Oribatid mite communities after ecosystem disturbance in Alberta

by

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ABSTRACT

Many northern Alberta soils have a thick forest floor that houses the majority of soil biogeochemical processes and biological interactions. Microarthropods dominate the faunal communities in these soils, and oribatid mites are the key detritivores that initiate litter decomposition and maintain forest floor structure. Soil disturbance is becoming more prevalent across Alberta and may threaten the long-term sustainability of the forest floor as both a nutrient reservoir and a habitat for oribatid mite communities. The objective of this research was to characterize oribatid mite abundance, richness, diversity, and species composition after two growing sources of soil disturbance in Alberta: oil sands mining and non-native earthworm invasion. Bitumen extraction in the Athabasca oil sands region has disrupted over 800 km^2 of boreal forest habitat to date, forcing soils to be reconstructed from the ground up. The specific objectives following soil reconstruction were to identify: i) which overstory vegetation may favor mite recovery, and ii) at what point in time would mite communities begin to resemble mite communities in natural stands. A chronosequence of 15 reclaimed soils was sampled to assess the influence of canopy (aspen or white spruce) and time-since-reclamation (8-31 yrs.) on oribatid mite communities, and was compared to five undisturbed soils. Species-level identification revealed that the presence of a novel forest floor at sites undergoing reclamation had the biggest impact on oribatid mite reestablishment. Reclaimed stands with a novel forest floor thickness ≥ 2 cm had similar oribatid mite species richness and diversity to that of undisturbed stands and at times had higher abundances than undisturbed stands regardless of time since reclamation or stand type.

Compared to soil reconstruction, non-native earthworm invasion is a less drastic disturbance. However, the presence of another keystone detritivore may threaten the stability of endemic oribatid mite communities in northern boreal forest floors. The objectives following non-native earthworm invasion were to: i) characterize earthworm and oribatid mite assemblage present in a boreal aspen stand and ii) assess how oribatid mite assemblages respond to changes in soil biogeochemical properties as a result of earthworm disturbance. An invaded aspen stand near Wolf Lake, Alberta was surveyed for earthworm invasion and divided into two areas representing different invasion stages: (1) a low density, single species invasion area (*Dendrobaena octaedra* only), and (2) a high density, multiple species invasion area (*Dendrobaena octaedra* and *Aporrectodea* spp.). At each area, oribatid mite communities were sampled. The high density invasion area had a higher forest floor bulk density and a thinner leaf litter. As a result, a drastic loss of the mite species *Gymnodamaeus ornatus* was observed and overall species richness decreased in the high density invasion area. Ultimately, it was the physical loss of and/or alteration of the forest floor habitat that was the main driver of oribatid mite community response to soil disturbance in both studies.

“And forget not that the earth delights to feel your bare feet and the winds long to play with your hair.”

-Kahlil Gibran

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1. CHAPTER 1—GENERAL INTRODUCTION

1.1. Boreal forest ecosystem

The boreal zone circles the Northern Hemisphere and is predominantly found in Russia (60% or 1.14 billion hectares) and Canada (28% or 552 million hectares). In Canada, about 270 million hectares of the boreal zone are forested (Brandt et al., 2013) and over half (145 million hectares) is considered managed (Kurz et al., 2014). The boreal forest is critical to Canada's natural resource industries and is culturally and ecologically significant (Hassan et al., 2005; Brant et al., 2013). One of the most vital ecosystem services provided by the boreal forest is carbon storage, and the Canadian boreal forest is considered one of the largest terrestrial carbon reservoirs (Watson et al., 2000; Kurz et al., 2014).

The boreal forest carbon reservoir is divided into five pools: above-ground biomass, below-ground biomass (roots), deadwood, litter, and soil organic matter (Kurz et al., 2014). Compared to carbon storage in tropical forests (where 56% C is stored in live biomass and 32% in soils), boreal forests only store 20% of the carbon in the live biomass and the majority (60%) is stored in soil (Pan et al., 2011). Litter (47 Mg-C/ha) and soil organic matter (80 Mg-C/ha) store the greatest proportion of ecosystem carbon (Kurz et al., 2014). Carbon storage in these two pools is controlled by climate, organisms, relief, parent material, and time (Jenny, 1941). Given the region's short growing season and long, cold winters, annual organic (live biomass) inputs into the soil system are limited (Brandt et al., 2013). The organic inputs that do occur form thick forest floors characterized by low nutrient status and productivity (Prescott et al., 2000).

Environmental issues such as climate change, deforestation, resource management, and invasive alien species pose a threat to the boreal forest's vital role as a global carbon reservoir

(Brandt et al., 2013). This thesis discusses two of these threats – natural resource management and invasive alien species – and assesses their effect on an indicator species: the endemic oribatid mite communities of the boreal forest. As anthropogenic activities are projected to increase in the future, it is essential to understand and quantify their impacts on the boreal forest floor and its endemic biological communities.

1.2. Target organism

Coleman et al. (2004) identified hotspots of biogeochemical activities in soil that include the rhizosphere, aggregates, litter and organic layers, and the drilosphere (mucus coated earthworm burrows (Bouche, 1977)). When present, the litter and organic layers (forest floor) of boreal forest soils host the highest proportion of plant roots, microbes, and soil fauna, and are where the majority of biological and chemical reactions occur within the soil (Coleman et al., 2004).

While often overlooked, soil fauna creates the complex food web within the forest floor and directly and indirectly associate with microorganisms to maintain soil biogeochemical cycling (Edwards, 2004; Diaz-Aguilar and Quideau, 2013). Soil fauna can be defined by body size (micro-, meso-, and macro-) and each group participates in one or more ecological functions. Microfauna directly graze on microorganisms, and meso- and macrofauna graze on microorganisms, fragment detritus, deposit fecal pellets, and participate in some degree of bioturbation (Coleman et al., 2004). Microarthropods are a group of soil mesofauna that link together many sectors of the soil food web by acting as grazers (fungivores and bacterivores), predators of microfauna (nematodes), and as prey for larger macrofauna (Coleman et al., 2004). Microarthropods play an important role in forest floor decomposition by fragmenting litter, which increases the litter surface area for further chemical transformation by microorganisms. In forest soils, mites and collembolans dominate the microarthropod community. Mites can be characterized into four suborders: oribatida (detritivores), prostigmata (detritivores, predators), mesostigmata (predators), and astigmata (detritivores). Prostigmatid mites are found in nearly all ecosystems, whereas astigmatid mites are found in nitrogen-rich decomposing organic matter (Lavelle and Spain, 2001; Phillips, 1990). Mesostigmatid mites are found in many ecosystems and are predatory on nematodes, enchytraeids, or other microarthropods (Krantz and Ainscough, 1990). When compared to the aforementioned suborders of Acari, oribatid mites are numerically dominant in forest soil and most directly influence organic matter decomposition and forest floor structure (Wallwork, 1983).

Oribatid mites (Acari: Oribatida) are found in abundances of several hundred thousand per square meter of forest soil (Norton, 1990; Behan-Pelletier, 1999). Globally, 7,000 oribatid mite species have been described into 1,000 genera from 150 families (Norton, 1990; Balogh and Balogh, 1992), and the organic horizons of a forest soil may reveal between 30-50 species (Norton, 1990). Additionally, oribatid mites can be categorized into three feeding guilds: (1) macrophytophages, which decompose higher plant material, (2) microphytophages, which feed on microflora, mainly fungi and yeasts, and (3) panophytophages, which consume both microbial and higher plant material (Luxton, 1972).

Oribatid mites have relatively slow metabolic rates compared to other microarthropods like collembolans, and have multiple reproductive cycles in a lifetime. Their lifespan ranges from two months to two years, but in cold climates can range up to seven years (Behan-Pelletier, 1999). These characteristics classify oribatid mites as “k-strategists”, and they are able to produce stable populations year-round (Norton, 1994; Behan-Pelletier ,1999). Some adult females are thelytokous, meaning that they reproduce asexually and have only female offspring.

Thelytoky is hypothesized to be a desirable trait that gives oribatid mites an advantage when reestablishing after habitat disturbance. Thelytokous species can be particularly beneficial as indicator species due to their dominance in the early stages of soil reclamation, and a decrease in their abundance over time may indicate successful soil recovery (Behan-Pelletier, 1999; Lindo and Visser, 2004). On the other hand, changes in oribatid mite assemblage composition (i.e., abundance, species richness, body size, reproduction strategy, and/or physiological response) may be a bioindicator of ecosystem stress (Siddig et al., 2016). Consequently, oribatid mites are hypothesized to be a useful microarthropod taxa to monitor after landscape disturbance.

A bioindicator is a species that is able to reflect any level of ecosystem disturbance within its community characteristics such as abundance and species richness (Siddig et al., 2016). A good bioindicator will be numerically dominant, have high diversity, stability, and play an important ecological role in the ecosystem of study (Behan-Pelletier, 1999). Small body size (150-2000 um) and resistance against fluctuations in soil moisture and temperature make oribatid mites excellent candidates as bioindicators. Upon disturbance, oribatid mites are unlikely to escape stressed conditions as their main mechanism of dispersal is through wind and active dispersal (Lehmitz et al., 2011). Of the species able to participate in active dispersal, their estimated maximum active dispersal rates range from 0.3-2.1 cm/day (Lehmitz et al., 2012). Moreover, oribatid mites play a critical role in litter decomposition in boreal forest ecosystems. The abundance of food resources and the microhabitat characteristic of the boreal forest floor attracts oribatid mites to dominantly inhabit this soil layer, often times in abundances exceeding 100,000/m^2 (Coleman et al., 2004). Here, oribatid mites graze on fungi, bacteria, and detritus, shredding organic matter into smaller fragments for further microbial transformation and nutrient cycling (Behan-Pelletier, 1999). The slow decomposition rates in boreal forest soils are due in part to the rate at which microarthropods are able to shred organic matter, which is much slower than other groups of detritivores such as earthworms. Grazing activities initiate litter decomposition, and enable oribatid mites to directly affect forest floor structure and indirectly affect nutrient cycling in boreal forest soils.

1.3. Target habitat

This thesis is comprised of two studies that investigated the impact on endemic oribatid mite communities after 1) oil sands mining and 2) invasion by exotic earthworms. Both study sites lie in the Central Mixedwood subregion of Alberta, which is the largest of the eight boreal forest subregions. This subregion spans eight degrees of latitude and many climatic zones. Annual precipitation falls at 478 mm and annual temperature ranges from a maximum of 22 ˚C in July and a minimum of -24.2 ˚C in January (Natural Regions, 2006). Precipitation and temperature notably decrease near the 57th parallel. The oil sands study was conducted in the Athabasca oil sands region between the 56th and 57th parallel; the earthworm study was conducted in the Wolf Lake region between the 54th and 55th parallel (Figure 1-1.).

Understory vegetation in the Athabasca oil sands region is dominated by bearberry (*Arctostaphylos uva-ursi* (L.) Spreng), bog cranberry (*Vaccinium vitus-idaea* L.), twinflower (*Linnaea borealis* L.), labrador tea (*Lendum groenlandicum* Oeder), feathermosses, and lichen (Fung and Macyk, 2000). Soils in the area formed under upland mixedwood and coniferous forests are Luvisols and Brunisols (Soil Classification Working Group, 1998; Fung and Macyk, 2000).

Understory vegetation in the Wolf Lake area is dominated by low bush cranberry (*Viburnum edule* (Michx.) Raf.), rose (*Rosa acicularis* Lind.), wild sarsaparilla (*Aralia nudicaulis* L.), dewberry (*Rubus pubescens* Raf.), bunchberry (*Corus canadensis* L.), and

Canada Buffaloberry (*Shehperdia canadensis* (L.) Nutt.) (Natural Regions, 2006). Soils in the area are Orthic Gray Luvisols and degraded Eutric Brunisols (Alberta Agriculture and Forestry, 2017).

1.4. Oil sands surface mining in the boreal forest

The Athabasca oil sands region is located north of Fort McMurray, Alberta (56°43'N 111°21'W) and is home to large bitumen deposits. Bitumen is a naturally occurring (reaching up to 18% sand by weight) viscous hydrocarbon (McRory, 1982; Fung and Mayck, 2000). Approximately 18% of Canada's total oil production is from two oil sands mining leases: Syncrude Canada Ltd. and Suncor Energy, Inc. Reclaimed stands at both mining leases were included this study.

Bitumen extraction via surface mining has disrupted nearly 1000 km^2 of boreal forest habitat, requiring entire forest ecosystems to be reconstructed from the ground up. Surface mining requires the complete removal of surface vegetation, soil, and geologic material. After bitumen extraction is complete, contractors are required by the Alberta Environmental Protection and Enhancement Act to: "reclaim disturbed land to equivalent land capability" (Macdonald et al., 2015; Government of Alberta, 2016). Land reclamation following surface mining involves reconstructing entire ecosystems in a matter of years by rebuilding soil-like profiles and revegetating and reforesting disturbed land. Contractors are bound to reclaim disturbed landscapes to ecosystems capable of supporting reforested vegetation, lakes, and wetlands (Fung and Mayck, 2000).

Materials used to reconstruct mineral soils include lean oil sand, which contains up to 10% oil; mineral soil, salvaged to a depth of 3 m; overburden, geologic material >3 m, and tailings sand, which is a byproduct of bitumen extraction (> 90% sand). Combinations of these materials comply to a reclamation prescription, and each prescription is capped by an organic layer most often comprised of peat mixed with mineral soil collected from lowlands surrounding Fort McMurray. This capping material is identified as a “peat-mineral mix” and ranges from 25-50% peat (by volume) to mineral soil. The availability of peat in the Athabasca oil sands region makes it the most viable capping material to reclaim soils in the region (Akala and Lal, 2000; Norris et al. 2013). The only government certified “reclaimed” area in the Athabasca oil sands region is Gateway Hill, which is included in this study.

There have been multiple studies focused on the recovery of organic matter quality and microbial communities in soils undergoing reclamation in the Athabasca Oil Sands Region. Turcotte et al. (2009) reported that soil organic matter quality in stands undergoing reclamation differed substantially from the natural range observed in undisturbed forest ecosystems of the area, but that there seems to be an evolution with time since reclamation towards that natural range. Turcotte et al. (2009) further hypothesized that this evolution reflected an increasing contribution of forest vegetation litter to soil organic matter at the reclaimed sites. Norris et al. (2013) found that the strongest n-alkane biomarkers in reclaimed soils originated from substrate types (peat vs. tree litter) rather than stand age. Additional studies have suggested that when peat-based materials are included in the reclamation prescription, microbial communities are different from those in undisturbed stands (Dimitri et al., 2010; Quideau et al., 2013). Hahn and Quideau (2013) found that the common peat amendment used in soil reclamation inhibited understory vegetation growth and microbial community development compared to salvaged forest floor. Microbial communities in reclaimed stands were more similar to those in natural stands when a forest floor material was used instead of a peat-based material. Lastly, Sorenson et al. (2011) determined that the development of a forest floor at the reclaimed sites rapidly occurred once a canopy cover of 30% was reached, and that this forest floor significantly influenced microbial community structure. Few studies have documented the recovery of mesofauna after oil sands mining compared to the soil characteristics discussed above. Battigelli (2011) reported that mesofauna densities remained different in reclaimed stands when compared to natural stands, but densities tended to be higher in stands reclaimed with peat-mineral mix and either overburden or tailings sand. No studies have directly investigated the use of oribatid mites as bioindicators after oil sands mining.

1.5. Earthworm invasion in the boreal forest

Boreal forest ecosystems have historically been characterized by limited human development and inhabitance, high quantities of stored ecosystem carbon, and very few invasive species due to the harsh climate (Brandt et al., 2013). With climate change, non-native species invasion is becoming more of a threat to northern boreal zones, including the presence of non-native vascular plants, bryophytes, lichens, spiders, ground beetles, earthworms, and few mammals, reptiles, and amphibians (Langor et al., 2014).

Of the non-native species currently invading the Canadian boreal forest, exotic earthworms belonging to the family Lumbricidae may have the most drastic effect on the soil ecosystem (Bohlen et al., 2004a, b; Hale et al., 2005; Eisenhauer et al., 2007; Addison, 2009). Slow colonization rates (~4 m/year) indicate that earthworm invasion can be greatly enhanced through anthropogenic activities (Marinissen and van den Bosch, 1992). Anthropogenic activities such as mining and logging are projected to increase non-native earthworm spread from 9% of the boreal forest to 49% by 2050 (Cameron and Bayne, 2009). James and Hendrix (2004) determined that a high tolerance of environmental variability is the dominant trait that enables earthworms to invade ecosystems with a harsh climate. Adverse environmental conditions have kept most of Alberta devoid of earthworms since Pleistocene glaciation, and the current invasion by Lumbricidae may threaten the sustainability of northern boreal forests as a long-term carbon reservoir (Gates, 1982; Reynolds and Clapperton, 1996).

Aristotle described earthworms as “the intestines of the earth” (Edwards, 2004). Today, we refer to earthworms more commonly as “ecosystem engineers” (Jones et al., 1994) and their influence on soil biogeochemical cycles has been recognized since Darwin’s *The Formation of Vegetable Mould through the Actions of Worms* (1881). No other soil fauna species or subspecies influences litter comminution and soil structure more than the earthworm (Coleman et al., 2004). Earthworms are divided into three ecological classes, primarily by their feeding preferences (Bouche, 1977). Epigeic are the smallest group (2-5 cm), feed on detritus, and cause little to no mixing of the organic and mineral soil horizons (Coleman et al., 2004). Epigeic species are most likely to be invasive and two species, *Dendrobaena octaedra* and *Dendrodrilus rubidus* Savigny, 1826*,* have been found in northern Alberta (Cameron et al., 2007). Endogeic species live and feed in the mineral soil and range in size from 2-12 cm in length. Two species have been found in northern Alberta: *Aporrectodea tuberculate* Savigny and *Aporrectodea turgida* Savigny (Bouche, 1977; Cameron et al., 2007). Anecic species are mineral dwelling detritivores that burrow to the surface to feed, and have the largest influence on soil structure, ranging in size from 8-15 cm in length. Only one species, *Lumbricus terrestris* L., 1758, has been found in northern Alberta.

To date, two major studies regarding non-native earthworm invasion in Alberta have been conducted: one series in the Kananaskis Valley of southern Alberta, and one series in the northern boreal forest of Alberta. Epigeic (litter-dwelling) species were first recorded invading the Kananaskis Valley of southern Alberta in the 1980s (Scheu and Parkinson, 1994), mainly the species *Dendrobaena octaedra* (Savigny, 1826). The influence of *D. octaedra* on organic matter, microbial activity, and microfungal and microarthropod communities was studied first in 3, 6, and 12-month laboratory incubations (McLean and Parkinson, 1997; McLean and Parkinson, 1998a; McLean and Parkinson, 1998b) and later in a two-year field study (McLean and Parkinson, 2000a; McLean and Parkinson, 2000b), all using soil and litter from a 90-year old lodgepole pine stand. As the invasion front progressed, endogeic species *Octolasion tyrtaeum* and *Aporrectodea caliginosa,* and anecic species *Lumbricus terrestris* were manipulated in laboratory incubations (Migge, 2001) and field studies (Migge, 2001; Eisenhauer et al., 2007; Straube et al., 2009) using soil and litter from a montane aspen stand. The second series focused on invasion mechanisms of non-native earthworms into northern Alberta, and found that invasion is likely a product of entry via bait at boat launches and transport in tire treads (Cameron and Bayne, 2007). Cameron and Bayne (2009) investigated further and found a correlation between road age and earthworm occurrence, where higher earthworm populations were seen at the most southwestern boreal sites in Alberta. A series of laboratory investigations were performed using soils devoid of earthworms from northern boreal forests with coniferous and deciduous litter. The presence of earthworm species from more than one functional group (specifically detritivores like epigeic and endogeic) may have additive effects in decreasing forest floor thickness, increasing soil bulk density, and decreasing microarthropod abundance (Cameron and Bayne, 2011; Cameron et al., 2013).

1.6. Ecological theory following disturbance

Ecosystem disturbance leading to habitat fragmentation and the creation of novel landscapes amongst “natural” landscapes presents a unique opportunity to monitor the succession and development of disturbed ecosystems. Traditional ecological theory, such as the

Island Biogeography Theory (IBT) (MacArthur and Wilson, 1967), has transcended beyond the bounds of "an island surrounded by an inhabitable sea" to "heterogeneous landscapes" of increasing insularity after human disturbance (MacArthur and Wilson, 1967; Haila, 2002; Laurence, 2008). While relying on the foundation of the IBT, landscape fragmentation is considered heterogeneous and remains influenced by interactions with the surrounding forest (Haila, 2002). These interactions introduce a suite of variables to consider when assuming disturbed environments are different from natural environments, including canopy-gap dynamics, carbon storage, and trophic structure of above-ground and below-ground food webs (Haila, 2002; Laurence, 2008).

We can use the framework of the IBT theory to assess the potential for immigration of oribatid mites into newly built soil profiles after oil sands mining. Equilibrium theory of the IBT describes species immigration rates as a function of the distance to the fragmented (disturbed) stand. Research regarding the immigration of oribatid mites after mining suggests that wind dispersal, while slow, is the dominant mode of dispersal (Wanner and Dunger, 2002). Depending on the distance of novel forests to natural forests, active dispersal may occur, but only for specific species with appropriate feeding and reproductive strategies (Lehmitz et al., 2011; Lehmitz et al., 2012). Therefore, we cannot anticipate that identical species will reestablish in novel forests. Rather, we can anticipate the preservation of biodiversity (number of species) with the development of abiotic and biotic factors resembling natural forests.

A second ecological concept, the Intermediate Disturbance Hypothesis (IDH), has been discussed in studies aiming to assess the impact of non-native species invasion to endemic biological communities. Connell (1978) describes the IDH as a biotic or abiotic disturbance with intermediate frequency and intensity that allows the maximum coexistence and diversity for all species (Straube et al., 2009). Hutson (1979) furthered this hypothesis by focusing on the intensity of the disturbance and reproductive rate of an organism, where successive disturbances maintain low levels of diversity for communities with slow reproductive rates.

Oribatid mites have slow reproductive rates and may react differently to different levels and intensities of disturbance. The introduction of non-native earthworms into previously earthworm free ecosystems can disrupt the ecosystem equilibrium to varying degrees depending on the earthworm species invading (epigeic, endogeic, anecic, or a combination) and may result in a “new” equilibrium for that ecosystem (James and Hendrix, 2004). Maraun (2003) investigated the effect of different levels of mechanical disturbance on oribatid mite composition and found that disturbance was detrimental even at low levels, concluding the IDH may not apply to soil microarthropods. In contrast, results of earthworm invasion on microarthropod communities in the Kananaskis Valley support the IDH by suggesting minor disturbances of *O. tyrtaeum* do not influence ecosystem function and support maximum coexistence of species (Straube, et al., 2009). Lastly, McLean and Parkinson (1998a) found that microarthropod abundances were maximized three months after earthworm invasion and decreased significantly after six months, which also supports the IDH. Depending on the time since invasion, habitats may reflect different levels of disturbance. While valuable, the IDH should be used cautiously as causation for changes in abundances and species richness in field studies without knowing when the invasion began.

1.7. Objectives and hypotheses

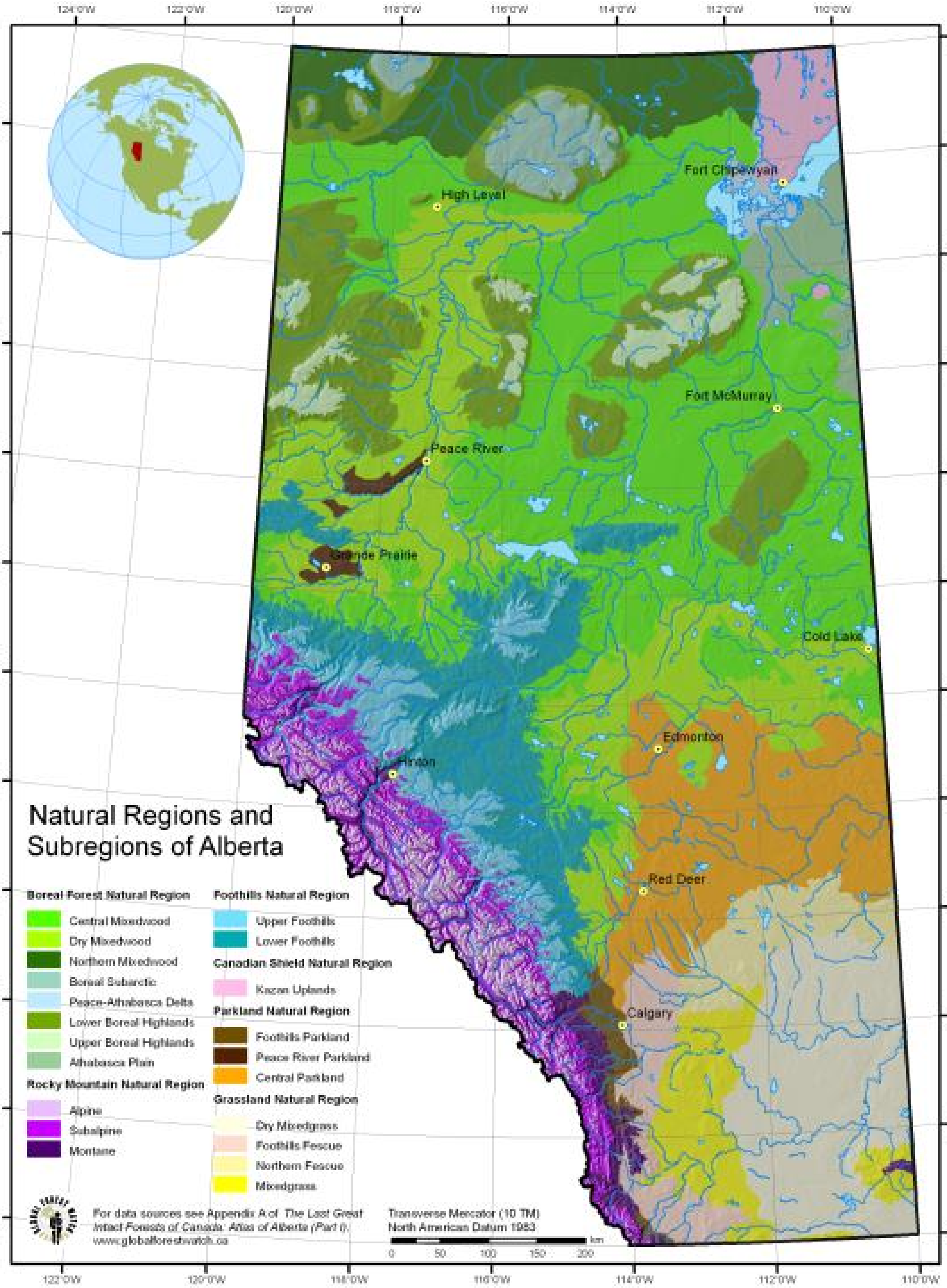
This research aimed to investigate the structure of oribatid mite assemblages after large-scale disturbance in Alberta. The first study investigated oribatid mite structure after oil sands mining and the second study investigated oribatid mite structure after non-native earthworm invasion.

