Nitrogen, plant and microbial community dynamics in sites recovering from wildfire and surface mining in the Athabasca Oil Sands Region

by

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A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

in

Soil Science

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ABSTRACT

For reclamation to be considered successful, an ecosystem must be self-sustaining and have a recovery trajectory that falls within the range of variability of ecosystem function in natural ecosystems. This study compared the soil nitrogen availability, soil microbial community, and understory vegetation following natural (wildfire) disturbance and anthropogenic (reclamation) disturbance, in the Athabasca Oil Sands Region. Eleven natural (aged 2-131 years) and five reclaimed sites (aged 4-27 years) from upland aspen/ spruce stands were compared. Soil available nitrogen was assessed *in-situ* with ionic resin capsules and potentially mineralizable nitrogen was determined by anaerobic incubation. Microbial respiration was measured as an indicator of activity, and microbial community fingerprints and biomass were determined using phospholipid fatty acid analysis. The vegetation was characterized by canopy cover, plant functional group, and composition survey at the genus level.

No significant difference for nitrate or ammonium availability was observed at the site level; however, there were trends with time and canopy cover. The potentially mineralizable nitrogen trend with time was much higher on the natural sites than the reclaimed sites. Non-metric multi-dimensional scaling ordinations of the soil microbial community and understory vegetation composition revealed that reclaimed and unburned sites had significantly different communities with a low degree of similarity. The burned sites (aged 2-39 years) were more variable and bridged the difference between the reclaimed and mature sites. The microbial community of the oldest reclaimed sites were most similar to naturally disturbed sites. This work shows that young naturally disturbed sites may be a more relevant comparison when evaluating reclamation trajectory than mature stands.

ACKNOWLEDGMENTS

My utmost thanks and sincere gratitude go to my thesis advisor, Dr. Derek Mackenzie. Your enthusiasm and passion first inspired my curiosity in this project and your endless support and encouragement made the completion of this thesis possible. I would also like to thank my committee members, Dr. Sylvie Quideau and Dr. Miles Dyck, for reviewing my research and their suggestions.

I would like to acknowledge multiple people who provided invaluable support with site description, field sampling, laboratory analysis and technical knowledge. My field and laboratory assistants, Caren Jones, Diana Dabrowa, and Megan Lewis. Allan Harms, from the Natural Resources Analytical Laboratory, and Emily Lloret for their support with laboratory analyses. Marty Yarmuch, from Syncrude Canada Ltd., and Francis Salifu, from Suncor Energy. Neil Stange from Alberta Environment and Sustainable Resource Developments (AESRD) who provided the Alberta historical wildfire GIS data. My fellow Pyrogenic Ecosystems Restoration Ecology Laboratory lab mates, Arezoo Amini, Sanatan Das Gupta, and JinHu Liu who provided encouragement and an exchange of knowledge and ideas throughout this entire project.

I would also like to acknowledge the assistance of the Canadian Oil Sands Network for Research and Development- Environmental and Reclamation Research Group (CONRAD-ERRG) and the Circumpolar/Boreal Alberta Research Grant (CBAR) and Northern Scientific Training Program Grant (NSTP) for providing financial assistance.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1 INTRODUCTION

1.1 The Athabasca Oil Sands Region

The Athabasca Oil Sands Region (AOSR) is located in the boreal forest of northeastern Alberta, Canada (Figure 1). It is one of the largest crude bitumen deposits in the world, with known recoverable reserves of 170 billion barrels (Government of Alberta, 2014). The shallow nature of the deposit means that 10 to 15 percent is suitable for open pit mining, a total surface mineable area spanning about 4800 km^2 (Government of Alberta, 2014). During mining, all vegetation, soil and underlying mineral overburden substrate is removed creating a disturbance comparable to glaciation in scale. The Alberta government requires mined land to be reclaimed to a sustainable boreal forest ecosystem with a desired end land use value (Fast and Mihajlovich, 2009). As such, innovative methods are being developed to reclaim the boreal landscape and jumpstart the formation of natural soil and plant community processes.

1.2 Reclamation

The goal of land reclamation is to replace soils and vegetation removed during mining, and to restore natural ecosystem function. Ecosystem function is the framework of biological, geochemical and physical processes and components that take place or occur within an ecosystem. Such processes include, nutrient cycling, soil and organic matter development, and microbial community activity and structure (MacDonald et al., 2012). For reclamation to be successful, the reconstructed system must be self-sustaining and have a reclamation trajectory, the developmental route of the reclaimed ecosystem function over time, which falls within natural variability.

Over the past 30 years, the practice of land reclamation has been recreating various target ecosystems. For upland boreal forest target ecosystems, soils are reconstructed using a prescription of a peat and mineral soil mixture atop overburden material that is then planted to aspen and white spruce (Fung and Macyk, 2000). Prior research has shown that nutrient availability, soil organic matter, and microbial community structure and function in upland reclaimed soils differ from that of mature upland forest soils (Turcotte et al. 2009; Rowland et al. 2009). However, comparing these rebuilt ecosystems to mature forests might not represent what happens after disturbance very well. Therefore, reclaimed systems should be compared to native forest recovering from wildfire as it is one of the main, large scale natural disturbances in the region.

1.3 Fire and Disturbance

Disturbance, both natural and anthropogenic, alters the physical environment and disrupts ecosystem structure which can change nutrient cycling and availability, and the composition, abundance and distribution of vegetation (White and Pickett, 1985). The predominant natural disturbance regime in the western Canadian boreal forest is wildfire (Johnson, 1998). Wildfire changes the soil microclimate, including temperature and moisture. It causes plant and microbial death, shifts the microbial and plant community structure, and deposits fire residues. All these changes alter the tight nitrogen (N) cycle and availability. Decades later, the system returns to a mature forest stand similar to its pre-fire state. While reclaimed soils differ from mature forest soils, perhaps they are on a similar recovery trajectory as naturally disturbed soils. Wildfire disturbance recovery can be used as a benchmark for evaluating reclamation recovery, and understanding the influence of wildfire disturbance on the natural forest soil structure, function, and biodiversity can help create more suitable land reclamation practices.

Wildfire is a key evolutionary agent in terrestrial and N-scarce systems, and it is important for rejuvenation of soil properties, encouraging regeneration and growth (Zackrisson et al., 1996).

Fire occurs regularly. Each ecosystem has a specific mean fire return interval, which is the historic average period between fires. Fires vary in both their intensity, which is how intense a fire burns, and severity, which is how much they consume (Keeley, 2009). They can either be ground, surface or crown fires, with crown fires being most intense and severe and ground fires the least.

The majority of fires in the boreal forest are characterized as high intensity crown fires (Johnson, 1992). However, surface fires are dominant in aspen-dominated mixedwood stands due to the high moisture content of their foliage (deGroot et al., 2013). The variable landscape (i.e. topography, climate, species composition) of the boreal forest results in a highly variable fire return interval ranging from 100-500 years (Hart and Chen, 2006; Johnson, 1998).

Fire has complex effects on ecosystem function (Figure 3). Fire results in organism mortality and the complete and/or partial combustion of organic matter. Depending on the magnitude of the fire, the entire plant community may be consumed, or just the understory ground cover. Fire can select certain species and affect forest species composition, as larger more robust species tend to be more fire resistant (Hart et al., 2005). Regardless, the organic soil layer is usually removed, depending on its thickness and fire magnitude, as is part of the microbial community contained in it. The consumed biomass is volatilized or converted to ash and charcoal. The heating and oxidation of organic matter releases stored nutrients into their labile forms (Vitousek and Howarth, 1991), significantly altering nutrient dynamics.

Soil properties and the soil microclimate are altered by fire (Figure 3). A short term increase in soil temperature is observed because of the initial heat of the fire and subsequent increased solar radiation in the absence of plant cover (Hart et al., 2005). Consumption of the soil organic layer decreases the forest floor thickness and releases the base cations, calcium (Ca), magnesium (Mg), potassium (K), and phosphorus (P). Cation release results in an increase in pH, and total soil N may decrease due to volatilization (Hart and Chen, 2006). Cation release may increase the activity of some soil microorganisms (Hart and Chen, 2006).

Wildfire causes substantial changes to N cycling. Immediately following a wildfire there is a spike in available N (Figure 4) (DeLuca and Sala, 2006). This is due, in part, to thermally altering organic matter and release of unavailable N previously stored in biomass, including soil microbes (Chen and Hart, 2006). The increased soil temperature created by the fire induces chemical oxidation of soil organic matter which alters N transformations and increases mineralization and nitrification rates (Choromanska and DeLuca, 2002*)*. With time since fire, available N is immobilized as soil microbes use it for metabolic processes and reproduction (MacKenzie et al., 2004). The form of available N changes from nitrate (NO_3^-) to ammonium (NH_4^+) with time since fire (Deluca et al., 2002; Zackrisson et al., 2004; Nilsson and Wardle, 2005) as a result of an increasingly tight N cycle between plants, soil, and micro-organisms. An increase in N content after fire has also been attributed to increased N fixation in the recovering plant community (Hart and Chen, 2006).

With increasing time since fire, a decrease in nitrification rates has been observed, due to inhibition of nitrifying bacteria (Mackenzie et al., 2006). Certain plants, such as ericaceous shrubs, release secondary allelopathic metabolites through their litter. This family is better adapted for NH_4^+ uptake (Persson, 2003), and these phenolic compounds reduce the activity of nitrifying soil microbes (Mackenzie et al., 2006; Wardle, 1997), essentially altering the N cycle for their benefit. It is also hypothesized that restricted production of the more easily lost NO_3^- is an adaptation for N conservation in an N-limited system, and prevents N loss by leaching and denitrification (MacKenzie and Deluca, 2006). Allelopathic compounds can also indirectly inhibit nitrification. Such compounds are phenolic based and can form polyphenol protein complexes with available N

(Hattenschwiler and Vitousek, 2000). A negative correlation between total phenols and available N has been observed (Mackenzie et al., 2004).

The period of increased post-fire N availability may span decades (MacKenzie et al., 2006). While initially caused by a short lived thermal pulse (DeLuca et al., 2002), it is maintained by charcoal, a primary residue of wildfire, which can alter plant and soil community processes (DeLuca et al., 2002, MacKenzie et al., 2006). Produced from partial combustion of woody biomass, charcoal is composed of aromatic carbon rings ordered to create a highly recalcitrant honeycomb like structure (MacKenzie et al, 2008). Its structure allows it to adsorb allelopathic compounds that would otherwise inhibit microbes, initiate immobilization and bind proteins (MacKenzie and DeLuca, 2006). It may also provide microbes a protected site with adequate resources away from predation, stimulating nitrification (Zackrisson et al., 1996). This adsorptive ability of charcoal diminishes with time, and is ineffective after about 100 years (Zackrisson et al., 1996*).* The period of charcoal activity coincides with both the natural fire return interval and the period of increased N availability (MacKenzie and DeLuca, 2006), which can vary by ecosystem.

The abiotic and nutrient availability changes in the soil cause a shift microflora and vegetation following wildfire (Hart et al., 2005). Resources such as nutrients, light and growing space are abundant and result in the rapid colonization of fast-growing vascular plants (Greene et al., 1999). Species diversity is high among the early colonizers (Greene et al., 1999), which are shade intolerant and nutrient demanding species (Hart and Chen, 2006). Regeneration is primarily from buried seeds and propagules located in the humus layer (Hart and Chen, 2006). Aspen, which are easily killed by low intensity surface fires that girdle their stems, survive by quickly re-sprouting from root stock (deGroot et al., 2013).

The newly established understory community helps drive N cycling. The abundantly available N is rapidly taken up as foliage-rich aboveground biomass is produced. Plants are short lived, and rapid decomposition recycles N back into the forest, mitigating nutrient loss following fire (Hart and Chen, 2006). As N availability decreases and the canopy begins to close, vascular plant diversity and the abundance of nutrient demanding species decrease (Hart and Chen, 2006*).* Slow growing vegetation such as feather mosses, woody plants and ericaceous species become more prevalent (Hart and Chen, 2006).

Much of the previous post-fire N and vegetation community work was done in conifer dominated forests, including the Swedish boreal forest (DeLuca et al., 2002; Zackrisson et al., 1996) and the Ponderosa pine ecosystem of western Montana and northern Arizona (Choromanska and DeLuca, 2002; DeLuca and Sala, 2006; Hart et al., 2005; MacKenzie and DeLuca, 2006; MacKenzie, et al., 2004, 2006). It is unclear if charcoal has the same effect on soil processes in Alberta boreal soils under aspen and spruce stands. A better understanding of the processes that shape recovery from natural wildfire is necessary if we want our reclaimed stands to emulate natural recovery and function.

1.4 Nitrogen Biogeochemistry

Nitrogen is of particular interest because it is an essential, frequently limiting nutrient in terrestrial ecosystems, such as the boreal forest (Vitousek et al., 1982; Vitousek and Howarth, 1991). It is a key element in the biological functioning of an ecosystem, required by organisms to produce proteins and DNA, and for basic metabolic functions. Although abundant in the atmosphere as nitrogen gas (N_2), most plants can only take up N as NH_4^+, NO_3^-, and in some cases as organic N (Kaye and Hart, 1997), forms referred to as available N. An intricate cycle of biological N transformations by soil microbes, plant uptake and recycling has resulted (Figure 2).

Almost all N found in terrestrial ecosystems comes from the atmosphere. N_2 in the atmosphere is converted into available forms, either by lightening or biological fixation by N-fixing organisms (Figure 2 A), such as *Rhizobia* spp. and *Frankia* spp., and then taken up by plants. Organic N returns to the soil as litter (Figure 2 H), where decomposers (bacteria and fungi) chemically modify the N from organic ammonia (NH_3) to inorganic NH_4^+. This process is known as mineralization (Figure 2 B). The NH_4^+ is often chemically altered by *Nitrosomonas* bacteria to nitrite (NO_2^-), then further modified by *Nitrobacter* bacteria to NO_3^-, a process known as nitrification (Figure 2 C). Both the NH_4^+ and NO_3^- can be immobilized (Figure 2 F, G,) by the soil microbial community, and NO_3^- can be returned to the atmosphere by denitrification (Figure 2 L), where denitrifying bacteria metabolically reduce NO_3^- to N or nitrous oxide (N_2O) gas (Kaye and Hart, 1997).

Nitrogen is highly reactive in the environment and some forms can be readily lost through leaching, adsorption to clay or by denitrification to the atmosphere. The N that remains is commonly in highly recalcitrant organic forms that require multiple enzyme systems to be broken down into available forms (Vitousek and Howarth, 1991). As a forest ages, woody species begin to dominate, incorporating more N into their biomass, which is more stable and thus more difficult to brake down.

