics will be imperative for predicting change and supporting soil carbon accrual processes in insect-disturbed landscapes.

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## Appendix A: Supplementary tables and figures

**Table A1.**

*Descriptions and forest characteristics of plots surveyed in the study in the summer of 2022. Sites located outside the nearest town of Grande Prairie, Alberta.*

Plot	Latitude	Longitude	Soil Texture		Stand age	% MPB death	Forest Canopy			Regeneration	
			Category	Class			Species	Stems/ha	DBH	Species	Stems/ha
1	54.650103	-118.93369	Fine	SiCL	44	0	PI, Aw	3000	12.6	Fb	1000
2	54.656829	-118.86664	Fine	SiCL	42	0	PI	6200	9.8	Fb	800
3	54.653068	-118.87155	Fine	L	43	0	PI, Aw, Fb	8000	8.8	Fb, Sw	800
4	54.631846	-119.01732	Fine	CL	38	0	PI	5600	11.2	–	0
5	54.636973	-119.00438	Fine	L	35	0	PI	6400	8.9	PI	200
6	54.630987	-119.11854	Fine	L	44	0	PI	5800	10.9	–	0
7	54.7688	-119.37137	Fine	L	101	100	PI	400	35.5	–	0
8	54.720033	-119.67754	Fine	CL	101	100	PI	800	31.3	–	0
9	54.561251	-118.66454	Fine	L	101	100	PI, Sw, Bw	1200	29.5	Sw	200
10	54.676216	-119.33304	Fine	L	91	100	PI	600	27.6	–	–
11	54.721244	-118.95111	Fine	L	108	80	PI, Sw	1600	23.8	–	0
12	54.639273	-119.16832	Fine	SiL	33	0	PI	1200	19.5	–	0
13	54.094589	-117.04949	Fine	L	111	0	PI, Sb	800	23.7	Sb	200
14	54.749159	-119.6658	Coarse	SL	114	0	PI, Sw	5000	24.1	Sw	1000
15	55.620105	-117.89568	Coarse	SL	74	100	PI	600	27.9	Sw	400
16	55.619572	-117.94771	Coarse	SL	61	100	PI	400	22.3	Sw	400
17	54.59692	-118.17765	Coarse	SL	118	100	PI	800	25.7	–	0
18	54.583374	-118.16337	Coarse	SL	124	0	PI, Sw	1200	23.4	–	0
19	54.50934	-118.96884	Fine	CL	53	0	PI, Sw	1800	14.8	–	0
20	55.05872	-118.2022	Coarse	LS	69	10	PI	2200	17.2	–	0
21	55.062096	-118.21736	Coarse	LS	70	0	PI	2000	16.9	–	0
22	54.817711	-116.74215	Fine	CL	72	0	PI, Sw	6000	12.3	–	0
23	54.528146	-118.16117	Coarse	LS	109	0	PI, Sw	1600	17.8	–	0
24	54.537795	-118.16855	Coarse	LS	114	0	PI, Sw	1200	20.1	–	0
25	54.573892	-118.1737	Coarse	LS	116	0	PI	1000	27.2	–	0
26	54.952729	-118.44125	Coarse	LS	70	0	PI	600	30.9	Sw	400
27	54.248038	-116.13313	Coarse	LS	70	0	PI	4000	10.6	Sw	200
28	54.934333	-118.47901	Coarse	LS	70	0	PI	2600	14.4	Sw	200
29	54.235242	-116.10701	Coarse	SL	68	0	PI	2600	15.4	Bw, Aw	600
30	54.236651	-116.08586	Coarse	SL	70	0	PI	6200	10.4	–	0
31	54.234749	-116.05797	Coarse	SL	72	0	PI	3200	19.2	Aw	200
32	54.224206	-116.05711	Coarse	SL	68	0	PI	3600	15.3	Sw	1400
33	54.206267	-116.11877	Coarse	LS	71	0	PI	3800	13.7	Sw	200
34	54.188572	-116.15254	Coarse	LS	55	0	PI	3800	12.8	Sw	200
35	54.186237	-116.18497	Coarse	LS	66	0	PI	4800	10.3	–	0
36	54.925243	-118.48169	Coarse	SL	56	100	PI	1400	19.0	–	0
37	55.642729	-117.95724	Coarse	SL	55	90	PI	1600	22.0	Aw	800
38	55.63292	-117.95752	Coarse	LS	76	90	PI, Sw, Bw	1600	14.3	Sw	1200
39	54.437267	-119.001	Fine	CL	40	0	PI	4400	12.1	Sw	200
40	54.451961	-118.99468	Fine	CL	40	0	PI	6400	11.2	–	0

41	55.019969	-118.55173	Coarse	LS	69	0	Pl, Sb	4000	14.1	–	0
42	54.4241	-118.00929	Fine	CL	55	0	Pl, Fb, Aw	5200	14.8	Fb	600
43	54.700178	-118.35358	Coarse	LS	66	0	Pl	600	19.7	Pl	400
44	54.61572	-118.20917	Fine	L	122	0	Pl, Sw, Bw	1800	24.2	Fb	200
45	55.639963	-117.72257	Coarse	SL	62	100	Pl	600	19.5	Sw	200
46	55.636954	-117.68939	Coarse	LS	42	100	Pl	600	22.9	Aw	1000
47	55.630726	-117.67863	Coarse	LS	68	100	Pl	600	24.3	Pl	2000
48	54.637415	-118.99144	Fine	SiC	110	75	Pl, Sw	1000	22.6	–	0
49	54.657337	-118.99561	Fine	SiCL	103	100	Pl, Sw	1200	26.3	–	0
50	54.687182	118.98351	Fine	SiC	91	100	Pl, Sw	1000	26.3	–	0
51	54.737101	-118.95463	Fine	L	105	100	Pl, Sw	1000	24.7	–	0
52	54.737902	-118.9684	Fine	L	109	100	Pl	1800	24.8	Sw, Fb	1200
53	54.96214	-118.50067	Coarse	SL	70	0	Pl	2200	15.3	–	0
54	54.55723	-118.68272	Fine	SiCL	90	100	Pl, Sw, Bw	800	30.8	Sw	200
55	55.624151	-117.93471	Coarse	SL	79	100	Pl	800	20.8	–	0
56	54.172542	-116.62004	Coarse	SL	83	0	Pl, Sb	2400	30.3	Sb	1400
57	54.637975	-119.14148	Fine	L	34	0	Pl	9600	9.3	Sb	600
58	54.569299	-119.00813	Fine	CL	33	0	Pl, Aw	2800	10.0	–	0
59	54.558976	-118.99383	Fine	SiC	45	0	Pl, Aw	2600	13.1	–	0
60	54.471855	-118.99305	Fine	SiCL	34	0	Pl	6600	11.4	Sw	600
61	55.621759	-117.97054	Coarse	LS	58	100	Pl	800	18.9	Sw, Pl	1000
62	54.775986	-118.9678	Fine	SiCL	68	0	Pl, Sw	1800	20.5	Sw	600
63	54.679704	-119.32405	Fine	L	99	100	Pl	400	51.4	–	0
64	54.640885	-119.1815	Fine	SiCL	110	86	Pl	1400	28.6	Fb	1000
65	54.643222	-119.24442	Fine	L	94	100	Pl	800	29.5	–	0
66	55.067715	-118.2062	Coarse	LS	110	100	Pl	600	–	Pl, Sw	600
67	55.091545	-118.19991	Coarse	LS	123	100	Pl	1000	23.7	Pl, Sw	1400
68	54.782947	-119.40873	Fine	SiCL	105	75	Pl, Bw	1000	33.0	–	0
69	55.074275	-118.19813	Coarse	LS	70	100	Pl, Sw	2400	27.8	Sw	1200
70	55.460088	-119.78244	Fine	SiCL	118	100	Pl	800	22.3	Pl, Sw	1800
73	55.072025	-118.20788	Coarse	LS	113	100	Pl	2200	16.8	Pl	600
71	55.752632	-119.79826	Fine	L	92	100	Pl, Sw	3000	13.9	Sw	600
74	55.616587	-117.96111	Coarse	SL	61	100	Pl	1400	19.8	–	0
72	55.561424	-119.69598	Fine	SiC	134	100	Pl, Sw	1800	23.0	–	0
75	55.637105	-117.85043	Coarse	LS	69	100	Pl	1000	18.6	Pl	600
76	55.647194	-117.74704	Coarse	SL	49	100	Pl, Aw	800	27.4	Aw, Sw	1200
77	55.618443	-117.91075	Coarse	SL	57	100	Pl	600	20.5	Sw, Fb	2000
78	55.61566	-117.92595	Coarse	SL	59	100	Pl	600	30.9	Pl, Sw	1200
79	55.527963	-119.10943	Fine	SiC	74	100	Pl, Sw	1000	21.1	Sw	4800
80	55.560074	-119.28406	Fine	SiCL	65	100	Pl, Sw	1800	12.7	Sw	2000

*Note.* Site location, texture category assigned by this study, soil texture class according to the Expert Committee on Soil Survey (1982), stand mortality level, and forest description. In total, surveys included 20 disturbed-coarse, 21 intact-coarse, 20 disturbed-fine, and 19 intact-fine sites. For texture classes: SiC= silty clay, SiCL= silty clay loam, CL= clay loam, SiL=silt loam, L= loam, SL=sandy loam, LS= loamy sand. For tree species: Pl = *Pinus contorta*; Aw = *Populus tremuloides*, Fb = *Abies balsamea*, Bw = *Betula papyrifera*, Sw = *Picea glauca*, Sb = *Picea mariana*.