The objective of the first study was to characterize oribatid mite species ≥ 0.3 mm throughout a chronosequence (8-31 years) of reclaimed soils in the Athabasca oil sands region to identify when and under what vegetative conditions successful oribatid mite community recovery, if any, occurred. Specifically, I wanted to identify: i) which vegetative conditions favored community recovery, ii) at what time since reclamation and under which vegetative conditions did oribatid mite community composition shift toward oribatid mite composition in natural stands, and iii) if any species could be used as a bioindicator of forest floor recovery. I hypothesized that i) oribatid mite communities would follow a linear trajectory with increasing abundance and species richness from young reclaimed stands to old reclaimed stands, and ii) indicator species analysis would associate the loss or gain of pioneer species as a bioindicator of community maturation and forest floor recovery.

The objectives of the second study were to i) characterize earthworm and oribatid mite assemblages present in a boreal aspen stand and ii) assess how oribatid mite assemblages respond to changes in soil biogeochemical properties as a result of earthworm disturbance. I hypothesized that i) oribatid mite assemblage diversity would increase in the area that had only epigeic earthworm species (and at low densities), and ii) diversity and abundance would decrease in stands with epigeic, endogeic, and/or anecic species (at high densities).

Tables and Figures

Figure 1-1. Natural Regions and Subregions of Alberta map. From Natural Regions, 2005.



2. CHAPTER 2—ORIBATID MITES AS A TOOL TO ASSESS SOIL RECOVERY AFTER OIL SANDS MINING

2.1. Introduction

The boreal forest is one of the largest terrestrial carbon sinks in the world (Kurz et al. 2014; Watson et al., 2000). The highest proportion of carbon within the boreal biome is stored below-ground, with an average of 47 Mg-C ha^{-1} present within the surficial organic horizons; i.e., the forest floor (Kurz et al. 2014). The forest floor hosts the highest proportion of plant roots, microbes and soil fauna, and when present, is where the majority of biological and chemical reactions occurs in the soil (Coleman et al., 2004). Soil fauna are part of the complex food web within the forest floor and both directly and indirectly interact with microorganisms to maintain soil biogeochemical cycling (Diaz-Aguilar and Quideau 2013). Included in these fauna are oribatid mites (Acari: Oribatida), which are microarthropods that range in size from 150 μm—2000 μm and are numerically dominant in upland boreal forest floors (Behan-Pelletier, 1999; Wallwork 1983).

Bioindicator species can act as a monitoring tool in disturbed ecosystems by reflecting disturbance within their community composition. This includes changes in abundance, species richness, age, body size, reproduction strategy, growth rate/fecundity, and/or physiological response (Siddig et al., 2016). Oribatid mites possess many of the desirable qualities of a bioindicator (Behan-Pelletier, 1999), including numerical dominance, high diversity, stability, and important ecological role. They are the most diverse microarthropod taxa and reach densities up to several hundred thousand individuals per square meter of forest soil (Behan-Pelletier, 1999; Norton, 1990). Some oribatid mite species are parthenogenetic, which may be a positive attribute to communities establishing after disturbance (Behan-Pelletier, 1999). Long life spans and few reproductive cycles exemplify oribatid mites as ‘k-strategists’, and in combination with limited dispersal, communities are able to create stable populations in undisturbed environments (Behan-Pelletier 1999; Norton 1994). When colonizing a disturbed area, most mite species are reliant on wind and vectors like larger species, while few species recolonize through active dispersal, diminishing the likelihood of escape in stressed conditions (Lehmitz et al., 2011, 2012; Wanner and Dunger, 2002). Lastly, oribatid mites dominantly inhabit the top 10 cm in the forest floor due to the high presence of food resources. Most oribatid mite species have a polyphagous feeding strategy, and they feed by grazing on bacteria, fungi, and detritus within the forest floor. Grazing promotes litter decomposition through the comminution of dead organic matter (Coleman et al., 2004; Walter 1987), and as a result, oribatid mites directly affect soil structure and formation in organic horizons and indirectly affect nutrient cycling.

Oribatid mites have historically been characterized in disturbed landscapes using metrics of abundance, species richness, diversity, and reproductive strategy. Previous research in the boreal forest includes the documentation of soil fauna recovery following spontaneous ecological succession on top of coal heaps in Central Europe (Frouz et al., 2001, 2006, 2008, 2013), in limestone quarries from Catalonia (Andrés and Mateos, 2006), in reclaimed forest stands post-coal mining in Eastern Germany (Dunger et al., 2001), on mine tailings in Ontario (St. John et al., 2002), and following prescribed and natural fire in Scandanavia (Malmström, 2006). More specifically, oribatid mite recovery was evaluated following forest harvest in a spruce chronosequence from Germany (Zaitsev et al., 2002), in white spruce stands from British Columbia (Battigelli et al., 2004), and in mixedwood forests in Alberta (Lindo and Visser, 2004) and Quebec (Dechene and Buddle, 2009). Yet, there is a dearth of knowledge regarding soil mesofauna recovery, specifically oribatid mites after oil sands mining reclamation activities.

Oil sands mining in Alberta has disrupted nearly 1000 km^2 of boreal forest habitat to date (Alberta Government, 2017). This invasive mining technique is used to extract bituminous sediment below the Earth's surface, which results in the complete removal of all surface vegetation, soil, and geologic material. Continuous reclamation of post-mining landscapes creates an inherently valuable area of research where novel ecosystems can be studied from the early stages of forest succession (Frouz et al. 2001, 2008, 2013). Reclaimed ecosystems in the Athabasca oil sands region may be referred to as novel, where new abiotic conditions and novel species exist and may follow a new successional path compared to natural stands in the area (Hobbs et al., 2009; Quideau et al., 2013). Previous research in the Athabasca oil sands region has examined the influence of reclamation practices on organic matter quality and its evolution with time since reclamation (Norris et al., 2013; Turcotte et al., 2009). Soil organic matter (SOM) quality was investigated by Hahn and Quideau (2013), who compared the influence of peat and forest litter amendments on microbial communities. Sorenson et al. (2011) assessed SOM evolution, and microbial community composition in older reclaimed stands (16-33 years since reclamation) under different canopy types. Additionally, the Alberta Biodiversity Monitoring Institute provides data on oribatid mite species richness, distribution, and extent of intactness in the Athabasca soil sands region, but does not provide an assessment of recovery (ABMI 2013). Only one study has assessed the effect of reclamation prescription on soil fauna (Battigelli, 2011) in the Athabasca oil sands region, and no studies have directly investigated the use of oribatid mites as bioindicators for this region.

The present study characterized oribatid mite species > 300 μm throughout a chronosequence (8-31 yrs.) of reclaimed soils in the Athabasca oil sands region. It aimed to identify when and under what vegetative conditions successful oribatid mite community recovery, if any, occurred. Specifically, we wanted to assess: i) which canopy type (white spruce (*Picea glauca* (Moench) Voss), trembling aspen (*Populus tremuloides*, Michx.)) favored community recovery, ii) at what time since reclamation did oribatid mite community composition begin to reflect that found in natural stands, and iii) if any particular oribatid mite species could be used as a bioindicator of forest floor recovery. We hypothesized that i) oribatid mite communities would follow a linear trajectory with time since reclamation and increase in abundance and species richness from young to old reclaimed stands, and ii) indicator species analysis would associate the loss of parthenogenetic or pioneer species as bioindicators of community maturation and forest floor recovery.

2.2. Materials and methods

2.2.1. Study area

The study area is located north of Ft. McMurray (56°43’N 111°21’W) in the Central Mixedwood subregion of the Boreal Forest region of Alberta (Natural Regions Committee, 2006). The climate is characterized by mean monthly temperatures of 17.1°C in July and -17.4°C in January, and there is an average of 97 frost-free days annually. Mean annual precipitation is 419 mm with 316 mm falling as rain (Environment Canada, 2016). Dominant tree species in this region include white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill.) B.S.P), jack pine (*Pinus banksiana* Lamb.), and trembling aspen (*Populus tremuloides* Michx.). White spruce is the principal climax species of upland forests, but aspen covers the largest land area due to its re-vegetative properties such as root suckering (Fung and Macyk, 2000; Stringer 1976; Thompson et al., 1978). Understory vegetation under these canopy types includes bearberry (*Arctostaphylos uva-ursi* (L.) Spreng), bog cranberry (*Vaccinium vitus-idaea* L.), twinflower (*Linnaea borealis* L.), Labrador tea (*Lendum groenlandicum* Oeder), feathermosses and lichen

(Fung and Macyk, 2000). Soils formed under upland mixedwood and coniferous forests are Luvisols and Brunisols (Fung and Macyk, 2000; Soil Science Classification Working Group, 1998), equivalent to Albic Luvisols and Dystric Cambisols (IUSS Working Group WRB, 2014), and have significant surface accumulations of organic matter and low productivity due to a short growing season.

Soils are reconstructed during land reclamation in the Athabasca oil sands region using a range of materials salvaged during the mine activities. Soil cover generally consists of a 2-layer design, including cover soil underlain by subsoil that are salvaged within the lease development area. Since approximately 50% of the pre-disturbance landscape consists of peatlands, a peat-mineral mix (PPM; <17% total organic carbon) salvaged from bogs and fens represents a large part of the cover soil in reclamation. Following soil reclamation, a new forest floor may begin to develop on top of the peat reclamation material. As this forest floor is developing in a novel ecosystem as defined by Hobbs et al. (2009), it will be referred to in the remainder of this manuscript as the “novel” forest floor.

Once constructed, soils are seeded either with barley (*Hordeum vulgare* L.) or native and non-native grasses in the initial year following reclamation to enhance soil stabilization and reduce erosion before they are planted to trees including white spruce, trembling aspen, and jack pine (Rowland et al., 2009; Turcotte et al., 2009). Novel soils are then left to undergo reclamation succession.

2.2.2. Site selection

Fifteen reclaimed stands were chosen from a network of stands previously described in Quideau et al. (2013) and Sorenson et al. (2011). In short, these stands were selected within an 80 km radius of Ft. McMurray to include a range of age classes, where "age class" refers to the time since soil reconstruction. As much as possible, sites were selected to include comparable slope, aspect, and salvaged materials used during soil reconstruction (reclamation prescription); in particular, all soils had been capped with about 20 cm of peat-mineral mix. These fifteen stands formed a chronosequence ranging in age from eight to thirty-three years (Table 1). Selected age classes included: young reclaimed (8-11 yrs.), mid-reclaimed (17-25 yrs.), and old reclaimed (30-31 yrs.) sites. Sites were further selected to include replicates of aspen and white spruce stands within each age class (Table 1). Young reclaimed stands represent the starting point of both the aspen and white spruce chronosequences; while they were planted to a combination of aspen and white spruce, to date they have no canopy development. Natural sites including a total of five replicates of undisturbed aspen and white spruce stands located in the surrounding undisturbed forest were chosen as references to the reclaimed stands.

2.2.3. Field sampling

Sample collection occurred in July and August 2015. Each site was surveyed at the stand level by establishing a 20 m x 20 m (400 m^2) plot around the central point to conduct vegetation surveys. Additionally, four plots were established within the 400 m^2 plot in the four cardinal directions, 10 m from a central point for oribatid mite sampling. Tree density (no. trees/ 400 m^2) and diameter at breast height (DBH) of all trees were measured within the plot. Tree age was determined in natural stands by analyzing the rings of core samples taken with an increment borer of the three trees with the largest DBH. At the oribatid mite sample plots, surveys were conducted to record leaf area index (LAI) using a Licor-2200C and included: understory LAI (30 cm above soil surface) and overstory LAI (100 cm above soil surface). Understory vegetation species were determined using a square that measured 1 m^2 with 25 individual 20 cm x 20 cm squares (Johnson, Kershaw, and MacKinnon, 1995). Additionally, percent ground cover was recorded using a 1 m^2 square for the following categories: moss, lichen, bare ground, leaf litter (all deciduous litter), coarse woody debris, conifer needles, and shrubs.

Oribatid mite sampling was based on the Alberta Biodiversity Monitoring Institute (ABMI) terrestrial protocol, using a modified version of the organic soil protocol for arthropods (Alberta Biodiversity Monitoring Institute, 2010). At each oribatid mite sampling plot, four forest floor and/or peat-mineral mix subsamples were collected to a total depth of 7.5 cm using a 7.5 cm diameter metal core and composited to one 500 cm^3 sample. Soils within reclaimed stands were sampled according to the thickness of the novel forest floor. When the forest floor thickness exceeded 2 cm, it was considered a novel forest floor (R.FF) and was sampled independently from the underlying peat-mineral mix (PMM). Novel forest floor thickness ≤ 2 cm (R.FF+PMM) was sampled collectively with the underlying PMM, resulting in three material types sampled from the reclaimed stands: R.FF, PMM, and R.FF+PMM. A total of 104 samples were collected in the chronosequence for oribatid mite extraction. In addition, at each oribatid mite sampling plot, novel forest floor ≥ 2 cm and natural forest floor were sampled for moisture content and bulk density using a 10 cm x 10 cm square and sampling to depth of the forest floor. The underlying PMM and novel forest floor ≤ 2 cm were sampled by collecting a 7.5 cm x 7.5 cm metal soil core.

2.2.4. Laboratory and chemical analyses

Bulk density (g/cm^3) and gravimetric moisture content (g/g; %) of all samples was determined by weighing samples before and after oven drying at 65°C for 48 hours (Kalra and Maynard, 1991). pH was measured on the air-dried samples following oribatid mite extraction with an Accument XL200 pH meter using a slurry of 1:4 organic sample to 0.01 M $CaCl_2$ solution (Kalra and Maynard, 1991). The remainder of each air dried sample used for oribatid mite extraction was then finely ground with a ball mill and analyzed for total carbon and nitrogen concentrations through dry combustion using a Thermo FLASH 2000 model combustion Elemental Analyzer.

2.2.5. Oribatid mite extraction and identification

Soil cores were extracted within seven days of field collection according to the ABMI processing of mites and springtails protocol (Alberta Biodiversity Monitoring Institute, 2014). Fresh soil samples were placed on a modified Tullgren type extractor for seven days as recommended by Crossley and Blair (1991). Extracted specimens were preserved in 95% ethanol until processing occurred, including sieving specimens to > 300 μm, separating oribatid mites from other mesofauna, and identifying to species when possible with a Leica M165-C stereomicroscope (7.3x-120x magnification). When necessary, specimens were cleared in 85% lactic acid for three days, mounted on slides using polyvinyl alcohol, and oven dried for seven days at 55-60°C. Specimens were identified to species using a Leica DM 2500 compound microscope and identification keys from the Almanac of Alberta Oribatida 2014 (Walter et al., 2014).

2.2.6. Statistical analysis

The study design included four age classes: young reclaimed (YR), mid-reclaimed (MR), old reclaimed (OR), and natural (NAT); two canopy types: white spruce (Sw) and trembling aspen (Aw); and four material types as explained in the Field Sampling methods: natural forest floor (N.FF), novel forest floor (R.FF), novel forest floor + peat-mineral mix (R.FF+PMM), and peat-mineral mix (PMM). The YR stands will only be referred to as YR with no canopy type designation as there was no developed canopy type at the time of sampling. All data were analyzed using packages in R statistical software version 3.2.4 (R Development Core Team, 2016). Trends were represented by the strength of the p-value in relation to the p-values of other comparisons within any single analysis (Hurlbert and Lombardi, 2009; Nuzzo, 2014).

Site characteristics were analyzed for differences among the seven age classes and canopy type combinations, and soil characteristics were analyzed for differences among the four material types. All site and soil analyses were performed using a permutational analysis of variance (ANOVA). Oribatid mite abundance, richness, and diversity were compared among canopy types, age classes, and material types. Abundance was represented as the count of individuals/sample (500 cm^3). Species richness was represented as the total count of different species in the four subsamples composited to 500 cm^3. Trend strength was computed using a permutational ANOVA followed by Tukey's Honest Significant Difference (HSD) *post-hoc* testing. In stands where a novel forest floor was formed and two materials were sampled (R.FF & PMM), data were standardized using the proportion (thickness) of each horizon in the 7.5 cm soil core. A non-linear regression was applied to the relationship between forest floor thickness and mean richness. The goodness of fit of the logarithmic curve was determined by calculating R^2 and root-mean squared error (RMSE). RMSE was calculated by squaring the mean residuals of the model and then taking the square root of that value. The best model is the model that produces the lowest RMSE and the highest R^2 (Sorenson et al., 2017). The non-linear regression equation was computed in R using package 'minpack.lm' (Elzhov et al., 2016). Permutational ANOVA was computed in R using the 'lmPerm' package (Wheeler and Torchiano, 2016).

Diversity indices were calculated for overall community diversity and evenness. Relative abundance ((no. individuals per species/ total individuals per site) x 100) was calculated and used to compute Hill numbers expressed as “Q” (Hill 1973; Jost 2006). Hill numbers translate traditional indices such as Shannon entropy (H’) and Simpson’s index (D) into the effective number of species (ENS) by taking the exp(H’) and the inverse Simpson’s (1/D). These indices are now in comparable units and follow the “doubling principle”, which better represents the magnitude of change in a community compared to traditional diversity indices (Jost, 2006). The exp(H’) (Q1) was plotted against 1/D (Q2), and diversity indices were calculated in R using the VEGAN package (Oksanen et al., 2015).

Oribatid mite community composition was analyzed using non-metric multidimensional scaling (NMDS) followed by permutational multiple analysis of variance (MANOVA). The NMDS organized the species data into 2D space and determined similarity between treatments using distance measures. As oribatid mite species data were zero-inflated, the Hellinger distance was used. Using the Hellinger transformation followed by Euclidean distance in an ordination is identical to the Hellinger distance between the original row vectors of species abundances (Legendre and Gallagher, 2001). This transformation is favorable for oribatid mite composition data as to not exclude rare species, but to assign them low weight in comparison to abundant species. Additionally, this transformation does not identify cells containing zeros as being more similar in ordination space; a common cause of inappropriate clustering of dissimilar sites due only to the fact of neighboring cells containing zeros. All measured site and soil characteristics were considered as potential vectors in the NMDS. Sites in the NMDS were distinguished by the independent variables canopy and material type. NMDS and vector fitting was performed using the VEGAN package in R version 3.2.4 (Oksanen et al., 2015), and permutational MANOVA was conducted using package RVAideMemoire (Hervé, 2017).

Indicator species analysis was used to identify species most strongly associated with the independent variables. Strong indicator species were analyzed based on their specificity and fidelity for each site group. Specificity (probable predictive value) represents exclusivity, where species x only belongs to site A. Fidelity (sensitivity) refers to species x that is always faithful to site A. Indicator species analysis was performed using R with the ‘indicspecies’ package (Cáceres and Legendre, 2009).

2.3. Results

2.3.1. Key site and soil characteristics

Tree diameter increased among reclaimed sites from young to old, and was largest within the natural sites; white spruce trees consistently had larger diameters than aspen trees at similar age classes (Table 2). Tree density in reclaimed aspen stands exhibited high variability, ranging from a minimum of 15 trees/400 m^2 in an old reclaimed stand to a maximum of 87 trees/400 m^2 in a mid-reclaimed stand. Reclaimed white spruce stands exhibited a narrower range of variability, with densities from a minimum of 15 trees/400 m^2 in a mid-reclaimed stand to a maximum of 66 trees/400 m^2 in a different mid-reclaimed stand. The wide range of variation led to very weak differences in tree densities among reclaimed aspen and white spruce stands ($p = 0.72$, Table 2). However, differences in both overstory and understory vegetation in reclaimed aspen and white spruce stands led to differences in percent ground cover. Leaf area index (LAI) in reclaimed stands measured at 100 cm was lowest in young (zero) and was highest in old reclaimed white spruce stands ($p = 0.28$). Similarly, understory LAI in reclaimed stands measured at 30 cm was lowest in young and highest in old reclaimed white spruce stands ($p = 0.22$).

Stands differed very strongly in percent ground cover by leaf litter (p = < 0.0001), especially between mid-reclaimed aspen stands vs. mid-reclaimed white spruce stands (p = 0.0004). Leaf litter originated in both aspen and white spruce stands from deciduous (dominant and non-dominant) trees and deciduous or grassy understory vegetation. Deciduous overstory species other than aspen found in reclaimed aspen stands included paper birch (*Betula papyrifera* (Marshall)), and only two reclaimed aspen stands were not purely aspen. Deciduous overstory species found within the reclaimed white spruce stands included trembling aspen, paper birch, balsam poplar (*Populus balsamifera* (L.)), and the large shrub red-osier dogwood (*Cornus sericea* (L.)). Five of the seven reclaimed white spruce stands were not purely white spruce and contained some deciduous overstory species. Understory species richness was higher in natural than reclaimed stands for both aspen (young reclaimed (p = 0.0001), mid-reclaimed (p = 0.0001), old reclaimed (p = 0.0002)) and white spruce (mid-reclaimed (p = 0.02), old reclaimed (p = 0.03)), but differences were very weak between reclaimed aspen and white spruce stands (mid-reclaimed (p = 1.0); old-reclaimed (p = 0.99)) within similar age classes (Table 2). Although differences in species richness among reclaimed stands were minor, there were differences in species composition. Grass (*Poaceae* spp.) dominated the understory vegetation in young reclaimed and mid-reclaimed aspen stands. Mid-reclaimed aspen stands also supported dandelion (*Taraxacum officinale* (F.H. Wigg)) and Canada thistle (*Cirsium arvense* ((L.) Scop.)). Conversely, reclaimed white spruce stands were dominated by moss spp. and wild strawberry (*Fragaria virginiana* (Duchesne)). Young and mid-reclaimed white spruce were the only stands with bare soil present, although this remained a very small percentage of ground cover (1%). Dominance by moss spp. in mid-reclaimed white spruce stands resulted in mid-reclaimed white spruce having the highest percent ground cover by moss (56%) among any other stand in the chronosequence. There were very weak differences between aspen and white spruce stands in all age classes for percent cover by lichen and coarse woody debris.

Four of the six stands that had developed a novel forest floor were under aspen canopies, and there was an equal split between mid-reclaimed (2 Aw; 1 Sw) and old-reclaimed (2 Aw; 1 Sw) stands. Forest floor characteristics varied very strongly depending on the material type sampled (Table 3). While the forest floor present at the natural stands was thicker than the novel forest floor developed within the reclaimed stands ($p = < 0.0001$), moisture content and bulk density were very similar for the two materials. Moisture content differed strongly among the four material types ($p = 0.006$), and was moderately higher in the natural and novel forest floors than in the novel forest floor + peat-mineral mix ($p = 0.02$; $p = 0.01$). Bulk density differed very strongly among the four material types ($p = < 0.0001$), and was moderately lower in the natural and novel forest floors than in the novel forest floor + peat-mineral mix ($p = 0.02$; $p = 0.01$) and peat-mineral mix ($p = 0.02$; $p = 0.01$). There were no strong differences in pH values or C: N ratios among the different materials (Table 3).

2.3.2. Oribatid mites

2.3.2.1. Abundance

When age was not confined by canopy type, there was a moderate difference in oribatid mite abundance between the natural and mid-reclaimed stands ($p = 0.03$); natural stands were weakly similar to both the old ($p = 0.09$) and young reclaimed ($p = 0.15$) stands (data not shown). However, neither age class or canopy type was a strong indicator of oribatid mite abundance in reclaimed stands (Figure 2a). Within each canopy type, there were weak differences among age classes. Mite abundance appeared to be decreasing in reclaimed aspen and white spruce stands with time since reclamation. Due to the wide range of variability among reclaimed stands, only a weak difference was detected in abundance between mid-reclaimed and natural white spruce stands (p = 0.18). All other comparisons showed little differences (p = > 0.5). On the other hand, material type was a strong predictor of oribatid mite abundance (Figure 2b). Both the natural and novel forest floors hosted the highest mite abundances. The novel forest floor sustained slightly higher abundances than those in natural forest floors (p = 0.99). While the difference in mean forest floor thickness was only 1.5 cm between the novel forest floor and the novel forest floor + peat-mineral mix, these two materials showed strong differences in abundance. The natural and novel forest floors supported higher oribatid mite abundances than the novel forest floor + peat-mineral mix (p = 0.006; p = 0.002) and peat-mineral mix (p = 0.007; p = 0.003).

2.3.2.2. Richness and diversity

When age was not confined by canopy type, species richness in natural stands was strongly different from the old reclaimed stands (p = 0.007), and decreased in similarity from the young (p = 0.0009) to the mid-reclaimed stands (p = <0.0001; data not shown). Natural aspen stands showed a distinctly higher species richness than both young (p = 0.07) and mid-reclaimed (p = 0.007) aspen stands (Figure 3b). Strong differences were also seen in reclaimed white spruce stands where young (p = 0.03), mid (p = 0.0005), and old reclaimed (p = 0.04) stands were all lower in species richness than natural white spruce stands. Further, like abundance, oribatid mite species richness was affected more by material type than by either canopy type or reclamation age (Figure 3b). The natural and novel forest floors exhibited very weak differences in species richness (p = 0.20). Very strong differences in species richness existed among material types, where the natural floor exhibited higher species richness than both the novel forest floor +

peat-mineral mix ($p = < 0.0001$) and peat-mineral mix ($p = < 0.0001$). Similarly to the natural forest floor, the novel forest floor supported higher species richness than both the novel forest floor + peat-mineral mix ($p = 0.0002$) and peat-mineral mix ($p = 0.008$). The novel forest floor + peat-mineral mix supported the fewest number of species. The logarithmic trend highlighted in Figure 4 had an R^2 of 0.51 and a root-mean square error (RMSE) of 3.8. This trend indicated that as forest floor thickness increased, so did species richness (Figure 4).