Nitrogen deficient plants produce tissue and litter that have high carbon to nitrogen ratios (C:N) and contain increased amounts of lignin and other recalcitrant compounds. Their tissue therefore decomposes relatively slowly, and the microorganisms decomposing it immobilize large quantities of N. This immobilization in turn reduces N availability to plants, and the cycle continues as long as N deficient litter continues to accumulate. A harsh northern climate further decreases decomposition rates and nutrient turnover (Vitousek and Howarth, 1991).

1.5 Key Questions

Nitrogen cycling is driven by the soil microbial community (Wagner, 1998) and influenced by a series of interactions between the soil environment, atmosphere and vegetation. To properly characterize N availability we must also characterize these influencing factors.

This study aims to characterize N availability trends over time in upland aspen and white spruce stands recovering from natural fire disturbance in the boreal forest of the AOSR. Furthermore, it aims to determine if natural N availability trends can be observed in aspen spruce stands planted on soils reconstructed following oil sands mining. Finally, it will look at the differences in the microbial community structure and vegetation cover, with respect to soil parameters in natural and reclaimed soils following disturbance.

Key Questions:

1. How does the availability of N change with time since fire in upland aspen/white spruce stands of the Alberta boreal forest?
2. Do reclaimed soils under aspen/white spruce stands have similar N availability trends over time as natural soils following disturbance?
3. What are the differences in microbial community structure on sites recovering from fire and reclamation, and is there a relationship with soil parameters?
4. What are the differences in vegetation cover on sites recovering from fire and reclamation, and is there a relationship with soil parameters?

Note: 1 km^2 = 1 square kilometre = 0.39 square miles

Figure 1. Map of Alberta, Canada, depicting the AOSR (Athabasca Deposit) (Adapted from Government of Alberta, 2014).

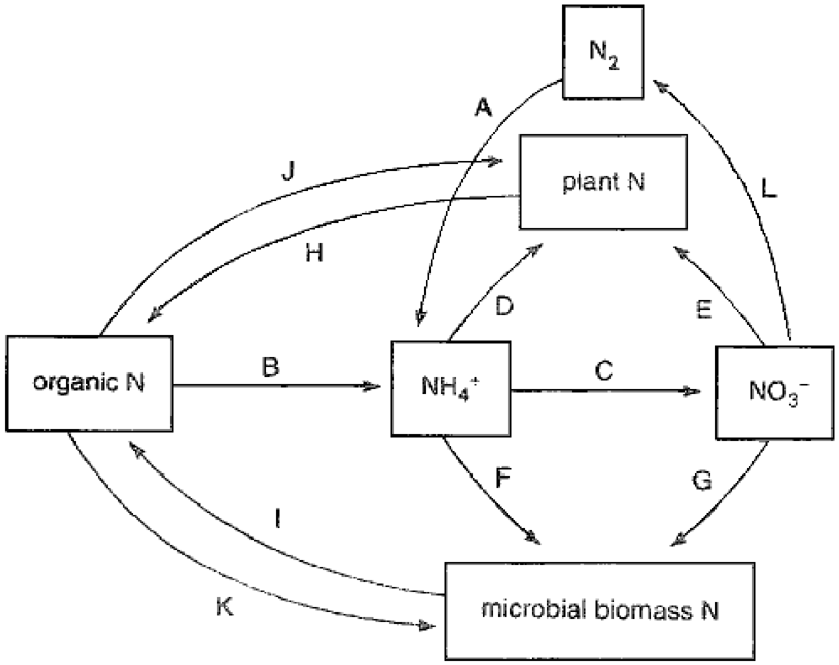


Figure 2. A schematic of the N cycle (Adapted from Kaye and Hart, 1997). A), N fixation; B), N mineralization; C), nitrification; D), plant uptake of NH_4^+; E), plant uptake of NO_3^-; F), immobilization of NH_4^+; G), immobilization of NO_3^-; H), plant detrital inputs; I), microbial detrital inputs; J), plant uptake of organic N; K), microbial uptake of organic N.

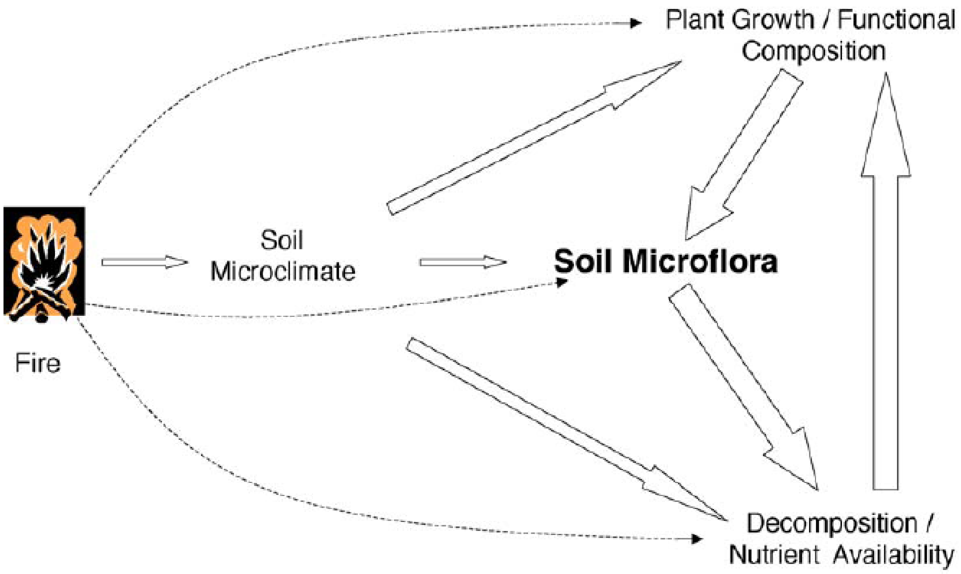


Figure 3. Conceptual model of the effects of fire on forest ecosystems (Adapted from Hart et al., 2005). Dotted arrows indicate short-term effects, which include plant and soil microbe mortality and nutrient release from combustion of organic matter. Changes to the soil microclimate cause changes in the soil microflora and vegetation (small arrows). With time, strong feedbacks (thick arrows) develop between the soil microflora, decomposition and nutrient availability, and plant growth and functional composition, which are responsible for the long-term stability of the ecosystem.

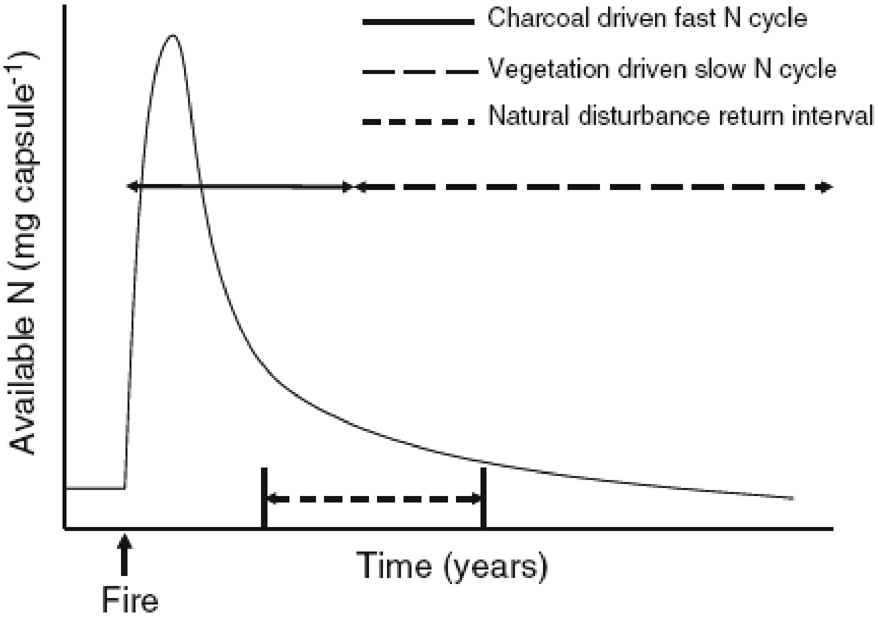


Figure 4. A theoretical framework for changing N availability with increasing time since fire in any pyrogenic forest ecosystem (Adapted from MacKenzie and DeLuca, 2006). Disturbance driven N availability dominates during the natural return interval and vegetation driven N availability dominates beyond the natural fire return interval.

CHAPTER 2 METHODOLOGY

2.1 Study Area and Site Selection

The study was conducted within the AOSR in northern Alberta, Canada (Figure 5). The area lies within the Central Mixedwood Subregion of the Canadian boreal forest (Natural Regions Committee, 2006). The area is characterized by a humid continental climate with mild summers and long cold winters (Peel et al., 2007). The mean annual temperature is 1.0° C, ranging from an average daily maximum of 23.7° C in July to an average daily minimum of -22.5° C in January. The mean annual precipitation is 418.6 mm, of which 102.3 mm falls as snow (Environment Canada, 2015).

In fall 2010, natural forest sites were selected within a 120 km radius of Fort McMurray, Alberta (56°39' N 111°13' W). To locate potential sites, an ArcGIS map of the area was constructed using data from the Alberta Environment and Sustainable Resource Developments (EASRD) historical wildfire database in conjunction with the Alberta Vegetation Inventory (AVI) data provided by Alberta Pacific Forest Industries Inc. (AL-PAC). The historical wildfire data indicated locations and ages of all significant wildfires occurring over the past 40 years. Using the AVI data, d ecosites, characterized by a mesic moisture regime, Orthic Luvisols, and a class 2 soil capability (Beckingham and Archibald, 1996), were located within the historic fire polygons. Furthermore, within these ecosites, only stands where aspen was the dominant crown species and contained no jack pine were selected. Finally, because of the difficulty traversing peatland to access upland areas, all potential sites were within 1 km of an access road. Over 20 potential sites, spanning multiple fires ages, were identified and visited.

Eleven sites were ultimately selected for this project, based on increasing time since fire (2, 4, 9, 16, 30, 39, 91, 102, 116, 121, 125 years since fire) (Figure 5). Burned sites (aged 2- 39 years) were paired with adjacent unburned sites (aged 71-131 years) of similar vegetation and soil characteristics. All sites were in upland mixedwood forest, dominated by aspen (*Populus tremuloides*, Michx.) and white spruce (*Picea glauca*, [Moench.] Voss). Stands with obvious signs of harvesting were avoided. The underlying soils were generally classified as Orthic Gray Luvisols (Soil Classification Working Group, 1998), developed in well to imperfectly drained sites, with sandy loam to clay loam textures, developed on glacial sediments (Turchenek and Lindsay, 1982).

A suite of reclaimed sites was added in summer 2011 from locations within the Syncrude and Suncor mine leases, located 45 km north of Fort McMurray. Like with the natural site selection, numerous potential reclamation sites were visited before ultimately selecting appropriate sites for this study. A total of 5 sites, with increasing age (4, 9, 13, 19, 27 years since reclamation) were chosen. Like the natural sites, all reclaimed sites were aspen and white spruce mixed stands. One-year-old aspen and white spruce container planting stock, grown from local seed sources at a commercial nursery, were planted the year following soil placement at densities between 2161 to 2855 stems/ ha (Sorensen et al., 2011). Reclamation soil profiles were built with clean capping materials, selectively sampled pre-mining (Fung and Macyk, 2000). As a large percentage of the pre-mining landscape is made up of wetlands, much of the salvaged soil is peat, generating a peat mineral mix (PMM) after salvaging. On the sites examined here, approximately 20 cm of PMM was placed over 80 cm of fine-textured geologic material (see Fung and Macyk, 2000; Rowland et al., 2009; Sorenson et al., 2011). Material was considered fine-textured, as it did not contain tailings sand or heavy clay, and had a parent geologic material of sandy loam to clay loam texture. Fertilizer application varied across sites, where some sites received a single fertilizer application while others received five consecutive annual applications; total fertilization of sites ranged from 35-80 kg N/ha, 18-46 kg P/ha, and 10-44 kg K/ha (Lanoue, 2003).

2.2 Soil Collection and Analysis

In September 2010, 110 forest floor and mineral soil samples were collected from all 11 natural sites to measure basic chemical and physical properties, and ensure comparable site characteristics across the chronosequence. Similarly, in late August 2011, 50 samples were collected from the 5 reclaimed sites. One sample was taken approximately every 20 m along 100 m transects, for a total of five samples per site. Forest floor material was collected using a 15 cm diameter core and measuring depth, while underlying mineral soil or PMM were sampled with a 7 cm diameter x 10 cm core. Samples were chilled until processed at 4°C, then air dried and weighed. Bulk density was calculated based on dry mass and soil volume (Kalra and Maynard, 1991). Samples were then sieved to 4 mm for forest floor and 2 mm for the underlying mineral soil. pH was measured using a glass electrode in a 2:1 slurry of 0.01 M CaCl (Kalra and Maynard, 1991). Soil texture of the mineral soil was determined by particle size analysis using the hydrometer method (Kalra and Maynard, 1991). A subsample was pulverized with a ball grinder until homogeneous then 20 mg (mineral soil) or 10 mg (forest floor) were encapsulated for total carbon (C) and N determination by dry combustion analysis on a Costech ECS 4010 CHNS-O Elemental Combustion System (Costech Analytical Technologies Inc., Valencia, CA).

In late August 2011, a second set of soil samples was collected from both fire and reclamation sites for microbial analysis. Mineral soil and forest floor samples were collected from undisturbed soil at each site along the same transect, for a total of 160 samples. The same sampling protocol was used as above, except all equipment was sterilized with 70% ethanol between samples. Soil samples were kept cool until they reached the lab where a subsample was stored at -20°C and then at -80°C until samples could be freeze-dried. The remainder was either subsampled for field-fresh analyses or air-dried.

2.3 Resin Available Nitrogen

Ionic resin capsules were used to measure soil available N *in situ* (MacKenzie and DeLuca, 2006). These are commercially available polyester mesh capsules that contain approximately 1 g of mixed anionic and cationic resins (PST-2, Unibest, Walla Walla, WA). Capsules were placed just below the forest floor/ mineral soil interface or approximately 10 cm into the PMM, along the same soil sampling transects, approximately every 10 m, for a total of 110 capsules on the natural sites and 50 capsules on the reclaimed sites. Each capsule was covered with soil and forest floor material, and secured to a marker with fishing line. Resin capsules were installed in September 2010 on the natural sites, left though winter, and collected following spring snow melt in May 2011. A second set was installed on the fire sites and the reclaimed sites in June 2011 and left until late August 2011, to measure available N through the growing season. Upon removal, the resin capsules were kept cool until they could be returned to the lab for extraction. Capsules were rinsed clean of soil particles with deionized water and extracted with three successive 20 mL rinses of 2 M KCl (MacKenzie and DeLuca, 2006), with 30 minutes on a reciprocal shaker and decanting between rinses. NH_4^+ and NO_3^- concentrations in KCl extracts were analyzed colourimetrically by segmented flow using a SmartChem Discrete Wet Chemistry Analyzer (Model 200, Westco Scientific Instruments, Inc., Brookfield, CT). NH_4^+ was quantified by the nitro-prusside/salicylate method and NO_3^- by the cadmium reduction method (Bundy and Meisinger, 1994).