**Table A2.**

List of understory plant species observed in the study and the number of stands in each site category where each species was present. Sites located outside the nearest town of Grande Prairie, Alberta.

Species	Coarse-textured		Fine-textured	
	Disturbed	Intact	Disturbed	Intact
<i>Actaea rubra</i> (Aiton) Willd.	1	0	0	5
<i>Agrimonia striata</i> Michx.	0	0	1	0
<i>Alnus viridis</i> var. <i>crispa</i> (Aiton) House	0	0	2	3
<i>Amelanchier alnifolia</i> (Nutt.) Nutt. ex M.Roem.	14	6	2	2
<i>Anemone canadensis</i> L.	2	0	0	0
<i>Anemone multifida</i> Poir.	1	0	0	0
<i>Aralia nudicaulis</i> L.	7	3	4	1
<i>Arctostaphylos uva-ursi</i> (L.) Spreng.	15	12	1	0
<i>Arnica cordifolia</i> Hook.	0	0	4	12
<i>Athyrium filix-femina</i> (L.) Roth ex Mert.	0	0	5	3
bryophytes	17	21	16	17
<i>Campanula rotundifolia</i> L.	1	0	0	0
<i>Carex</i> spp.	0	0	1	0
<i>Clematis occidentalis</i> (Hornem.) DC.	1	0	0	0
<i>Cornus canadensis</i> L.	12	13	10	19
<i>Dryopteris carthusiana</i> (Vill.) H.P.Fuchs	2	0	2	0
<i>Epilobium angustifolium</i> L.	12	11	13	8
<i>Equisetum arvense</i> L.	0	0	1	0
<i>Equisetum hyemale</i> L.	1	0	0	0
<i>Equisetum pratense</i> Ehrh.	3	2	3	1
<i>Equisetum sylvaticum</i> L.	0	0	13	2
<i>Fragaria virginiana</i> Mill.	6	0	2	5
<i>Galearis rotundifolia</i> (Banks ex Pursh) R.M.Bateman	0	0	0	1
<i>Galium aparine</i> L.	1	0	1	1
<i>Galium boreale</i> L.	5	1	0	0
<i>Galium trifidum</i> L.	2	1	7	6
<i>Geocaulon lividum</i> (Richardson) Fernald	3	5	3	0
graminoids	18	15	13	10
<i>Gymnocarpium dryopteris</i> (L.) Newman	0	0	10	6
<i>Heracleum maximum</i> W.Bartram	0	0	2	2
<i>Lathyrus ochroleucus</i> Hook.	9	2	1	2
<i>Ledum groenlandicum</i> Retz.	3	13	2	5
<i>Linnaea borealis</i> L.	12	16	6	13
<i>Lonicera dioica</i> L.	2	2	3	0
<i>Lonicera involucrata</i> (Richardson) Banks ex Spreng.	0	1	5	6

<i>Lycopodium annotinum</i> L.	3	1	11	4
<i>Lycopodium digitatum</i> Dill. ex A.Braun	1	0	0	0
<i>Maianthemum canadense</i> Desf.	19	13	1	9
<i>Maianthemum racemosum</i> (L.) Link	1	0	1	1
<i>Melampyrum lineare</i> Desr.	0	4	0	0
<i>Mertensia paniculata</i> (Aiton) G.Don	0	0	3	3
<i>Mitella nuda</i> L.	0	1	8	5
<i>Oplopanax horridus</i> (Sm.) Miq.	0	0	4	0
<i>Osmorhiza depauperata</i> Phil.	0	0	1	0
<i>Petasites frigidus</i> (L.) Fr.	0	1	4	11
<i>Petasites palmatus</i> (Aiton) Cronquist	0	0	0	2
<i>Prunus pensylvanica</i> L.f.	0	0	0	1
<i>Ribes hudsonianum</i> Richardson	0	0	2	0
<i>Ribes oxyacanthoides</i> L.	0	0	5	5
<i>Rosa acicularis</i> Lindl.	19	13	10	6
<i>Rubus chamaemorus</i> L.	0	0	3	0
<i>Rubus idaeus</i> L.	7	1	10	4
<i>Rubus parviflorus</i> Nutt.	0	0	2	1
<i>Rubus pedatus</i> Banks & Sol.	0	0	3	6
<i>Rubus pubescens</i> Raf.	0	0	6	9
<i>Salix</i> spp.	0	1	2	0
<i>Shepherdia canadensis</i> (L.) Nutt.	10	5	0	0
<i>Sonchus arvensis</i> L.	1	0	0	0
<i>Sorbus scopulina</i> Greene	0	0	1	2
<i>Spiraea alba</i> DuRoi	0	1	0	0
<i>Spiraea betulifolia</i> Hook.	0	0	1	1
<i>Streptopus amplexifolius</i> (L.) DC.	0	0	6	3
<i>Symphoricarpos albus</i> (L.) S.F.Blake	0	1	0	3
<i>Symphoricarpos occidentalis</i> Hook.	2	1	4	1
<i>Taraxacum officinale</i> F.H.Wigg.	1	0	0	0
<i>Thalictrum venulosum</i> Trel.	0	0	1	0
<i>Urtica dioica</i> L.	0	0	1	0
<i>Vaccinium myrtillus</i> L.	15	16	3	2
<i>Vaccinium vitis-idaea</i> L.	5	15	2	3
<i>Viburnum edule</i> (Michx.) Raf.	0	1	6	3
<i>Viola</i> spp.	0	1	3	8

Note. In total, surveys included 20 disturbed-coarse, 21 intact-coarse, 20 disturbed-fine, and 19 intact-fine sites.

Species authority retrieved from Brouillet et al. (2010) and Meades et al. (2004).



**Table A3.**

*Mycorrhizal fungal identity of all plant species observed in sites of this study, assigned using available databases and root-scoring results. Sites located outside the nearest town of Grande Prairie, Alberta.*

Species	Source		Identity
	DB	RS	
<i>Abies balsamea</i> (L.) Mill.	x		EM
<i>Actaea rubra</i> (Aiton) Willd.	x		AM
<i>Agrimonia striata</i> Michx.	x		AM
<i>Alnus viridis</i> var. <i>crispa</i> (Aiton) House	x	x	EM
<i>Amelanchier alnifolia</i> (Nutt.) Nutt. ex M.Roem	x	x	AM
<i>Anemone canadensis</i> L.	x		AM
<i>Anemone multifida</i> Poir.	x		AM
<i>Aralia nudicaulis</i> L.	x	x	AM (and EM)
<i>Arctostaphylos uva-ursi</i> (L.) Spreng.	x	x	arbutoid
<i>Arnica cordifolia</i> Hook.	x		AM
<i>Athyrium filix-femina</i> (L.) Roth ex Mert.	x		AM
<i>Betula occidentalis</i> Hook.	x		AM/EM
<i>Betula papyrifera</i> Marshall	x	x	AM/EM
<i>Betula pumila</i> L.	x		EM
<i>Campanula rotundifolia</i> L.	x		AM
<i>Clematis occidentalis</i> (Hornem.) DC.	x		AM
<i>Cornus canadensis</i> L.	x	x	AM
<i>Dryopteris carthusiana</i> (Vill.) H.P.Fuchs	x		AM
<i>Epilobium angustifolium</i> L.	x		AM
<i>Equisetum arvense</i> L.	x		n/a
<i>Equisetum hyemale</i> L.	x		n/a
<i>Equisetum pratense</i> Ehrh.	x		n/a
<i>Equisetum sylvaticum</i> L.	x		n/a
<i>Fragaria virginiana</i> Mill.	x	x	AM
<i>Galium aparine</i> L.	x		AM
<i>Galium boreale</i> L.	x		AM
<i>Galium trifidum</i> L.	x		AM
<i>Geocaulon lividum</i> (Richardson) Fernald	x		n/a
<i>Gymnocarpium dryopteris</i> (L.) Newman	x		AM
<i>Heracleum maximum</i> W.Bartram	x		AM
<i>Lathyrus ochroleucus</i> Hook.	x		AM
<i>Ledum groenlandicum</i> Retz.	x	x	ericoid (EM)
<i>Linnaea borealis</i> L.	x		AM
<i>Lonicera dioica</i> L.	x		AM
<i>Lonicera involucrata</i> (Richardson) Banks ex Spreng.	x	x	AM
<i>Lycopodium annotinum</i> L.	x		n/a
<i>Lycopodium digitatum</i> Dill. ex A. Braun	x		n/a
<i>Lycopodium obscurum</i> L.	x		n/a