Similar to mite abundance and species richness, when compared among age classes, community diversity and evenness were highest in the natural aspen and white spruce stands (Figure 5a). The distance between old reclaimed aspen and natural aspen stands was substantially smaller than the distance between old reclaimed white spruce and natural white spruce stands. Oribatid mite diversity and evenness were slightly higher in young than mid-reclaimed aspen and white spruce stands, but differences were small. In contrast, the notable increase in diversity and evenness in both the old reclaimed aspen and old reclaimed white spruce stands distinguished them from the earlier age classes and indicated a trend towards natural mite diversity in aspen and white spruce stands. Material type was a stronger predictor of community diversity recovery than age class or canopy type. Diversity followed an almost identical trend to the one seen for species richness in Figure 3b, where diversity and evenness were lowest in the novel forest floor + peat-mineral mix, followed by the peat-mineral mix and novel forest floors, and was highest in natural forest floors (Figure 5b).

2.3.2.3. Species composition

In order to visually assess potential differences in the species makeup of oribatid mite communities among sites, non-metric multidimensional scaling (NMDS) was performed, resulting in a 2D solution with a final stress of 15.8% after 104 iterations (Figure 6). Material and canopy types resulted in the closest groupings in the ordination. Natural stands grouped together regardless of their differences in canopy type. In addition, the novel forest floor and the peat-mineral mix materials grouped closely to one another at each reclaimed site from which they were sampled. Contrastingly, communities in the novel forest floor + peat-mineral mix samples differed greatly from one another and from all other material types. Results from the permutational MANOVAs indicated that canopy type moderately influenced community variation within the reclaimed aspen and white spruce stands ($p = 0.02$). Oribatid mite communities found under aspen differed moderately from those found under white spruce stands ($p = 0.024$) and white spruce communities differed moderately from those in young reclaimed stands ($p = 0.028$). On the other hand, only weak differences existed among the four material types ($p = 0.12$).

The variation in mite communities shown in the NMDS was correlated with several environmental variables. The strength of the environmental variable is indicated by the length and direction of the vector arrow in ordination space, and is related to mite communities that cluster in a similar ordination space as the vectors point. Correlation vectors indicated that the percent cover by leaf litter ($p = 0.04$, $R^2 = 27\%$) and tree density within the 400 m^2 plot ($p = 0.08$, $R^2 = 13\%$) were moderately associated with material types found under reclaimed aspen canopies. Additionally, percent cover by moss ($p = 0.01$, $R^2 = 42\%$) and moisture content ($p = 0.03$, R^2 23%) were moderately correlated with material types formed under reclaimed white spruce canopies. Other environmental variables associated with forest floor characteristics indicated no relationship to the variation in oribatid mite communities, such as pH ($p = 0.89$) and C: N ratio ($p = 0.40$)

A total of 1198 adult oribatid mites (> 300 μm), including 54 species from 23 families, were identified in both natural and reclaimed stands (Table 4). Of the seven species found in all material types, *Ceratozetes gracilis* (Michael, 1884) (9 individuals /500 cm^3) and *Chamobates cuspidatus* (Michael, 1884) (8 individuals/500 cm^3) had the highest mean abundance in all material types. Of the 36 species found in the natural forest floor, 15 (42%) were unique to the natural forest floor and not found in any other material type. Twenty-nine species were found in the novel forest floor, and 7 (24%) were unique to the novel forest floor and not found in any other material type. Finally, of the fifteen species found in the novel forest floor + peat-mineral mix, four (26%) were unique to the novel forest floor + peat-mineral mix. The peat-mineral mix had no unique species. Further, 14 (93%) of the species found in the peat-mineral mix were shared with the novel forest floor. When comparing the natural and novel forest floors only, eighteen species were shared between the natural forest floor (50%) and the novel forest floor (62%). The natural forest floor had 18 species (50%) that were not shared in common with the novel forest floor, and the novel forest floor had 11 species (38%) that were not shared in common with the natural forest floor.

2.3.2.4. Indicator species

The strongest evidence of an indicator species was associated with unique species established in natural aspen and white spruce stands (Table 5). Among the reclaimed stands, the old reclaimed aspen stands were the only group where an indicator species was identified. This indicator species (*Pilogalumna* sp. 1 DEW) was only supported in fidelity, meaning that it was always found in the old reclaimed aspen stands. Additionally, it was one of the seven species found in at least one age class/canopy type replicate of all sites in the chronosequence (Table 4). The natural aspen and natural white spruce stands were the only stands associated with species that were exclusively found at these sites (Table 5). The strongest indicator potential was seen in natural aspen stands as one species (*Ceratoppia quadridentata arctica*) was exclusive to these stands and two species were always found at these stands.

2.4. Discussion

2.4.1. Oribatid mite abundance, richness, and diversity

While time since reclamation may play a role, it was a weaker predictor of oribatid mite abundance, richness, and diversity than material type. We hypothesized that abundance would follow a linear trajectory from young to old reclaimed stands, as this was previously reported after spontaneous succession and soil reclamation in Eastern Europe (Frouz and Nováková, 2005; Frouz et al., 2001). However, neither aspen or white spruce stands reflected this trend. Abundance was highest in the natural white spruce stands, which aligns with high abundances found in coniferous stands vs. deciduous and mixedwood stands in Quebec (Sylvain and Buddle, 2010). The minimal effect of time since reclamation on mite communities as observed in this study, has also been documented for soil microbial communities in the Athabasca oil sands region (Dimitriu et al., 2010). In our study, the accumulation of novel forest floor materials was the principal factor affecting the recovery of mite abundance, richness, and diversity. Similarly, Frouz and Nováková (2005) found that microbial abundance and biomass began to reflect that of natural stands after organic matter increased at the soil surface. Additionally, they reported that once vegetation shifted away from primarily shrub-dominated, the presence of overstory species (*Populus tremuloides* and *Betula* spp.; 25-41 years since reclamation) increased, and microbial communities grew more similar to those in undisturbed forests.

The resemblance observed between mite abundances found in the natural and novel forest floors may be a result of mite species that were already present in the peat-based materials when soils were reconstructed and that are beginning to establish in the novel forest floors (Fig. 3a). This may be supported by the similarity in species identified between the peat-mineral mix and the novel forest floor (93%). Similar to abundance, species richness was comparable in both the natural and novel forest floors (Fig 3b), and this may be a result of the increased habitat complexity at the soil surface provided by the novel forest floor (Anderson, 1977). The logarithmic relationship observed in our study between forest floor thickness and mite species richness suggests that species richness will continue to increase as the novel forest floor thickens (Fig. 4). Future increases in novel forest floor species richness may come from the dispersal of species present in adjacent undisturbed stands, but long-term monitoring and comprehensive community descriptions in adjacent stands are necessary to investigate this assumption further.

In addition to abundance and richness, oribatid mite communities were assessed for overall diversity. Measuring diversity is essential to understanding colonization patterns in disturbed landscapes (Zaitsev et al., 2002). Material type was again a stronger predictor of mite community diversity than either age class or canopy type (Fig. 5a/b). Compared to abundance, diversity more closely followed the hypothesized linear trajectory with reclamation age, and old reclaimed aspen and white spruce stands were separating out from other reclaimed stands (Fig. 5a). Natural forest floors had the highest mite diversity, followed by novel forest floors (Fig. 5b). The presence of a novel forest floor also boosted mite diversity in the underlying peat-mineral mix. This close relationship between mite diversity and the forest floor thickness has been recorded after other large-scale ecological disturbances, such as fire and forestry. In post-fire landscapes, burn severity (depth) of the forest floor was reported as the biggest contributor to mite diversity loss after both natural and prescribed burns in Scandinavia (Malmström, 2006). This relationship was further supported by observations by Battigelli et al. (2004), who documented the lowest levels of mite diversity in soils where the forest floor had been removed or compacted. In the present study, the lowest measures of diversity were recorded in the peat based materials with minimal forest floor (Fig. 5b). On the other hand, industrial practices that leave the forest floor somewhat intact, such as low-impact forest harvesting practices have noted minimal changes in mite diversity following disturbance (Bird and Chatarpaul, 1986; Lindo and Visser, 2004). This reinforces the importance of the nascent novel forest floor observed at the reclaimed stands, which, if left intact, may provide mite communities with increased stability and resilience against future disturbance.

2.4.2. Oribatid mite species composition

Species composition differed between natural and novel forest floors and was most similar between the novel forest floor and underlying peat-mineral mix (Fig. 6). The high percentage of unique species in natural forest floors (15/36, 42%) and novel forest floors (7/29, 24%) indicate that these communities are distinctly different. These results suggest that species in novel forest floors are not simply a subset of the same species found in natural forest floors (Table 4), concurring with the distinct communities observed by Lindo and Winchester (2006) in suspended (canopy) forest soils vs. grounded forest soils within the same stand. Parthenogenetic species have been hypothesized to dominate disturbed landscapes, but in our study, only two parthenogenetic species, *Tectocepheus sarekensis* Trägårdh, 1910 and *Trhypochthonius tectorum* (Berlese, 1896) *s.l.,* were detected in the novel forest floors. *T. sarekensis* has been found in high abundances at sand and manganese quarry dumps (Murvanidze et al., 2013), and has dominated soil communities at coal dumps (Frouz et al., 2001). Its relatively small body size (295-360 μm) may have limited the number of specimens detected in our study as only species > 300 μm were analyzed. Conversely, *T. tectorum* has a body size well within the range of what was analyzed in this study, and was still detected at low abundances in reclaimed soils (< 1 individual/ sample). A complete species analysis (< 300 µm) would be necessary to make further inferences regarding differences in species composition.

Lastly, indicator species analysis identified species unique to natural stands as indicators, but no pioneer or parthenogenetic species were identified as indicators (Table 5). Lindo and Visser (2004) saw no clear pattern in the changes in abundance of detected partheogenetic species after soil disturbance in Alberta. These results indicate that differences in species composition between natural and novel forest floors is likely due to the loss of unique or rare species in novel communities as opposed to the inflation of parthenogenetic or pioneer species. The former has been documented as a cause of increased community evenness after fire in Scandanavia (Malmström, 2006), and after forest floor removal in British Columbia (Battigelli et al., 2004). These findings suggest that while species composition remains different, a novel forest floor is essential for recovering initial mite abundance, richness, and diversity.

2.4.3. Novel habitat development

Environmental variables that promoted novel forest floor formation included percent ground cover by leaf litter and tree density (Table 2, Fig. 6). Reclaimed stands with novel forest floors that formed under aspen canopies (4/6, 67%) were correlated with a high percentage of ground cover by leaf litter. This factor may have resulted in thicker novel forest floors formed under aspen canopies, which Sorenson et al. (2011) reported as an outcome of aspen canopies vs. either spruce or pine canopies; they further attributed this to the early establishment of aspen canopies compared to spruce or pine canopies at similar reclamation ages. Similarly, tree density was positively correlated with mite communities under reclaimed aspen canopies (Fig. 6). The correlation of these factors to mite communities in reclaimed aspen stands (4/6 novel forest floors) may have mimicked the rapid regeneration of aspen suckers (2.5 years) after clearcutting as observed in Lindo and Visser (2003, 2004); rapid regeneration further caused only marginal differences in mite abundances between clear-cut and undisturbed aspen stands, which can be compared to the similarities in abundances observed in novel and natural forest floors in this study. These environmental variables appear to have played the biggest role in forming a novel forest floor. The recovery of mite abundance, richness, and diversity is likely a result of the increased habitat complexity in novel forest floors, creating microhabitats for the formation of food resources, breeding, and reproduction (Hansen, 2000).

In addition to the aforementioned environmental variables, several soil properties may have played a role in mite recolonization. Bulk density was strongly reduced in novel forest floors compared to the peat-mineral mix and novel forest floor + peat-mineral mix (Table 3). Similar results have been documented in Battigelli et al. (2004) and Lindo and Visser (2003), who identified forest floor compaction as a main factor causing a reduction in oribatid mite diversity and mesofauna abundances, respectively. Additionally, Battigelli et al. (2004) reported that if preserved, the forest floor may act as a buffer against changes in mineral soil bulk density when compared to soils where the forest floors were removed. Conversely, a decrease in bulk density in the peat-mineral mix underlying the novel forest floor was not observed in this study. Future decomposition of the peat-mineral mix and an increase in biological activity in these reclaimed soils may create a more suitable habitat for mite recolonization in the peat-mineral mix. Moisture content and litter thickness have also been noted to impact mite species richness in suspended and grounded forest floors of red cedar stands (Lindo and Winchester, 2006). While forest floor thickness was only slightly higher in the novel forest floor compared to the novel forest floor + peat-mineral mix, its moisture content was significantly higher (Table 3). A combination of these habitat traits in novel forest floors appear to be increasing the inhabitability of both novel forest floors and the underlying peat-mineral mix by mite communities (Fig. 5b, 6).

2.4.4. Reclamation success and future monitoring

After resource extraction, it is important to reconstruct soils in a way that will promote the restoration of biogeochemical cycling in reconstructed soils (Bradshaw, 1984; Chapin et al., 1996; Quideau et al., 2013). The successful recovery observed in mite abundance, richness, and diversity during this study (8-31 yrs.) in novel forest floors suggests that the capacity of the mite community to function has likely been restored; but this is only one way to characterize "reclamation success". Success can also be characterized in regards to the conservation of species found before disturbance, as the differences observed in species composition between natural and disturbed landscapes may be permanent (Marshall, 2000). Natural forest floor communities remain distinctly different from those in novel forest floors, peat-mineral mix, and novel forest floor + peat-mineral mix (Fig. 6). Fifteen of the 36 species in natural forest floors were unique, but not all unique species are rare. *Atropacarus striculus* (C.L. Koch, 1835) was unique to natural forest floors, but is recorded as being common and even abundant in Alberta's boreal forest (Walter et al., 2014). Therefore, the presence of these common but unique species to boreal forests in novel forest floors may be a sign of reclamation success. On the other hand, rare species that were present in the natural forest floors were likely supported by a level of habitat complexity that took decades to develop (Anderson, 1977), and we may not see these species return to novel forest floors for many years, if ever.

The original habitat of mites is reduced in soils undergoing reclamation, and the novel forest floor habitat may foster distinct ecological processes (Haila, 2002). Indeed, these novel forests are essentially “habitat islands”, representing areas of the landscape that now have a different distribution and orientation of soil and/or above-ground vegetation. The biogeochemical properties in these novel habitats may continue to be different from the surrounding undisturbed forest matrix for the long-term. If reclaimed stands remain different from natural stands, the recovery of unique and/or rare boreal forest mite species may be low (MacArthur and Wilson, 1967; Maraun et al., 2007), which was the case in all reclamation materials in this study. We also found that even in some of the older stands (~31 yrs.), a novel forest floor had not yet formed, indicating a lack of physical soil recovery that may have resulted from a thin stand density or lower litter inputs in white spruce stands. As a result, species composition was different between reclaimed and natural soils, and can be anticipated to stay different until a thicker novel forest floor is developed. Additionally, major limitations for oribatid mite dispersal may interfere with the immediate possibility of mite communities in the novel and natural forest floors to become similar. Research regarding the immigration of oribatid mites after mining suggests that wind dispersal, while slow, is the dominant mode of mite immigration into disturbed stands (Wanner and Dunger, 2002). Depending on the distance of novel forests to the undisturbed forest matrix, active dispersal may occur, but may be only possible for specific species with appropriate feeding and reproductive strategies (Lehmitz et al., 2011; Lehmitz et al., 2012).

Although results on mite abundance, richness, and diversity support the idea of a successful recovery at the studied sites, it is necessary to determine if rare and/or unique species will also be able to eventually re-inhabit these reclaimed sites as tree stands mature and the novel forest floor continues to develop. In addition, while there were definite trends in the > 300 μm size class included in this study, further research into community characteristics of specimens <

300 µm is necessary to identify if recovery is possible for the whole mite community. In particular, species from families Suctobelbidae and Oppiidae have been found to be the most likely to immigrate into novel ecosystems via active dispersal (Lehmitz et al., 2012). Species from these families and of the included size range (>300 um) are documented for the Athabasca oil sands region (Walter et al., 2014) but were not detected in the present study. Future analyses of the whole mite community must include both abundance and taxonomic approaches in order to identify and correctly interpret trends in mite communities in these post-mining landscapes. In addition to mite community analyses, it is important to include analyses involving other faunal groups that comprise the soil food web. It is anticipated that the soil food web and its interaction with the soil environment will increase in complexity after disturbance, emphasizing the need for research regarding soil fauna responses to ecosystem disturbance with a focus on the relationship of soil fauna to vital soil processes (Coyle et al., 2017).

Oribatid mites are crucial regulators of forest floor habitat and decomposition in boreal forest soils, and may provide useful information regarding soil development and habitat sustainability after oil sands mining. The development of a novel forest floor in reclaimed stands is the most effective way to restore levels of mite abundance, richness, and diversity similar to those found in undisturbed stands. Percent ground cover by leaf litter and tree density were positively correlated with oribatid mite community composition, and four of the six stands with a novel forest floor were aspen stands. Hence it appears that rapid mite community reestablishment could be enhanced by planting more reclaimed stands with deciduous overstory species (aspen). Additionally, diversity indices revealed that reclaimed aspen stands were on a faster trajectory toward community recovery than reclaimed white spruce stands. The similarities between the novel and natural forest floor in terms of mite abundance, richness, and diversity indicate that these reclaimed stands are likely on track to ecosystem recovery. However, the overall composition of the mite communities developing in the novel forest floors at reclaimed sites is still distinctly different from those in natural sites. Monitoring reclaimed sites over time is essential to understand oribatid mite recolonization patterns following oil sands mining in Alberta.

Tables and Figures

Table 2-1. Experimental design of the chronosequence in the Athabasca Oil Sands Region of Alberta, Canada. Age classes include: young reclaimed (YR, 8-11 yrs.), mid-reclaimed (MR, 17-25 yrs.), old-reclaimed (OR, 30-31 yrs.), and natural (NAT) stands.

Site ID	Location (°N, °W)	Age class	Stand age (yrs) †	Dominant tree species‡	Reclamation prescription/soil type§
1	56.9987, -111.6154	YR	11	Aspen/White spruce	PMM/MS/OB
2	57.0101, -111.7224	YR	8	Aspen/White spruce	PMM/MS/OB
8	57.0100, -111.7224	YR	8	Aspen/White spruce	PMM/MS/OB
3	57.0012, -111.6087	MR	24	Aspen	PMM/OB
4	56.9956, -111.6191	MR	17	Aspen	PMM/OB
11	57.0833, -111.6121	MR	27	Aspen	PMM/MS/TS
13	56.9925, -111.5631	MR	25	White spruce	PMM/LOS
16	56.9910, -111.5369	MR	24	White spruce	PMM/OB
17	56.9922, -111.5369	MR	23	White spruce	PMM/OB
18	56.9977, -111.5336	MR	24	White spruce	PMM/OB
12	56.9911, -111.5641	OR	31	Aspen	PMM/MS/OB
20	56.9984, -111.5480	OR	30	Aspen	PMM/OB
14	56.9933, -111.5710	OR	30	White spruce	PMM/MS/OB
15	57.0237, -111.4997	OR	31	White spruce	PMM/OB
19	56.9987, -111.5472	OR	31	White spruce	PMM/OB

6	56.9638, -111.7217	NAT	54	Aspen	Gleyed Gray Luvisol
7	56.9586, -111.7229	NAT	60	Aspen	Gleyed Gray Luvisol
10	57.2567, -111.6238	NAT	42	Aspen	Orthic Dystric Brunisol
5	56.9440, -111.7392	NAT	35	White spruce	Gleyed Gray Luvisol
9	57.0201, -111.7271	NAT	103	White spruce	Orthic Gray Luvisol

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[†] Reclamation age is ‘time since reclamation’; natural stand age is from tree ring counts.

[‡] Age class “YR” had no canopy development but was planted to aspen and white spruce.

[§] PMM: peat and mineral substrate. MS: subsoil; TS: tailings sand; LOS: lean oil sand. See AMEC and Paragon, 2005 for more detailed information and reclamation prescriptions.

Table 2-2. Mean and standard error of site characteristics at natural stands and stands undergoing reclamation after oil sands mining in the Athabasca Oil Sands Region of Alberta, Canada. Age classes include: young reclaimed (YR, 8-11 yrs.), mid-reclaimed (MR, 17-25 yrs.), old-reclaimed (OR, 30-31 yrs.), and natural (NAT) stands. Dominant canopy types include trembling aspen (Aw) and white spruce (Sw). Different letters indicate differences between age/canopy groups within row variables with a strong p-value ($p<0.05$).

Age	YR	MR		OR		NAT		p-value
Canopy	Both (*n* = 3)	Aw (*n* = 3)	Sw (*n* = 4)	Aw (*n* = 2)	Sw (*n* = 3)	Aw (*n* = 3)	Sw (*n* = 2)	
Tree density (400 m^2)	23 ± 5	48 ± 20	35 ± 12	43 ± 28	40 ± 9	33 ± 4	17 ± 6	0.72
Diameter at breast height (DBH)	3.2 ± 2.1	5.3 ± 1.2	8.5 ± 3.1	8.7 ± 4.1	12.5 ± 1.0	10.3 ± 1.1	14.6 ± 3.1	0.06
Leaf Area Index (m^2 m^{-2}) 30 cm	0.8 ± 0.6	2.4 ± 0.2	3.9 ± 1.1	2.9 ± 0.5	4.6 ± 1.7	3.0 ± 0.6	3.7 ± 0	0.22
Leaf Area Index (m^2 m^{-2}) 100 cm	0 ± 0	2.3 ± 0.5	3.2 ± 1.4	2.6 ± 0.3	3.9 ± 1.2	2.3 ± 0.4	3.3 ± 0.3	0.28

Moss (%)	10 ± 8	0 ± 9	56 ± 22	13 ± 2	13 ± 3	6 ± 3	13 ± 10	0.07
Bare soil (%)	1 ± 0	0 ± 0	1 ± 1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.54
Leaf litter (%)	49 ± 15bcd	100 ± 0a	22 ± 2cd	71 ± 3ab	10 ± 5d	91 ± 4ab	66 ± 30abc	**<0.0001**
Shrub (%)	7 ± 5	4 ± 3	0 ± 0	1 ± 0	1 ± 1	12 ± 1	5 ± 3	0.07
Coarse woody debris (%)	9 ± 8	2 ± 1	6 ± 4	9 ± 1	6 ± 1	7 ± 2	10 ± 5	0.91
Lichen (%)	0 ± 0	0 ± 0	0 ± 0	0 ± 0	4 ± 4	0 ± 0	1 ± 1	0.75
Understory richness (no. spp. m^{-2})	12 ± 1bc	9 ± 0c	9 ± 2c	8 ± 1c	9 ± 0c	24 ± 2a	18 ± 3ab	**<0.0001**
Dominant understory species	*Fragaria virginiana* (Duchesne)	*Cirsium arvense* (L.) Scop.	*Fragaria virginiana* (Duchesne)	*Fragaria virginiana* (Duchesne)	*Fragaria virginiana* (Duchesne)	*Cornus canadensis* (L.)	*Equisetum pratense* (Ehrh.)	
	Poaceae spp.	*Poaceae* spp.	Moss spp.	*Pyrola* spp.	Moss spp.	*Linnaea borealis* (L.)	*Mitella nuda* (L.)	
	Rubus idaeus (L.)	*Taraxacum officinale* (F.H Wigg)	*Taraxacum officinale* (F. H. Wigg.)	*Shepherdia canadensis* (L.) Nutt.	*Rubus idaeus* (L.)	*Rosa acicularis* (Lindl.)	*Rosa acicularis* (Lindl.)	

Table 2-3. Forest floor and peat-mineral mix characteristics of natural stands and stands undergoing reclamation after oil sands mining. Materials include novel forest floor + peat-mineral mix (R.FF+PMM), peat-mineral mix (PMM), novel forest floor (R.FF), and natural forest floor (N.FF). Values represent the mean and one standard error from the mean. Different letters indicate differences between material types within row variables with a strong p-value (p<0.05).

Material Type	R.FF+PMM (*n* = 9)	PMM (*n* = 6)	R.FF (*n* = 6)	N.FF (*n* = 5)	p-value
Bulk density (g/cm^3)	0.35 ± 0.08a	0.38 ± 0.04a	0.08 ± 0.01b	0.08 ± 0.01b	**<0.0001**
Gravimetric moisture content (g/g; %)	19 ± 4b	35 ± 7ab	53 ± 11a	51 ± 7a	**0.006**
Forest floor thickness (cm)	1.3 ± 0.1b	n/a	2.8 ± 0.4b	10.9 ± 2.1a	**<0.0001**
pH	6.5 ± 0.1	5.9 ± 0.3	6.3 ± 0.2	5.9 ± 0.3	0.06
C:N	29.3 ± 4.9	23.8 ± 2.4	21.5 ± 1.9	33.9 ± 4.8	0.2

Table 2-4. Mean oribatid mite species abundance in natural forest floor (N.FF), novel forest floor (R.FF), novel forest floor + peat-mineral mix (R.FF+PMM), and peat-mineral mix (PMM). Values in parentheses represent one standard error from the mean.