2.4 Potentially Mineralizable Nitrogen

Potentially mineralizable N of all natural forest floor, reclaimed forest floor and PMM samples, collected in summer 2011, was determined by an anaerobic incubation (MacKenzie et al., 2004). Approximately 10 g of air dried soil was placed into 100 mL sealed glass jars and incubated in the dark at approximately 50 % water holding capacity at room temperature for 2 ½ weeks. Water holding capacity for each soil type was calculated on a gravimetric basis at 0.1 bar (Topp et al., 2008), as an average of 3 random samples of each soil type. Soils were aerated periodically and deionized water added to replace any loss to water vapour. Following the pre-incubation, soils were saturated with deionized water (20- 40 mL) and placed in an incubator at 40 °C for 7 days. Soils were then removed from the incubator and NH_4^+ extracted by adding 40 to 80 mL of 4 M KCl (final concentration of deionized water and KCl added was 2 M) (Curtin and Campbell, 2006). NH_4^+ was then quantified colourmetrically by the nitro-prusside/salicylate method (Bundy and Meisinger, 1994) using a SmartChem Discrete Wet Chemistry Analyzer (Model 200, Westco Scientific Instruments, Inc., Brookfield, CT).

2.5 Soil Microbial Community Analysis

Microbial respiration was analyzed by the closed chamber alkali trap method (Hopkins, 2008) and was used as an indicator of microbial activity. Approximately 25 g of field-fresh soil was added to 1 L incubation jars. A 20 mL glass vial containing either 0.5 M NaOH for mineral soil, reclaimed forest floor, and PMM, or 1.0 M NaOH for natural forest floor was added to each jar as a carbon dioxide trap. The jars were sealed and incubated at room temperature in the dark for 7 days. Excess NaOH was back titrated with 0.5 M HCl using a Schott TitroLine Easy autotitrator (SI Analytics, Mainz, Germany). The metabolic quotient (qCO_2) of the forest floor samples was determined as the ratio of basal respiration (mg CO_2–C g^{-1} dry soil hr^{-1}) to total microbial biomass (ug C g^{-1} dry soil) from PLFAs (see below Anderson and Domsch, 1985).

Microbial community composition and microbial biomass in the forest floor soils were determined using phospholipid fatty acid (PLFA) analysis. PLFAs were extracted with a modified

Bligh and Dyer technique (Bligh and Dyer, 1959; Frostegard et al., 1991; White and Ringelberg, 1998) to isolate polar lipids from 0.9 g (run 1) or 0.5 g (run 2) of freeze-dried soil. Phospholipids were then fractionated with pre-packed silicic acid columns (Agilent Technologies, Wilmington, DE, USA) and methanolysed to form fatty acid methyl esters (FAMEs). The FAMEs were then quantified on an Agilent 6890 series capillary gas chromatograph (Agilent Technologies, Wilmington, DE, USA) equipped with a 25 m Ultra 2 (5%-phenyl)-methylpolysiloxane column and hydrogen as the carrier gas. Individual PLFAs were identified using bacterial fatty acid standards and the MIDI peak identification software (Sherlock 3.0, MIDI, Inc., Newark, DE). Standardized nomenclature for fatty acids (Hannam et al., 2007) was used to identify peaks and PLFAs were expressed as mole % of total microbial biomass to standardize for differences in total amount of PLFAs produced, after being relativized by an internal standard (Hannam et al., 2007). PLFA biomarkers were used to identify organisms in specific functional groups (bacteria, actinomycetes, fungi, protists). The abundance of each group was estimated as the sum on the percentage molar fractions of: bacteria, 15:0, a15:0, i15:0, i16:0, 16:1u9c, 17:0, a17:0, i17:0, cyc17:0 18:1u7c (Frostegård and Bååth, 1996), 14:0, 10Me16:0, 18:0 (Myers et al., 2001), 18:1u5c (Hasset and Zak, 2005), 16:1 2OH, i17:0 3OH and 17:0 3OH (Hamman et al., 2007); fungi, 18:2u6,9 (Bååth et al., 1995), 18:1u9c, 20:1u9c (Myers et al., 2001), 16:1u5c, 18:3u6c (Hamman et al., 2007); actinomycetes, 10Me16:0 and 10Me 18:0 (Myers et al., 2001); and protists, 20:4u6c (Myers et al., 2001). PLFA biomarkers with <7 non-zero numbers were removed to reduce the effect of rare molecules. The fungal/bacterial ratio was calculated from the sum of PLFAs specific to each group (Strickland and Rousk, 2010). Total microbial biomass was calculated by summing all PLFAs on a nmol PLFA g-^{1} dry soil basis.

2.6 Vegetation Assessment

A general vegetation assessment was conducted in July, 2011. Circular plots with 1.79 m radii (10 m^2) were established at each soil sample site, for a total of 160 plots. Within each plot, functional group percent cover (shrubs, forbs, grasses and non-vascular) was visually estimated. Canopy cover was measured at the center of each plot using a convex spherical densitometer (Model A, Forest Densiometers, Bartlesville, OK, USA), determined as an average of four measures, one in each cardinal directions. The tree density, species, tree height and diameter at breast height (DBH) on trees taller than 1.3 m were determined. Tree height was calculated from measuring distance to tree and angles to tree top and base using a clinometer (PM-5, SUUNTO, Vantaa, Finland*)*. The vascular understory community was characterized by recording the presence and percent cover of each genus present within three randomly located 50 cm^2 quadrats (data subsequently averaged), within the plot. Understory percent cover of the vascular understory was determined as a total percent cover of all understory. Diversity of the vascular understory cover was quantified using the Shannon-Weiner index (H'). Richness was determined as the total number of genera found within the quadrat, and evenness was calculated using the formula: H'/(ln(S)), where S is genera richness.

2.7 Data Analysis

For each of the sixteen study sites, the five individual sample site measurements were averaged to create site averages to be used for the statistical analysis. Outliers were detected and removed (>2 standard deviations from the mean). These values were used in subsequent data analyses, except the microbial community structure analysis. With respect to the microbial community, because the effects of fire are heterogeneous at the micro scale, each sample site was considered to be an independent experimental unit.

Linear regressions were used to characterize variables (potentially mineralizable N; vascular understory richness, evenness and Shannon-Weiner biodiversity index; and understory and canopy percent cover) with time since disturbance, using Microsoft Excel (2013). A linear regression was done for NO_3 with percent canopy cover. A non-linear regression (logarithmic) on the ionic resin data with time since fire was completed.

R version 3.0.2 was used to perform paired t-tests for the paired burned and unburned winter ionic resin data (NH_4^+ and NO_3^-). Burned sites were considered <40 years since fire, while unburned site >70 years since fire.

A one-way analysis of variance, followed by a Tukey's post hoc test, was used to determine significant differences among means of burned, unburned and reclaimed sites for all other measured variables. Residuals of most data conformed to the assumptions of normality and homogeneity of variance. The summer NO_3^- and NH_4^+ availability data were inversely transformed to meet assumptions. Total soil N and C data for the mineral soil/PMM were unable to be transformed to meet assumptions. The data was normally distributed with unequal variances, therefore a non-parametric Welch F test, with a post-hoc Games-Howell test was performed.

Non-metric multi-dimensional scaling (NMS) ordination (Kruskal, 1964; Mather, 1976) was used to examine patterns of PLFAs using PC-ORD software (version 6.0, MjM Software Design, Gleneden Beach, OR). Only PLFAs with ≤20 C in length were included in the analysis. PLFA data was relativized and an arcsine square-root transformation was performed due to its suitability for proportional data (McCune and Grace, 2002). The Sorensen (Bray-Curtis) distance measure was used in the analysis. To test for significant differences among the disturbance type groups the Multi-Response Permutation Procedure (MRPP) was used with a minimum α of 0.05. Results from an MRPP analysis include the following three variables: a T value, which represents the difference between groups, a more negative value indicates a greater difference; an A value, which represents the variation within groups, where 1 indicates similarity between values and 0 indicates dissimilarity; and a p value, which represents the significance of the comparison (Zimmerman et al., 1985).

The NMS ordination using PC-ORD software (version 6.0, MjM Software Design, Gleneden Beach, OR) was also used to characterize the understory vascular plant community. Uncommon genera (<7 occurrences) were excluded and the data was relativized and an arcsine square-root transformation performed. The Sorensen (Bray-Curtis) distance measure was used in the analysis.

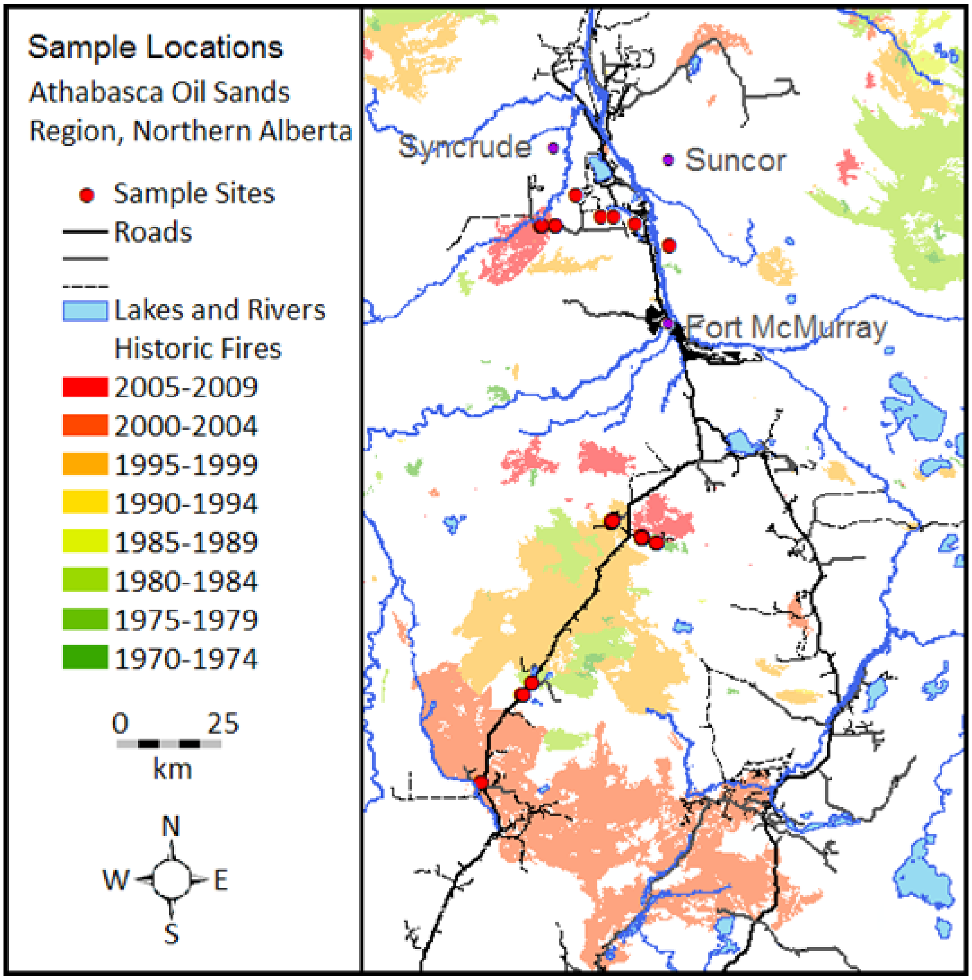


Figure 5. Map of sample site locations and historic fire sites within the AOSR, Alberta, Canada.

CHAPTER 3 RESULTS

3.1 Total Soil Carbon and Nitrogen

Total soil C and N (%) in the forest floor of the reclaimed sites was lower than what was observed naturally (Figure 6a, b), but both increase with time. C concentrations (Figure 6a) were found to be statistically different among disturbance types (df=2, F=12.92, p=0.00082), where reclaimed sites were significantly lower than both the burned (p=0.0011) and unburned (p=0.0034) sites. N concentrations (Figure 6b) were also statistically different between disturbance types (df=2, F=4.04, p=0.043). Reclaimed sites and unburned sites differed (p=0.037), but no significant difference was found between burned and the reclaimed sites (p=0.19).

Total soil C and N (%) in the PMM was higher than that of the mineral soil (Figure 7a, b), and increasing with time. C concentrations (Figure 7a) were found to be statistically different among disturbance types (df=2, F=34.87, p= 0.00039). Reclaimed sites had significantly different total C concentrations from both the burned (p= 0.0015) and unburned (p= 0.0020) sites. Similarly, N concentrations (Figure 7b) were statistically different among disturbance types (df=2, F=16.66, p=0.0027), with reclaimed sites differing from both the burned (p=0.0080) and unburned (p=0.0081) sites. The reclaimed sites had comparable total C and N to the overlying forest floor, while the mineral soil was relatively low compared to the natural forest floor. The C:N ratio had no trends with time.

3.2 Soil Nitrogen Availability

3.2.1 Resin Available Nitrogen

Resin capsule analysis showed the youngest burned sites (aged 2 to 9) had higher NO_3^- levels (11.72-68.44 ug/capsule) when compared to the older sites (1.14-4.68 ug/capsule) (Figure

8a). Average site NO_3^- with time since fire (Figure 9a) has a trend of elevated soil NO_3^- in the years immediately following fire and decreasing with time since fire ($y = 31.171x^{-0.585}$, $R^2 = 0.501$). NH_4^+ levels were highly variable, spanning from 7.39-107.23 ug/capsule across all sites (Figure 8a).

Total N availability over the growing season, which also included a suite of reclaimed sites, showed no trends in total soil N availability over time (Figure 8b). NH_4^+ levels varied widely (10.46-35.93 ug/capsule) and NO_3^- levels were low with little difference between sites (3.14-7.85 ug/capsule). The reclaimed sites had similar N availability as the natural sites for both NH_4^+ (10.10-26.34 ug/capsule) and NO_3^- (4.03-7.70 ug/capsule) (Figure 8b). Overall, soil N availability was higher following the spring melt than during the summer growing season.