<i>Maianthemum canadense</i> Desf.	x	x	AM ( <b>none</b> )
<i>Maianthemum racemosum</i> (L.) Link	x		AM
<i>Melampyrum lineare</i> Desr.	x		<i>n/a</i>
<i>Mertensia paniculata</i> (Aiton) G.Don	x		AM
<i>Mitella nuda</i> L.	x		<i>n/a</i>
<i>Oplopanax horridus</i> (Sm.) Miq.	x		<i>n/a</i>
<i>Osmorhiza depauperata</i> Phil.	x		<i>n/a</i>
<i>Petasites frigidus</i> (L.) Fr.	x		AM
<i>Petasites palmatus</i> (Aiton) Cronquist	x		AM
<i>Picea glauca</i> (Moench) Voss	x	x	EM ( <b>and AM</b> )
<i>Pinus contorta</i> Doug ex Loud.	x	x	EM ( <b>and AM</b> )
<i>Populus tremula</i> L.	x	x	EM
<i>Prunus pensylvanica</i> L.f.	x		AM
<i>Ribes hudsonianum</i> Richardson	x		AM
<i>Ribes oxyacanthoides</i> L.	x		AM
<i>Rosa acicularis</i> Lindl.	x	x	AM
<i>Rubus chamaemorus</i> L.	x		AM
<i>Rubus idaeus</i> L.	x	x	AM
<i>Rubus parviflorus</i> Nutt.	x		AM
<i>Rubus pedatus</i> Banks & Sol.	x		AM
<i>Rubus pubescens</i> Raf.	x		AM
<i>Salix</i> spp.	x	x	AM/EM
<i>Shepherdia canadensis</i> (L.) Nutt.	x	x	AM
<i>Sonchus arvensis</i> L.	x		AM
<i>Sorbus scopulina</i> Greene	x		AM
<i>Spiraea alba</i> DuRoi	x		AM
<i>Spiraea betulifolia</i> Hook.	x		AM
<i>Streptopus amplexifolius</i> (L.) DC.	x		AM
<i>Symphoricarpos albus</i> (L.) S.F.Blake	x		AM
<i>Symphoricarpos occidentalis</i> Hook.	x		AM
<i>Taraxacum officinale</i> F.H.Wigg.	x		AM
<i>Thalictrum venulosum</i> Trel.	x		AM
<i>Urtica dioica</i> L.	x		AM
<i>Vaccinium myrtillus</i> L.	x	x	ericoid ( <b>none</b> )
<i>Vaccinium vitis-idaea</i> L.	x	x	ericoid ( <b>none</b> )
<i>Viburnum edule</i> (Michx.) Raf.	x	x	AM
<i>Viola</i> spp.	x		AM

*Note.* List of all plant species observed in study and mycorrhizal type. Identity determined from databases (DB) (Akhmetzhanova et al., 2012; Bueno et al., 2017; Hempel et al., 2013) and root scoring (RS) results from this study. Root scoring results that are inconsistent with databases are indicated in parentheses in bold. *n/a* indicates no known mycorrhizal fungal associates.

**Table A4.**

*Mycorrhizal root scoring results of the 20 most commonly observed plant species in this study. Samples obtained from study sites, located outside the nearest town of Grande Prairie, Alberta.*

Species	%Colonization						Identity	
	EM	AM hyphae	AM arbuscules	AM vesicles	Arbutoid	Ericoid	Database	Scoring
<i>Alnus viridis</i>	3.1	0.6	–	–	–	–	EM	EM
<i>Amelanchier alnifolia</i>	–	9.4	3.4	5.0	–	–	AM	AM
<i>Aralia nudicaulis</i>	6.5	11.2	5.0	2.5	–	–	AM	AM/EM
<i>Arctostaphylos uva-ursi</i>	–	–	–	–	22.8	–	arbutoid	arbutoid
<i>Betula papyrifera</i>	24.0	1.6	0.2	0.2	–	–	EM/AM	EM/AM
<i>Cornus canadensis</i>	–	19.6	16.9	1.1	–	–	AM	AM
<i>Fragaria virginiana</i>	–	45.9	14.9	12.2	–	–	AM	AM
<i>Ledum groenlandicum</i>	10.0	–	–	–	–	–	ericoid	EM
<i>Lonicera involucrate</i>	–	–	6.7	4.3	–	–	AM	AM
<i>Maianthemum canadense</i>	–	–	–	–	–	–	AM	none
<i>Picea glauca</i>	30.0	0.6	0.9	–	–	–	EM	EM/AM
<i>Pinus contorta</i>	31.0	1.1	0.3	0.3	–	–	EM	EM/AM
<i>Populus tremuloides</i>	28.0	–	–	–	–	–	EM	EM
<i>Rosa acicularis</i>	–	16.2	10.6	2.4	–	–	AM	AM
<i>Rubus idaeus</i>	–	27.3	11.1	4.4	–	–	AM	AM
<i>Salix spp.</i>	24.0	–	–	–	–	–	AM/EM	EM
<i>Shepherdia canadensis</i>	–	24.8	5.9	5.3	–	–	AM	AM
<i>Vaccinium myrtillus</i>	–	–	–	–	–	–	ericoid	none
<i>Vaccinium vitis-idaea</i>	–	–	–	–	–	–	ericoid	none
<i>Viburnum edule</i>	–	17.6	9.6	4.4	–	–	AM	AM

*Note.* Percent colonization by ectomycorrhizal fungal structures, arbuscular mycorrhizal hyphae, arbuscules, and vesicles, arbutoid mycorrhizal structures, and ericoid mycorrhizal structures (from left to right). Identity determined from databases (Akhmetzhanova et al., 2012; Bueno et al., 2017; Hempel et al., 2013) were compared to identity determined from root scoring (RS) results of this study.

**Table A5.**

*Post-hoc test comparing the living basal area between sites of different disturbance and soil texture categories.*

<i>Site category</i>	disturbed-coarse	intact-coarse	disturbed-fine
intact-coarse	<b>&lt; .001</b>	—	—
disturbed-fine	.490	<b>&lt; .001</b>	—
intact-fine	<b>&lt; .001</b>	1.00	<b>&lt; .001</b>

*Note.* Results from Nemenyi's non-parametric all-pairs comparison test for Kruskal-type ranked data with chi-square approximation, comparing tree living basal area between site categories ( $n = 20$  for disturbed-coarse,  $n = 21$  for intact-coarse,  $n = 20$  for disturbed-fine, and  $n = 19$  for intact-fine sites). 'Disturbed'= lodgepole pine dominant sites with >70% basal area killed by mountain pine beetle; 'Intact'= lodgepole pine dominant sites free of mountain pine beetle activity. Values represent  $P$ -values. Bolded text represents significant difference.

**Table A6.**

Post-hoc test comparing the shrub abundance between sites of different disturbance and soil texture categories.