Family **Species**	N.FF	R.FF	R.FF+PMM	PMM	Location (Site ID) †
Euphthiracaridae					
Euphthiracarus flavus (Ewing, 1908)	0.55 (0.15)	0.13 (0.09)			5- 7, 9, 10-12
Rhysotritia ardua (C.L. Koch, 1841)	0.10 (0.10)	0.04 (0.04)			5, 12
Phthiracaridae					
Atropacarus striculus (C.L. Koch, 1835)	0.21 (0.16)			0.04 (0.04)	3P, 13, 15
Phthiracarus boresetosus Jacot, 1930	0.20 (0.15)	0.79 (0.55)			5, 10, 12, 15
Phthiracarus cf *borealis* (Trägårdh, 1910)		0.08 (0.05)			12, 15
Trhypochthoniidae					
Trhypochthonius tectorum (Berlese, 1896) s.l.		0.17 (0.17)		0.04 (0.04)	12P, 13
Hermanniellidae					
Hermanniella robusta Ewing, 1918	0.25 (0.25)				5
Gymnodamaeidae					
Gymnodamaeus cf *ornatus* Hammer, 1952	1.20 (1.14)				9, 10
Pleodamaeus sp. 1 DEW	2.05 (2.05)				10
Damaeidae					
Epidamaeus cf *fortispinosus* Hammer, 1967			0.03 (0.03)		16

Epidamaeus floccosus Behan-Pelletier & Norton, 1985		1.21 (0.76)		0.50 (0.45)	3, 12, 12P, 13, 13P, 15
Epidamaeus sp. 2 *DEW*	0.10 (0.10)	0.50 (0.32)			9, 11
Epidamaeus sp. 3 DEW			0.03 (0.03)		14
Compactozetidae					
Cepheus sp. 1 DEW	0.05 (0.05)	0.46 (0.46)			5, 10, 15
Cepheus sp. 2 DEW	0.05 (0.05)	0.04 (0.04)			15
Oribatodes mirabilis Banks, 1895	0.60 (0.30)				5, 7, 9, 10
Eremaeidae					
Eueremaeus quadrilamellatus (Hammer, 1952)	0.20 (0.20)				5
Eueremaeus marshalli Behan-Pelletier, 1993	0.05 (0.05)	0.21 (0.14)	0.03 (0.03)		13, 15, 19
Liacaridae					
Dorycranosus acutidens (Aoki, 1965)		0.04 (0.04)			15
Dorycranosus parallelus (Hammer, 1967)				0.04 (0.04)	15P
Peloppiidae					
Ceratoppia bipilis (Hermann, 1804)	0.05 (0.05)				6
Ceratoppia quadridentata arctica Hammer, 1955	0.25 (0.19)				5, 9
Carabodidae					
Carabodes granulatus Banks, 1895	0.05 (0.05)				6
Oppiidae					
Multioppia sp. 1 DEW		0.04 (0.04)			16
Thyrisomidae					
Banksinoma spinifera (Hammer, 1952)					8
Tectocepheidea					
Tectocepheus sarekensis Trägårdh, 1910		0.04 (0.04)			13

Phenopelopidae					
Eupelops sp. 2 DEW		0.79 (0.79)		0.04 (0.04)	15, 15P
Peloptulus sp. 1 DEW		0.21 (0.12)			3, 8, 12, 15
Propelops alaskensis (Hammer, 1955)	0.60 (0.38)				5, 6, 7
Propelops sp. 3 DEW	0.10 (0.10)				7
Tegoribatidae					
Tegoribates cf *americanus* Hammer 1958	0.05 (0.05)				5
Achipteriidae					
Achipteria sp. 1 DEW	2.55 (1.03)	2.04 (1.59)	0.06 (0.04)	0.13 (0.09)	3, 3P, 5-9, 15, 18, 19, 20P
Anachipteria cf *howardi* (Berlese, 1908)	0.05 (0.05)				10
Anachipteria sp. 1 DEW					8
Oribatulidae					
Lucoppia burrowsii (Michael, 1890)	0.05 (0.05)		0.09 (0.09)		2, 6
Oribatula sp. 1 DEW	0.15 (0.10)		0.03 (0.03)		2
Oribatula sp. 2 LML			0.03 (0.03)		
Zygoribatula bulanovae Kulijew, 1961		0.13 (0.13)			12
Haplozetidae					
Peloribates pilosus Hammer, 1952		2.21 (1.84)	1.00 (0.93)	0.71 (0.56)	4, 12, 12P, 13, 13P, 14, 20P
Peloribates sp. 3 DEW	0.25 (0.19)				6, 10
Neoribates sp. 1 DEW	0.05 (0.05)				7
Scheloribates pallidulus (C.L. Koch, 1841)	0.25 (0.19)	1.00 (0.42)	0.06 (0.06)	0.33 (0.24)	3, 7, 10-12, 12P, 13, 13P, 14, 15, 15P
Scheloribatidae					
Scheloribates pallidulus(C.L. Koch, 1841)	0.25 (0.19)	1.00 (0.42)	0.06 (0.06)	0.33 (0.24)	3, 7, 10-12, 12P, 13, 13P, 14, 15, 15P
Parakalummidae					
Neoribates sp. 1 DEW	0.05 (0.05)				7

Chamobatidae					
Chamobates cf *cuspidatus* (Michael, 1884)	4.00 (1.63)	3.38 (2.42)	0.09 (0.07)	0.42 (0.37)	6, 7, 9, 10, 12, 13, 13P, 14, 15, 15P
Chamobates sp. 2 DEW		0.04 (0.04)			12
Ceratozetidae					
Ceratozetes cuspidatus Jacot, 1939	0.05 (0.05)				6, 18
Ceratozetes gracilis (Michael, 1884)	4.65 (2.00)	2.29 (0.71)	1.69 (1.45)	0.46 (0.22)	1-3, 3P, 4-11, 11P, 12, 12P, 13, 13P,
Diapterobates humeralis (Hermann, 1804)	0.40 (0.20)	0.33 (0.15)			3, 5, 6, 9, 12, 13, 15
Fuscozetes fuscipes (CL. Koch, 1844)					8
Sphaerozetes arcticus Hammer, 1952	1.00 (1.00)	0.04 (0.04)			9, 20
Trichoribates striatus Hammer, 1952	0.05 (0.05)	0.04 (0.04)		0.08 (0.05)	3, 3P, 9, 20P
Mycobatidae					
Mycobates incurvatus Hammer, 1952	0.05 (0.05)	0.04 (0.04)		0.04 (0.04)	5, 15, 15P
Galumna sp. 1 DEW	0.15 (0.10)	3.63 (3.33)	0.34 (0.23)	0.25 (0.20)	1, 4, 7, 9, 11, 11P, 12, 20
Pergalumna sp. 1 DEW	0.20 (0.05)	0.71 (0.41)	0.19 (0.13)	0.04 (0.04)	1-5, 7-11, 15, 20P
Pilogalumna sp. 1 DEW	0.60 (0.20)	1.33 (0.69)	0.22 (0.22)	0.46 (0.33)	1, 3, 5-7, 10-12, 12P, 13, 20, 20P
Mycobatidae					
Mycobates incurvatus Hammer, 1952	0.05 (0.05)	0.04 (0.04)		0.04 (0.04)	5, 15, 15P

† See Table 1 for site ID descriptions.

Table 2-5. Indicator species analysis for natural (NAT) stands and old reclaimed (OR, 30-31 yrs.) stands with varying canopy type. Exclusivity corresponds to the specificity of a species to that site. Fidelity corresponds to the faithfulness of a species to that site. Strength of the indicator is determined by a strong p-value (p<0.05).

Age	Canopy	Exclusivity	Fidelity	p-value
OR	Aspen		*Pilogalumna sp. 1 DEW*	0.013
NAT	Aspen	*Ceratoppia quadridentata arctica*	*Ceratoppia quadridentata arctica*	0.004
			Oribatodes mirabilis	0.007
NAT	White spruce	*Peloribates sp. 3 DEW*		0.025

Figure 2-1. Chronosequence of natural and reclaimed stands in the Athabasca Oil Sands Region in Alberta, Canada.

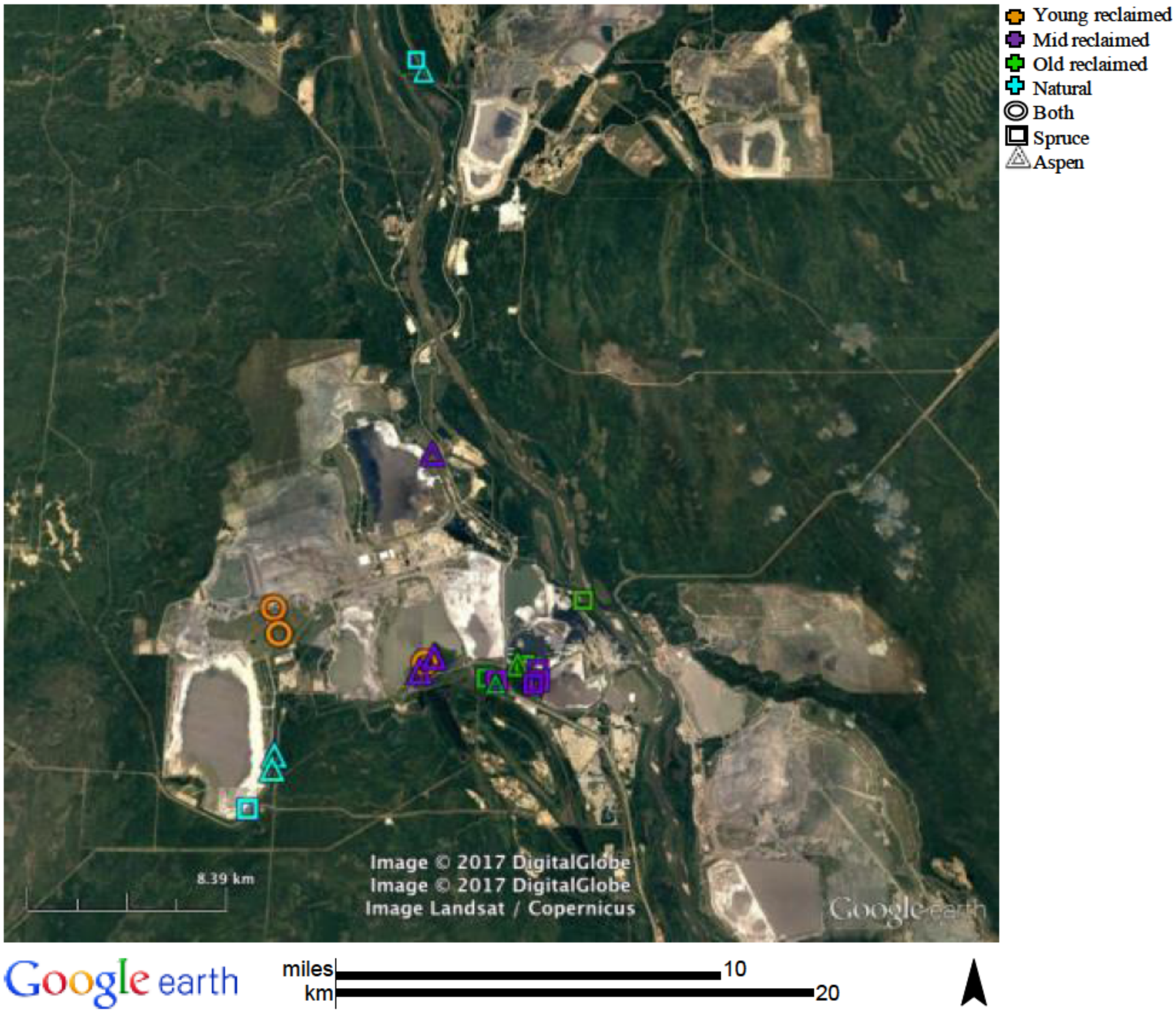


Figure 2-2. Mean oribatid mite (a) abundance and (b) richness per 500 cm^3 in young reclaimed (YR, 8-11 yrs.), mid-reclaimed (MR, 17-25 yrs.), old reclaimed (OR, 30-31 yrs.), and natural (NAT) aspen and white spruce stands. Each error bar corresponds to one standard error from the mean. Differences are represented by connected dotted lines with corresponding p-values determined by a permANOVA followed by Tukey's Honest Significance Difference (HSD).

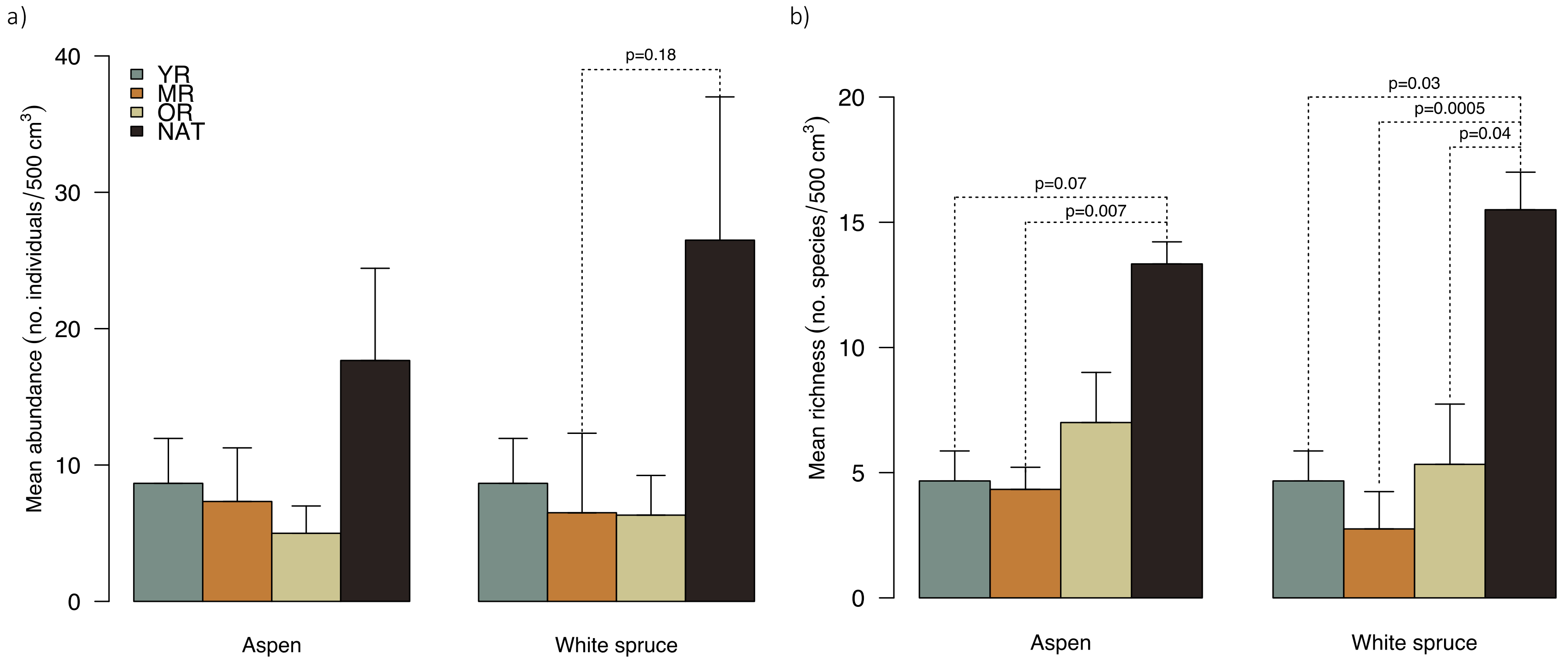


Figure 2-3. Mean oribatid mite (a) abundance and (b) richness per 500 cm^3 in natural forest floor (N.FF), novel forest floor (R.FF), novel forest floor + peat-mineral mix (R.FF+PMM), and peat-mineral mix (PMM). Each error bar corresponds to one standard error from the mean. Differences are represented by connected dotted lines with corresponding p-values determined by permANOVA followed by Tukey's Honest Significance Difference (HSD).

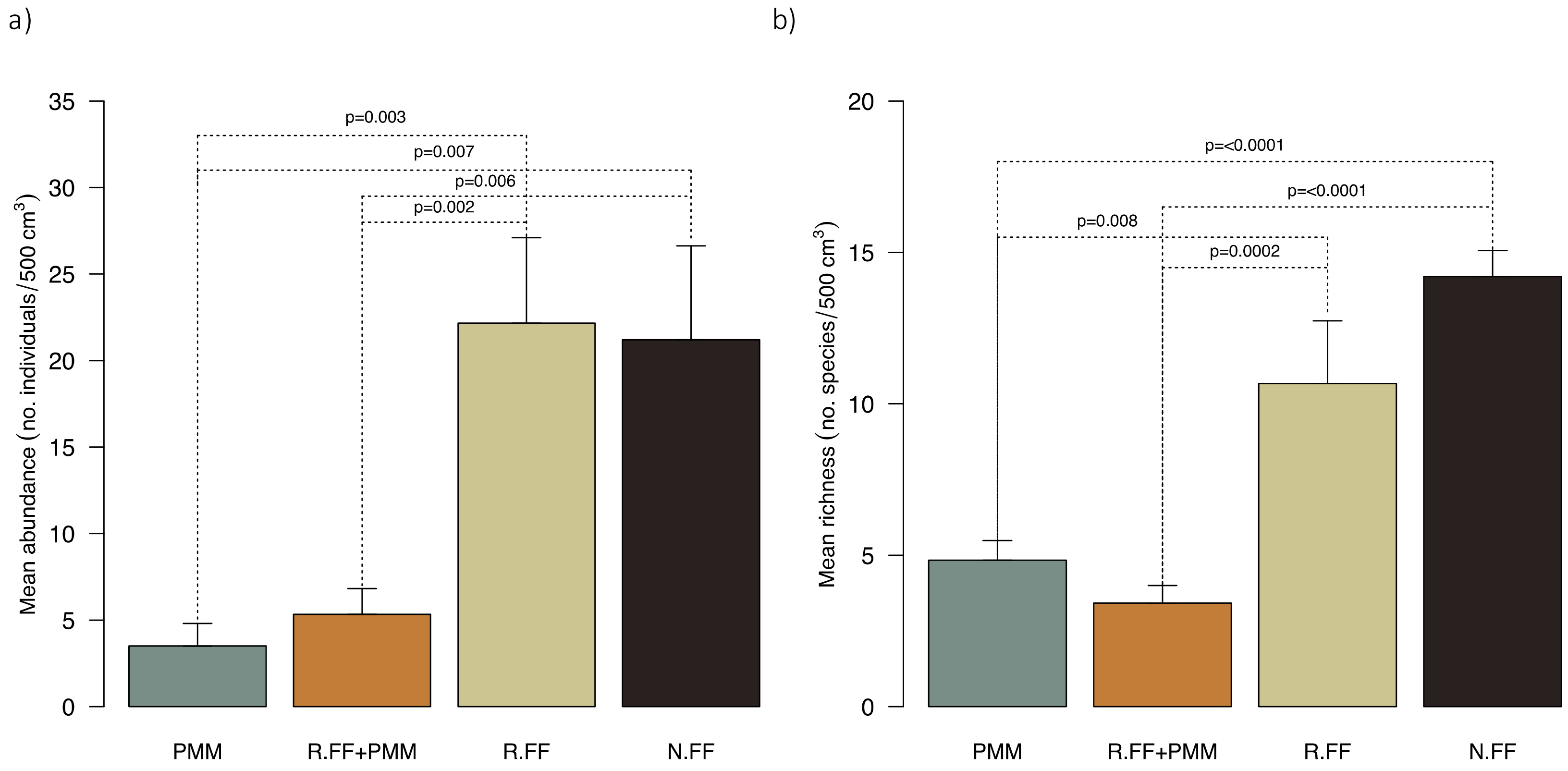


Figure 2-4. Scatterplot of forest floor thickness (cm) vs. oribatid mite species richness (no. individuals/500 cm^3) in natural forest floor (N.FF), novel forest floor (R.FF), and novel forest floor plus peat-mineral mix (PMM).

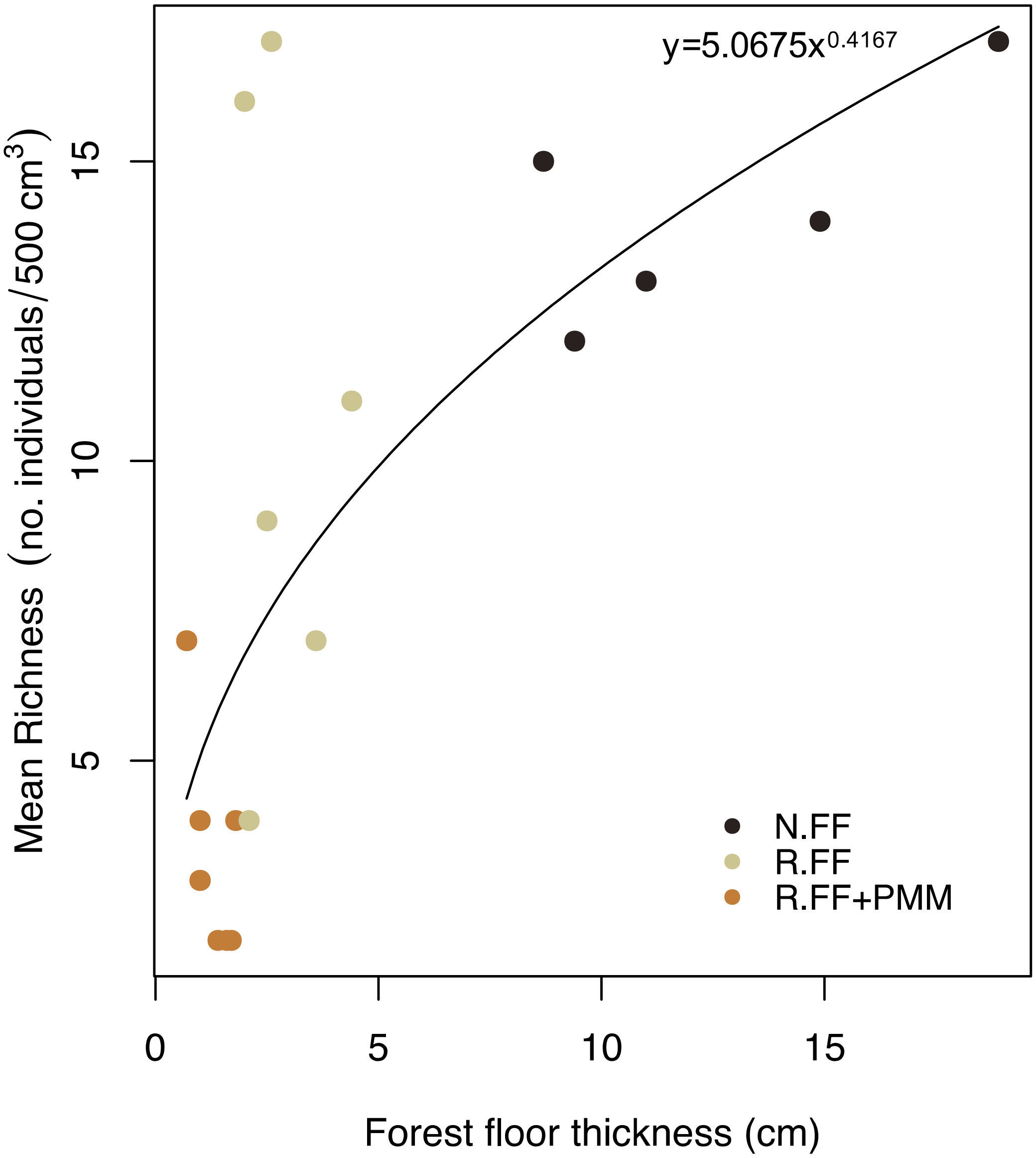


Figure 2-5. Diversity orders using Hill numbers expressed as Q_1 (exp(H’)) and Q_2 (1/D) for factors (a) ‘age class x stand type’ and (b) material type. Age classes include young reclaimed (YR, 8-11 yrs.), mid-reclaimed (MR, 17-25 yrs.), old reclaimed (30-31 yrs), and natural (NAT). Stand types include aspen (Aw) and white spruce (Sw). Material types include natural forest floor (N.FF), novel forest floor (R.FF), novel forest floor + peat-minearl mix (R.FF+PMM), and peat-mineral mix (PMM). Each error bar corresponds to one standard error from the mean. Diversity is represented as the effective number of species (ENS).

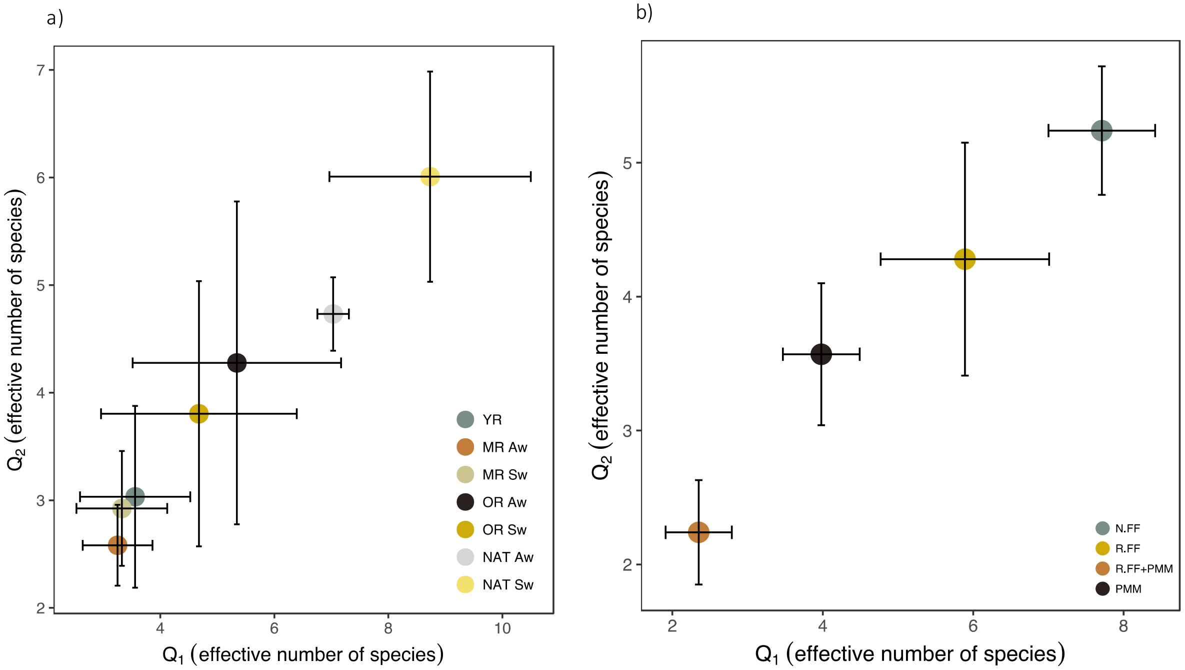
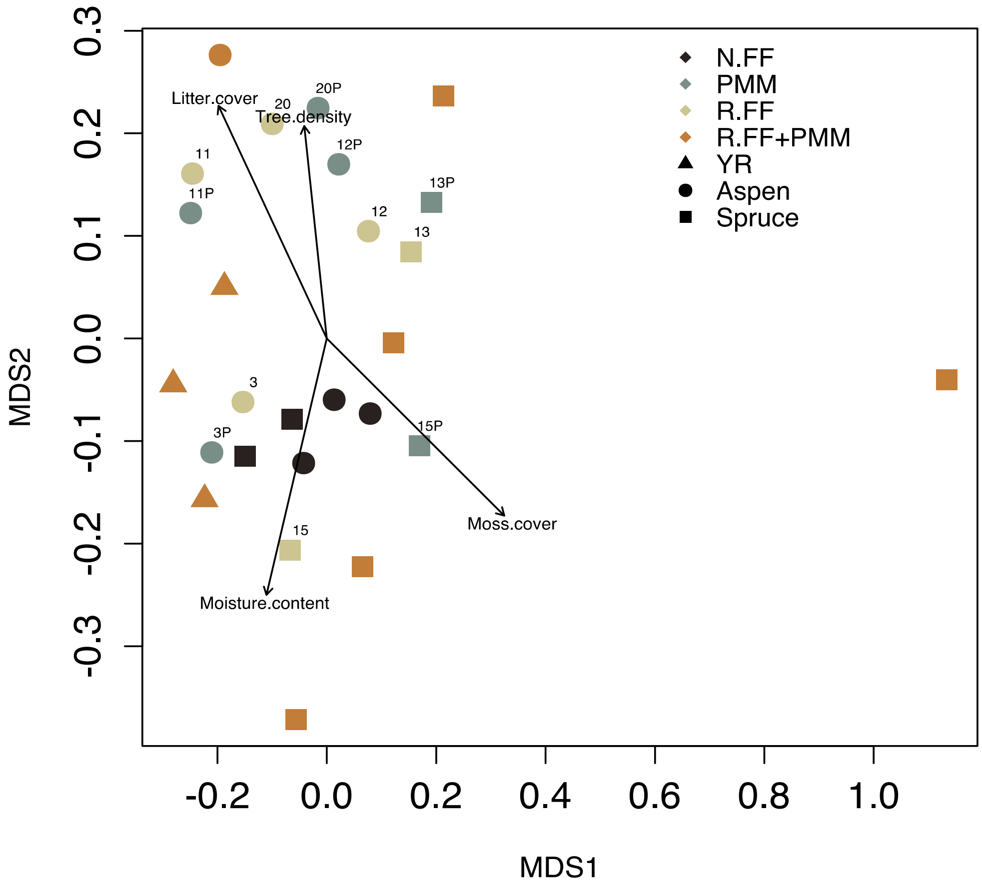


Figure 2-6. Non-metric multidimensional scaling (NMDS) with Hellinger-transformed oribatid mite abundance data coded for material and stand type. Material type includes natural forest floor (N.FF), novel forest floor (R.FF), novel forest floor + peat-mineral mix (R.FF+PMM), and peat-mineral mix (PMM). Young reclaimed stands are represented as YR. Numbers associated with points represent sites where peat-mineral mix (P) and R.FF (≥ 2 cm) were collected separately Vectors correspond to environmental associations. Litter cover is represented as the percent ground cover of all deciduous litter, moss is represented as the percent ground cover of all moss species, and tree density is number of trees in 400 m^2 plot.