Burned sites had higher NO_3^- levels than the unburned sites for both the summer and winter data sets, but not for NH_4^+ (Figure 8a, b). Paired t-tests for averaged site data did not indicate a significant difference between paired burned and unburned sites (NO_3^-, df = 5, t = 1.22, p= 0.27) (NH_4^+, df = 5, t = -0.03, p = 0.98) during the winter. No significant difference was found between the disturbance types for either NO_3^- (df=2, F=0.96, p=0.41) or NH_4^+ (df=2, F=0.24, p=0.79).

Available N correlated with canopy cover rather than time (Figure 9b), did not highlight any further trends ($y = -0.5013x + 47.172$, $R^2 = 0.2933$). Similar to time, NO_3^- on the natural sites decreased with increasing canopy cover over the winter months.

3.2.2 Potentially Mineralizable Nitrogen

Potentially mineralizable N of the reclaimed PMM and newly developed forest floor was initially low relative to the natural forest floor (Figure 10). Natural sites had increasing potentially mineralizable N with time ($y = 1.2228x + 440.7$, $R^2 = 0.1726$). The potentially mineralizable N remained low with time, but the reclaimed forest floor developing on the PMM increased sharply to values that fall within the natural variability of the burned natural sites.

3.3 Microbial Community

3.3.1 Microbial Biomass

The percent recovery of the 19:0 standard determined in the PLFA analysis was relatively similar across substrates within each PLFA analysis run, but it varied between the two. Run A had an average percent recovery of 17.2%, while run B had a recovery of 6.1%. Microbial biomass for each run is therefore reported separately. Overall, microbial biomass varies across sites (Figure 11a, b), and only unburned sites in run B (Figure 11b) showed a decreasing trend with time. A significant difference among disturbance types was found for run A (Figure 11a) (df=2, F=5.28, p=0.021), where the reclaimed and burned sites found to be significantly different (p=0.022). No difference was determined between disturbance types in run B (df=2, F=1.43, p= 0.27).

3.3.2 Soil Respiration

Respiration increased with time in the forest floor of burned sites, but was variable for all other sites in both forest floor and mineral soil (Figure 12a, b). No significant differences were found between disturbance types for either the forest floor (Figure 11b) (df=2, F=1.47, p=0.27) or mineral soil (Figure 11b) (df=2, F=2.81, p=0.097). The NaOH solution was made in advance of the alkai trap analysis and likely reacted with both the CO_2 in the atmosphere and the glass of the jar it was contained within to reduce its initial concentration. This would have been equal among samples and the relative comparison between sites is still valid.

3.3.3 Metabolic Quotient

Metabolic quotient is a function of microbial biomass it was therefore represented as run A (Figure 13a) and run B (Figure 13b). Neither showed any trends with time or statistical differences between disturbance types for either run A (df=2, F=1.85, p=0.20) or run B (df=2, F=0.71, p=0.51).

3.3.4 Microbial Community Structure

An NMS ordination of the soil microbial community composition produced a three dimensional solution, which explained 39.0%, 38.7%, and 11.2% of the variation on the axes respectively (Figure 14). A stress of 13.9 was reached after 117 iterations. Disturbance type (burned, unburned, reclaimed) was found to be the strongest grouping factor. The MRPP concluded that the disturbance types groups are significantly different. There was an overall significance of the comparisons (p=0.000), a difference between groups (T=-18.30), and little variation within groups (A=0.077).

The ordination reveals a distinct community structure. Reclaimed and unburned sites were found to have largely different microbial communities, with little overlap on the ordination diagram (Figure 14). When excluding the burned sites from the MRPP analysis, the reclaimed and unburned sites were the most dissimilar (T=-19.11, A=0.097, p=0.00), the burned and reclaimed sites were slightly less dissimilar (T=-16.64, A=0.072, p=0.00), and the burned and unburned quite similar (T=-2.33, A=0.0099, p=0.027), with a very low A-value. The burned sites (aged 2 to 39) were more variable and the microbial community bridged that of the unburned and reclaimed sites. No environmental variables or functional groups were found to have a significant correlation with an ordination axis.

Separate ordinations of the soil microbial community from each of the three disturbance types was completed, using age as the grouping variable. An ordination for the reclaimed sites produced a three dimensional solution, which explained 56.2%, 17.1%, and 15.5% of the variation on the axes, and had a stress of 11.45 was reached after 266 iterations (Figure 15a). The MRPP concluded that the age groups are significantly different. There was an overall significance of the comparisons (p=0.00), a difference between groups (T=-8.34), and a variation within groups (A=0.18). The microbial community of the reclaimed sites is changing with time, possibly on a trajectory towards natural variability (Figure 15 a). The microbial community at the youngest reclaimed sites is least similar to the natural sites, while the oldest (27 yrs) is most similar (Figure 15 b).

An ordination for the burned sites produced a two dimensional solution, which explained 75.7% and 14.6% of the variation on the axes, and had a stress of 13.97 was reached after 75 iterations. The MRPP concluded that the age groups are significantly different. There was an overall significance of the comparisons (p=0.00), a difference between groups (T=-8.17), and little variation within groups (A=0.13). An ordination for the unburned sites produced a three dimensional solution, which explained 29.2%, 29.6%, and 28.5% of the variation on the axes, and had a stress of 11.55 was reached after 92 iterations. The MRPP concluded that the age groups are significantly different. There was an overall significance of the comparisons (p=0.0015), a difference between groups (T=-3.49), and little variation within groups (A=0.076). None of the natural sites displayed a temporal trend.

The percent of total PLFA biomass that is fungi is increasing with time on the reclaimed sites (Figure 16 b), while protist PLFAs are initially way above the natural variability, decreasing with time to within/below natural variability (Figure 16 d). The fungi:bacteria ratio (FBR) is increasing slightly on the natural burned sites (Figure 17). It is slightly lower on the unburned sites compared to the burned sites, and appears to be increasing on the reclaimed sites. The FBR of the reclaimed sites falls within the natural variability.

3.4 Plant Community

3.4.1 Understory Composition

The most common understory genera on the burned sites were *Cornus* (red-oiser dogwood, bunchberry), *Epilobium* (fireweed), *Vaccinium* (blueberry, bog cranberry, bob billberry), and grasses (*Poa sp., Bromus sp., Calamagrostis canadensis*) (Table 1). The most common understory genera on the unburned sites were *Cornus* (red-oiser dogwood, bunchberry), *Lycopodicum* (ground pine and cedar), *Viburnum* (low bush cranberry), grasses (*Poa sp., Bromus sp., Calamagrostis canadensis)*, *Rubus* (wild red raspberry, dewberry), *Linnaea* (twinflower), and *Alnus* (green alder) (Table 1). The most common species on the reclaimed sites were grasses (*Poa sp., Bromus sp., Calamagrostis canadensis)*, *Taraxacum* (dandilion), *Epilobium* (fireweed), *Equistem* (horsetail), and *Melilotus* (clover) (Table 1).

An NMS ordination of the understory vascular plant community composition produced a three dimensional solution, which explained 61.9%, 12.8%, and 12.9% of the variation on the axes, respectively (Figure 18). A stress of 12.93 was reached after 98 iterations. There was an overall significance of the comparisons (p=0.00), a difference between groups (T=-27.66), and some variation within groups (A=0.16). Grouped by disturbance type (burned, unburned, reclaimed), like the microbial community, the reclaimed and unburned sites were found to have considerably different microbial communities, with little overlap on the ordination diagrams. When excluding a disturbance type from the MRPP analysis, unburned and reclaimed sites were found to have the most dissimilar understory communities (T=-25.91, A=0.21, p=0.00), while the unburned and burned sites the most similar (T=-11.68, A=0.057, p=0.00), relatively. Genera on the burned and reclaimed sites were less dissimilar (T=-19.01, A=0.12, p=0.00) than between the unburned and reclaimed. The genera found in the understory of the burned sites (aged 2 to 39) were more variable and bridged that of the unburned and reclaimed sites.

Ericaceous genera found on the sites include *Vaccinium, Pyrola* and *Rhododendron*. There does not appear to be a relationship between Ericoid genera found and available N. *Ranuncalus* and *Taraxacum* are the only genera on the reclaimed sites to have species listed as a noxious or nuisance weed species in the "Guidelines for reclamation to forest vegetation in the Athabasca Oil Sands Region" (Alberta Environment, 2010).

3.4.2 Canopy Cover

Canopy cover reaches >80% within 20 years on both reclaimed and natural sites (Figure 19 a). Mature unburned natural stands have a canopy cover > 80%, except the oldest site (ML-UB, 71.1%) due to gaps opening, and have a peak cover of 91.1% (HR-UB). Overall, the unburned sites are decreasing with time ($y = -0.274x + 112.09$, $R^2 = 0.7362$). Comparable canopy cover is reached within 16 years on the burned sites (JA-B95, 80.4%) and 19 years on the reclaimed sites (BL-R92, 87%). The burned sites initially have a faster developing canopy, only two years following fire, the naturally disturbed sites are already at 46.9% cover. The initial canopy development slows over time (slope, $m = 1.4532$). The planted seedlings are much slower to grow, at the 4 year mark there is essentially no canopy (0.2%). While initially much lower, canopy cover on the reclaimed sites does increase over time (slope, $m=4.3456$) to full closure in a similar time frame as naturally disturbed sites.

3.4.3 Understory Cover

Understory cover of vascular genera on the natural sites ranges from 69 % to 222%, with the burned sites ranging from 69% to 155% and the unburned sites from 112% to 222% (Figure 19 b). Understory percent cover is increasing with time ($y = 0.5013x + 105.31$, $R^2 = 0.3057$). The reclaimed sites ranged from 71% to 139% understory percent cover. It is decreasing with time, with a fairly steep slope (slope, $m=-2.2887$), unlike the natural sites, with the oldest site (GH-R84, 71%) falling below the natural variability of the disturbed (burned) natural sites.

3.4.4 Understory Functional Group Cover

Shrub cover is increasing overall with time since disturbance. Forbs are decreasing with time on the reclaimed sites. Grasses are decreasing on the reclaimed and burned sites with time, while increasing on the unburned sites. This coincides with changes in canopy cover, which is correlated to time since disturbance (Figure 19 a). Reclaimed sites have more grass on the youngest sites compared to the burned sites. Non-vascular species are increasing with time on the reclaimed sites.

3.4.5 Understory Diversity

Shannon-Weiner index of understory genera ranged from 1.19 to 2.41 (Figure 20 a). The burned sites are initially decreasing in diversity ($y = -0.0092x + 1.8142$, $R^2 = 0.1928$), but overall the natural sites have a slightly increasing trend with time since disturbance ($y = 0.004x + 1.67$, $R^2 = 0.2757$) (Figure 20 b). The oldest two sites (HS-US, ML-UB) display a slight decrease, causing the unburned sites to decrease with time ($y = -0.0052x + 2.6965$, $R^2 = 0.4284$). On the reclaimed sites, the Shannon-Weiner index ranged from 1.26 to 1.62 (Figure 20 a) and decreased with time

(Figure 20b) ($y = -0.0146x + 1.6703$, $R^2 = 0.3734$). Biodiversity was significantly different between disturbance types (df=2, F=8.58, p=0.0042), with unburned sites being significantly different from burned (p=0.021) and reclaimed (p=0.0043) sites, which were similar to each other (p=0.57) (Figure 20 a).

The genera richness (Figure 21 a) of the natural sites ranged from 7.6 to 17 and showed the same trends with time as biodiversity (Figure 21 b). The genera richness on the reclaimed sites ranged from 7.0 to 10.8, was highest on the youngest site, then consistently lower on all other sites. There was a significant difference between disturbance types (df=2, F=9.98, p=0.0024). Unburned sites were significantly different from burned (p=0.014) and reclaimed (p=0.0024) sites, which were similar to each other (p=0.50).

Genera evenness (Figure 22 a) on the natural sites ranged from 0.70 to 0.88, was relatively consistent, with no obvious trends over time (Figure 22 b). We can see that on the natural sites, the indices are initially decreasing slightly with time ($y = -0.0042x + 0.8187$, $R^2 = 0.5111$), but eventually increase, creating an overall increasing trend on the natural sites ($y = 0.0007x + 0.7515$, $R^2 = 0.1861$). The reclaimed genera evenness ranged from 0.58 to 0.79 (Figure 22 a), with a slight decrease with time ($y = -0.0052x + 0.7827$, $R^2 = 0.36950$) (Figure 22 b). No significant difference between disturbance types was found (df=2, F=3.29, p=0.070) (Figure 22 a).

Overall, all indices on the reclaimed sites were within the natural variability of the natural sites. The trajectory (slope) of the vegetation diversity indicators (Shannon-Weiner, richness, evenness) of the reclaimed sites is similar to that of the burned sites (Figure 20 b, 21 b, 22 b).

3.4.6 Forest Floor Depth

The average forest floor depth of the natural sites (Figure 23) was 6.2 cm, while it was only 2.6 cm for reclaimed sites. However, over time the forest floor depth of the reclaimed sites is increasing ($y = 0.0949x + 1.2635$, $R^2 = 0.6477$) and with more time may reach depth seen on the natural sites.

3.4.7 Tree Density, Species, Tree Height, DBH

Tree height and DBH are increasing on the burned sites, while both are decreasing on the unburned sites. Number of trees are decreasing on the disturbed sites, while remaining relatively consistent on the older unburned sites.

Table 1. Average percent cover of vascular plant understory genera.