Site category	disturbed-coarse	intact-coarse	disturbed-fine
<i>AM</i>			
intact-coarse	<b>.024</b>	—	—
disturbed-fine	.937	.120	—
intact-fine	<b>&lt; .001</b>	.490	<b>.002</b>
<i>EM</i>			
intact-coarse	.570	—	—
disturbed-fine	.069	<b>&lt; .001</b>	—
intact-fine	.342	<b>.014</b>	.887
<i>Total</i>			
intact-coarse	<b>.012</b>	—	—
disturbed-fine	.965	<b>.002</b>	—
intact-fine	<b>.020</b>	1.00	<b>.004</b>

*Note.* Results from Nemenyi's non-parametric all-pairs comparison test for Kruskal-type ranked data with chi-square approximation, comparing average abundance of arbuscular mycorrhizal (AM) shrubs (*top*), ectomycorrhizal (EM) shrubs (*middle*), and total shrubs (*bottom*) between site categories ( $n = 20$  for disturbed-coarse,  $n = 21$  for intact-coarse,  $n = 20$  for disturbed-fine, and  $n = 19$  for intact-fine sites). Shrub abundance recorded as the number of stems intersecting the 20 m line transect in each site. 'Disturbed'= lodgepole pine dominant sites with >70% basal area killed by mountain pine beetle; 'Intact'= lodgepole pine dominant sites free of mountain pine beetle activity. Values represent  $P$ -values. Bolded text represents significant difference.

**Table A7.**

*Post-hoc test comparing understory species richness between sites of different disturbance and soil texture categories.*

<i>Site category</i>	disturbed-coarse	intact-coarse	disturbed-fine
<i>AM</i>			
intact-coarse	<b>&lt; .001</b>	—	—
disturbed-fine	.728	<b>.007</b>	—
intact-fine	.986	<b>&lt; .001</b>	.905
<i>EM</i>			
intact-coarse	.99	—	—
disturbed-fine	.92	.75	—
intact-fine	.90	.73	1.00
<i>Total</i>			
intact-coarse	<b>&lt; .001</b>	—	—
disturbed-fine	.850	<b>.006</b>	—
intact-fine	1.00	<b>&lt; .001</b>	.907

*Note.* Results from Nemenyi's non-parametric all-pairs comparison test for Kruskal-type ranked data with chi-square approximation, comparing average understory species richness of arbuscular mycorrhizal (AM) plants (*top*), ectomycorrhizal (EM) plants (*middle*), and total plants (*bottom*) between site categories ( $n = 20$  for disturbed-coarse,  $n = 21$  for intact-coarse,  $n = 20$  for disturbed-fine, and  $n = 19$  for intact-fine sites). Richness recorded as the number of species observed within two 1 m<sup>2</sup> quadrats per site. 'Disturbed'= lodgepole pine dominant sites with >70% basal area killed by mountain pine beetle; 'Intact'= lodgepole pine dominant sites free of mountain pine beetle activity. Values represent *P*-values. Bolded text represents significant difference.

**Table A8.**

*Two-way ANOVA tests comparing mean forest floor thickness between sites of different disturbance and soil texture categories.*

Predictor	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>p</i>
Disturbance	1	1.58	1.58	0.451	.504
Texture	1	36.62	36.62	10.436	<b>.002</b>
Interaction	1	13.55	13.55	3.862	.053
Residuals	76	266.69	3.51		

*Note.* Summary of two-way ANOVA comparing mean forest floor thickness with disturbance and soil texture as predictor variables ( $n = 20$  for disturbed-coarse,  $n = 21$  for intact-coarse,  $n = 20$  for disturbed-fine, and  $n = 19$  for intact-fine sites). ‘Disturbed’= lodgepole pine dominant sites with >70% basal area killed by mountain pine beetle; ‘Intact’= lodgepole pine dominant sites free of mountain pine beetle activity. Degrees of freedom (*df*), sum of squares (*SS*), mean squares (*MS*). Bolded p-values represent effects deemed significant.

**Table A9.**

Two-way ANOVA tests comparing mean % carbon in bulk soil and forest floors between sites of different disturbance and soil texture categories.

Predictor	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>p</i>
<i>Bulk</i>					
Disturbance	1	0.269	0.269	1.666	.201
Texture	1	18.814	18.814	116.346	<b>&lt; .001</b>
Interaction	1	0.370	0.370	2.286	.135
Residuals	75	12.128	0.162		
<i>Forest Floor</i>					
Disturbance	1	0.762	0.762	1.881	.174
Texture	1	0.304	0.304	0.750	.389
Interaction	1	6.045	6.045	14.924	<b>.001</b>
Residuals	75	30.378	0.405		

*Note.* Summary of two-way ANOVA comparing ln-transformed % carbon means in bulk (top) and forest floor (bottom) soil with disturbance and soil texture as predictor variables ( $n = 20$  for disturbed-coarse,  $n = 21$  for intact-coarse,  $n = 20$  for disturbed-fine, and  $n = 19$  for intact-fine sites). 'Disturbed'= lodgepole pine dominant sites with >70% basal area killed by mountain pine beetle; 'Intact'= lodgepole pine dominant sites free of mountain pine beetle activity. Removed extreme outliers: 1 intact-coarse bulk and 1 intact-coarse forest floor. Degrees of freedom (*df*), sum of squares (*SS*), mean squares (*MS*). Bolded p-values represent effects deemed significant.



**Table A10.**

Two-way ANOVA tests on mean % nitrogen in bulk soil and forest floors between sites of different disturbance and soil texture categories.

Predictor	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>p</i>
<i>Bulk</i>					
Disturbance	1	0.72	0.72	1.945	.167
Texture	1	55.08	55.08	147.849	<b>&lt; .001</b>
Interaction	1	1.08	1.08	2.889	.093
Residuals	76	28.31	0.37		
<i>Forest Floor</i>					
Disturbance	1	0.096	0.096	0.690	.409
Texture	1	0.159	0.159	1.140	.289
Interaction	1	0.955	4.955	6.864	<b>.011</b>
Residuals	76	10.574	0.139		

*Note.* Summary of two-way ANOVA comparing ln-transformed % nitrogen means in bulk (top) and forest floor (bottom) soil with disturbance and soil texture as predictor variables ( $n = 20$  for disturbed-coarse,  $n = 21$  for intact-coarse,  $n = 20$  for disturbed-fine, and  $n = 19$  for intact-fine sites). 'Disturbed'= lodgepole pine dominant sites with >70% basal area killed by mountain pine beetle; 'Intact'= lodgepole pine dominant sites free of mountain pine beetle activity. Degrees of freedom (*df*), sum of squares (*SS*), mean squares (*MS*). Bolded *p*-values represent effects deemed significant.

**Table A11.**

*Two-way ANOVA tests on mean forest floor carbon and nitrogen stocks between sites of different disturbance and soil texture categories.*

Predictor	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>p</i>
<i>Carbon Stock</i>					
Disturbance	1	0.01	0.01	0.010	.919
Texture	1	9.71	9.71	10.886	<b>.001</b>
Interaction	1	7.22	7.22	8.093	<b>.006</b>
Residuals	76	67.79	0.89		
<i>Nitrogen Stock</i>					
Disturbance	1	0.46	0.46	0.615	.438
Texture	1	10.82	10.82	14.396	<b>&lt; .001</b>
Interaction	1	3.95	3.95	5.258	<b>.025</b>
Residuals	76	57.14	0.75		

*Note.* Summary of two-way ANOVA comparing ln-transformed mean carbon (top) and nitrogen (bottom) stocks in forest floors with disturbance and soil texture as predictor variables ( $n = 20$  for disturbed-coarse,  $n = 21$  for intact-coarse,  $n = 20$  for disturbed-fine, and  $n = 19$  for intact-fine sites). 'Disturbed'= lodgepole pine dominant sites with >70% basal area killed by mountain pine beetle; 'Intact'= lodgepole pine dominant sites free of mountain pine beetle activity. Degrees of freedom (*df*), sum of squares (*SS*), mean squares (*MS*). Bolded p-values represent effects deemed significant.

**Table A12.**

Two-way ANOVA tests on the relative abundance of carbon in the mineral-associated organic matter and particulate organic matter fractions between sites of different disturbance and soil texture categories.