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3. CHAPTER 3—THE EFFECT OF INVASIVE EARTHWORMS ON ORIBATID MITE COMMUNITIES IN A BOREAL ASPEN STAND

3.1. Introduction

A considerable amount of boreal forest soil is covered by a thick layer of surface accumulated organic matter known as the forest floor (Prescott et al., 2000), which stores ~24% of the boreal forest ecosystem carbon (Kurz et al., 2014). Not only is the forest floor a massive carbon reservoir, but when present, it is the zone where the majority of the biological and chemical reactions occur in soil and is the habitat to many soil-dwelling species (Coleman et al., 2004). Within the forest floor, oribatid mites are keystone detritivores where they initiate litter decomposition, nutrient cycling, and maintain forest floor structure (Walter 1987; Coleman et al., 2004; Behan-Pelletier, 1999). Due to their dominance in relation to other soil meso- and macro-faunal groups in the boreal forest, oribatid mites are key regulators of organic matter decomposition, aiding in the long-term maintenance of the forest floor as an important global carbon reservoir (Kurz et al., 2014).

The recent invasion of non-native earthworm species into northern boreal forests of Alberta may threaten the long term sustainability of this global carbon reservoir. Like oribatid mites, earthworms are a detritivorous group of macrofauna (Coleman et al., 2004; Frelich et al., 2006), and have long been classified as “ecosystem engineers” for their substantial influence on soil biogeochemical processes (Jones et al., 1994; Edwards, 2004). Due to the size (5-15 cm) and the spatial distribution of earthworms in the landscape (40 m patches), they have the ability to drastically alter soil biogeochemical cycling, specifically litter decomposition (Lavelle and Spain, 2001). Earthworms greatly increase organic matter decomposition rates throughout the soil profile when introduced into previously earthworm-free ecosystems (Frelich et al., 2006). The rate and extent of habitat alteration and organic matter decomposition are dependent on the ecological group that the invading earthworms belong to (Bohlen et al., 2004b): epigeic (litter-dwelling), endogeic (mineral-dwelling), and anecic (litter and mineral dwelling) (Bouche, 1977). Individually, anecic species would cause the greatest extent of habitat alteration through bioturbation of the mineral and organic layers, but studies have observed the greatest extent of habitat alteration in the presence of multiple ecological groups (Hale et al., 2008; Cameron et al., 2013). Most similar to oribatid mites in size and ecological function are the epigeic species (2-5 cm), which often lead the invasion front of non-native earthworms into new environments (Hendrix, 2006; Eisenhauer, 2010).

The magnitude of the impacts caused by an earthworm invasion within an ecosystem greatly depends on its previous land use (Bohlen et al., 2004a). As such, a previously disturbed or plowed soil will see less drastic biogeochemical changes, while earthworms pose a high risk of significantly altering an undisturbed forested landscape. Earthworm invasion into previously earthworm-free forests has the potential to increase microbial activity and litter decomposition rates, alter biotic communities, and cause a shift from fungal dominated communities to bacterial dominated communities (Wardle, 2002; Bohlen et al., 2004b; Frelich et al., 2006). The current earthworm invasion poses a unique opportunity to observe shifts in the detritivore community and associated biogeochemical processes at a landscape scale (Frelich et al., 2006). At this time, there have been few field studies regarding the influence of non-native earthworms in northern boreal soils on endemic soil fauna (Cameron et al., 2007; Cameron and Bayne, 2009).

The recent invasion by earthworms into the Canadian boreal forest has sparked two major studies in Alberta. Documentation of the epigeic species *Dendrobaena octaedra* Savigny, 1826 invasion into aspen and pine forests of southwestern Alberta was noted in the 1990s and has been investigated in both field studies (Dymond, Scheu, and Parkinson, 1997; McLean and Parkinson, 2000a; McLean and Parkinson, 2000b) and laboratory studies (Scheu and Parkinson, 1994; McLean and Parkinson, 1997; McLean and Parkinson, 1998a; McLean and Parkinson, 1998b). With the advancement of the invasion front, later field studies documented the presence of epigeic, endogeic, and anecic species (Eisenhauer et al., 2007; Straube et al., 2009). The second series of studies targeted *D. octaedra* in the forests of northern Alberta (Cameron et al., 2007; Cameron and Bayne, 2009). Initial research indicated that the extent of spread into the northern parts of Alberta was dominated by hotspots of earthworm presence near roads, boat launches, and places where human activity had occurred (Cameron et al., 2007). Later, the investigation into introduction mechanisms revealed that earthworm presence in northern boreal forests of Alberta may have begun as early as the 1950s (Cameron and Bayne, 2009) with the construction of roads as a result of the growing natural resource industry. The most dominant species found near boat launches were anecic bait species such as *Lumbricus terrestris* Linnaeus, 1758*,* endogeic bait species such as *Aporrectodea* spp., and distant forests were dominated by epigeic species such as *Lumbricus rubellus* Hoffmeister, 1843, *D. octaedra,* and *Dendrodrilus rubidus* Savigny, 1826 (Cameron et al., 2007; Cameron and Bayne, 2009). These findings launched a series of laboratory studies using boreal forest soil to study the effect of *D. octaedra* on ectomycorrhizal fungi and microarthropods (Cameron et al., 2012; Cameron et al., 2013). To date, there have been limited field studies regarding non-native species interactions with soil biota in northern Alberta. Field studies regarding non-native earthworm invasion historically require either the inoculation of plots with desired populations of earthworms or the active removal of earthworms to represent an "earthworm-free" system (Parkinson et al., 2004). These methods introduce challenges in data interpretation, for example, identifying if the data is a result of earthworm elimination or the physical changes caused previously by the earthworms

(Parkinson et al., 2004). The occurrence of areas with little to no earthworm invasion in northern Alberta presents the ideal environment to study non-native earthworm presence on endemic soil biological communities in the field (Parkinson et al., 2004). This environment represents a natural, uninvaded ecosystem where data can more precisely be related back to the soil biogeochemical changes caused by earthworms.

The objectives of this study were to (1) assess the current state of earthworm invasion in a boreal aspen stand and (2) determine the response of oribatid mite assemblages to changes in soil physical and chemical properties as a result of earthworm disturbance. Based on previous earthworm surveys in the area, we hypothesized that earthworm invasion (density) would decrease with distance from the road. We also hypothesized that the high density, multiple species invasion area would have a higher degree of mineral and organic layer mixing, higher bulk density, and lower oribatid mite abundance and species richness than the low density, single-species invasion area as a result of the intermediate disturbance hypothesis.

3.2. Materials and Methods

3.2.1. Study Area

The study area is located south of Wolf Lake Provincial Recreational Area (53.2116N, -116.0742W) in the Central Mixedwood subregion of the Boreal Forest region of Alberta (Natural Regions, 2006). The climate is characterized by long cold winters and cool short summers. The mean monthly air temperature ranges from -15.1˚C in January to 17.4˚C in July, with an average of 116 frost free days annually. Mean annual precipitation is 421.0 mm with 319.2 mm falling as rain (Environment Canada, 2017). Composition of Central Mixedwood forests include trembling aspen (*Populus tremuloides* Michx.) dominated, white spruce (*Picea glauca* (Moench) Voss) dominated, mixedwood aspen and white spruce, and jack pine (*Pinus banksiana* Lamb.)

dominated stands (Natural Regions, 2006). Common understory vegetation includes low bush cranberry (*Viburnum edule* Michx.), rose (*Rosa acicularis* Lindl.), wild sarsaparilla (*Aralia nudicaulis* L.), dewberry (*Rubus pubescens* Raf.), bunchberry (*Cornus canadensis* L.), and Canada buffaloberry (*Shepherdia canadensis* L.) (Natural Regions, 2006). Central Mixedwood forests are dominated by Gray Luvisols, and soils specific to our study site include Orthic Gray Luvisols formed over moderately to strongly calcareous glacial till and degraded Eutric Brunisols formed over sandy-skeletal glaciofluvial material (Alberta Agriculture and Forestry, 2017).

3.2.2. Site Selection and Field Sampling

The study area was in proximity to one of the many locations used in a previously published non-native earthworm survey that investigated the relationship between road age and earthworm density in northern Alberta (Cameron et al., 2007; Cameron and Bayne, 2009). The chosen forest area was identified as having only epigeic species *D. octaedra* and *Dendrodrilus rubidus* approximately five years ago (E. Cameron, personal communication). To control for site variation, one aspen stand was selected with consistent canopy type, soil type, and slope. Soils were classified as an Orthic Gray Luvisol and consistency in soil type was determined by augering at points along transects moving from the forest edge to the forest interior (Eisenhauer et al., 2007). Slope was measured with a Suunto clinometer and varied between 0.5-2%.

Field sampling occurred in August 2016 (Figure 3-1). To investigate the extent of earthworm invasion, three transects (10 m apart) were set up from the forest edge (~10 m from the road) to the forest interior (~350 m from the road). Earthworm surveys were conducted every 20 meters using the first two transects. Non-linear invasion was apparent and there was no obvious invasion front or leading edge from the road to the interior forest, unlike field studies in

Minnesota (Hale et al., 2005; Schlaghamersky et al., 2014). Therefore, two 400 m^2 areas were identified within the aspen stand as (1) a low density area 300 m from the road, and (2) a high density area 150 m from the road. The low density area was occupied by epigeic species only and was characterized by the presence of distinct L, F, and H layers (Hale et al., 2005; Holdsworth et al., 2007; Schlaghamersky et al., 2014). The high density area was occupied by multiple species (epigeic, endogeic/anecic) and was characterized by the obvious mixing of mineral and organic horizons with many casts present. Four subplots (4 m^2) were established just beyond each corner boundary of the 400 m^2 plot to ensure that a distance of at least 20 m was respected between sampling replicates as recommended in previous studies (Hale et al., 2005; Eisenhauer et al., 2007; Straube et al., 2009; Schlaghamersky et al., 2014).

3.2.2.1. Earthworm and oribatid mite sampling

At each of the four subplots, two 0.0625 m^2 quadrats were excavated to a depth of 0.1 m to assess the presence and distribution of earthworm species; a 0.0625 m^2 quadrat size was chosen as Cameron and Bayne (2009) showed that this was a sufficient size. Plots were excavated using a hand trowel and the soil was placed on a plastic tarp where earthworm specimens were hand-sorted. Next, a liquid extraction was performed in all excavated earthworm quadrats. A solution of 40 g of Coleman’s hot mustard powder in 1 L of water was combined and left for three hours to allow the “hotness” to develop. Half of the hot mustard solution was applied immediately to the excavated quadrat, and the remaining solution was applied 10 minutes after the first application (University of Minnesota, 2011). All collected earthworms were placed in 90% isopropyl alcohol until they could be taken back to the laboratory for identification. Additionally, oribatid mites were sampled using a modified version of the Alberta Biodiversity Monitoring Institute (ABMI) terrestrial protocol for arthropod extraction from organic soils (ABMI, 2010). Four composited samples (500 cm^3) were collected 10 cm from each earthworm quadrat using a 7.5 x 7.5 cm metal soil core, resulting in a total of eight oribatid mite samples and two earthworm quadrats per subplot in each invasion area. A total of eight earthworm quadrats were excavated and 32 oribatid mite samples were collected at each of the two areas under study (low-density and high-density areas).

At each of the four subplots per area, the forest floor was sampled in its entirety for bulk density and moisture content using a 10 cm^2 square. Understory vegetation richness was determined prior to all soil sampling by identifying understory vegetation species within a 1 m^2 area (Johnson et al., 1995).

3.2.3. Laboratory analyses: Specimen identification and soil properties

Earthworm specimens were preserved with formalin and stored in 90% isopropyl alcohol (University of Minnesota, 2011). Specimens were counted and identified to genus and species level when possible (Reynolds 1977). Earthworms were grouped into two groups: mineral burrowing (*Apporectodea* spp.) and litter-dwelling (*Dendrobaena octaedra).* Oribatid mite samples were extracted within seven days of field collection on a modified Tullgren funnel (Crossley and Blair, 1991). Extracted oribatid mites were sieved, and specimens ≥ 300 µm were identified to species. All specimens (earthworms and oribatid mites) were identified using a Leica M165-C stereomicroscope (7.3x-120x magnification). If necessary, oribatid mite specimens were cleared in 85% lactic acid, mounted on slides using polyvinyl alcohol, and oven dried at 55-60°C. Slide-mounted specimens were identified to species using a Leica D 2500 compound microscope. All oribatid mite species were identified using the Almanac of Alberta

Oribatida-Part I (Walter et al., 2014). All specimens and residuals will be stored at the Royal Alberta Museum in Edmonton, Alberta, Canada.

Nutrient status (total organic C, N) and pH were determined from the air-dried forest floor samples used for oribatid mite extraction. For nutrient analyses, samples were finely ground with a ball mill and analyzed for total carbon and nitrogen through dry combustion using a Thermo FLASH 2000 model combustion Elemental Analyzer. The pH was determined by making a 1:4 slurry of air-dried sample and 0.01 M $CaCl_2$ solution. Then, pH was measured with an Accument XL200 meter (Kalra and Maynard, 1991). Bulk density and gravimetric moisture content were calculated by weighing samples before and after oven drying at 65°C for 48 hours (Kalra and Maynard, 1991).

3.2.4. Statistical Analyses

All variables were analyzed for differences between earthworm areas at (1) high density + multiple species earthworm invasion (high density (H.D.)) and (2) low density + single species earthworm invasion (low density (L.D.)) using packages in R statistical software version 3.2.4 (R Development Core Team, 2016).

A one-way permutational analysis of variance (ANOVA) was performed to test the effect of earthworm invasion on site and soil characteristics including bulk density, moisture content, forest floor thickness, pH, C: N ratio, understory vegetation richness, and soil mite assemblage characteristics including abundance and species richness. Oribatid mite abundance was represented as the number of individuals/sample (500 cm^3), and species richness was represented as the total number of different species per sample. Permutational analysis of variance (permANOVA) followed by Tukey's adjustment for multiple inference (Tukey HSD) was computed in R using the ‘lmPerm’ package (Wheeler and Torchiano, 2016). Assemblage diversity was visualized using a diversity profile where diversity orders (Q) represent different measures of diversity. For example, Q_0 represents species richness, Q_1 represents the exponential of the Shannon entropy (diversity), and Q_2 represents the inverse of Simpson’s Index (evenness). Changes in assemblage diversity are indicated by the rate of change between diversity orders and the number of species equivalence found in each diversity order. The rate of change is illustrated by the continuous points between each diversity order on the x-axis, where each point represents the estimated species equivalent (ENS) with increasing succession of Q in 0.1 increments.

Non-metric multidimensional scaling (NMDS) was used to visualize oribatid mite composition using species count data. Each oribatid mite sample (n = 64) was used as a data point rather than the mean per replicate due to the limitations in the analysis where the ordination stress was too low to run. The NMDS was performed on Hellinger-transformed oribatid mite data. This data transformation favors zero-inflated species data and gives low-weight to rare species when configuring the NDMS solution; it also avoids grouping sites containing zeros as being more similar in ordination space. Following NMDS, a permutational multivariate analysis of variance (MANOVA) was conducted to identify differences in community composition between the two earthworm density areas. Additionally, all site and soil characteristics were considered for vectors in the NMDS but only those with strong p-values ($p<0.05$) were applied. The NMDS analysis was performed using the VEGAN package in R version 3.2.4 (Oksanen et al., 2015), and permutational MANOVA was conducted using package RVAideMemoire (Hervé, 2017). Finally, indicator species analysis was used to identify if any species were more strongly associated with high density or low density earthworm areas. Indicator species were identified using R with the ‘indicspecies’ package (Cáceres and Legendre, 2009).

3.3. Results

3.3.1. Earthworm distribution and habitat characteristics

Only one earthworm species, *Dendrobaena octaedra* was found in the low density area, with an average of 17 adults/m^2 and 13 juveniles/m^2 (Table 3-1). *Dendrobaena octaedra* was also found in the high density area, but at a reduced average adult density of 10 individuals/m^2 and an increased average juvenile density of 27 individuals/m^2. In addition to *D. octaedra*, species from the *Aporrectodea* genus were also detected in the high density area. The highest adult earthworm densities were observed in the high density area and individuals from the *Aporrectodea* genus were present at densities of 29 adults/m^2. There were no mineral-burrowing species found in the low density area.

Both forest floor and surface vegetation were altered by the high density earthworm invasion (Table 3-2). Forest floor bulk density notably increased in the high density area when compared to the low density area ($p = 0.02$), and the moisture content was notably increased in the low density than the high density area ($p = 0.07$). Additionally, the thickness of the litter layer was notably reduced in the high density area when compared to the low density area ($p = 0.007$). Aboveground, the high density earthworm invasion negatively affected understory vegetation richness. Species richness of the understory vegetation was notably reduced in the high density area ($p = 0.02$) and species dominance by *Calamagrostis canadensis* ((Michx.) P.Beauv.) was observed. Contrastingly, the low density area had sparse amounts of grassy vegetation and was dominated by *Linnaea borealis* (L.), *Rubus idaeus* (L.), and *Rosa acicularis* (Lindl.). Additionally, NMDS analysis revealed correlation vectors that were both positively and moderately related with oribatid mite communities in the high density areas: C: N ratio ($p = 0.05$) and bulk density ($p = 0.03$).

3.3.2. Oribatid mite assemblage

A total of 940 oribatid mite individuals were extracted from the forest floor samples and 26 species were identified from 18 families. Mite abundance decreased by 27% (149 individuals) in the high density area compared to the low density area (p = 0.1; Figure 3-2a). Similarly, mite species richness decreased by 36% in the high density area (p = 0.03; Figure 3-2b). A total of 16 oribatid mite species were found in the high density area while the low density area supported a total of 25 species. The nine species not found in the high density area were identified as rare in the low density area (singletons/doubletons).

NMDS revealed that oribatid mite composition differed between the two earthworm areas (p = 0.004; Figure 3-3), and reached a final solution in 2D space with a stress of 18.2%. The dominant species found in both areas were *Ceratozetes gracilis* (Michael,1884), *Pilogalumna* sp. 1 DEW, and *Gymnodamaeus ornatus* Hammer, 1952. The number of *C. gracilis* individuals was evenly distributed between areas (H.D: 180, L.D: 183), followed by *Euphthiracarus flavus* (H.D: 49, L.D: 36) and *Pilogalumna* sp. 1 DEW (H.D: 60, L.D: 75). In the high density area, the abundance of *Gymnodamaeus ornatus* was 28 individuals, which was notably lower than the 109 *G. ornatus* individuals found in the low density area. Overall, the high density area had a notably lower diversity than the low density area (Figure 3-4). The low density area had more singletons and doubletons (n = 11) when compared to the high density area (n = 6; Table 3-3). Moving from Q_1 to Q_2, the high density area had a slower rate of decrease, indicating that it may have a higher overall community evenness than the low density area. Additionally, of the 26 species found in both areas, 16 species (62%) were shared. The high density area possessed no unique species, and in contrast, 10 species (32%) found in the low density area were unique and not found in the high density area.

Indicator species analysis further supported the differences seen in oribatid mite assemblages between the low density and high density earthworm areas (Table 3-4). Indicator species were identified only in the low density area and included *Gymnodamaeus ornatus* ($p = 0.001$) and *Achipteria* sp. 1 DEW ($p = 0.003$). No species were identified as indicators in the high density earthworm invasion area.

3.4. Discussion

In this study we found that the largest density of adult *Dendrobaena octaedra* was in the low density area with 17 individuals/m^2, which is larger than densities previously recorded by Cameron et al. 2007 at 5 individuals/m^2. Adult species densities in the *Aporrectodea* genus were largest in the high density area with 29 individuals/m^2. Other studies report varying field densities of earthworm species after an invasion (Eisenhauer, 2010). For example, the Kananaskis Valley study series first reported field densities of epigeic species *D. octaedra* at 854 individuals/m^2. As the invasion front increased, endogeic species *Octolasion tyrtaeum* Savigny, 1826 were reported at densities of 287 individuals/m^2 and 107 individuals/m^2 (Eisenhauer et al., 2007; Straube et al., 2009), and *Aporrectodea caliginosa* and *O. tyrtaeum* at 125 individuals/m^2 (Migge, 2001). These high densities suggest that as the invasion continues to spread throughout the aspen stand in this study, it is likely that earthworm densities will increase in all ecological groups, but specifically in endogeic and anecic species groups (Eisenhauer et al., 2007).

Oribatid mite abundance and richness were both negatively affected as a result of the overall increased earthworm density and the presence of *Aporrectodea* genus in the high density area. While mite abundance was lower in the high density area, it was only lower by 27%, which is similar to the decrease in abundance observed in other studies investigating the effects of earthworm invasion on microarthropods in the forest floor (Cameron et al., 2013). Greater losses in mite abundances have been observed as an earthworm invasion progressed (McLean and Parkinson, 1998a), and may also occur as multiple ecological groups began to invade a specific stand (Hale et al., 2008).

Mite species richness more strongly decreased in the high density earthworm invasion than did mite abundance (Fig. 3-1b). The low density earthworm area supported nine more species than the high density area in terms of the overall community, and identified five more species as singletons and doubletons (Table 3-3). The lack of these nine species in the high density area may not be a direct result of the high density earthworm invasion, as these species were all found to be singletons and doubletons in the low density area. This suggests that these rarer species were either already found at low abundances in the low density area, or that the presence of *D. octaedra* at low densities yielded similar effects as the presence of multiple ecological groups at high densities. Cameron et al. (2013) observed the latter, where oribatid mite species richness and abundance did not differ in treatments with *D. octaedra* only and treatments with both D. *octaedra* and *Lumbricus terrestris* (anecic species). Therefore, these species may be very sensitive to earthworm effects, or may have been detected in low abundances as a product of sampling effort.

The mite assemblage composition was different in the high density and low density earthworm areas, and indicator species analysis identified *Gymnodamaeus ornatus* and *Achipteria sp. 1* DEW as indicators of the low density area (Fig. 3-3; Table 3-4). Both the high and low density earthworm areas had almost the same dominant species with similar abundances, excluding *G. ornatus*. The high earthworm density strongly reduced *G. ornatus* abundance (-75%), affecting the species composition in both areas. Overall community diversity was also lower in the high earthworm invasion area, supporting the same diversity loss seen in aspen litter after a multiple species earthworm invasion (Migge, 2001). Most notable was the difference in the Shannon index between areas, which was higher in the low density area as a result of greater species richness and the increased number of rare species (Fig. 3-4).

The high density area had a substantially greater mean bulk density and a thinner litter layer, which aligns with changes to the soil habitat observed after a multiple species invasion in Minnesota (Hale et al., 2008). The presence of species in the *Aporrectodea* genus in the high density area caused a substantial decrease in forest floor bulk density, which may have negatively affected mite communities (Table 3-2). Straube et al. (2009) noted that oribatid mite abundance decreased moving down the profile from the litter layer to the mineral layer after earthworm invasion; therefore, the incorporation of a species-poor mineral soil into a species-rich litter layer may have contributed to the decrease in forest floor species richness observed in this study. Additionally, the feeding and burrowing activities common to species in the *Aporrectodea* genus may have led to the thinner litter layer observed in the high density area. Loss of the litter layer appeared to negatively influence both the abundance of oribatid mites and the epigeic earthworm *D. octaedra*. Eisenhauer et al. (2007) also observed lower densities of *D. octaedra* in thinner aspen litter compared to thicker aspen litter, which may be a result of the loss of resources when the organic and mineral soil layers become mixed (Dymond et al., 1997). To our surprise, the C: N ratio was positively correlated with the forest floor in the high density area, indicating that high C: N ratio values were associated with the high density area. This may be due to the addition of more recalcitrant soil organic matter from deeper soil horizons or a result of earthworm feeding, leaving behind less palatable, woodier debris like leaf stems.