Genera	Species	Common Names	Average Cover (%)
Burned Sites			
Cornus	*stolonifera, canadensis*	red-oiser dogwood, bunchberry	16.4
Epilobium	*angustifolium*	fireweed	13.0
Vaccinium	*myrtilloides, caespitosum, vitis-idaea, uligmosum*	common blueberry, dwarf blueberry, bog cranberry, bob billberry	12.4
Grasses	*Poa sp., Bromus sp., Calamagrostis canadensis*		11.5
Rhododendron	*groenlandicum*	common labrador tea	8.8
Viburnum	*edule*	low bush cranberry	7.9
Equisetum	*sylvaticum, arvense, palustre*	woodland horsetail, common horsetail, marsh horsetail	6.4
Petasites	*palmatus, safittatus*	palmate leaved coltsfoot, arrow leaved coltsfoot	6.2
Rosa	*acicularis*	prickly rose	5.0
Lathyrus	*ochroleucus*	cream coloured vetching	3.0
Aster			2.9
Fragaria	*virginiana*	wild strawberry	2.5
Linnaea	*borealis*	twinflower	2.3
Rubus	*idaeus, pubescens*	wild red raspberry, dewberry	2.3
Maianthemum	*canadense*	wild lily of the valley	1.6
Ribes	*triste, oxyacanthoides*	wild red currant, wild gooseberry	1.2
Taraxacum	*officianle*	dandilion	1.1
Pyrola	*asarifolia, secunda*	common pink wintergreen, one-sided wintergreen	1.0
Achillea	*millefolium, sibirica*	common yarrow, siberian yarrow	0.9
Lycopodicum	*obscurum, complanatum*	ground pine, ground cedar	0.8
Trientalis	*borealis*	northern starflower	0.7
Mettensia	*paniculata*	tall lungwort/bluebell	0.5
Mitella	*nuda*	bishop's cap	0.5
Vicia	*americana*	wild vetch	0.4
Galium	*boreale, triflorum*	northern bedstraw, sweet scented bedstraw	0.4
Lonicera	*sp.* (possibly *utanensis*)	honeysuckle	0.2
Shepherdia	*canadensis*	canadian buffaloberry	0.2
Prunus	*virginianana, prunus pensylvanica*	choke cherry, pin cherry	0.1
Hieracium	*umbellatum*	narrow leaved hawkweed	0.1
Salix	*sp., exigua, wolfii*	sandbar willow, wolfwillow	0.1

Aralia	*nudicaulis*	wild sarsparilla	0.1
Unburned Sites			
Cornus	*stolonifera, canadensis*	red-oiser dogwood, bunchberry	22.5
Lycopodicum	*obscurum, complanatum*	ground pine, ground cedar	12.7
Viburnum	*edule*	low bush cranberry	12.1
Grasses	*Poa sp., Bromus sp., Calamagrostis canadensis*		11.5
Rubus	*idaeus, pubescens*	wild red raspberry, dewberry	11.4
Linnaea	*borealis*	twinflower	11.0
Alnus	*viridis spp. crispa*	green alder	10.8
Aralia	*nudicaulis*	wild sarsparilla	8.1
Petasites	*palmatus, safittatus*	palmate leaved coltsfoot, arrow leaved coltsfoot	7.7
Rosa	*acicularis*	prickly rose	7.2
Vaccinium	*myrtilloides, caespitosum, vitis-idaea, uligmosum*	common blueberry, dwarf blueberry, bog cranberry, bob billberry	6.3
Mitella	*nuda*	bishop's cap	5.8
Aster			5.5
Epilobium	*angustifolium*	fireweed	4.8
Rhododendron	*groenlandicum*	common labrador tea	3.5
Pyrola	*asarifolia, secunda*	common pink wintergreen, one-sided wintergreen	3.0
Maianthemum	*canadense*	wild lily of the valley	2.8
Galium	*boreale, Triflorum*	northern bedstraw, sweet scented bedstraw	2.7
Fragaria	*virginiana*	wild strawberry	2.5
Ribes	*triste, oxyacanthoides*	wild red currant, wild gooseberry	2.4
Lathyrus	*ochroleucus*	cream coloured vetching	1.6
Trientalis	*borealis*	northern starflower	1.0
Equisetum	*sylvaticum, arvense, palustre*	woodland horsetail, common horsetail, marsh horsetail	0.9
Achillea	*millefolium, sibirica*	common yarrow, siberian yarrow	0.9
Vicia	*americana*	wild vetch	0.5
Mettensia	*paniculata*	tall lungwort/bluebell	0.2
Ranunculus	*sp.*	buttercup	0.2
Lonicera	*sp.* (possibly *utanensis*)	honeysuckle	0.1
Reclaimed Sites			
Grasses	*Poa sp., Bromus sp., Calamagrostis canadensis*		25.9
Taraxacum	*officianle*	dandilion	16.3
Epilobium	*angustifolium*	fireweed	11.1

Equisetum	*sylvaticum, arvense, palustre*	woodland horsetail, common horsetail, marsh horsetail	10.4
Melilotus	*alba, officinalis*	white sweet clover, yellow sweet clover	10.3
Cornus	*stolonifera, canadensis*	red-oiser dogwood, bunchberry	6.9
Salix	*sp., exigua, wolfii*	sandbar willow, wolfwillow	5.4
Achillea	*millefolium, sibirica*	common yarrow, siberian yarrow	3.3
Fragaria	*virginiana*	wild strawberry	3.2
Vicia	*americana*	wild vetch	3.1
Trifolium	*hybridum*	alsike clover	2.9
Rubus	*idaeus, pubescens*	wild red raspberry, dewberry	2.7
Rosa	*acicularis*	prickly rose	1.9
Aster			1.5
Vaccinium	*myrtilloides, caespitosum, vitis-idaea, uligmosum*	common blueberry, dwarf blueberry, bog cranberry, bob billberry	1.3
Hieracium	*umbellatum*	narrow leaved hawkweed	0.5
Cirsium	*arvense*	Canada thistle	0.4
Carex		sedges	0.4
Petasites	*palmatus, safittatus*	palmate leaved coltsfoot, arrow leaved coltsfoot	0.4
Pyrola	*asarifolia, secunda*	common pink wintergreen, one-sided wintergreen	0.3
Aquilegia	*brevistyla*	blue columbine	0.3
Lathyrus	*ochroleucus*	cream coloured vetching	0.2
Amelanchier	*alnifolia*	saskatoon	0.2
Mentha	*avensis*	wild mint	0.2

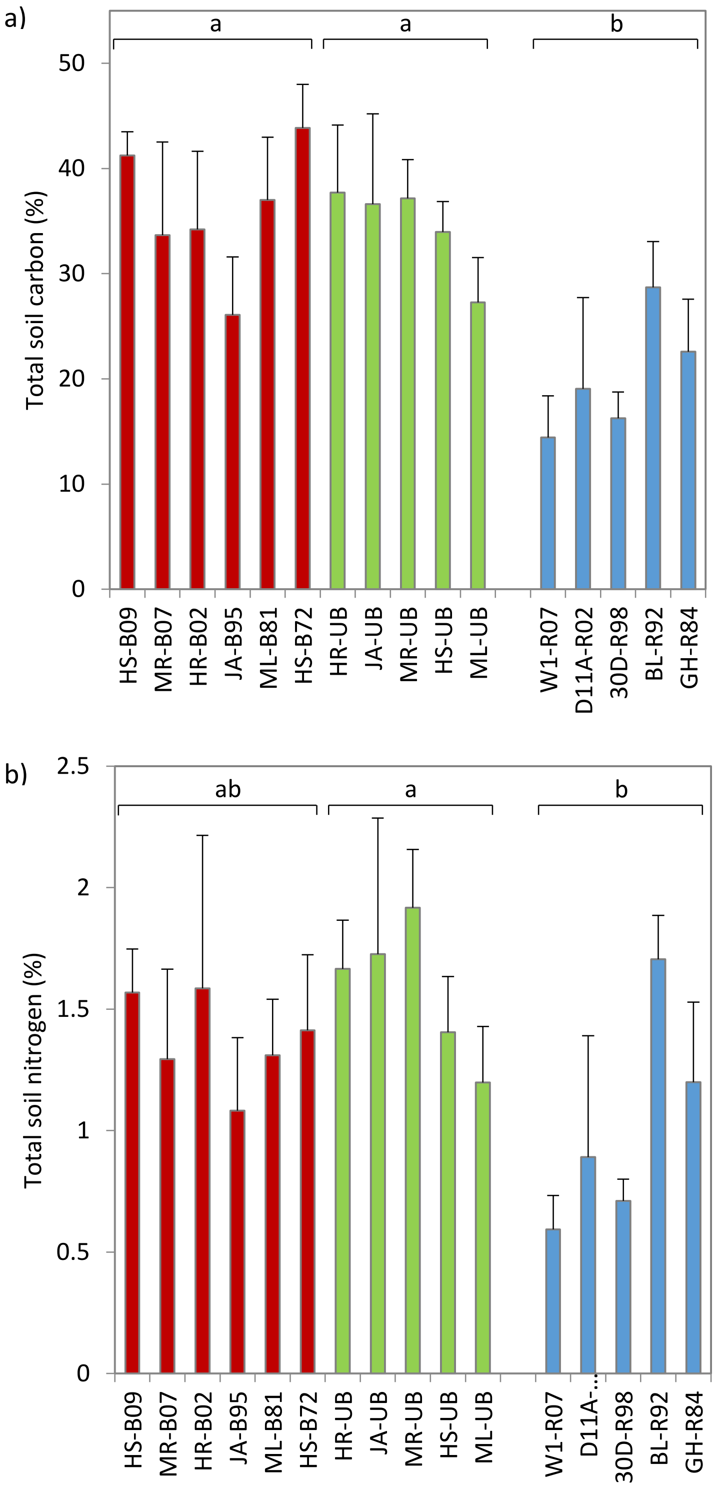


Figure 6. Total percent soil C (a) and N (b) of forest floor. Red bars indicate burned sites, green unburned, and blue reclaimed. Sites are arranged chronologically, by disturbance type. Error bars represent one standard deviation away from the mean. Different letters indicate statistically significant differences among disturbance type at α=0.05.

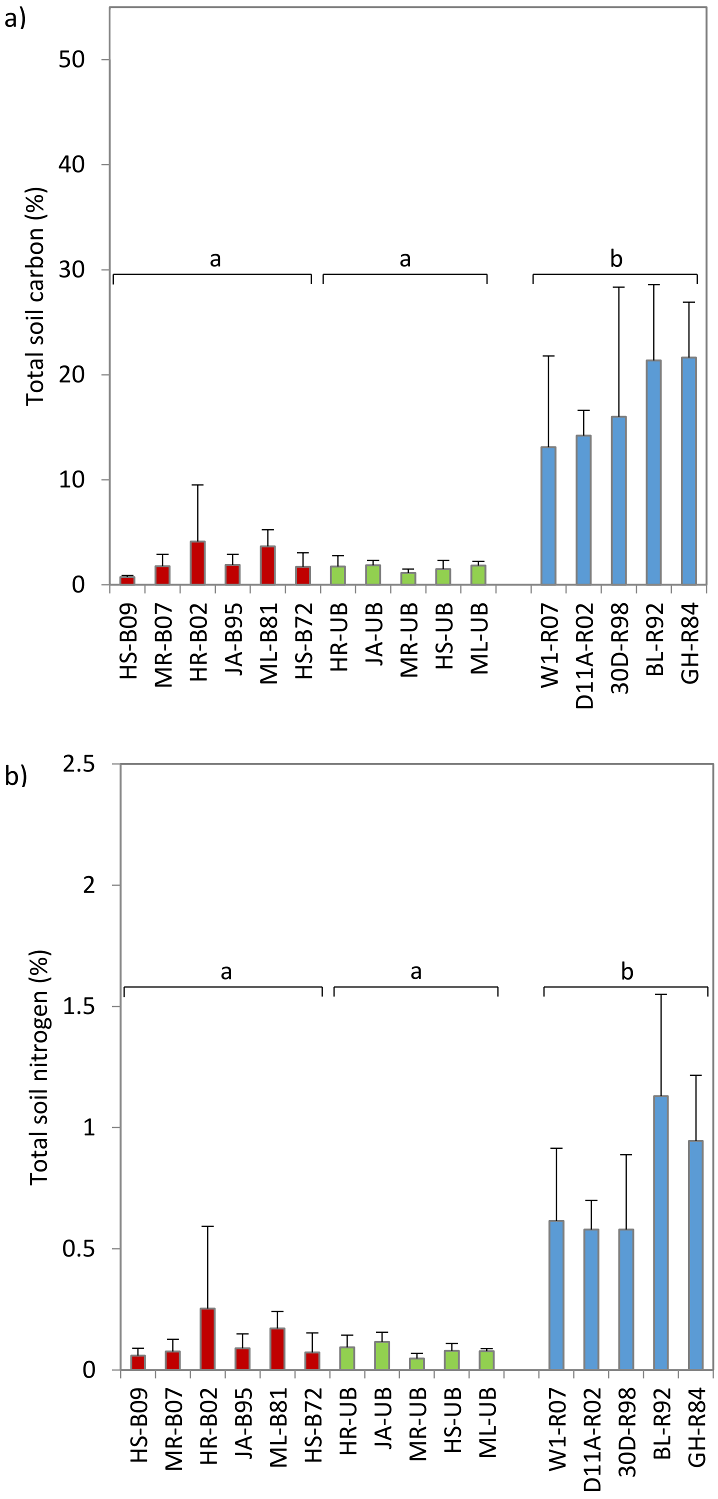


Figure 7. Total percent soil C (a) and N (b) of mineral soil or peat mineral mix. Red bars indicate burned sites, green unburned, and blue reclaimed. Sites are arranged chronologically, by disturbance type. Error bars represent one standard deviation away from the mean. Different letters indicate statistically significant differences among disturbance type at α=0.05.

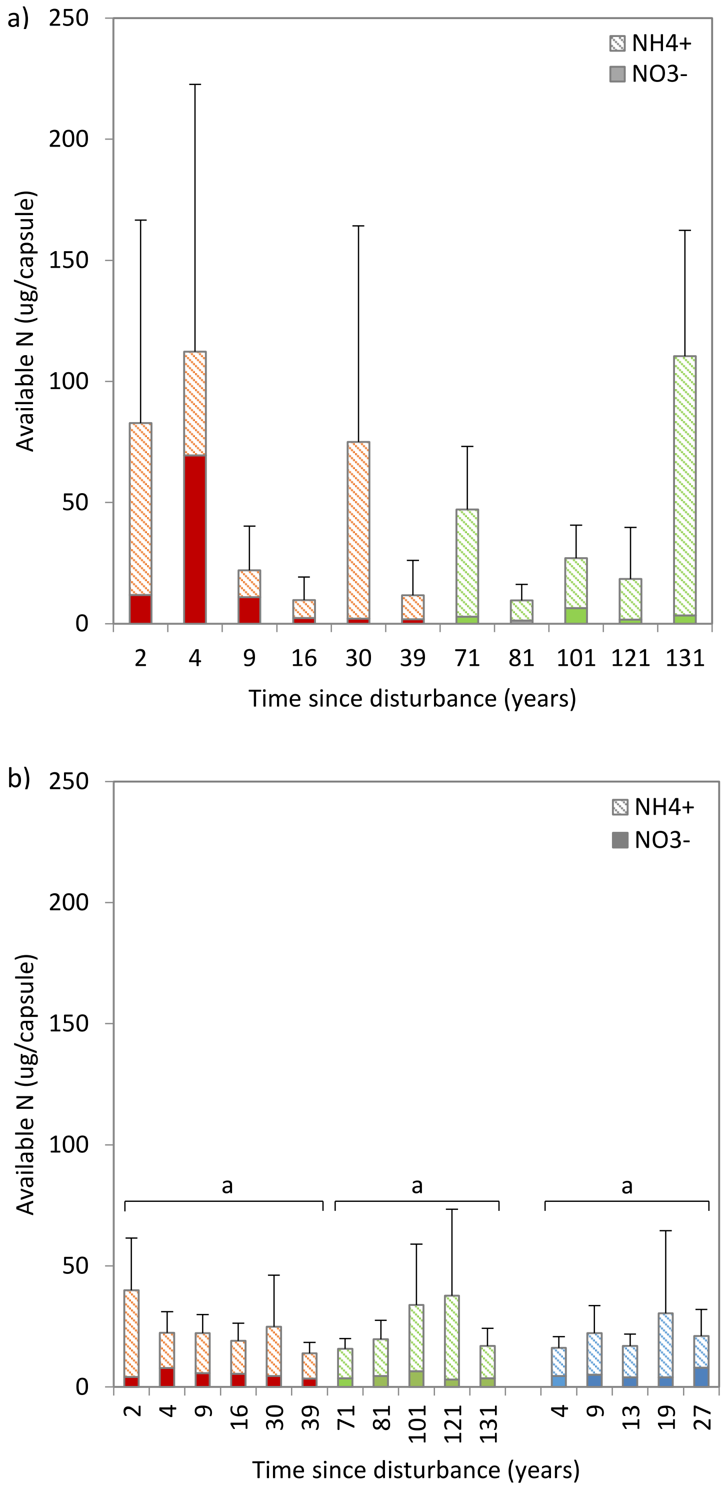


Figure 8. Total available N from ionic resin capsules. Incubated *in situ* during winter 2011 (a) and summer 2011 (b). Red bars indicate burned sites, green unburned, and blue reclaimed. Error bars represent one standard deviation away from the mean of total available N. Different letters indicate statistically significant differences among disturbance type at α=0.05.