Predictor	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>p</i>
<i>MAOM</i>					
Disturbance	1	0.093	0.093	6.729	<b>.011</b>
Texture	1	0.151	0.151	10.899	<b>.001</b>
Interaction	1	0.020	0.020	1.409	.239
Residuals	76	1.055	0.014		
<i>POM</i>					
Disturbance	1	0.093	0.093	6.729	<b>.011</b>
Texture	1	0.151	0.151	10.899	<b>.001</b>
Interaction	1	0.020	0.020	1.409	.239
Residuals	76	1.055	0.014		

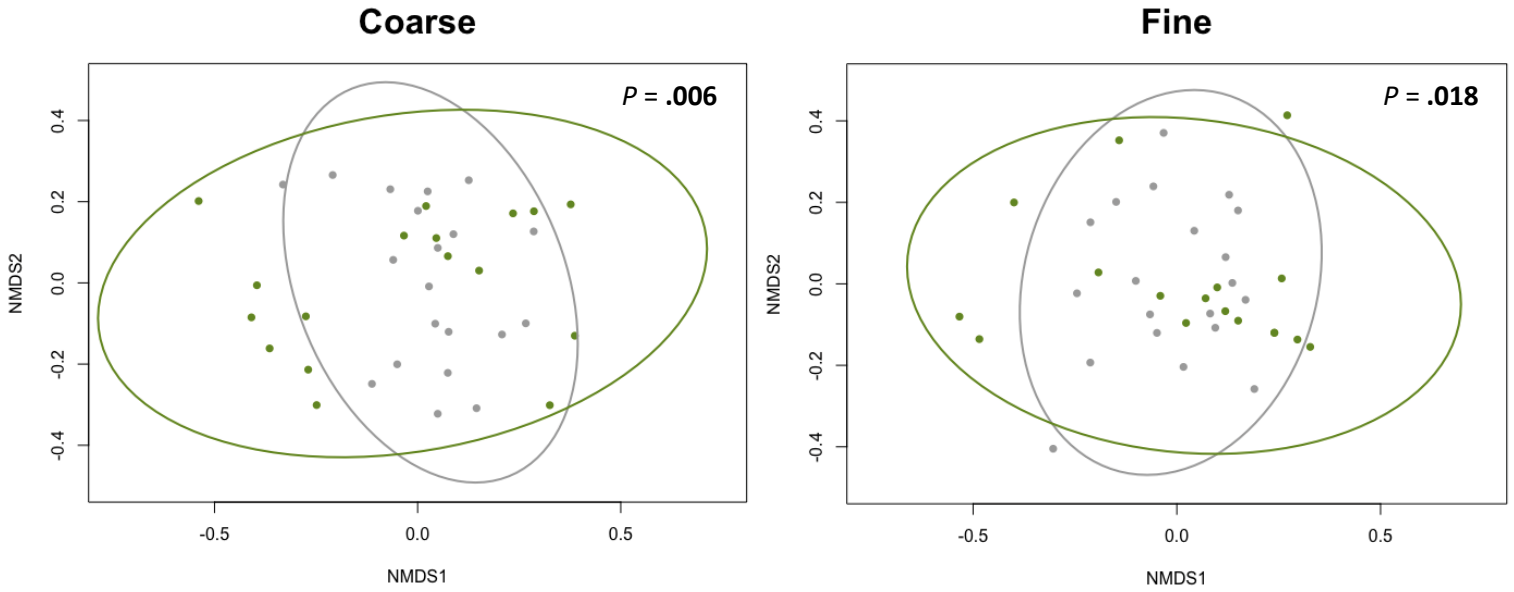
*Note.* Summary of two-way ANOVA comparing means of the relative abundance of carbon in the mineral-associated organic matter (MAOM) (*top*) and particulate organic matter (POM) (*bottom*) fractions with disturbance and soil texture as predictor variables ( $n = 20$  for disturbed-coarse,  $n = 21$  for intact-coarse,  $n = 20$  for disturbed-fine, and  $n = 19$  for intact-fine sites). ‘Disturbed’= lodgepole pine dominant sites with >70% basal area killed by mountain pine beetle; ‘Intact’= lodgepole pine dominant sites free of mountain pine beetle activity. Degrees of freedom (*df*), sum of squares (*SS*), mean squares (*MS*). Bolded p-values represent effects deemed significant.

**Table A13.**

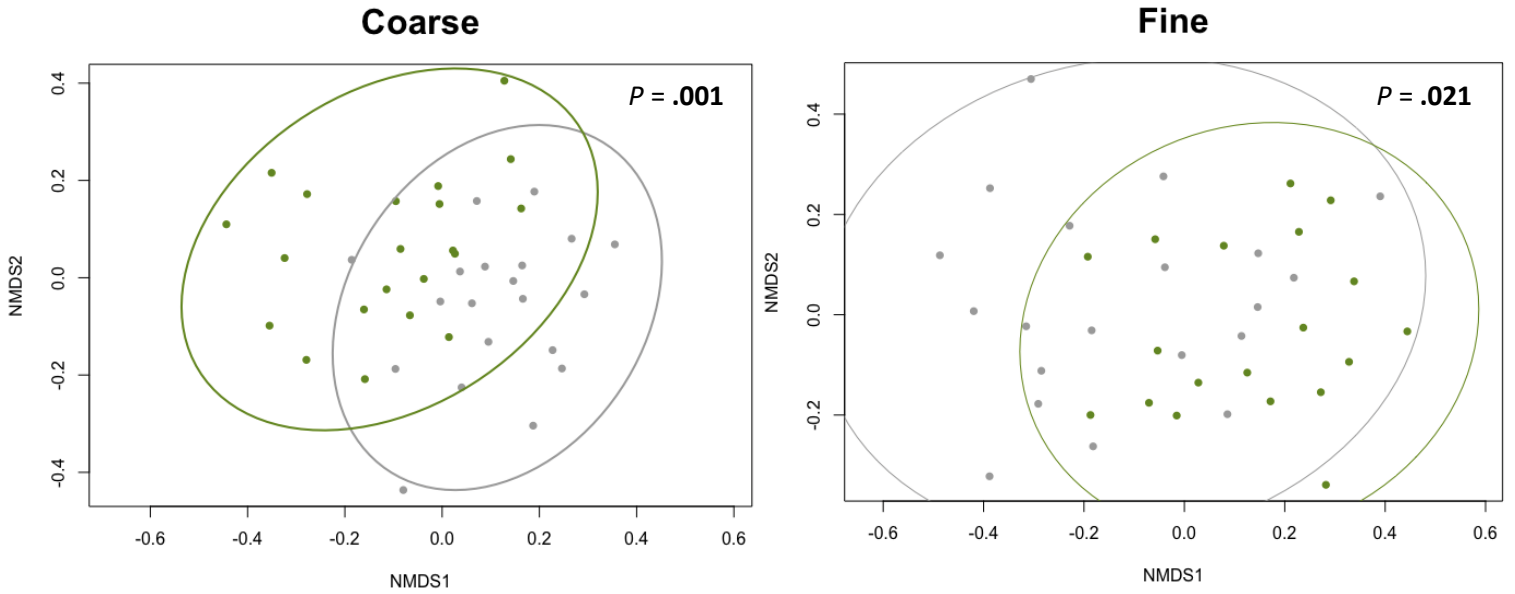
*Two-way ANOVA tests on % carbon in sites with soil depth and disturbance.*

Predictor	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>p</i>
<i>Coarse-textured</i>					
Depth	2	2.126	1.063	9.776	<b>&lt; .001</b>
Disturbance	1	0.147	0.147	1.351	.248
Interaction	2	0.143	0.072	0.659	.519
Residuals	114	12.396	0.109		
<i>Fine-textured</i>					
Depth	2	2.065	1.032	7.157	<b>.001</b>
Disturbance	1	0.209	0.209	1.449	.231
Interaction	2	0.722	0.361	2.504	.087
Residuals	107	15.434	0.144		