We cannot determine if the higher oribatid mite abundance, species richness, and diversity observed in the low density area is a result of the presence of *D. octaedra* at low densities or if it is actually representative of the oribatid mite communities in the uninvaded forest. Other studies looking at non-native earthworm invasion have suggested that increases in oribatid mite abundance in the early stages of invasion or in the presence of *D. octaedra* were a result of greater habitat heterogeneity. This concept has been discussed in terms of the intermediate disturbance hypothesis (IDH), where intermediate levels of disturbance allow maximum coexistence and diversity for all species (Connell, 1978). To corroborate this, McLean and Parkinson (1998) observed greater habitat heterogeneity in the forest floor shortly after *D. octaedra* invasion (three months), which resulted in increased oribatid mite abundances. Even deep burrowing species like *O. tyrtaeum* have resulted in greater microarthropod abundances when present at low densities (Straube et al., 2009). Conversely, when present at high densities, this species had negative effects on microarthropod abundance when studied three years previously in the same forest stand (Eisenhauer et al., 2007). Therefore, the density of the invading species may be more influential than the ecological group to which the invading species belongs when considering the IDH (Eisenhauer et al., 2007; Straube et al., 2009; Cameron et al., 2013). For example, Cameron et al. (2013) observed a greater change in microarthropod abundances at high densities of *D. octaedra* than at low densities of *Lumbricus terrestris.* Other studies have suggested that even low levels of habitat disturbance, such as those caused by low densities of *D. octaedra,* negatively influence oribatid mite assemblages (Maraun et al., 2003). The wide range of effects on soil-dwelling microarthropods at different stages of earthworm invasion makes it difficult to identify at what time since invasion and at what density of earthworms the IDH would be observed. In order to determine if the IDH was observed in this stand, the addition of areas with no earthworm impact is necessary.

3.5. Conclusion

It is apparent that earthworm invasion into previously earthworm-free forests can cause drastic changes to oribatid mite communities and forest floor characteristics such as bulk density and leaf litter thickness. In our experiment, high density earthworm invasion resulted in a drastic loss of mite species *G. ornatus* (-75%), and decreased overall species richness (-36%). Because we were unable to identify the exact time of invasion into this particular forest, it is difficult to say why we only saw a relatively small decrease in abundance (-27%) when compared to other community metrics. Most likely it is a result of the invasion being recent or earthworm densities being relatively low compared to other invaded forests in Alberta. It may also be that rare species were impacted in a similar way within both the high and low density invasion areas. Long term monitoring of this invasion is necessary to better understand the data presented in this study. Additionally, definite increases in bulk density and the loss of the litter layer decreased mite abundance, richness, and altered community diversity and composition. It would be worthwhile to further separate the forest floor into respective L, F, and H layers to investigate whether mite communities relocate within the forest floor in the presence of *D. octaedra*. Complete analyses of communities in the mineral soil layer would also help us better address if the mixing observed by the *Aporrectodea spp.* in the high density area caused an increase in similarity in forest floor and mineral soil oribatid mite communities.

Table and Figures

Table 3-1. Mean earthworm densities (m^2) and one standard error from the mean of adult and juvenile epigeic and other (endogeic/anecic) earthworms detected in high density (H.D.) and low earthworm invasion areas (L.D.).

Area	Earthworm species			
	Adult		Juvenile	
	Dendrobaena octaedra	*Aporrectodea* spp.	*Dendrobaena octaedra*	*Aporrectodea* spp.
H.D.	10 ± 6	29 ± 14	27 ± 14	20 ± 8
L.D.	17 ± 5	0 ± 0	13 ± 5	0 ± 0

Table 3-2. Mean site characteristics of the high density (H.D.) invasion area and low density (L.D.) invasion areas. Different letters indicate differences between earthworm invasion areas within row variables with a strong p-value ($p<0.05$)

	H.D.	L.D.	p-value
Bulk density (g/cm^3)	0.26 ± 0.03a	0.11 ± 0.03b	**0.02**
Gravimetric moisture content (g/g; %)	59.1 ± 8.9	114.3 ± 23.6	0.07
Forest floor thickness (cm)	1.7 ± 0.1b	2.4 ± 0.5a	**0.007**
pH	5.62 ± 0.07	5.76 ± 0.07	0.22
C: N ratio	19.9 ± 0.4	18.5 ± 0.5	0.06
Vegetation species richness (no. spp.)	7.0 ± 1.1b	11.0 ± 0.9a	**0.02**
Dominant vegetation	*Calamagrostis canadensis* ((Michx.) P.Beauv.) *Rubus idaeus* (L.) *Viburnum opulus* (L.)	*Linnaea borealis* (L.) *Rubus idaeus* (L.) *Rosa acicularis* (Lindl.)	

Table 3-2. Mean earthworm densities (m^2) and one standard error from the mean of adult and juvenile epigeic and other (endogeic/anecic) earthworms detected in high density (H.D.) and low earthworm invasion areas (L.D.).

	Earthworm species			
Area	Adult		Juvenile	
	Dendrobaena octaedra	*Aporrectodea* spp.	*Dendrobaena octaedra*	*Aporrectodea* spp.
H.D.	10 ± 6	29 ± 14	27 ± 14	20 ± 8
L.D.	17 ± 5	0 ± 0	13 ± 5	0 ± 0

Table 3-3. Mean oribatid mite species abundance in the high density (H.D.) and low density (L.D.) earthworm invasion areas. Values in parenthesis represent one standard error from the mean.

Family	**Species**	**H.D.**		**L.D.**	
Euphthiracaridae					
	Euphthiracarus flavus (Ewing, 1908)	1.58	(0.47)	1.13	(0.25)
Phthiracaridae					
	Phthiracarus boresetosus Jacot, 1930			0.06	(0.06)
Trhypochthoniidae					
	Trhypochthonius tectorum (Berlese, 1896) s.l.	0.06	(0.04)	0.06	(0.04)
Hermanniellidae					
	Hermanniella robusta Ewing, 1918	0.06	(0.04)	0.03	(0.03)
Gymnodamaeidae					
	Gymnodamaeus ornatus Hammer, 1952	0.90	(0.29)	3.41	(0.58)
Damaeidae					
	Epidamaeus sp. 2 DEW	0.03	(0.03)	0.06	(0.04)
	Epidamaeus coxalis (Hammer, 1952)			0.09	(0.07)
	Quatrobelba montana Norton, 1980			0.03	(0.03)
Compactozetidae					
	Oribatodes mirabilis Banks, 1895	1.42	(0.75)	0.88	(0.25)
Peloppiidae					
	Ceratoppia bipilis (Hermann, 1804)			0.03	(0.03)
	Ceratoppia quadridentata arctica Hammer, 1955	0.42	(0.10)	0.63	(0.13)
Tectocepheidae					

Tectocepheus sarekensis Trägårdh, 1910			0.09	(0.05)
Phenopelopidae				
Propelops alaskensis (Hammer, 1955)	0.16	(0.09)	0.38	(0.13)
Achipteriidae				
Achipteria sp. 1 DEW	0.10	(0.05	1.09	(0.27)
Oribatellidae				
Oribatella jacoti Behan-Pelletier, 2011	0.03	(0.03)	0.13	(0.07)
Haplozetidae				
Peloribates sp. 3 DEW			0.06	(0.04)
Scheloribatidae				
Paraleius leontonycha (Berlese, 1910)			0.03	(0.03)
Parakalummidae				
Neoribates sp. 1 DEW	0.03	(0.03)	0.03	(0.03)
Chamobatidae				
Chamobates cuspidatus (Michael, 1884)				
Ceratozetidae				
Ceratozetes gracilis (Michael, 1884)	5.81	(1.30)	5.72	(0.74)
*Diapterobates humeralis (*Hermann, 1804)	0.13	(0.06)	0.22	(0.09)
Trichoribates striatus Hammer, 1952			0.06	(0.04)
Galumnidae				
Pilogalumna sp. 1 DEW	1.87	(0.33)	2.34	(0.31)
Pergalumna sp. 1 DEW	0.16	(0.08)	0.16	(0.08)

Table 3-4. Indicator species analysis for the low density earthworm invasion area (L.D.). Strength of the indicator species is determined by a strong p-value ($p<0.05$).

Site	Species	p-value
L.D.	*Gymnodamaeus ornatus*	0.001
L.D.	*Achipteria sp. 1*	0.003

Figure 3-1. Field sampling schematic of organism sampling at each earthworm invasion areas. Dashed boxes represent the four sampling subplots per 400 m^2 plot and the blue circle represents the soil pit that was described.

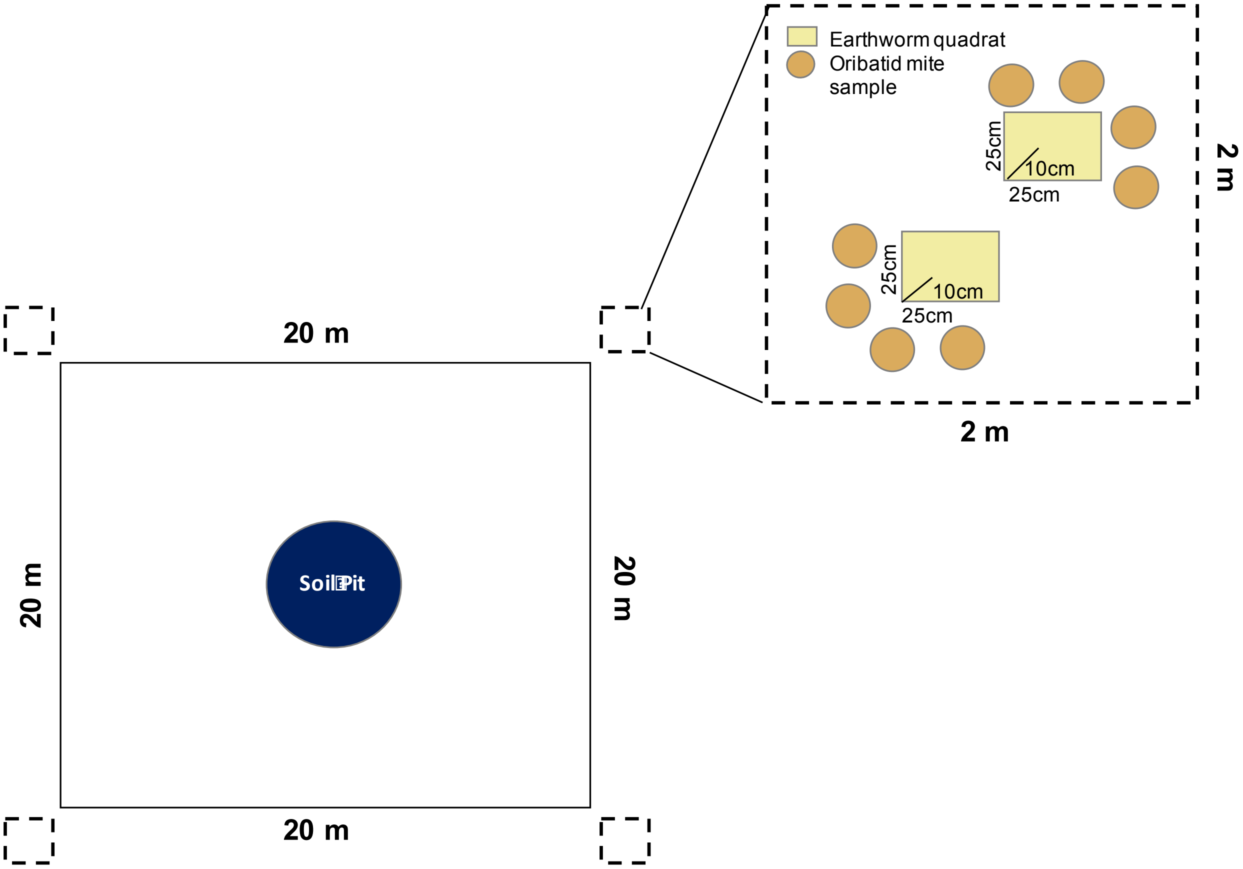


Figure 3-2. Mean oribatid mite (a) abundance and (b) species richness per 500 cm^3 in the high density invasion area (H.D.) and in the low density invasion area (L.D.). Each error bar corresponds to one standard error from the mean. Differences between invasion areas are represented by p-values listed above each comparison.

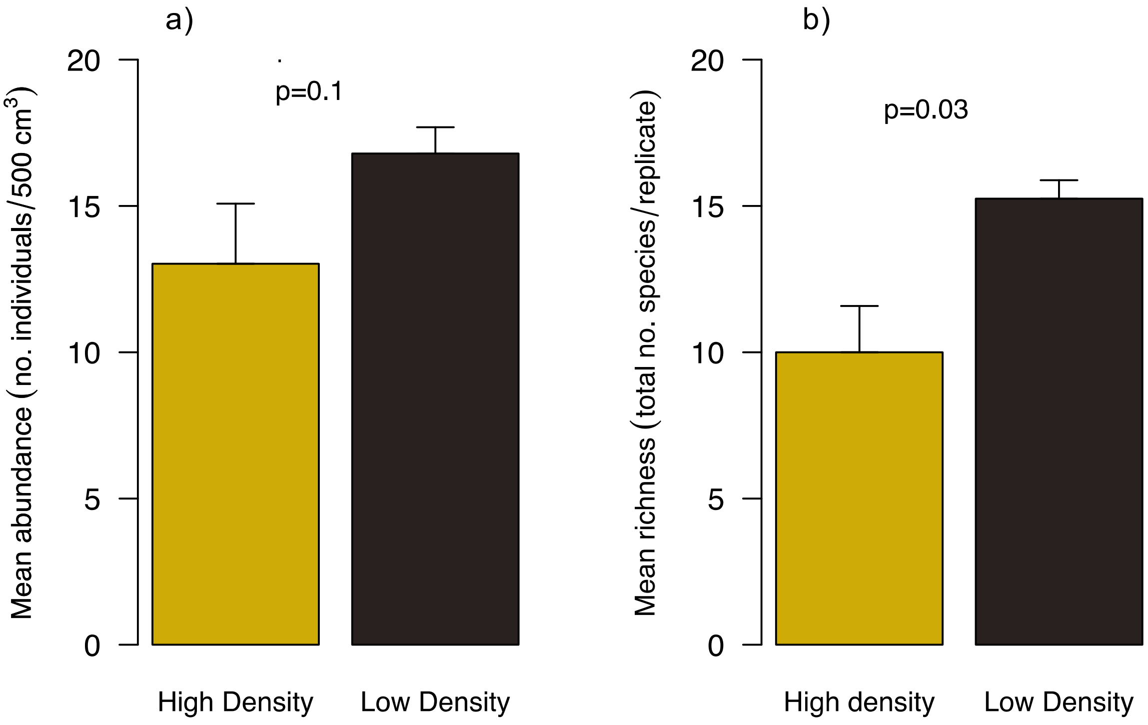


Figure 3-3. Non-metric multi-dimensional scaling (NMDS) using Hellinger-transformed oribatid mite abundance data in the high density invasion area (H.D.) and in the low density invasion area (L.D.). Vectors correspond to soil and site associations with a strong p-value ($p<0.05$). and were identified for bulk density (dB) and C: N ratio (C.N). A permMANOVA was performed and differences in mite assemblages in the two earthworm areas was indicated by the p-value listed in the upper right-hand corner of the ordination.

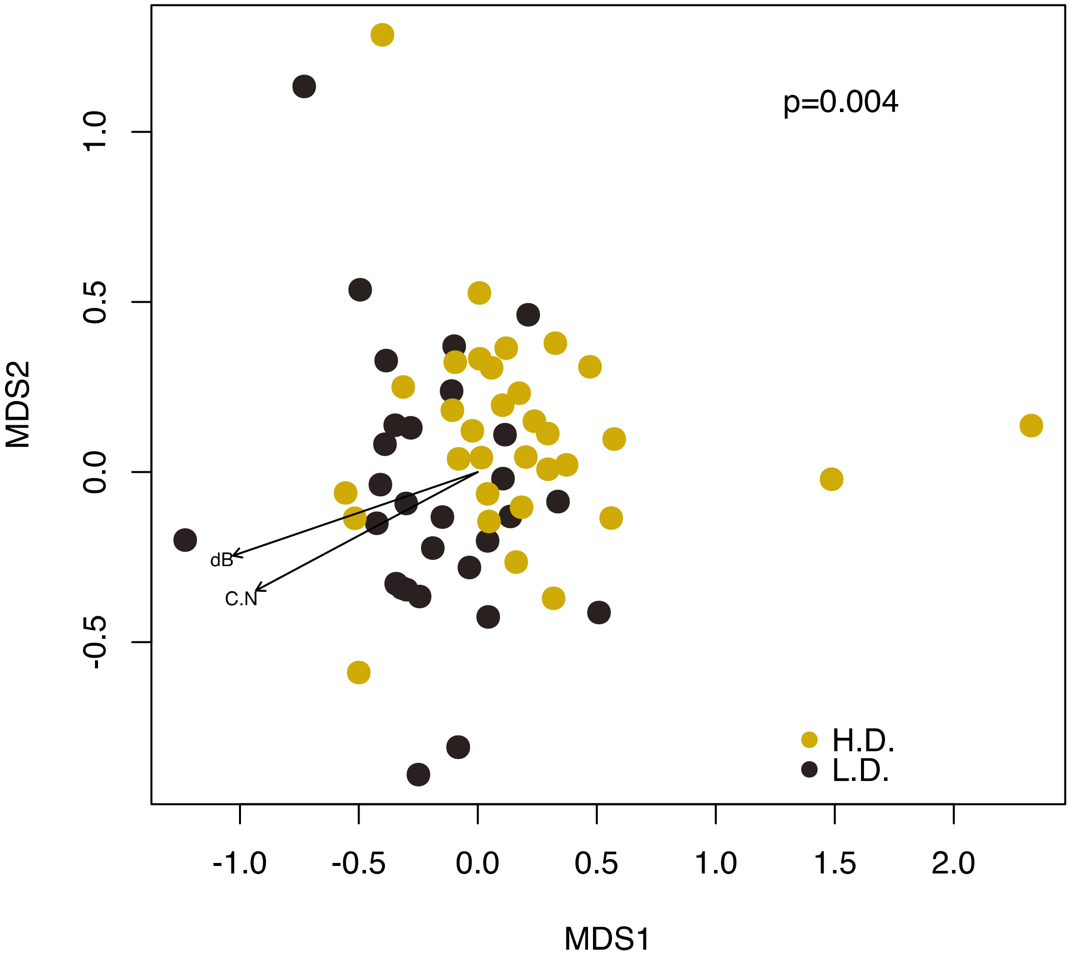
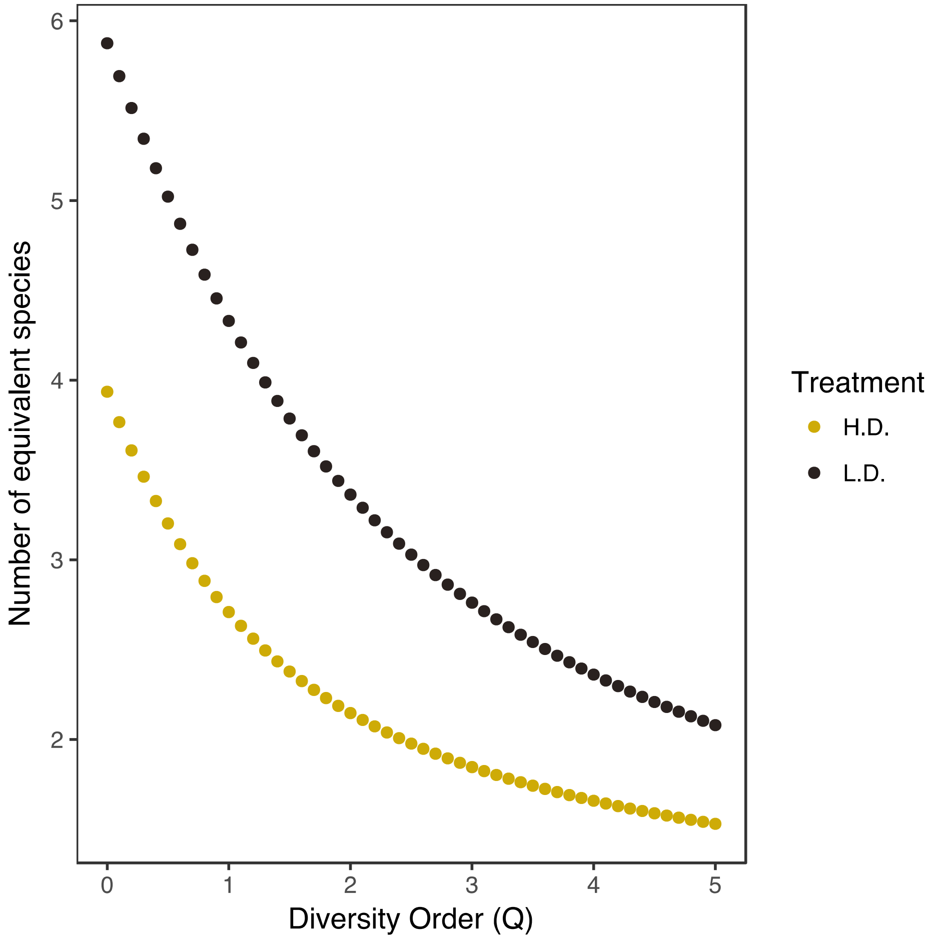


Figure 3-4. Diversity profiles of the high density invasion area (H.D.) and in the low density invasion area (L.D.) where Q_0 has the highest sensitivity to rare species, and rare species sensitivity decreases with increasing diversity order (Q_5).



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4. CHAPTER 4—CONCLUSIONS

The top 10 cm of boreal forest soil is where the majority of biological and chemical activities occur and is where the highest densities of oribatid mites are found (Coleman et al., 2004). In both studies presented in this thesis, oribatid mite community richness and diversity were negatively affected when the forest floor had been disturbed. While different variables may have contributed to either the formation or loss of the forest floor in the two studies, in both it was the physical presence of a forest floor and the associated habitat characteristics (specifically forest floor thickness and bulk density) that were the main drivers of oribatid mite community response to soil disturbance.

4.1. Landscape scale: surface mining in the AOSR

Surface mining was the most drastic disturbance studied, where soils had been completely reconstructed using pre-mining materials and capped with a peat-mineral mix in place of forest floor material. The soil material present in reclaimed stands was the most influential factor affecting oribatid mite reestablishment. While there was some positive development in terms of mite community diversity in the peat-mineral mix (PMM), it was less favorable for reestablishing mite communities than the novel forest floor in stands 8-31 years since reclamation. Both peat-based materials (i.e.; materials with or without forest floor mixed in) had virtually the same abundances. Species richness was also affected, and stands with a novel forest floor had the closest species richness to the forest floor present in surrounding undisturbed forest stands. The influence of the novel forest floor persisted into the underlying PMM, and species found in the PMM were very similar to species found in the novel forest floor. While there were strong differences in richness and diversity between PMM and the novel forest floor, assemblages in the novel forest floor + peat-mineral mix had the lowest overall richness, diversity, and community dissimilarity. Therefore, the establishment of a novel forest floor with a thickness of ≥ 2 cm on top of the PMM substrate substantially increased the inhabitability of the PMM by oribatid mites.

Age and canopy did not influence mite reestablishment as much as the presence of a novel forest floor. Of the stands with a novel forest floor, four were aspen (67%). These aspen stands were either planted to a higher stem density or supported more voluntary aspen growth than other reclaimed stands, which may have increased annual litter inputs into the soil system and aided in the development of a forest floor. Additionally, mite diversity was very close between old-reclaimed aspen and natural aspen stands. This is likely a result of both of the old reclaimed aspen replicates having developed a novel forest floor.

While metrics of abundance, richness, and diversity appeared to be recovering in novel forest floors, the mite species present were different from those found in natural forest floors. This supported my hypothesis of biodiversity preservation rather than species preservation in the novel forest floor within the context of the island biogeography theory (IBT). Not all species found in the natural forest floor that were missing in the novel forest floor (42%) were rare. Some species, such as *Atropacarus striculus* (C.L. Koch, 1835), were unique to the natural forest floor but are abundant in undisturbed boreal soils. This suggests that mite reestablishment may be a combination of reclaiming the habitat found in undisturbed stands and mite immigration into reclaimed stands. According to the IBT equilibrium theory, the more isolated the disturbed habitat, the lower the species equilibrium will be from the undisturbed habitat. While species richness appeared to be recovering in reclaimed stands aged 8-31 years since reclamation, it remained lower than that in undisturbed stands. Additionally, all stands undergoing reclamation in this study were at a minimum 500 m radius away from any undisturbed forest. Based on a maximum oribatid mite active dispersal rate of 2.1 cm/day estimated by Lehmitz et al., 2012, it would take at least 65 years for mite species to immigrate into stands undergoing reclamation. This suggests that the species present in the novel forest floor most likely originated from the PMM, and 89% of the species found in the PMM were also found in the novel forest floor. We can hypothesize that as the forest floor continues to thicken, more species will immigrate into these reclaimed stands, but that the species present may not be the same as those in undisturbed stands.

4.1.1. Management recommendations in the Athabasca Oil Sands Region

It is necessary to restore biogeochemical cycling in soils undergoing reclamation for nutrient cycling and overall ecosystem functions to recover. The most influential factor to oribatid mite recovery was the development of a novel forest floor on top of the PMM. This indicates that both the quantity and quality of the organic capping material influences the reestablishment of oribatid mite communities. Some reclamation prescriptions use a salvaged "forest floor-mineral mix", but this material is less commonly used in comparison to the PMM due to the high availability of peat in lowlands surrounding Fort McMurray. Lower mite abundance, species richness, and diversity in the PMM compared to the novel forest floor observed in this study suggests that mite communities may take longer than 31 years since reclamation to reestablish in the PMM. Further, with time since reclamation, the inhabitability of the PMM by mite communities may increase as a more natural soil-like profile beings to develop. The abundance of peat in the area surrounding Ft. McMurray indicates that it will likely continue to be used for reclamation, so future management practices may consider incorporating methods that accelerate novel forest floor development. The results from this study indicate that reclaimed stands planted to high densities of aspen were more successful in forming a novel forest floor than white spruce.

Aspen canopies develop more quickly and provide greater annual litter fall compared to white spruce stands, which may be why more aspen stands had a novel forest floor in this study. Therefore, incorporating high planting densities of aspen trees into reclamation protocols may result in a more rapid development of a novel forest floor.