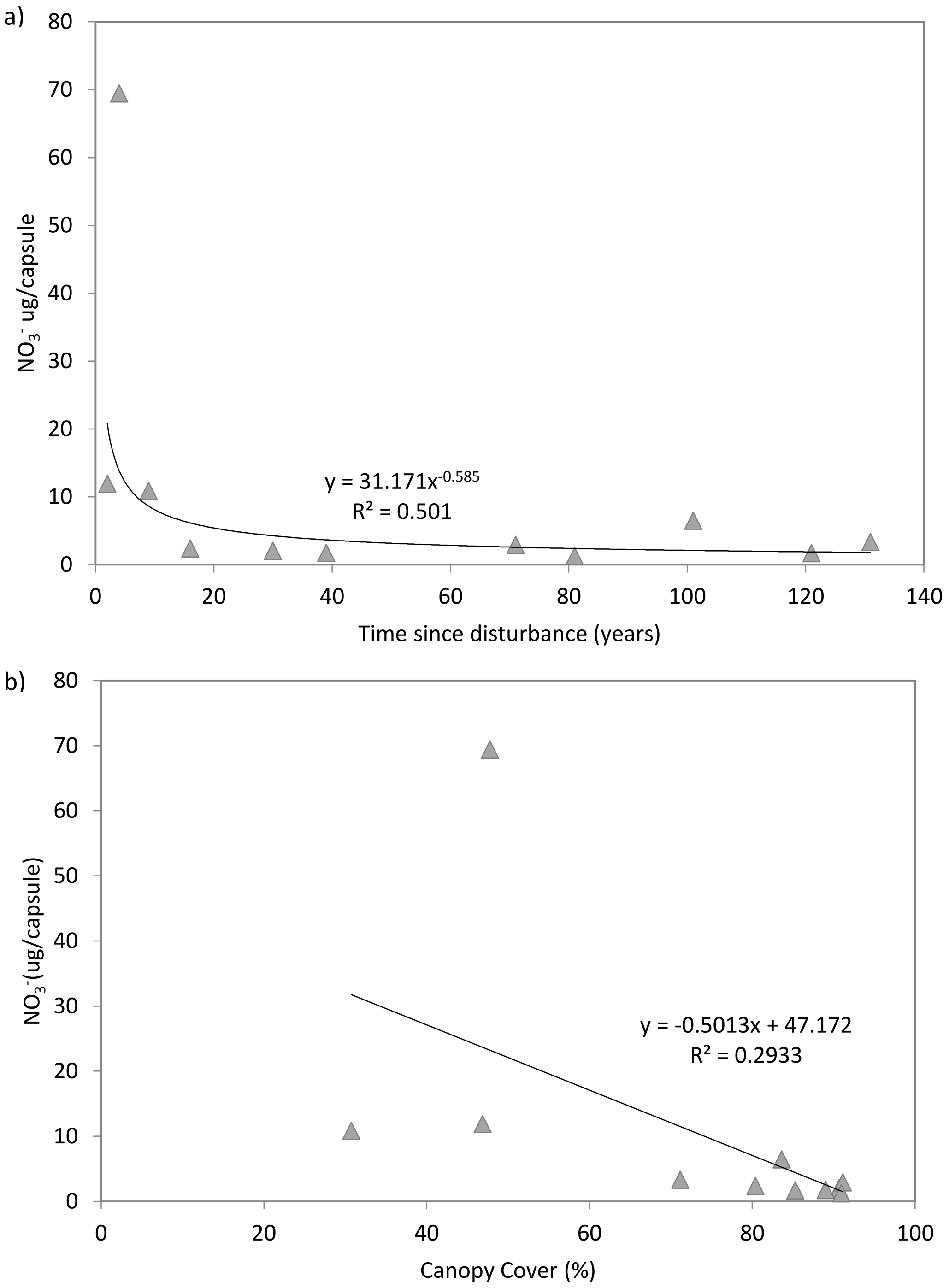


Figure 9. Regression analysis of available NO_3^- from ionic resin capsules. Incubated *in situ* on natural sites during winter 2011. Non-linear regression analysis (power) with time since disturbance (a) and linear regression with percent canopy cover (b).

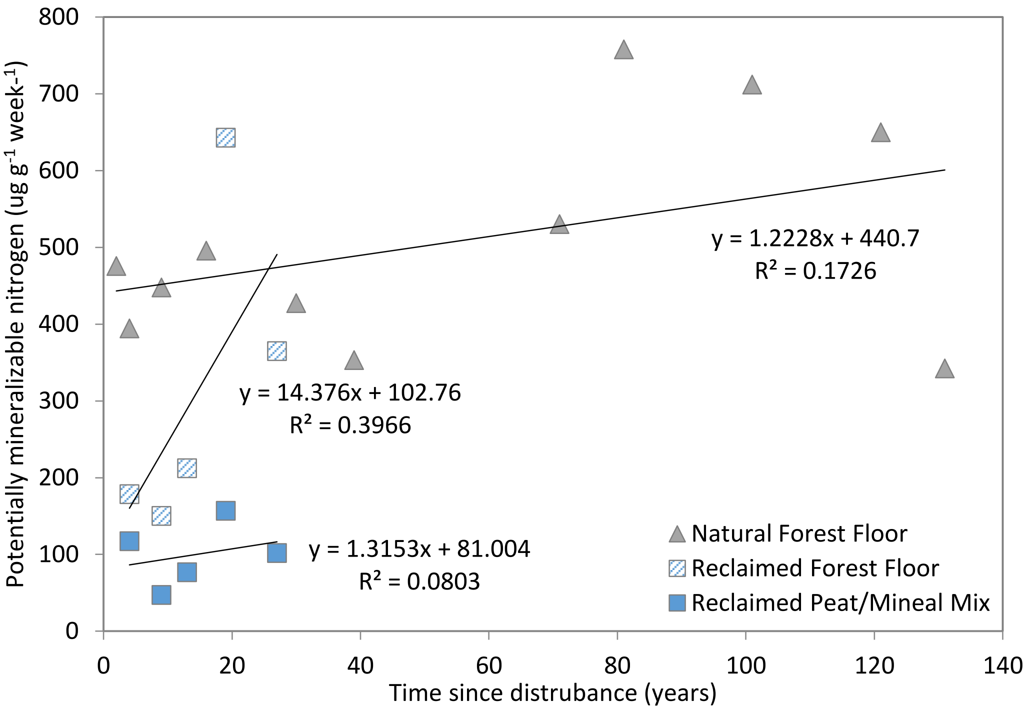


Figure 10. Linear regression analysis of potentially mineralizable N with time since disturbance. Natural is combined burned and unburned sites.

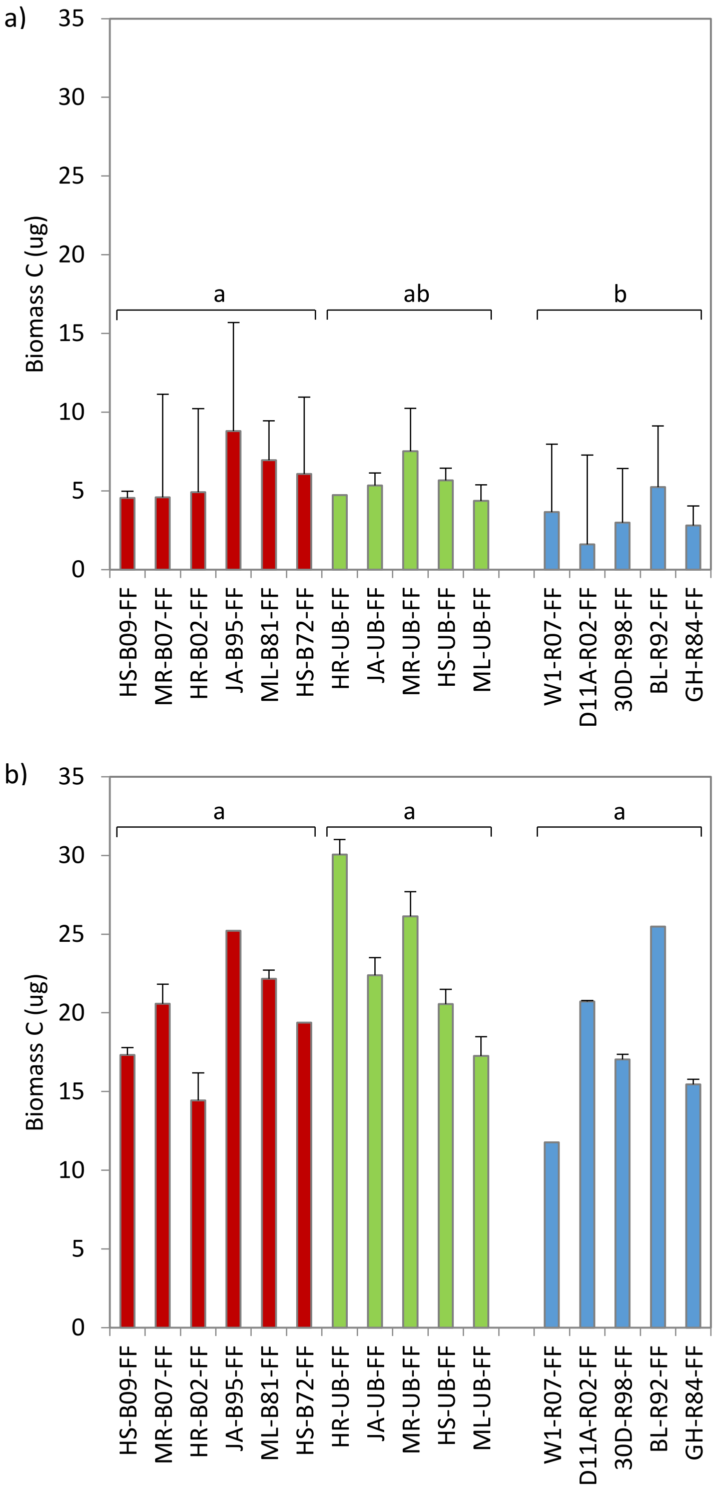


Figure 11. Microbial Biomass C measured by PLFA analysis for run A (a) run B (b). Red bars indicate burned sites, green unburned, and blue reclaimed. Sites are arranged chronologically, by disturbance type. Error bars represent one standard deviation away from the mean. Different letters indicate statistically significant differences among disturbance type at α=0.05.

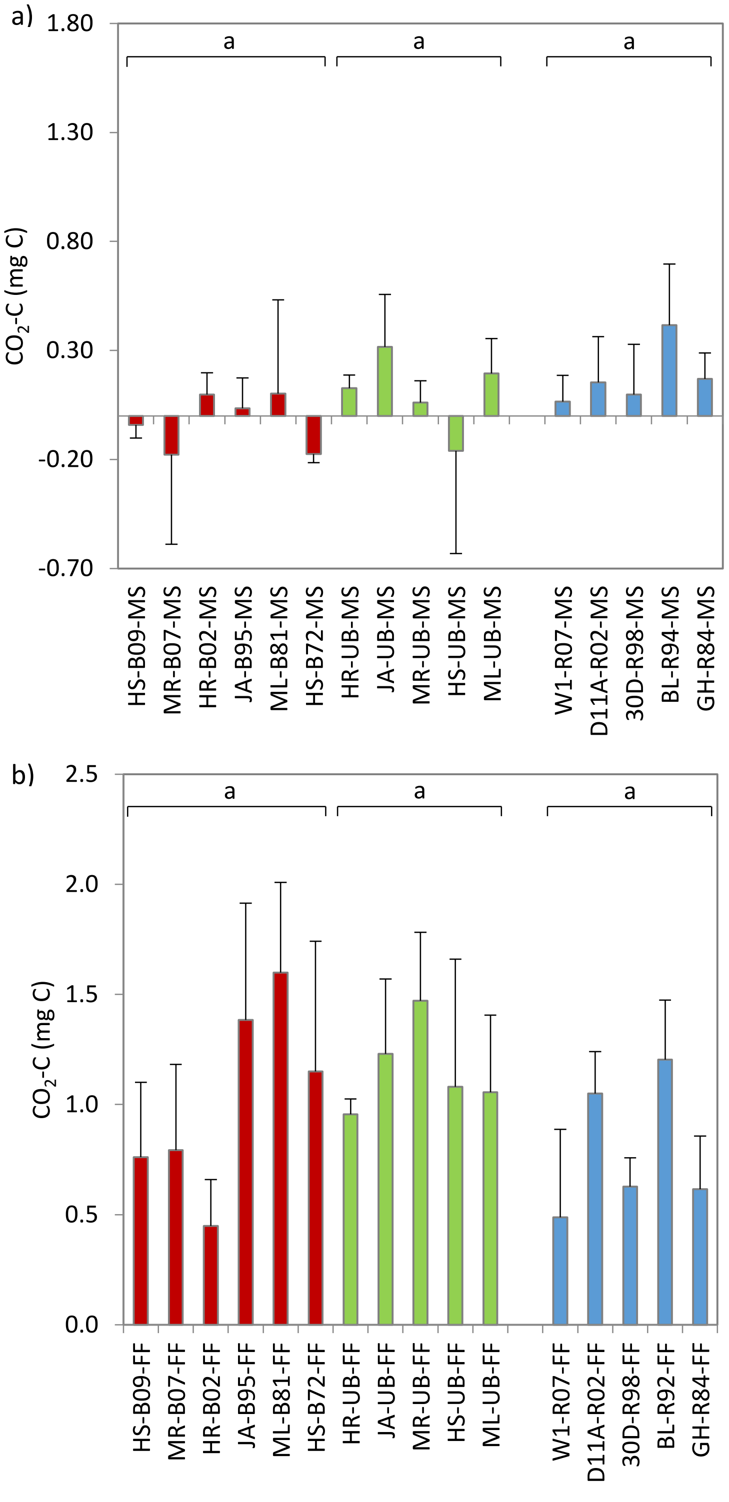


Figure 12. Soil respiration measured by alkali trap method for mineral soil (a) and forest floor (b). Red bars indicate burned sites, green unburned, and blue reclaimed. Sites are arranged chronologically, by disturbance type. Error bars represent one standard deviation away from the mean. Different letters indicate statistically significant differences among disturbance type at α=0.05.