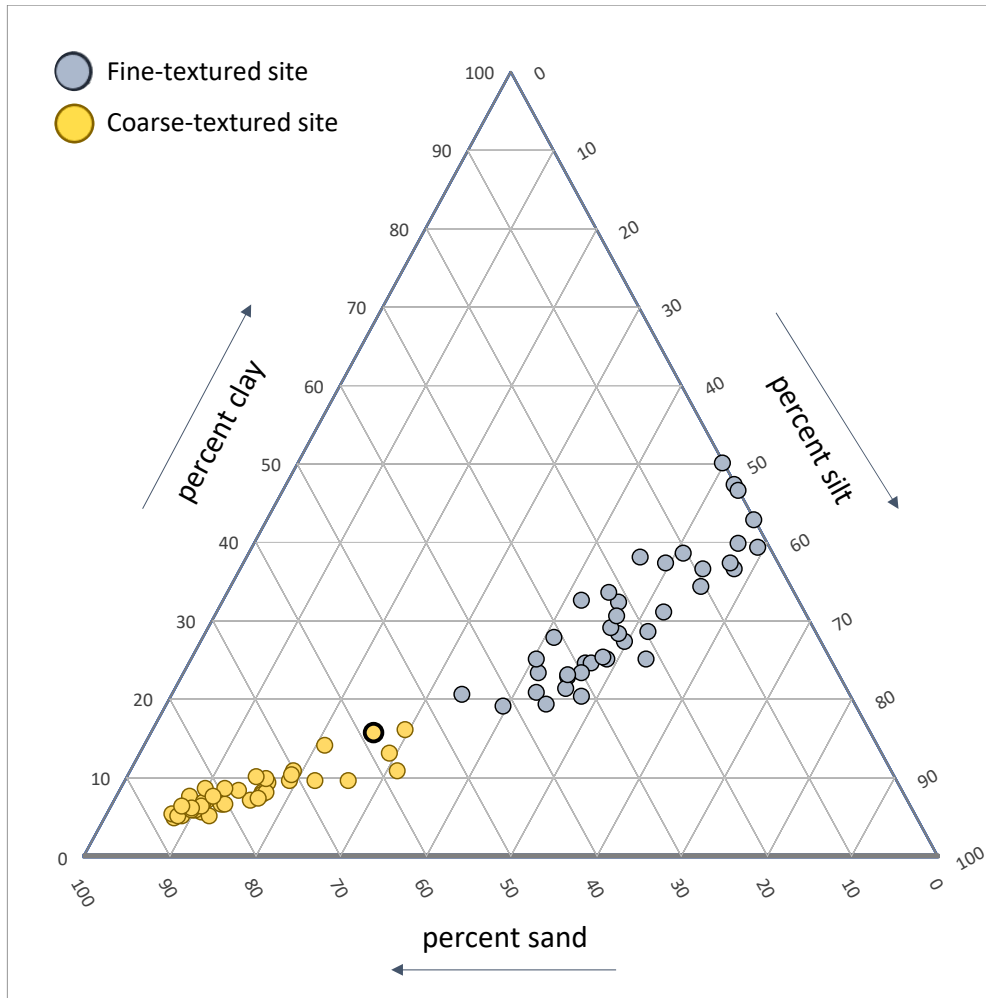
*Note.* Summary of two-way ANOVA comparing ln-transformed means of carbon concentration in coarse-textured (*top*) and fine-textured (*bottom*) soils with soil depth (0-15 cm, 15-30 cm, 30-45 cm) and disturbance as predictor variables ( $n = 20$  for disturbed-coarse,  $n = 21$  for intact-coarse,  $n = 20$  for disturbed-fine, and  $n = 19$  for intact-fine sites). ‘Disturbed’= lodgepole pine dominant sites with >70% basal area killed by mountain pine beetle; ‘Intact’= lodgepole pine dominant sites free of mountain pine beetle activity. Removed extreme outliers: one 15-30 cm disturbed-coarse, one 30-45 cm disturbed-coarse, one 15-30 cm intact-fine; one 30-45 cm intact-coarse. Degrees of freedom (*df*), sum of squares (*SS*), mean squares (*MS*). Bolded *p*-values represent effects deemed significant.



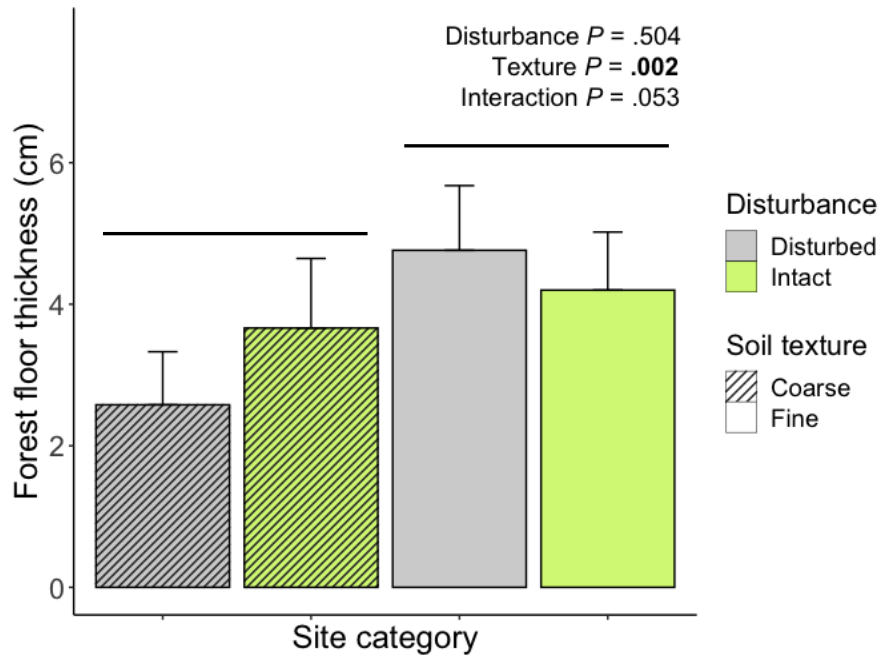
**Figure A1.** Non-metric Multi-dimensional Scaling plots of shrub abundances in each plot. Each point represents one site ( $n = 20$  for disturbed-coarse,  $n = 21$  for intact-coarse,  $n = 20$  for disturbed-fine, and  $n = 19$  for intact-fine sites). Ellipses show standard deviation of points by group. Sites for each soil texture group (fine and coarse) are divided by disturbance category: Grey = 'disturbed', lodgepole pine dominant sites with >70% basal area killed by mountain pine beetle; Green = 'Intact', lodgepole pine dominant sites free of mountain pine beetle activity.



**Figure A2.** Non-metric Multi-dimensional Scaling plots of understory plant species richness in each plot. Each point represents one site ( $n = 20$  for disturbed-coarse,  $n = 21$  for intact-coarse,  $n = 20$  for disturbed-fine, and  $n = 19$  for intact-fine sites). Ellipses show standard deviation of points by group. Sites for each soil texture group (fine and coarse) are divided by disturbance category: Grey = 'disturbed', lodgepole pine dominant sites with >70% basal area killed by mountain pine beetle; Green = 'Intact', lodgepole pine dominant sites free of mountain pine beetle activity.

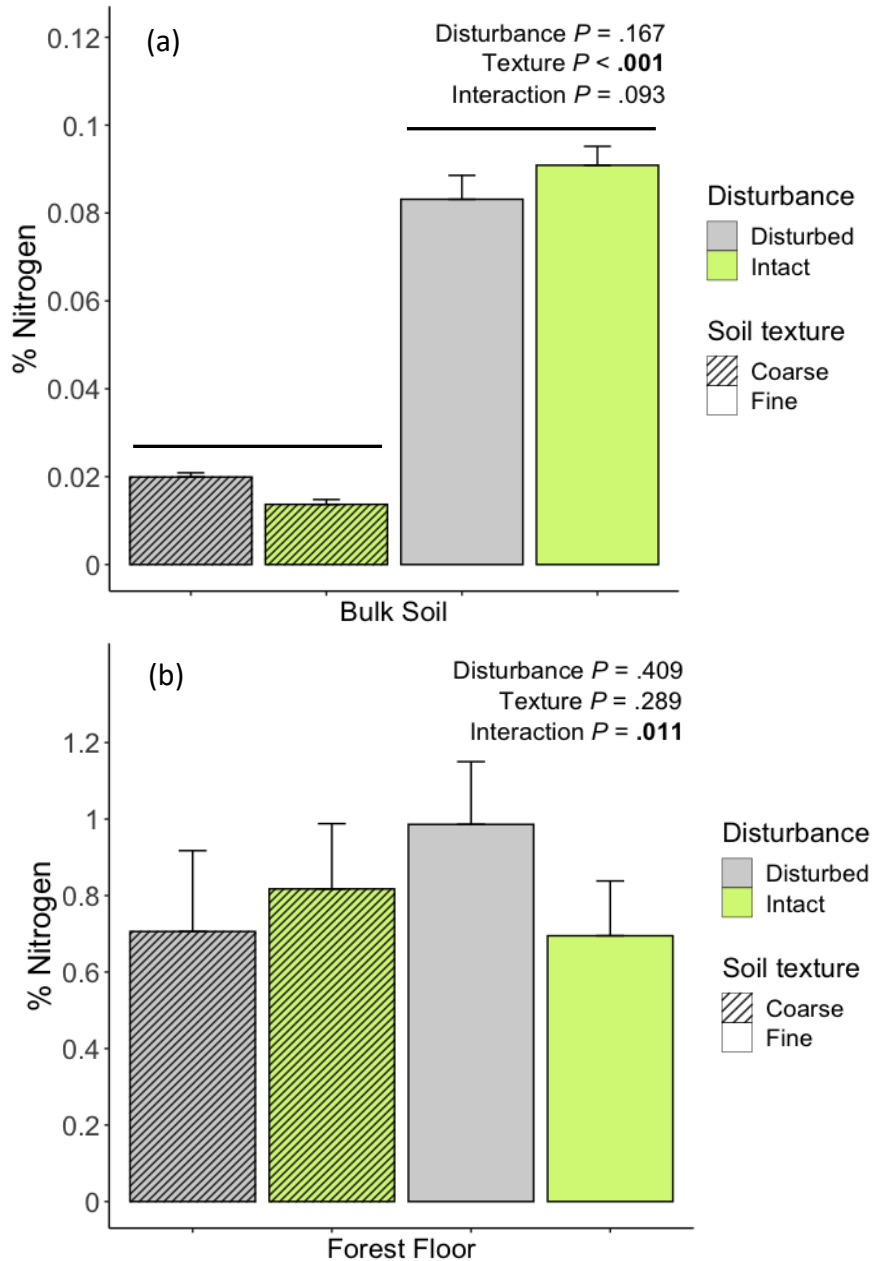


**Figure A3.** Placement of pooled soil samples from each surveyed site on soil texture triangle. 80 sites surveyed in the study, located outside the nearest town of Grande Prairie, Alberta. The bolded point represents the coarse-textured site originally misclassified as fine-textured in the field. With this correction,  $n = 41$  for coarse-textured sites,  $n = 39$  for fine-textured sites.