As previously mentioned, PMM will likely continue to be the dominant organic reclamation material. Results from this study suggest it is not as favorable as the novel forest floor material for oribatid mite reestablishment between 8-31 years since reclamation. Results from this study also suggest that when a novel forest floor of ≥ 2 cm is present, oribatid mite communities become strikingly more similar in abundance, richness, and diversity to undisturbed forest floors. Therefore, it may be worthwhile to include a thin layer of salvaged leaf litter on the surface of the peat-mineral mix upon reclamation, or selecting revegetation techniques that will accelerate forest floor development (i.e., higher planting densities of aspen). Further research is needed to support the inhabitability of the salvaged forest floor material by mite communities before altering reclamation protocols. In particular, the comparison of reclamation plots capped with PMM and plots capped with salvaged forest floor is necessary to compare their potential for native mite reestablishment. The importance of using a salvaged forest floor material in soil reclamation has previously been observed for the establishment of native plant seeds and propagules after oil sands mining (Mackenzie and Naeth, 2010). It can be hypothesized that native mite communities may establish similarly to plant propagules if this material is used. However, the salvaged forest floor would be disturbed and would lack the physical structure provided by a naturally developing forest floor. A combination of salvaged forest floor and naturally developing forest floor on reclaimed soils may maximize both oribatid mite community recovery and the conservation of native species that would otherwise be absent after soil reconstruction. Ultimately, the results from this study indicate the importance of novel forest floor development in reclaimed stands for oribatid mite reestablishment.

4.2. Stand scale: non-native earthworm invasion

When compared to surface mining, non-native earthworm invasion is less disruptive to the native soil system. For example, surface mining requires entire soils to be completely reconstructed from salvaged materials; typically, after an earthworm invasion, the most drastic physical change imposed on soil is the disappearance of the forest floor and the incorporation of organic materials into deep mineral layers via earthworm burrowing (Frelich, 2006; Eisenhauer, 2010). Therefore, in my study, many of the soil properties remained similar in both earthworm areas, including pH. The most drastic changes in forest floor properties were observed in the high density earthworm invasion area, where bulk density increased by 0.15 g/cm^3 and litter thickness decreased by 0.7 cm on average. These habitat changes are likely what resulted in the significant loss of *Gymnodamaeus ornatus* (-75%) in the high density invasion. Interestingly, both earthworm invasion areas had similar abundances of dominant oribatid mite species. Additionally, the species that were absent in the high density invasion but found in the low density invasion were characterized as rare (singletons/doubletons) in the low density invasion. This effect on rare species in both invasion areas suggests that the presence of *Dendrobaena octaedra* at low densities may strongly influence rare species or species naturally found at low abundances.

We cannot determine if rare species in the low density invasion are rare as a result of disturbance by *D. octaedra* or if these species are indeed rare in the overall undisturbed forest matrix. In order to determine if the intermediate disturbance hypothesis (IDH) is supported in this system, a completely uninvaded stand needs to be included and analyzed. Varied results in the literature make it difficult to determine at what time since invasion and at what earthworm density the IDH is most likely to be observed. The IDH has been both supported and rejected in previous studies involving the same earthworm species where the only difference between the studies was the earthworm density (Eisenhauer et al., 2007; Straube et al., 2009). This suggests that the density of the invading species may be a better predictor of the IDH than the time since invasion or the ecological class of the invading species (i.e., epigeic, endogeic, anecic).

4.2.1. Management and future research following earthworm invasion

Long term monitoring of the earthworm invasion into Alberta is necessary to better understand the data presented in this study. Physical forest floor changes such as increased bulk density and the loss of the litter layer decreased mite abundance, richness, and altered community diversity and composition. Therefore, it may be worthwhile to further separate the forest floor into the respective L, F, and H layers. This would allow us to investigate whether mite communities relocate within the forest floor in the presence of *D. octaedra*, and into the mineral soil in the presence of mineral burrowing species like *Aporrectodea* spp. Complete analyses of communities in the mineral soil layer would also help us better address if soil mixing by the *Aporrectodea* genera in the high density invasion area caused an increase in similarity in forest floor and mineral soil oribatid mite communities.

Non-native earthworm invasion has been documented since the 1950s in northern Alberta (Cameron and Bayne, 2009) and different projects and public awareness programs have been implemented. Globally, efforts to spread awareness and promote citizen science to map the current extent of non-native earthworm invasion have been growing. Projects like EarthwormWatch UK, Minnesota Worm Watch, WormWatch Canada, and the Alberta Worm Invasion Worm Tracker App greatly increase the likelihood of tracking earthworm spread, but these methods rely on citizen participation. Alberta has a unique opportunity to gather annual earthworm data across the province by incorporating an earthworm sampling protocol at the Alberta Biodiversity Monitoring Institute (ABMI). The ABMI conducted annual oribatid mite sampling using a province-wide grid, and the addition of an earthworm protocol to the terrestrial arthropod protocol could provide extremely valuable data to track earthworm invasion across the province. This data would serve as a baseline dataset allowing researchers to more accurately design field studies.

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Appendix 1. Athabasca Oil Sands region site and soil description sheets

Site 1

Site and Soil Assessment Form				**Observers: Cassandra, Brittany**					
Slope: N: -13% , 7.5° S: -8% , 45° E: -6% , 3° W: -1% , 0.5°		**Aspect (deg):** North (w) ,334°		**Slope position: Middle**		**Reclaimed**			
				Other Notes: Syncrude 30D - on the L while walking towards Bill's Lake Next to research plot					
Date: August 21,2015		**Site 1**		**GPS Coordinates: N 56.99871 W -111.61543**					
Tree species: Sw, Aw			**Number of trees (20 m by 20 m)**		20	**Average Sw DBH**: 6.44			
dbh (cm): Aw	2.8	1	1.5	5.7					
dbh (cm): Sw	5.1	5.1	3	4.4	9.9	8	10.4	4.5	4.3
	4.9	6.2	7.5	10.3	6.5	5.4	4.8		
Understory	**N:**		**E:**		**S:**		**W:**		**Dominant understory**
	Rubus idaeus, Fireweed, Dandelion, Grass, Creamy peavine, Yellow sweet clover, Alfalafa		Rubus idaeus, Dandelion, Grass, Fireweed, Purple peavine , Bedstraw		Fireweed, Rubus idaeus, Canada thistle		Rubus idaeus, Fireweed, Canada thistle, Purple peavine, Grass		Grass (Poaceae spp), Fireweed (Epilobeum angustifolium), Raspberry (Rubus idaeus)
Ground cover (1 m by 1 m)		**Ground cover (%)**							**Sampling distance to nearest tree**
	lichen	moss	leaf litter	needles	bare soil	CWD (twigs)	live	shrubs	
N	0	0	100	0	0	0	100	10	**N** 145 cm (Aw)
E	0	0	100	0	0	0	100	6	**E** 155 cm (Sw)
S	0	0	8	0	0	100	47	42	**S** 100 cm (Aw)
W	0	0	100	0	0	2	95	12	**W** 150 cm (Sw)
Site Average	0	0	77	0	0	25.5	85.5	17.5	

Site 2

Summer 2015		**Observers: Cassandra, Brittany**	
Slope (%): N: -2% , 1° S: -3% , 2° E: -3% , 2° W: -4% , 2°	**Aspect (deg):** SouthEast facing, 150°	**Slope position: Middle** **Other Notes** Syncrude Could not install rebar	**Reclaimed**
Date: August 20,2015	**Site 2 aka W1-2**	**GPS Coordinates: N 57.01005 W -111.72236**	
Tree species: Aw, Sw, Salix spp.	**Number of trees (20 m x 20 m)** 42	**Average Aw DBH** 2.01	

dbh (cm): Aw	2.5	2.9	1.8	0.5	1.3	3.2	1.2	1.3 (10+)	1.3 (10+)	1.9 (10+)	1.7
	1.3	1.9	0.8	0.9	1.7	4.4	1.3	1.7	2.8	.5 (10+)	2.7
	0.7	1.4 (10+)	3	3.5	1.7	0.7	2.8	2.5	2.7	2.6	
dbh (cm): Sw	1	2.7	3 (10+)	3.5 (10+)	1.5 (10+)	2.8 (10+)	2.7 (10+)	1.3 (10+)	3.0 (10+)	2.5 (10+)	

	N:	**S:**	**E:**	**W:**	**Dominant understory**
Understory	Wild strawberry, grass, dandelion , Aster ciliolatus, vetch, Achillea millefolium, Equisetum pratense, Arctostaphylos uva-ursi, Rubus idaeus	Fragaria virginiana. Arctostaphylos uva-ursi, Equisetum pratense, Vetch, Achillea millefolium, Dandelion, Grass, Rubus idaeus, Aster ciliolatus, Narrow-leaved hawkweed, Unknown lichen (same as E)	Fragaria virginiana, Equisetum pratense, Rubus idaeus, Grass , Dandelion, Arctostaphylos uva-ursi, Vetch, Achillea millefolium, Rosa acicularis. Aster ciliolatus, Unknown lichen (collected)	Fragaria virginiana, unknown vetch spp. (same as N), grass, Arctostaphylos uva-ursi, Rubus idaeus, Achillea millefolium, Dandelion	Wild strawberry (Fragaria virginiana), Bearberry (Arctostaphylos uva-ursi), Vetch (Vicia spp.)

Ground cover (1 m by 1 m)	**Ground cover (%)**								**Sampling distance to nearest tree**
	lichen	moss	leaf litter	needles	bare soil	CWD (twigs)	live	shrubs	
N	0	30	44	0	0.5	2	92	0	**N 76 cm**
E	2	53	24	0	0	2	120	6	**E 71 cm**
S	0.5	14	11	0	0	0	114	0	**S 110 cm**
W	0	5	21	0	0	0.5	97	8	**W 77 cm**
Site Average	0.625	25.5	25	0	0.125	1.125	105.75	3.5	

Site 3

Summer 2015		**Observers: Cassandra, Brittany**	
Slope (%):N: -6% , 5.5° S: -6% , 3.5° E: -2% , 1° W: -4% , 2.5°	**Aspect (deg):** SouthEast, 174°	**Slope position:** **Flat** **Other Notes** : Syncrude 30D - Bill's Lake lots of Salix spp. Or pincherry?	**Reclaimed**
Date: August 21,2015	**Site 3**	**GPS Coordinates: N 57.00123 W -111.60873**	

Tree species: Aw, Pb	**Number of trees (10 m by 10 m)**	43	**Average Aw DBH**	5.89

dbh (cm): Aw	4.6	7	6.5	2.3	3.3	2.2	2 (10+)	20.5	2.3	10.5
	4	14.3	2.2	0.2	2.2	6.2	1.3	16.7	9.8	4.5
	2.8	3.9	3.1	3.9	17.4	8.5	6	3.5	3.7	2
	3.3	7	8.7	3.7	9.4	1.3	1.5			
dbh (cm): Pb	17	16.1	19.5	16.5	15	19.5				

	N:	**S:**	**E:**	**W:**	**Dominant understory**
Understory	Aster cilliolatus, Grass, Dandelion, Canada thistle, Wintergreen spp, Rubus pubescens, Blunt leaved sandwort	Dandelion, Fireweed, Grass, Canada thistle, White spruce, Rubus pubescens (same as N), Hempnettle (collected)	Fireweed, Dandelion, Grass, Rubus idaeus	Dandelion, Grass, Rubus pubescens, Wintergreen spp. (same as N), White spruce, Fireweed, Yellow sweet clover	Dandelion (Taraxacum officianale), Fireweed, Raspberry (Rubus ideaus)

Ground cover (1 m by 1 m)			**Ground cover (%)**						distance to nearest tree (Aw)	
	lichen	moss	leaf litter	needles	bare soil	CWD	live	shrubs		
N	0	0	96	0	3	1	39	0	N	159 cm
E	0	0	100	0	0	8	10	7	E	47 cm
S	0	0	100	0	0	2	60	0	S	61 cm
W	0	0	100	0	0	0	49	0	W	27 cm
Site Average	0	0	99	0	0.75	2.75	39.5	1.75		

Site 4

Summer 2015		**Observers: Cassandra, Brittany**	
Slope (%): NW: -10% , SE: -15% , 8.5° NE: -12% , 7° SW: -13% , 7.5°	**Aspect (deg):** NorthWest facing, 320°	**Slope position:** **Other Note** Sampled July 11, 2015, Measured DBH Aug 21	**Middle** **Reclaimed**
Date: August 21,2015	**Site 4**	**GPS Coordinates: N 56.99556 W -111.61914**	
Tree species: Aw, Pb	**Number of trees (20 m by 20 m)**	215 Aw, 21 Sw = 236	**Average DBH** 4.04

dbh (cm): Aw	2.2	1.9	3.7	5.5	3.8	2.6	0.9	3.2	1.3	3.3
	3.7	3.9	2.5	1.8	2.8	1.3	3.6	3.2	4.5	1.7
	8.7	3.7	8.6	5.4	5.7	9.1	2.5	8.4	1.3	7
	9.5	2.5	4.3	9.1	2	2.4	3.3	2.5		

	SW:	**SE:**	**NE:**	**NW:**	**Dominant understory**
Understory	Rubus idaeus, Dandelion, Canada thistle, Trifloium hybridum	Fragaria virginiana, Canada thistle, Achillea millefolium, Dandelion, Alsike clover, Yellow sweet clover, Grass	Fireweed, Dandelion, Alsike clover, Achillea millefolium, Rubus idaeus, Purple peavine	Dandelion, alsike clover, Achillea millefolium, Canada thistle, Rubus idaeus, Yellow sweet clover, Grass	Dandelion (Taraxacum officinale) Achillea millefolium, Alsike clover (Trifolium hybridum)

Ground cover (1 m by 1 m)			**Ground cover (%)**						Sampling distance to nearest tree	
	lichen	moss	leaf litter	needles	bare soil	CWD	live	shrubs		
SW	0	0	100	0	0	4	31	1	SW	39 cm
NW	0	0	100	0.5	0	2	50	0	NW	52 cm
SE	0	0	100	0	0	10	13	1	SE	69 cm
NE	0	0	100	0	0	2	17	0	NE	59 cm
Site average	0	0	100	0.125	0	4.5	27.75	0.5		

Site 5

2015		**Observers: Cassandra, Brittany**	
Slope N: -1% , 0.5° E: -4% , 2.5° S: +2% , 1° W: -0% , 0°	**Aspect (deg):** NE 60˚	**Slope position:** **Flat**	**Natural**
Date: August 23,2015	**Site 5**	**Other Notes** : Syncrude Sw Stand *Thick cover of dust on everything. B/w 2 roads Hill of sand across road that runs on the NW side of the site	
Tree species: Sw, Lt, Pb, Aw	**Number of trees (20 m by 20 m): 46**	**GPS Coordinates: N 56.94395 W -111.73924**	

dbh (cm): Sw	3.7	9.3	23.3	6.1	11	14	1.5	23.3	**Average DBH** 9.07
	1.7	24.7	2.4	34.2	10.1	1.7	24.7	1.7 (10+)	
	21.7	4.9	3.9	3.9	4.5	2.4 (10+)	8.7		
dbh (cm): Pb	16.5	1.6	13.2	2.5	2.1				
dbh (cm): Aw	1.6	6.1	9	5.4	11.6	12.8			
dbh (cm): Lt	4.9	1.6	1.5	3.3	1.5	9.6			
	5.1	11.3	14.3	4.3	2.8	3			

Understory	**N:** Palmate leaved coltsfoot, Wild strawberry, Buffaloberry, Bunchberry, Rosa acicularis, Northern Bedstraw, Twinflower, Moss, Wild lily of the valley, Trintalis borealis, Bog cranberry, Shrubby cinquefoil, Grass, lily spp., Aster cilliolatus	**S:** Wild strawberry, Labrador tea, Moss, Palmate leaved coltsfoot , Bunchberry, Rosa acicularis, Grass, Achillea millefolium, Twinflower, Buffaloberry	**E:** Rosa acicularis, Dwarf birch, Wild strawberry, Moss, Palmate leaved coltsfoot, Labrador tea, Twinflower, Grass Bog cranberry, Willow spp., Lily spp., Northern starflower	**W:** Rosa acicularis, Labrador tea , Wild straw, Bog cranberry, Palmate leaved coltsfoot, Buffaloberry, Grass, Moss, Bunchberry, Twinflower, Bishop's cap, Meadow horsetail, Aster cilliolatus	**Dominant understory** Palmate leaved coltsfoot (Petasites palmatus), Rosa acicularis, Bunchberry (Cornus canadensis)

Ground cover (1 m by 1 m)	**Ground cover (%)**							**Sampling distance to nearest tree (Sw)**	
	lichen	moss	leaf litter	needles	bare soil	CWD	live	shrubs		
N	0	18	46	28	0	24	39	0	N	220 cm
E	0	27	47	25	0	6	10	7	E	95 cm
S	0	44	21	3	0	30	60	0	S	200 cm
W	0	1	30	1	0	0	49	0	W	114 cm
Site Average	0	22.5	36	14.25	0	15	39.5	1.75		

Site 6

Site and Soil Assessment Form		**Observers: Cassandra & Brittany**	
Slope: N: 3.2%, 2˚ E: 5%, 3˚ W: 0% 0˚	**Aspect (deg):** NorthWest, 279°	**Slope position:** **Flat**	**Natural**
		Other Notes: Syncrude SWSS	
Date: August 24,2015	**Site 6**	**GPS Coordinates: N 56.96378 W -111.72173**	
Tree species: Aw, Sw	**Number of trees (20 m by 20 m)** 40	**Average Aw DBH**: 9.73	

dbh (cm): Aw	20.9	23.8	21.7	1.5	1.5	31.4	1.4	23.6	4
	1.5	2.5	4	0.9	29.4	24.3	2.3	1.8	1.5
	29.8	2.2	0.9	24	3.3	1.5	2.3	1.6	1.3
	16.9	0.5	1.6	25.7	1.3	2.3	26.6	3	1
dbh (cm): Sw	7	14.2	12.8	11.5					

N: Bunchberry, Rosa acicularis, Twinflower, Lab. Tea , Northern Bedstraw, Wild lily of the valley, Lycopodium annotinum, Northern Star-flower, Wild strawberry, Small bog cran., moss (collected), Labrador lousewort	**S:** Stair-step moss, Twin flower, Northern bedstraw, Bunchberry, Bog cranberry, Wild lily of the valley , moss (collected), Rosa acicularis, Labrador lousewort, Fireweed, common yarrow, fabaceae spp.. Red oiser dogwood	**E:** Bunchberry, buffaloberry, Labrador tea, wild strawberry, Twinflower, Wild lily of the valley, Bog cranberry, Fireweed, Blueberry, High bush cranberry, Moss Grass, Northern Starflower, Northern black currant - Ribes hudsonianum	**W:** Palmate-leaved coltsfoot, Red-oiser dogwood, Bunchberry, Wild strawberry, Buffaloberry, Rosa acicularis, Twinflower, Bishop's cap, Wild sarsparilla, Moss, Wild lily of the valley, Lab. Lousewort, Wild red raspberry	**Dominant understory:** Bunchberry (Cornus canadensis), Twinflower (Linnaea borealis), Rosa acicularis

Ground cover (1 m by 1 m)		**Ground cover (%)**						**Sampling distance to nearest tree (Aw)**
	lichen	moss	leaf litter	needles	bare soil	CWD	live	shrubs	
N	0	4	98	0	0	7	66	23	N 85 cm
E	0	2	98	0	0	12	60	17	E 143 cm
S	0	30	44	0	0	21	60	2	S 150 cm
W	0	11	94	0	0	9	50	13	W 70 cm
Site Average	0	11.75	83.5	0	0	12.25	59	13.75	

Site 7

Summer 2015		**Observers: Cassandra, Brittany**	
Slope %	N: -1% , 0.5° E: -2% , 1° S: -1% , 0.5° W: -1% , 0.5°	**Slope position: Flat**	**Natural**
		Other Notes: Syncrude SWSS	
Date: August 24,2015	**Site 7**	**GPS Coordinates: N 56.95859 W -111.72289**	
Tree species: Aw, Sw		**Number of trees (20 m by 20 m)** 41	**Average Aw DB** 9.72

dbh (cm): Aw	1.5	20.6	22.4	21.7	20	0.7	3.8	2.3	1.2	2.3
	21.4	21	1.8	0.6	0.4	2.3	1	28.6	21.1	2.4
	3.5	3.6	2.7	20.8	8.8	20.7	0.5	3.7	2.3	4.7
	26.5	1.2	1.5	19.5	22.9	25.6	2.3	1.4		
dbh (cm): Pb	3.5	3	**dbh (cm): Sw**	1.1						

N: Wild strawberry, bunchberry, prickly rose, palmate leaved coltsfoot, low bush cranberry, bog cranberry, wild red raspberry northern bedstraw, twinflower, wild lily of the valley, buffaloberry, labradoe lousewort, grass, lindley's aster.	**S:** Bunchberry, Fireweed, Prickly rose, Palmate leaved coltsfoot, Bog cranberry, Northern bedstraw, Twinflower, Wild lily of the valley, grass, Lindley's aster, Bishop's cap, Labrador tea	**E:** Bunchberry, Fireweed, Prickly rose, Palmate leaved coltsfoot, Bog cranberry, Twinflower, Grass, Lindley's aster, Common blueberry, Northern starflower	**W:** Wild strawberry, Bunchberry, Prickly rose, Bog cranberry, Northern bedstraw, Twinflower, Wild lily of the valley, Grass, Lindley's aster, Common blueberry, Moss spp, Northern starflower, Lichen spp.	**Dominant understory:** Bunchberry (Cornus canadensis), Palmate leaved coltsfoot (Petasites palmatus), Twinflower (Linnaea borealis)

Ground cover (1 m by 1 m)	**Ground cover (%)**							Sampling distance to nearest tree (Aw)	
	lichen	moss	leaf litter	needles	bare soil	CWD	live	shrubs	
N	0	0	93	0	0	7	74	12	N	86 cm
E	0	0	100	0	0	10	68	10	E	136 cm
S	0	0	100	0	0	0	84	8	S	90 cm
W	0.5	10	92	0	0	10	77	12	W	129 cm
Site Average	0.125	2.5	96.25	0	0	6.75	75.75	10.5		

Site 8

2015		**Observers: Cassandra, Brittany**	
Slope (%): N: -4% , 1.5°	**Aspect (deg):** NW 344°	**Slope position:** Lower-middle	**Reclaimed**
E: -8% , 4° S: -8% , 4° W: -4% , 2.5°		**Other Notes** : Syncrude W1 Site	
Date: August 24,2015	**Site 8**	**GPS Coordinates: N: 57.01005 W: -111.72236**	

Tree species: Aw, Sw	**Number of trees (20 m x 20 m)**	35	**Average Aw DBH** 1.29

dbh (cm): Aw	0.8	2.3	1 (10+)	1.4 (10+)	0.7 (10+)	1.5	2.4	1.6	1	0.8	1.3
	0.5	1.5	0.8 (10+)	1 (10+)	1.2	1.5	1.8	1.8	0.7	1.5	
dbh (cm): Sw	2.3	1.3	1.3	1.4	2.5 (10+)	1	1 (10+)	1.3	1.7	1.3	1.2
	1.1	1	1.4								

Understory	**N:** Wild vetch (Vicia americana), Wild strawberry, Fireweed, Alsike clover, Dandelion, White sweet clover (Melilotus albus), Grass, Meadow horsetail, Moss, Achillea millefolium, Dwarf raspberry?, Aster ciliolatus	**S:** Wild red straw., Dwarf rasp? (same as N), Grass, Meliolatus albus, Vicia americana, Fireweed, Dandelion, Red-oiser dogwood, Achillea millefolium , Alsike clover, Moss (collected),	**E:** Grass, Wild red rasp., Dandelion	**W:** Achillea millefolium, Alsike clover, Dandelion, White sweet clover, Meadow horsetail Grass , Strawberry, Wild vetch, Achillea millefolium , Moss (same as S)	Dominant understory: Meadow horsetail, Grass, Wild vetch

Ground cover (1 m by 1 m)	**Ground cover (%)**								**Sampling distance to nearest tree (Aw)**	
	lichen	moss	leaf litter	needles	bare soil	CWD	live	shrubs		
N	0	3	37	0	0.5	0	67	0	N	70 cm
E	0	0	100	0	0	0	100	0	E	170 cm
S	0	6	22	0	5	1	101	4	S	60 cm
W	0	3	22	0	0	1	100	0	W	100 cm
Site Average	0	3	45.25	0	1.375	0.5	92	1		

Site 9

Summer 2015		**Observers: Cassandra, Brittany**		
Slope (%): N: -7% , 4.5° E: -7% , 4.5° S: -0% , 0° W: -5% , 3°	**Aspect (deg):** NW 274°	**Slope position: Lower - Middle**	**Natural**	
		Other Notes : N Hwy 63 Sw Stand	* Rebar placed	
Date: August 22,2015	**Site 9**	**GPS Coordinates: N 57.26284 W -111.63018**		
Tree species: Sw, Aw, Bw	**Number of trees (20m x 20m)**	28	**Average Sw DBH**	17.28

dbh (cm): Sw	18.4	8.1	47.6	23.1	17.7	36.2	36	37.2	16.3	
dbh (cm): Pb	1.2	0.9	0.7	1.5	2.6	0.7	1.1	25.8	35.9	
dbh (cm): Aw	0.8	0.8	1.2 (10+)	2.1	1.2	1.5	0.6	0.4	1.5	0.8

	N:	**S:**	**E:**	**W:**	Dominant understory
Understory	Cornus canadensis, Rosa acicularis, Pleurozium schreberi, Wild red currant (Ribes triste), Palmate leaved coltsfoot, Equisetum pratense, Gallium trifitum, Linnaea borealis, Mitella nuda, Maianthemum canadense	Rubus ideaeus, Equisetum pratense, Mitella nuda, Cornus canadensis, Rosa acicularis, Moss (collected)	Wild sarsaparilla, Bunchberry, Labrador tea, Rosa acicularis, Mitella nuda, Equisetum pratense (6), Rubus idaeus , Low bush cranberry, Moss (collected)	Petasites palmatus, Mitella nuda, Cornus canadensis, Equisetum pratense, Rubus idaeus, Gallium trifitum, Wild sarsaparilla, Moss (collected)	Mitella nuda, Prickly rose, Equisetum pratense

Ground cover (1 m by 1 m)	**Ground cover (%)**							Sampling distance to nearest tree	
	lichen	moss	leaf litter	needles	bare soil	CWD	live	shrubs	
N	0	100	50	40	0	9	178	4	N 227 cm Pb
E	4	48	58	30	0	20	123	6	E 211 cm Sw
S	0	43	20	40	0	20	105	18	S 112 cm Sw
W	0	25	17	40	0	10	112	4	W 105 cm Sw
Site Average	1	54	36.25	37.5	0	14.75	129.5	8	