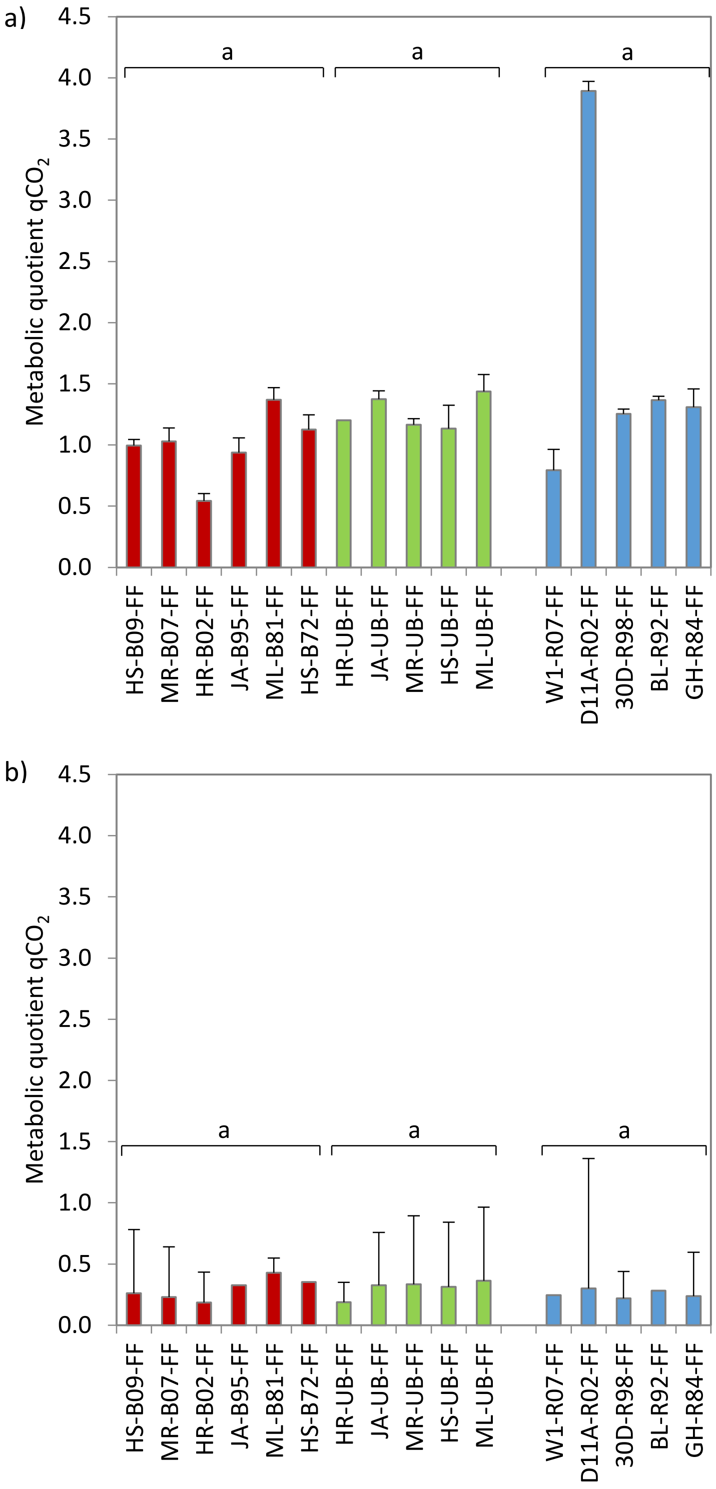
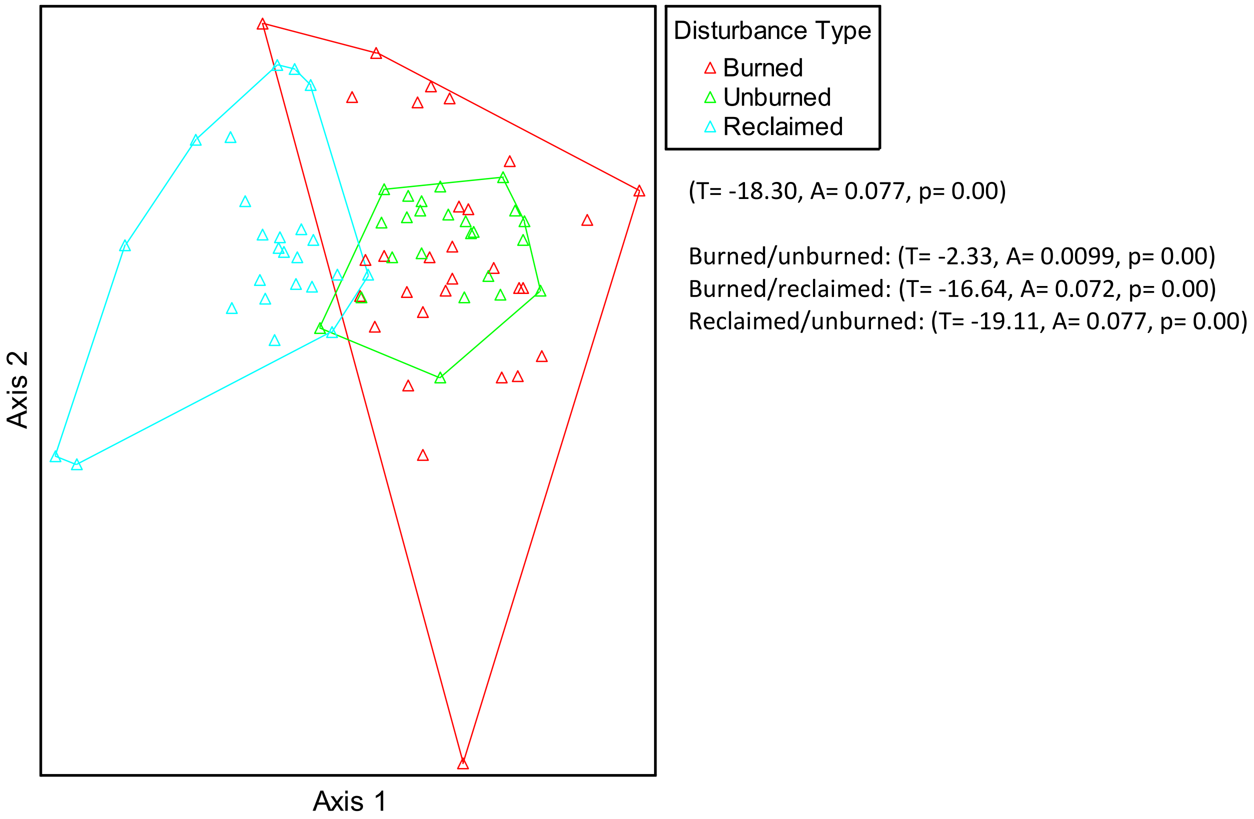


Figure 13. Metabolic quotient from forest floor for run A (a) and run B (b). Red bars indicate burned sites, green unburned, and blue reclaimed. Sites are arranged chronologically, by disturbance type. Error bars represent one standard deviation away from the mean. Different letters indicate statistically significant differences among disturbance type at α=0.05.



(T= -18.30, A= 0.077, p= 0.00)

Burned/unburned: (T= -2.33, A= 0.0099, p= 0.00)
Burned/reclaimed: (T= -16.64, A= 0.072, p= 0.00)
Reclaimed/unburned: (T= -19.11, A= 0.077, p= 0.00)

Figure 14. NMS ordination diagram of forest floor PLFA profiles. Grouped by disturbance type, from burned, unburned and reclaimed sites. Sites that are close together are more similar in terms of their microbial community structure than sites that are further apart. MRPP analysis includes T (difference between groups), A (variation within groups), and p (significance of the comparison) values.

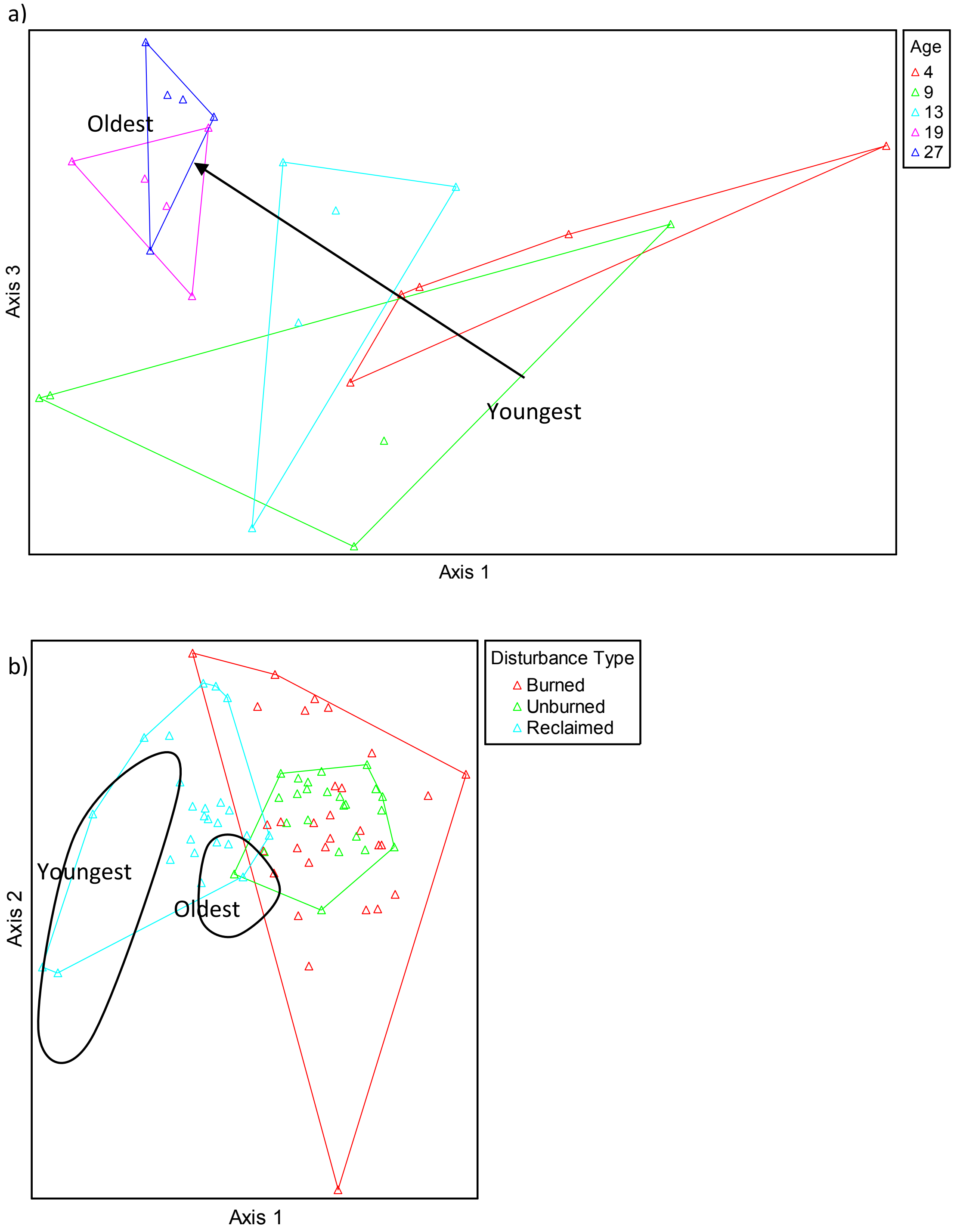
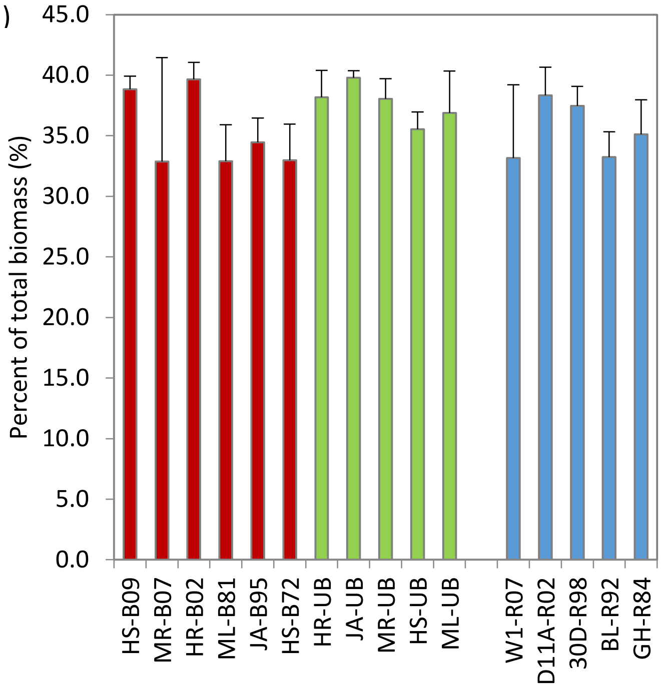