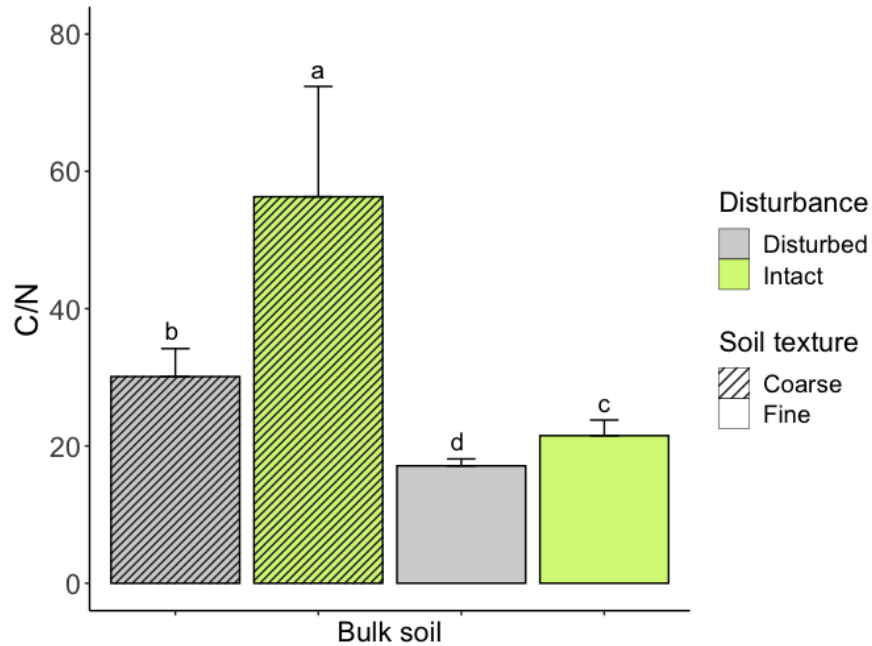


**Figure A4.** Forest floor thickness (mean  $\pm$  95% confidence interval). Surveys included 20 disturbed-coarse, 21 intact-coarse, 20 disturbed-fine, and 19 intact-fine sites. ‘Disturbed’= lodgepole pine dominant sites with >70% basal area killed by mountain pine beetle; ‘Intact’= lodgepole pine dominant sites free of mountain pine beetle activity. Statistically significant main effect from texture ( $F(1, 76) = 10.436, P = .002$ ), tested with two-way ANOVA. Means not sharing a horizontal line are significantly different (Tukey HSD Test,  $P < .05$ ).

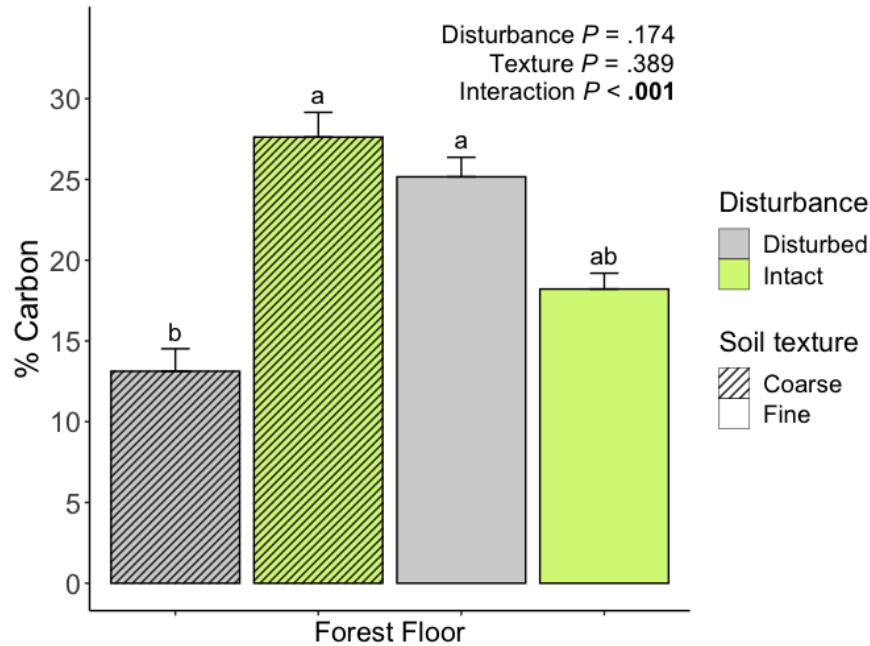




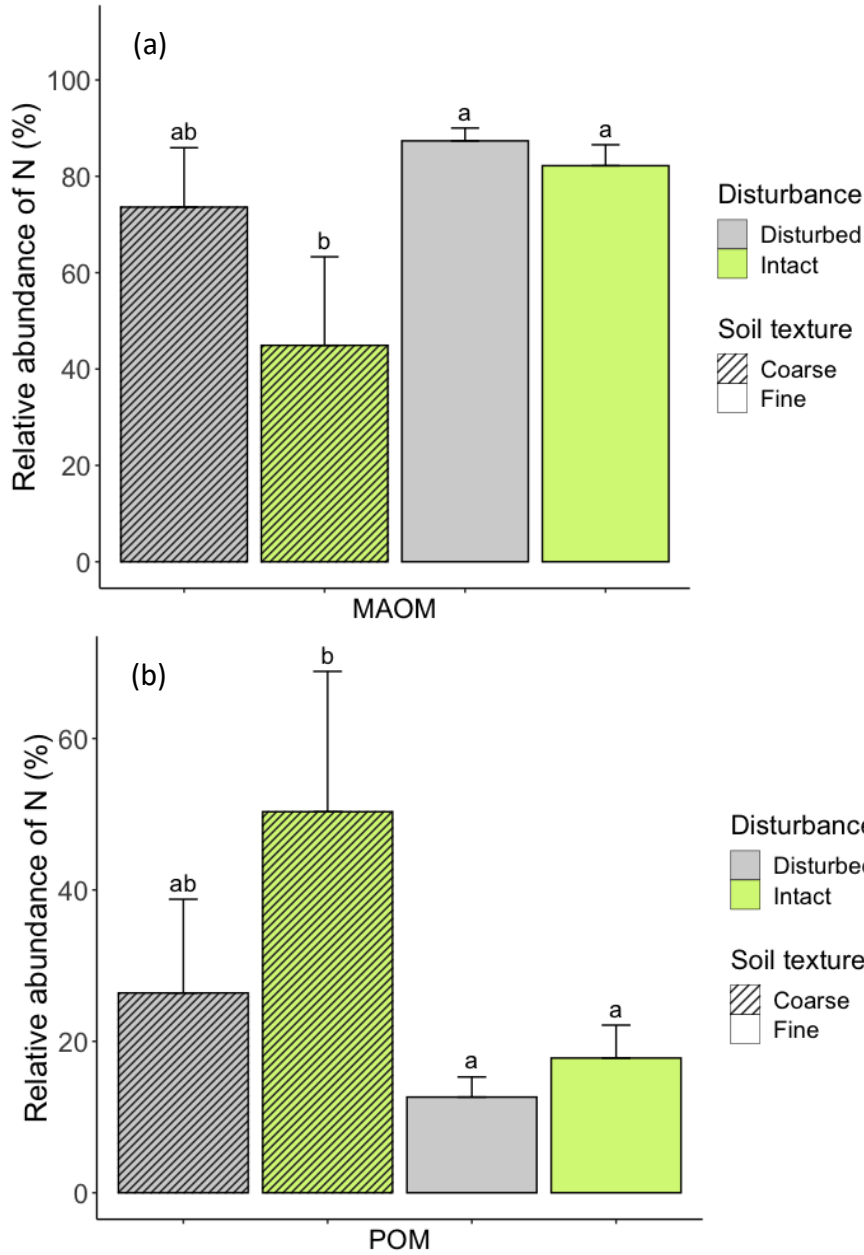
**Figure A5.** Nitrogen concentration in (a) bulk soil (back-transformed ln-mean  $\pm$  95% confidence interval), and (b) forest floor (mean  $\pm$  95% confidence interval). Surveys included 20 disturbed-coarse, 21 intact-coarse, 20 disturbed-fine, and 19 intact-fine sites. ‘Disturbed’= lodgepole pine dominant sites with >70% basal area killed by mountain pine beetle; ‘Intact’= lodgepole pine dominant sites free of mountain pine beetle activity. Statistically significant main effects from texture in bulk soil ( $F(1, 76) = 147.849, P < .001$ ), and statistically significant interaction effect from disturbance with texture in forest floor ( $F(1, 76) = 6.864, P = .011$ ), tested with two-way ANOVA. Means not sharing a horizontal line are significantly different (Tukey HSD Test,  $P < .05$ ).