Site 10

Summer 2015				**Observers: Cassandra, Brittany**					
Slope (%): N: -14% , 8° E: -25%, 14° S: -13%, 7.5° W: -		Aspect (deg): SW 226°		Slope position: Middle(S,W) and upper (N, E)			Reclaimed		
Date: Aug 22,2015		**Site 10**		**GPS Coordinates:**	**N: 57.25674, W: -111.62381**				
Tree species: Aw		**Number of trees (20 m x 20 m)**			26	Avg Aw DBH	10.98		
	1.5	22.1	19.4	18.7	0.7	0.6	0.9	0.6	0.7
dbh (cm)	17.2	17.1	0.6	17.4	17.7	16.2	1.1	19.1	19.3
	16.5	14.6	16.4	24.2	1.8	1	1.7	18.2	
Understory	**N**: Maianthemum canadense, bunchberry, twinflower, saskatoon, wild sasparilla, fireweed, fragaria virginiana,grass, rosa acicularis, gallium boeral		**E** twinflower, bunchberry, rosa acicularis, wild sasparilla, saskatoon, symphoricarops occidentalis, bearberry, bog cranberry, strawberry, gallium boreal, moss		**S**: buffaloberry, bunchberry, twinflower, rosa acicularis, palmate-leaved coltsfoot, labrador tea, mitella nuda, foreweed, bog cranberry, moss, northern bedstraw, grass, wild red currant, blueberry, wild lily of the valley, northern starflower		**W**: Rosa acicularis, Buffaloberry, Grass, Bunchberry, Wild lily of the valley, twinflower, bog cranberry, northern bedstraw, showy aster		**Dominant understory** Bunchberry (Cornus canadensis), Twinflower (Linnaea borealis), Rosa acicularis
Ground cover (1 m by 1 m)		**Ground cover (%)**							Sampling distance to nearest tree
	lichen	moss	eaf litter	needles	bare soil	CWD (twigs)	live	shrubs	
N	0	3	98	0	0	6	63	8	N: 300 cm Aw
E	0	0.5	80	0	0	15	88	5	E: 280 cm Aw
S	0	5	98	0	0	9	80	20	S: 127 cm Aw
W	0	1.5	93	1	0	11	46	16	W: 110 cm Aw
Site Average	0	2.5	92.25	0.25	0	10.25	69.25	12.25	

Site 11

Summer 2015		**Observers: Cassandra, Brittany**	
Slope (%): N: -15% , 8.5° E: -17%, 9.5° S: -13%, 7.5° SW: -18%, 10°	Aspect (deg): NE, 61 deg	Slope position: Middle	**Reclaimed**
Date:Aug 24, 2015	**Site 11**	**GPS: N: 57.08326, W: -111.61208**	
Tree species: Aw	**Number of trees (20 m by 20 m): 87**	Average Aw DBH	5.98
dbh (cm)	Aw: 2.5, Aw: 2, Aw: 9.4, Aw: 10.7, Aw: 2.2, Aw: 11.9, Aw: 7.8, Aw: 10.7, Aw: 6.8, Aw: 14.1, Aw: 9.7, Aw: 4.4, Aw: 1.3, Aw: 0.9, Aw: 2.8, Aw: 1.5, Aw: 1, Aw: 0.8, Aw: 10, Aw: 3.5, Aw: 5.8, Aw: 6.9, Aw: 9.3, Aw: 4.3		

Understory	**N:** wild red raspberry, grass, dandelion, fabaceae spp., aster ciliolatus, alsike clover, lotus corniculatus	**E:** grass, dandelion, wild red raspberry, wild strawberry	**S:** Raspberry, aster ciliolatus, grass, dandelion, fabaceae spp. lotus corniculatus	**W:** Rasp. Yellow flowerings, grass, fabaceae spp., lotus corniculatus	NOTE: Red osier dogwood throughout site	**Sampling distance to nearest tree (Aw)** N: 50 cm E: 70 cm S: 130 cm W: 100 cm	**Dominant understory:** Grass (Poaceae spp.), Dandelion (Taraxacum officinale), Wild red raspberry (Rubus ideas),

Ground cover (1 m by 1 m)	**Ground cover (%)**						
	lichen	moss	leaf litter	needles	bare soil	CWD (twigs)	live	shrubs
N	0	0	100	0	0	0	33	5
E	0	1	100	0	0	0	44	1
S	0	0	100	0	0	0	40	26
W	0	0	100	0	0	0	37	8
Site Average	0	0.25	100	0	0	0	38.5	10

Site 12

2015		**Observers: Cassandra, Brittany**	
Slope (%): NE: 1% , -1° SE: 0 NW: 1%, 1° SW: 1%, 1°	Aspect (deg)	**Slope position:** Flat	**Reclaimed**
Date:July 18,2015	**Site 12**	**GPS Coordinates:** N: 56.99108, W: -111.56409	
Tree species: Aw, Sw, Aw, Sw	**Number of trees (20m x 20m):** 15	**Average Aw DBH:**12.22	
dbh (cm)	Aw: 12.8, Aw: 10.3, Aw: 14.2, Aw: 8.5, Aw: 10.1, Aw: 5.2, Aw: 14.8, Aw: 13.7, Aw: 14.2, Aw: 11.1, Aw: 11.9, Aw: 10.1, Aw: 14.2, Aw: 16.4, Aw: 15.8		

Understory	**NE:**meadow horsetail, wild smooth strawberry, marsh redd grass, dandelion, common pink wintergreen, prickly rose	**SE:**wild red raspberry, wild smooth strawberry, dandelion, meadow horsetail	**SW:** dandelion	**NW:** common pink wintergreen	**Dominant understory:** Common pink **w**intergreen, Wild strawberry, Marsh reed grass	Sampling distance to nearest tree (Aw):

Ground cover (1 m by 1 m) **Ground cover (%)**

	lichen	moss	leaf litter	needles	bare soil	CWD (twigs)	live	shrubs
NE	0	0.2	100	25	0	12	10	0
SE	0	0.4	75	40	0	10	6	1
SW	0	0.2	70	40	0	9	18	0
NW	0	3	50	50	0	8	3	0
Site Average	0	0.95	73.75	38.75	0	9.75	9.25	0.25

Site 13

Site and Soil Assessment Form				Observers: Cassandra, Brittany				
Slope (%): N: -3% , 2° E: -2%, 1° S: -2%, 1˚		Aspect (deg): S,181°		**Slope position:** Flat		Reclaimed		
Date:Aug 19 2015		**Site 13**		**GPS Coordinates N: 56.99253, W: -111.56313**				
Tree species: Sw, Dogwood, Aw		**Number of trees (20m x 20m):** 27						
DBH (cm) Sw	Sw: 14.5, Sw: 21, Sw: 10.9, Sw: 14.7, SwL 16.5, Sw: 15.2, Sw: 15.9, Sw: 13.8, Sw: 19.1, Sw: 14.2, Sw: 5.5, Sw: 18.5, Sw: 15.8, Sw: 20.2, Sw: 14.1, Sw: 20.5							
DBH (cm) Aw	Aw: 5.5, Aw: 7.5, Aw: 5.6, Aw: 6.5, aw: 7.0, Aw: 6.0, Aw: 9.3, (??): 0.9, Aw: 12.9, Aw: 7.3							
Understory	**N:** wild strawberry, 3 mosses, 2 lichen, aster ciliolatus	**E:** grass, rosa acicularis	**S:** lesser wintergree, grass, moss, unkonwn shrub	**W:** dandelion, lesser wintergreen, moss	**Dominant understory:** Lindley's Aster (Aster ciliolatis), Moss spp., Lesser wintergreen (Pyrola minor)		**Sampling distance to nearest tree (Sw)** N: 100 cm E: 52 cm S: 81 cm W: 92 cm	
Ground cover (1 m by 1 m)			**Ground cover (%)**					
	lichen	moss	leaf litter	needles	bare soil	CWD (twigs)	live	shrubs
NE	2	4	0	100	0	4	7	0
SE	0	0	12	100	0	6	2	0.4
SW	0	4	22	100	0	20	11	4
NW	0	2	50	100	0	40	0	0
Site Average	0.5	2.5	21	100	0	17.5	5	1.1

Site 14

Site and Soil Assessment Form **Summer 2015**
Observers: Cassandra, Brittany
Slope (%): NE: -15% , 8.5° E: -15%, 8.5° S: -16%, 9° W: -20%,
Slope position: Middle
Reclaimed
20-Aug-15
Site 14
GPS Coordinates N: 56.99326, W: -111.57085
Tree species: Sw
Number of trees (20 m x 20m): 58

Notes: Lots of dead dogwood. Upslope from N and E sampling locations is Jack Pine

DBH (cm) Sw: Sw: 11.5, Sw: 8.3, Sw: 9.9, Sw: 9.6, Sw: 11.8, Sw: 13.1, Sw: 11.2, Sw: 7.4, Sw: 14.5, Sw: 13.8, Sw: 14.4, Sw: 11.9

Understory	**N:** Moss (knights plume),	**E:** wild strawberry, aster cilliolatus, 2 mosses(?)	**S:** same two mosses as E, blue columbine	**W:** 2 mosses (same as E), dandelion, blue columbine	**Around the site:** prickly rose, rubus idaeus, grass	**Dominant understory:** Moss (Pleurozium schreberi), blue columbine (Aquilegia brevistyla), Lindley's aster (Aster ciliolatus)

Ground cover (1 m by 1 m)	**Ground cover (%)**								Sampling distance to neartest tree (Sw) N: 100cm E: 24cm S: 30cm W:32cm
	lichen	moss	leaf litter	needles	bare soil	CWD (twigs)	live	shrubs	
NE	0	1	0	100	0	8	1	0	
SE	0	5	0.5	100	0	16	6	0	
SW	0	3	6	100	0	2	4	0	
NW	0	15	2	95	0	5	15	0	
Site Average	0	6	2.125	98.75	0	7.75	6.5	0	

Site 15

Site and Soil Assessment Form		**Observers: Cassandra, Brittany**	
Slope (%): N: -10% , 6° S: -37%, 20.5° E: -10%, 6° W: -39%, 21.5°	Aspect (deg): NE facing	Slope position: Flat	Reclaimed
July 20,2015	**Site 15**	**N: 57.02367 W: -111.49973**	
Tree species: Sw, Pj, Bw	**Number of trees (20m x 20m):** 40		
DBH (cm): Sw	15.6, 15.0, 14.7, 11.8, 11.9, 14.4, 11.8, 14.0, 10.3, 10.8, 14.3, 15.1, 11.0, 10.9, 16.7, 14.6,		
DBH (cm): Pj	Pj: 8.7 Pj: 10.7, Pj: 9.3, Pj: 9.8, Pb: 3.5, Pj: 9.3		
DBH (cm) Pb	Bw: 4.0, Bw: 1.5, Bw: 2.0, Bw: 6.1,		

Understory	**N:** wild strawberry, rasberry, grass, dandelion, unknown fern, moss	**E** wild strawberry, raspberry, dandelion, moss, lichen	**S:** prickly rose, moss, wild strawberry, unknown	**W:** Wild strawberry, baby Aw, rubus idaeus, moss, danelion, mushroom	**Dominant understory:** Fern spp, wild strawberry, moss	**Sampling distnace to nearest tree (Sw):** N: 110 cm E: 130 cm S: 90 cm W: 98 cm

Ground cover (1 m by 1 m)	**Ground cover (%)**						
	lichen	moss	leaf litter	needles	bare soil	CWD (twigs)	live	shrubs
N	0	0.5	6	100	0	2	12.5	1
E	0.50	5	6	100	0	2	20	3
S	0	5	2	100	0	3	7	2
W	0	53	20	60	0	8	67	9
Site Average	0	15.875	8.5	90	0	3.75	26.625	3.75

Site 16

Summer 2015		**Observers: Cassandra, Brittany**	
Slope (%): N: -5% , 3° S: +2%, 1.0° E: -5%, 3° W: -11%, 6°	Aspect (deg): W, 270°	Slope position: Upper	Reclaimed
July 20,2015	**Site 16**	**N: 56.99092 W: -111.53693**	
Tree species: Sw	**Number of trees (20m x 20 m):** 66		

DBH (cm) Sw	5.4, 7.5, 6.5, 6.1, 4.2, 2.6, 5.2, 1.1, 8.7, 6.2, 4.3, 5.2, 6.6, 6.8, 1.9, 7.0, 6.7, 5.2, 5.6, 7.3, 6.2, 4.0, 0.7, 2.9, 1.0, 4.4, 5.7, 2.8, 6.3, 3.5, 2.4, 5.4, 3.8, 5.9, 7.0, 5.9, 4.4, 4.9, 5.4, 7.3, 6.6, 5.5, 7.5, 5.7, 6.0, 5.6, 9.1, 3.0, 2.8, 6.6, 5.1, 3.4, 8.9, 5.1, 6.4, 6.6, 8.9, 5.5, 6.1, 5.8, 6.0, 5.5, 6.1, 5.8, 6.0, 5.5, 3.0, 6.3, 4.9, 10c m from ground: 4.8

Understory	**N:** Wild strawberry, whitet sweet clover, dandelion, fireweed, alsike clover, grass, mushrooms, unkown moss (glowmoss?), unkown lichen	**E:** alfalfa, dandilion, mushrooms, same two mosses as N	**S:** Wild smooth strawberry, fireweek, mushroom, alsike clover, frogpelt, mosses, stair-step moss, pleuroium schreberi tonetypnum knightands	**W:** wild strawberry, dandelion, fireweed, alfalfa, clover, mushroom, mosses	**Dominant understory:** Moss, wild straw, alfalfa (Medicago sativa)

Ground cover (1 m by 1 m)	**Ground cover (%)**								
	lichen	moss	leaf litter	needles	bare soil	CWD (twigs)	live	shrubs	**Sampling distance to neartest tree (Sw)** N: 64cm, E: 50cm, S: 56cm, W: 73cm
1	2	92	16	6	1	0	112	0	
2	1.00%	98	24	1	0.5	1	103	0	
3	2.5	98	24	3	0	0	100	0	
4	1	98	20	2	2	0	108	0	
Site Average	0	96.5	21	3	0.875	0.25	105.75	0	

Site 17

Summer 2015				**Observers: Cassandra, Brittany**				
Slope (%): N: -1% , 0.5° S: -1.5%, 1.0° E: 0%, 0° W: -5%,		Aspect (deg): E, 101°		Slope position: Flat		Reclaimed		
July 20,2015		**Site 17**		**N: 56.99222 W: -111.53276**				
Tree species: Sw, Pb			**Number of trees (20 m by 20 m): 44**					
DBH (cm) Sw	9.8, 8.7, 7.5, 3.7, 6.4, 5.8, 11.7, 13.1, 9.4, 2.9, 2.8, 10.4, 2.4, 2.4, 9.5, 8.7, 10.2, 11.3, 9.7, 6.8, , 1.7, 5.5, 7.4, 5.7, 4.0, 6.9, 7.4, 10.7, 7.0, 4.8, 8.8, 10.3, 8.4, 9.3, 7.7, 6.7, 13, 4.2, 8.8, 10.0, 3.0, 6.2, 9.8							
Understory	**N:** dandelion, clover (purple), alfalfa, wild red raspberry, wild smooth strawberry, fireweed, moss [stairstep]		**E:** dandelion, alsike clover, fireweed, wild red raspberry, mosses (2)	**S:** Wild smooth strawberry, alfalfa, fungi/mushrooms, vetch spp., dandelion, 2 mosses (unknown)		**W:** white sweet clover, dandelion, fireweek, alsike clover, mosses (2-3)	Dominant understory: Moss (Pleurozium schreberi), Wild strawberry, Dandelion	Sampling distance to neartest tree (Sw) N: 70cm E: 70cm S: 119cm W: 80cm
Ground cover (1 m by 1 m)			**Ground cover (%)**					
	lichen	moss	leaf litter	needles	bare soil	CWD (twigs)	live	shrubs
1	0	88	2	11	0	5.5	89	0.5
2	0.00%	100	24	1	0	0	124	1
3	0.5	79	24	0.5	10	0.5	97	0
4	0	77	18	0	4	0	97	0
Site Average	0.125	86	17	3.125	3.5	1.5	101.75	0.375

Site 18

Site and Soil Assessment Form		**Summer 2015**		**Observers: Cassandra, Brittany**				
Slope (%): NE: -27% , 15° SE: -25%, 14° NW: -27%, 15° SW: -25%, 14°		Steep slope: Mid		**Reclaimed**				
July 19,2015		**Site 18**		**GPS Coordinates: N:56.99769 W: -111.53362**				
Tree species: Sw, Aw		**Number of trees (20 m x 20 m): 79**						
DBH (cm) Sw:	7.5, 9.9, 11.5, 9.9, 8.9, 7.4, 6.0, 7.6, 5.6, 7.3, 10.4, 7.4, 0.4, 6.2, 5.7, 7.7, 10.0, 10.0, 9.2, 7.7, 9.8, 11.8, 9.2, 8.5, 9.1, 10.6, 6.0, 2.5, 8.8, 7.2, 6.0, 5.5, 11.4, 8.3, 10.5, 8.8, 8.8, 11.5, 9.7, 9.6, 7.0, 6.8, 6.0, 5.7, 9.8, 11.3, 10.9, 6.1, 11.7, 10.4, 13.5, 9.0, 8.3, 9.8, 11.4, 7.7, 11.7, 9.0, 10.2, 9.4, 9.4, 5.7,9.2, 11.5, 7.5							
DBH (cm)	Aw:9.1, Aw:3.5, Aw:7.0, Aw:7.6, Aw:9.2, Aw:7.2, Aw:7.5, Aw:7.8, Aw:3.4, Aw:4.7, Aw:4.3, Pb:5.4,							
Understory	**NE:** blue columbine, dandilion, many mosses, many lichen, Jameson liverwort	**SE:** Unknown moss	**SW:** same as SE	**W:** moss	**Dominant understory:** Moss (Pleurozium schreberi), Lichen (Leptobryum pyriforme), Dandelion		Sampling distance to nearest tree (Sw) NE: 71cm, SE: 47cm, SW: 67cm, NW: 77cm	
Ground cover (1 m by 1 m)				**Ground cover (%)**				
	lichen	moss	leaf litter	needles	bare soil	CWD (twigs)	live	shrubs
NE	3.5	82	2	32	0	1.5	85	0
SE	0	60	13	98	1	11	6	0
SW	0	8.5	60	92	0.5	4	8.5	0
NW	0	3	34	98	0	7	3	0
Site Average	0.875	38.375	27.25	80	0.375	5.875	25.625	0

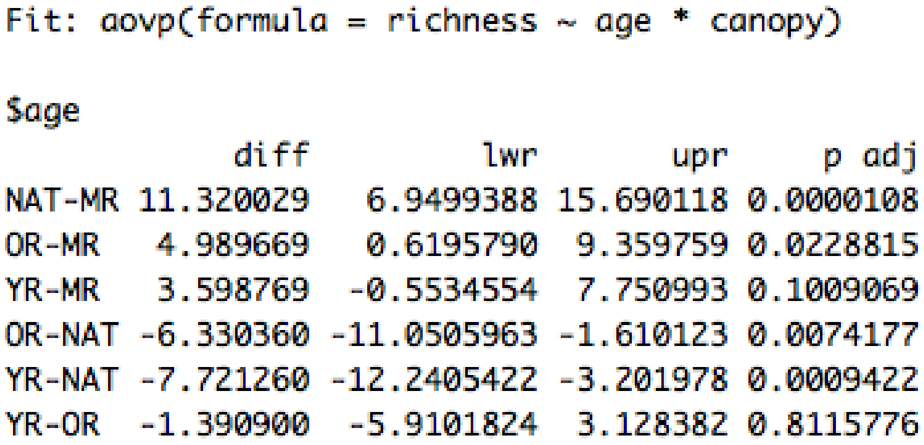
Site 19

Site and Soil Assessment Form			**Summer 2015**	**Observers: Cassandra, Brittany**				
Slope (%): NE: -29% , 16° SE: -28%, 15° NW: -28%, 15.5° SW: -29%, 17°		Aspect (deg): N,0°		Slope position: Mid		**Reclaimed**		
July 19,2015		**Site 19**		**N: 56.99865 W: -111.54722**				
Tree species: Sw, Pb, Aw		**Number of trees (20m x 20m): 54**						
DBH (cm) Sw	11.6, 15.1, 9.5, 10.3, 12.3, 11.2, 5.2, 7.7, 3.4, 11.4, 11.2, 11.6, 11.1, 11.4, 9.1, 12.1, 12.7, 12.1, 12.4, 12.3, 12.5, 7.0, 7.5, 4.5, 17.5, 13.7, 15.8, 11.6, 16.6, 13.8, 16.1, 14.0, 14.6, 14.7,							
DBH (cm) Pb	Pb: 7.4, Pb: 5.4, Pb 13.7, Pb:3.1, Pb:1.5, Pb:3.7, Pb:5.7, Pb:2.3, Pb:2.3, Pb:6.3, Pb:6.3, Pb:5.6,							
dbh (cm)	Aw:10.0, Aw:1.7, Aw:6.1, Aw:4.3, Aw:2.7, Aw:2.5, Aw:2.5, Aw:5.8							
Understory	**NW:** prickly rose, wild smooth strawberry, aspen, lichen (2), moss(1), red osier dogwood	**SE:** unknown moss (1)	**NE:** fireweed, wild smooth strawberry, grass, aspen, stairstep moss, lichen (2), unkown moss [aulacomnium palustre?]	**SW:** aspen, clover, wintergreen unknown	**Dominant understory:** Moss, lichen (Peltigera spp.), Common pink wintergreen (Pyrola asarifola)		Sampling distance to neartest tree (Sw) NE: 116cm, SE: 109cm, NW: 116cm, SW: 60cm	
Ground cover (1 m by 1 m)			**Ground cover (%)**					
	lichen	moss	leaf litter	needles	bare soil	CWD (twigs)	live	shrubs
NW	5	4	4	98	0	3	8	0
NE	40	45	11	25	0	7	87	0
SE	0	6	31	100	0	10	6	0
SW	0.5	8	29	100	0	7	12.5	0
Site Average	11.375	15.75	18.75	80.75	0	6.75	28.375	0

Site 20

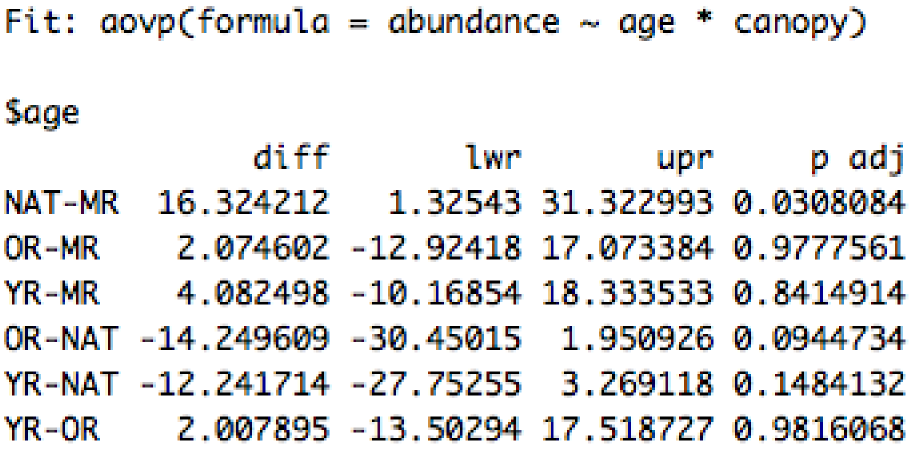
2015				**Observers: Cassandra, Brittany**				
Slope (%): N: -24% , 14° E: -25%, 14° S: -30%, 17° W: -30%, 17°		Aspect (deg): N,0°		Slope position: Mid - Upper		Reclaimed		
19-Jul-15		**Site 20**		**N: 56.99837 W: -111.54800**				
Tree species: Aw		**Number of trees (20m x 20 m): 69**						
dbh (cm)	2.2, 0.9, 7.7, 10.1, 2.0, 3.3, 3.2, 2.9, 11.6, 15.6, 1.1, 1.6, 4.7, 4.5, 1.1, 0.8, 7.6, 6.4, 0.8, 2.0, 2.9, 1.6, 2.3, 1.2, 3.8, 0.8, 1.9, 0.8, 2.2, 1.2, 3.8, 2.9, 7.7, 11.1, 1.6, 2.3, 3.8, 8.4, 6.5, 2.1, 1.8, 1.4, 1.6, 5.0, 1.2, 1.4, 2.2, 2.5, 6.3, 9.4, 3.3, 5.3, 1.0, 3.5, 4.3, 1.1, 1.3, 7.4, 7.0, 1.1, 7.4, 6.3, 2.2, 0.7, 3.7, 3.7, 1.5, 2.1, 13.4, 2.9, 11.1, 2.5							
Understory	**N:** White sweet clover, alsike clover, prickly rose, grass, moss, unkown wintergreen [common pink], buffaloberry	**E:** white sweet clover, wild strawberry, stairstep moss	**S:** alsike clover, grass, moss	**W:** buffaloberry, alsike clover, red-osier dogwood	**Dominant understory:** Grass (Fescue spp.), Moss (Pleurozium schreberi), Alsike clover (Trifolium hybridum)		**Sampling distance to neartest tree (Aw)** N: 36cm, E: 66cm, S: 72cm, W: 101cm	
Ground cover (1 m by 1 m)			**Ground cover (%)**					
	lichen	moss	leaf litter	needles	bare soil	CWD (twigs)	live	shrubs
N	0	12	72	0	0	10.5	23	2
E	0	72	22	0	0	4	75	0
S	0	14	78	0	0	10.5	25	0
W	0	1.2	100	0	0	8.5	6.5	1.5
Site Average	0	24.8	68	0	0	8.375	32.375	0.875

Appendix 2. permANOVA tables for age only in Figure 2-2a/b.



```
Fit: aovp(formula = richness ~ age * canopy)

$age
             diff         lwr       upr     p adj
NAT-MR 11.320029   6.9499388 15.690118 0.0000108
OR-MR   4.989669   0.6195790  9.359759 0.0228815
YR-MR   3.598769  -0.5534554  7.750993 0.1009069
OR-NAT -6.330360 -11.0505963 -1.610123 0.0074177
YR-NAT -7.721260 -12.2405422 -3.201978 0.0009422
YR-OR  -1.390900  -5.9101824  3.128382 0.8115776
```



```
Fit: aovp(formula = abundance ~ age * canopy)

$age
             diff       lwr       upr     p adj
NAT-MR  16.324212   1.32543 31.322993 0.0308084
OR-MR    2.074602 -12.92418 17.073384 0.9777561
YR-MR    4.082498 -10.16854 18.333533 0.8414914
OR-NAT -14.249609 -30.45015  1.950926 0.0944734
YR-NAT -12.241714 -27.75255  3.269118 0.1484132
YR-OR    2.007895 -13.50294 17.518727 0.9816068
```