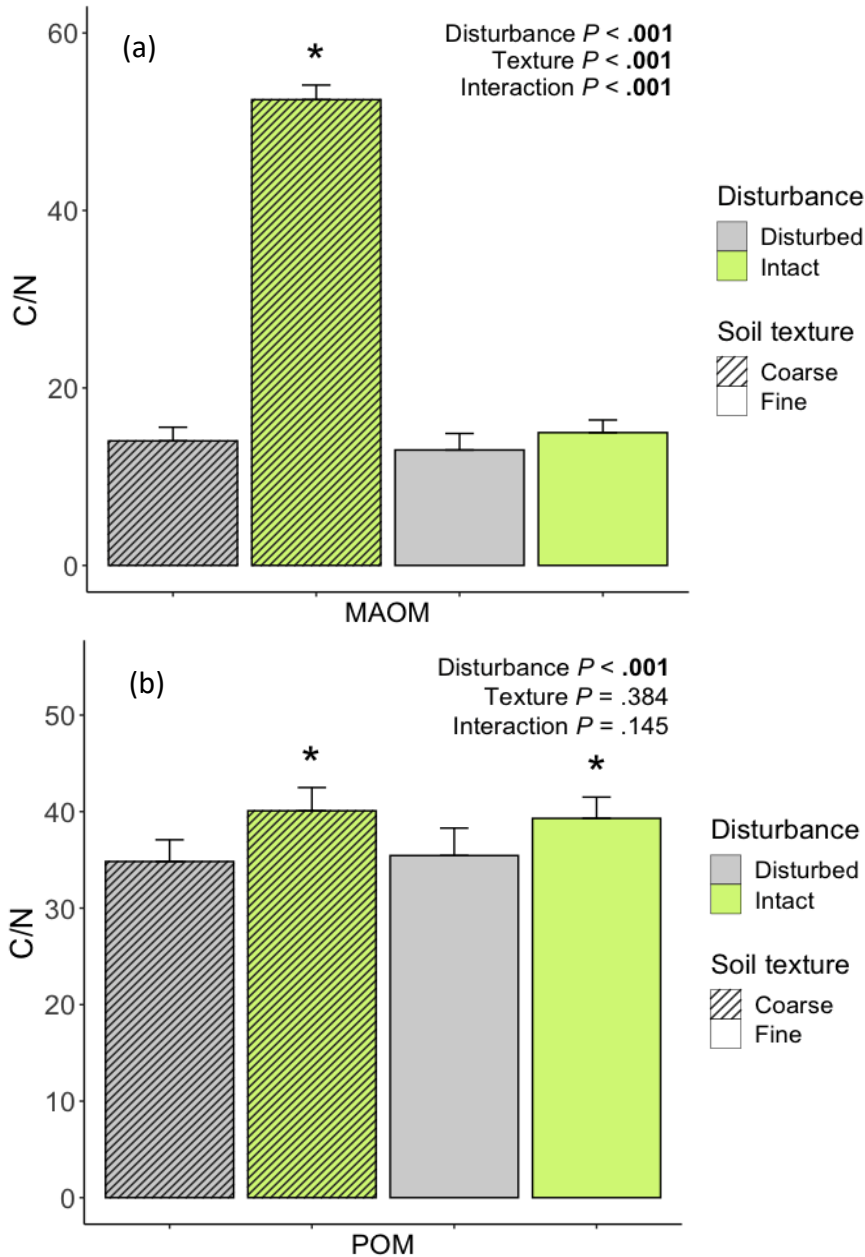
**Figure A6.** Carbon to nitrogen ratio in bulk mineral soil (mean  $\pm$  95% confidence interval). Surveys included 20 disturbed-coarse, 21 intact-coarse, 20 disturbed-fine, and 19 intact-fine sites. ‘Disturbed’= lodgepole pine dominant sites with >70% basal area killed by mountain pine beetle; ‘Intact’= lodgepole pine dominant sites free of mountain pine beetle activity. The Welch’s ANOVA for unequal variances found significant differences between the four site categories ( $F(3, 35.032) = 31.668, P < .001$ ). Means not sharing the same letter are significantly different (Tukey WSD Test,  $P < .05$ ).



**Figure A7.** Carbon concentration in the forest floor (back-transformed  $\ln$ -mean  $\pm$  95% confidence interval). Surveys included 20 disturbed-coarse, 21 intact-coarse, 20 disturbed-fine, and 19 intact-fine sites. ‘Disturbed’= lodgepole pine dominant sites with >70% basal area killed by mountain pine beetle; ‘Intact’= lodgepole pine dominant sites free of mountain pine beetle activity. Statistically significant interaction effect from disturbance with texture in forest floors ( $F(1, 75) = 14.924, P < .001$ ), tested with two-way ANOVA. Removed extreme outlier: 1 intact-coarse. Means not sharing the same letter are significantly different (Tukey HSD Test,  $P < .05$ ).



**Figure A8.** Relative abundance of nitrogen in (a) mineral-associated organic matter (MAOM), and (b) particulate organic matter (POM) fractions (mean  $\pm$  95% confidence interval), where 100% represents the sum of nitrogen in both fractions. Surveys included 20 disturbed-coarse, 21 intact-coarse, 20 disturbed-fine, and 19 intact-fine sites. ‘Disturbed’= lodgepole pine dominant sites with >70% basal area killed by mountain pine beetle; ‘Intact’= lodgepole pine dominant sites free of mountain pine beetle activity. The Kruskal-Wallis rank sum test found significant differences between site categories in both fractions ( $H(3) = 22.786, P < .001$ ). Means not sharing the same letter are significantly different (Nemeyi’s All-Pairs Rank Comparison Test,  $P < .05$ ).



**Figure A9.** Carbon to nitrogen ratio in (a) mineral-associated organic matter (MAOM), and (b) particulate organic matter (POM) fractions (mean  $\pm$  95% confidence interval). Surveys included 20 disturbed-coarse, 21 intact-coarse, 20 disturbed-fine, and 19 intact-fine sites. ‘Disturbed’= lodgepole pine dominant sites with >70% basal area killed by mountain pine beetle; ‘Intact’= lodgepole pine dominant sites free of mountain pine beetle activity. Statistically significant main effects of disturbance and texture and their interaction effects on MAOM C/N, and significant main effects of disturbance on POM C/N, identified with two-way ANOVA. Removed extreme outliers: 1 fine-intact POM, 3 disturbed-coarse MAOM. Asterisks denote significantly different means (Tukey HSD Test,  $P < .05$ ).

## **Appendix B: Supplementary results**

### **Power analysis.**

The power analyses determined that given the effect size, the probability of detecting a difference in carbon concentration between disturbed and intact forests if such a difference does exist was only 16.8% in fine-textured soils and 13.5% in coarse-textured soils. To achieve the standard accepted power level of 80% between the disturbances, 152 samples would be required for each group in fine-textured soils, and 210 samples would be required for each group in coarse-textured soils. Conversely, the power analysis between soil texture types determined a 98.6% probability of detecting a difference in soil carbon concentration in disturbed stands and a 100% probability in intact stands. To achieve a power level of 80% between the soil texture groups, only nine samples would be required per group in disturbed stands and five per group in intact stands.