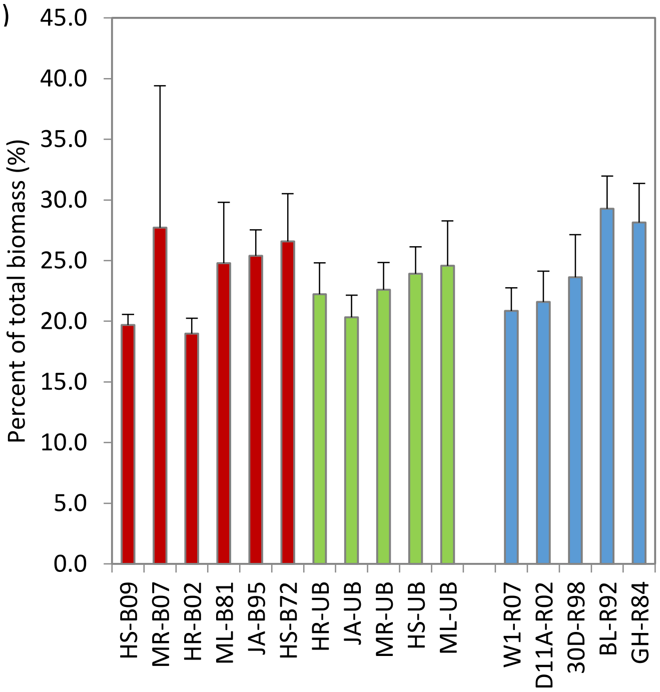
Figure 15. NMS ordination diagram showing temporal trend of reclaimed forest floor PLFA profiles. Reclaimed sites grouped by age (a) show a microbial community shift from youngest to oldest. All sites grouped by disturbance type (b) show the youngest reclaimed sites to be least similar to the natural sites, while the oldest reclaimed sites are most similar. Sites that are close together are more similar in terms of their microbial community structure than sites that are further apart.

a)



45.0
40.0
35.0
30.0
25.0
20.0
15.0
10.0
5.0
0.0
Percent of total biomass (%)
HS-B09
MR-B07
HR-B02
ML-B81
JA-B95
HS-B72
HR-UB
JA-UB
MR-UB
HS-UB
ML-UB
W1-R07
D11A-R02
30D-R98
BL-R92
GH-R84

b)



45.0
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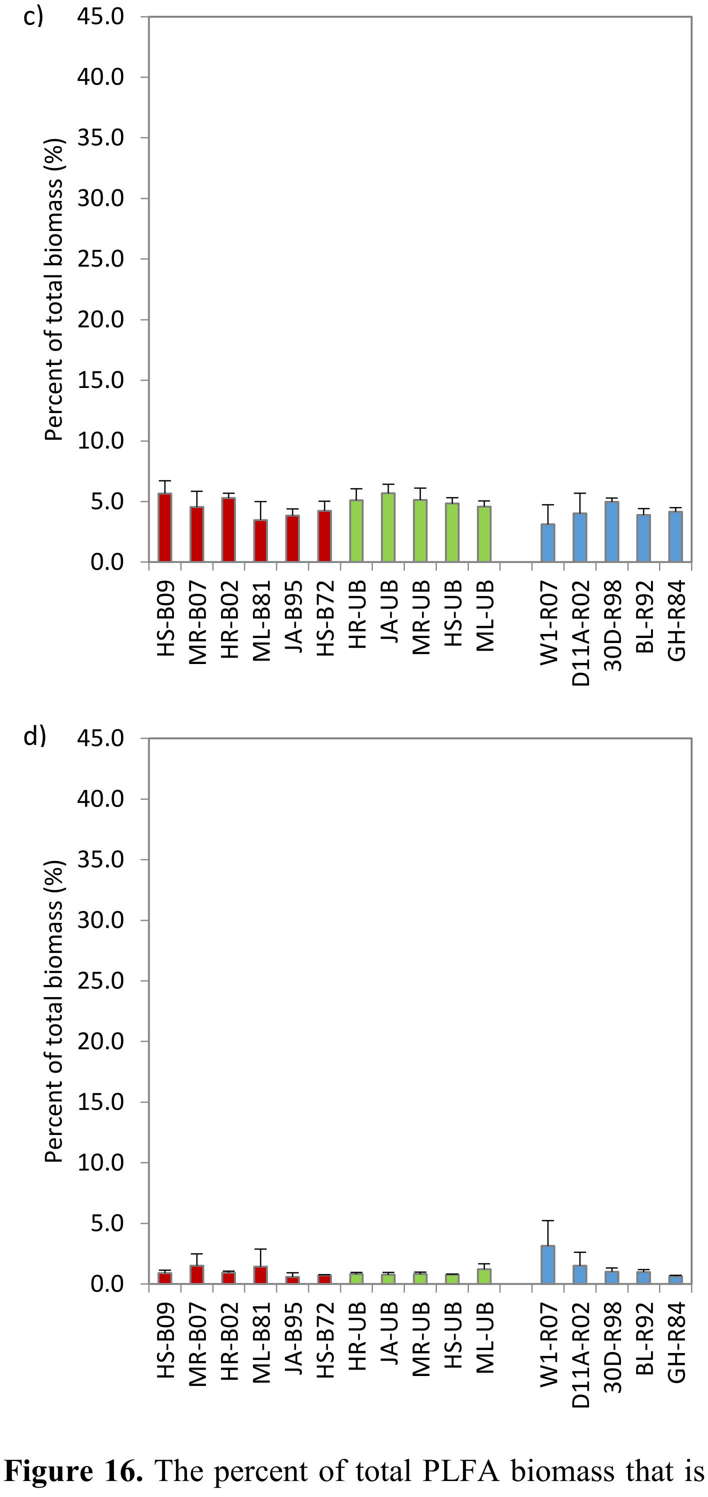


Figure 16. The percent of total PLFA biomass that is bacteria (a), fungi (b), actinomycetes (c), and protists (d). Red bars indicate burned sites, green unburned, and blue reclaimed. Sites are arranged chronologically, by disturbance type.

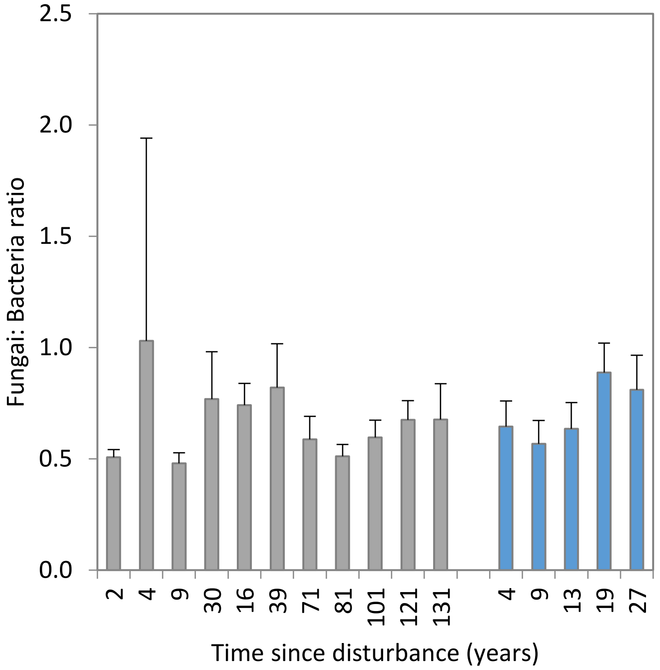
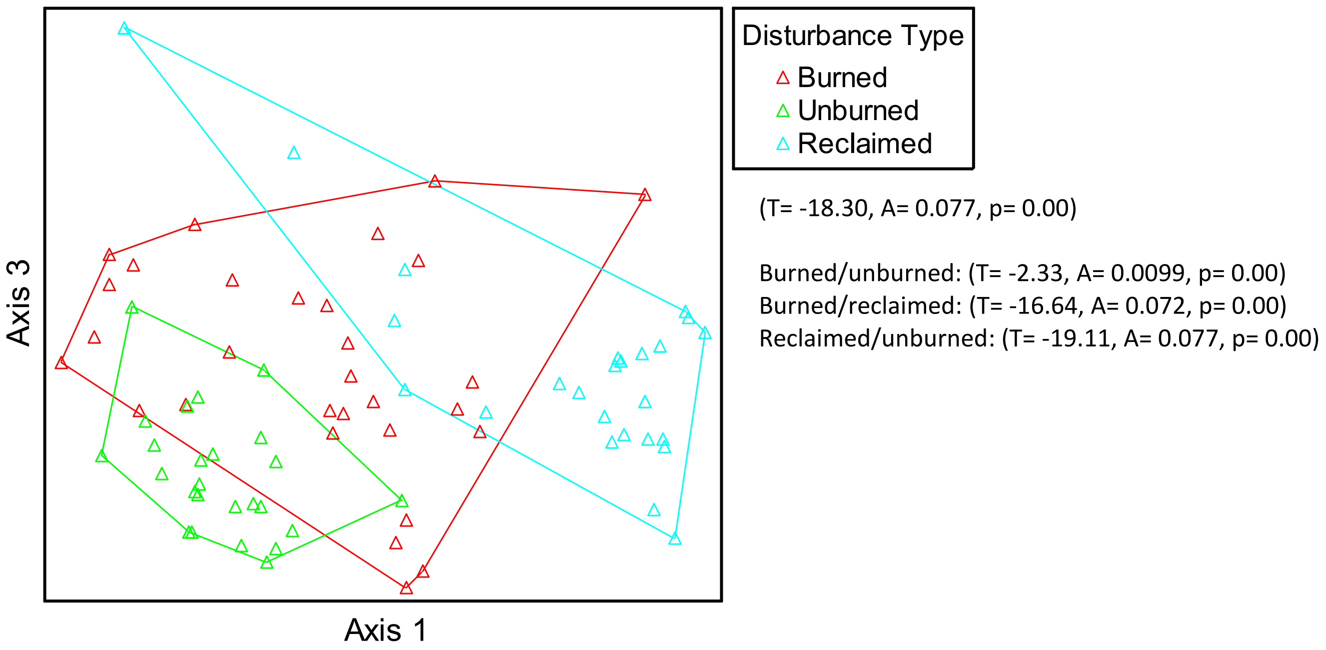


Figure 17. Fungi:bacteria ratio of percent of total PLFA biomass. Grey bars indicate natural (burned and unburned) sites and blue reclaimed.



(T= -18.30, A= 0.077, p= 0.00)

Burned/unburned: (T= -2.33, A= 0.0099, p= 0.00)
Burned/reclaimed: (T= -16.64, A= 0.072, p= 0.00)
Reclaimed/unburned: (T= -19.11, A= 0.077, p= 0.00)

Figure 18. NMS ordination diagram of vascular understory genera. Sites are grouped by disturbance type. Sites that are close together are more similar in terms of their microbial community structure than sites that are further apart. Arrows indicate the vectors for environmental variables. MRPP analysis includes T (difference between groups), A (variation within groups), and p (significance of the comparison) values.

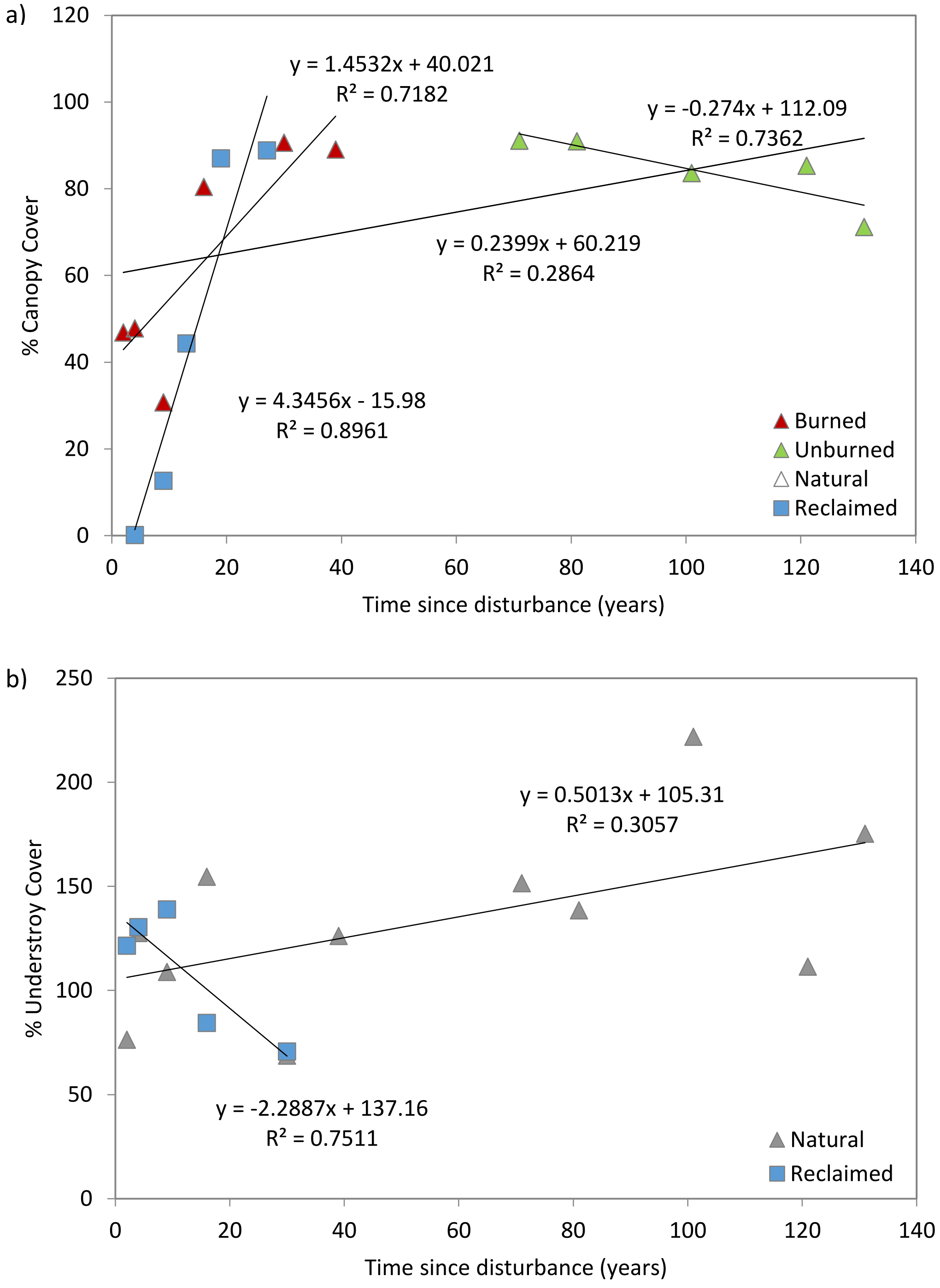


Figure 19. Linear regression analysis of percent canopy cover (a) and vascular understory cover (b) with time since disturbance. Natural is combined burned and unburned sites.

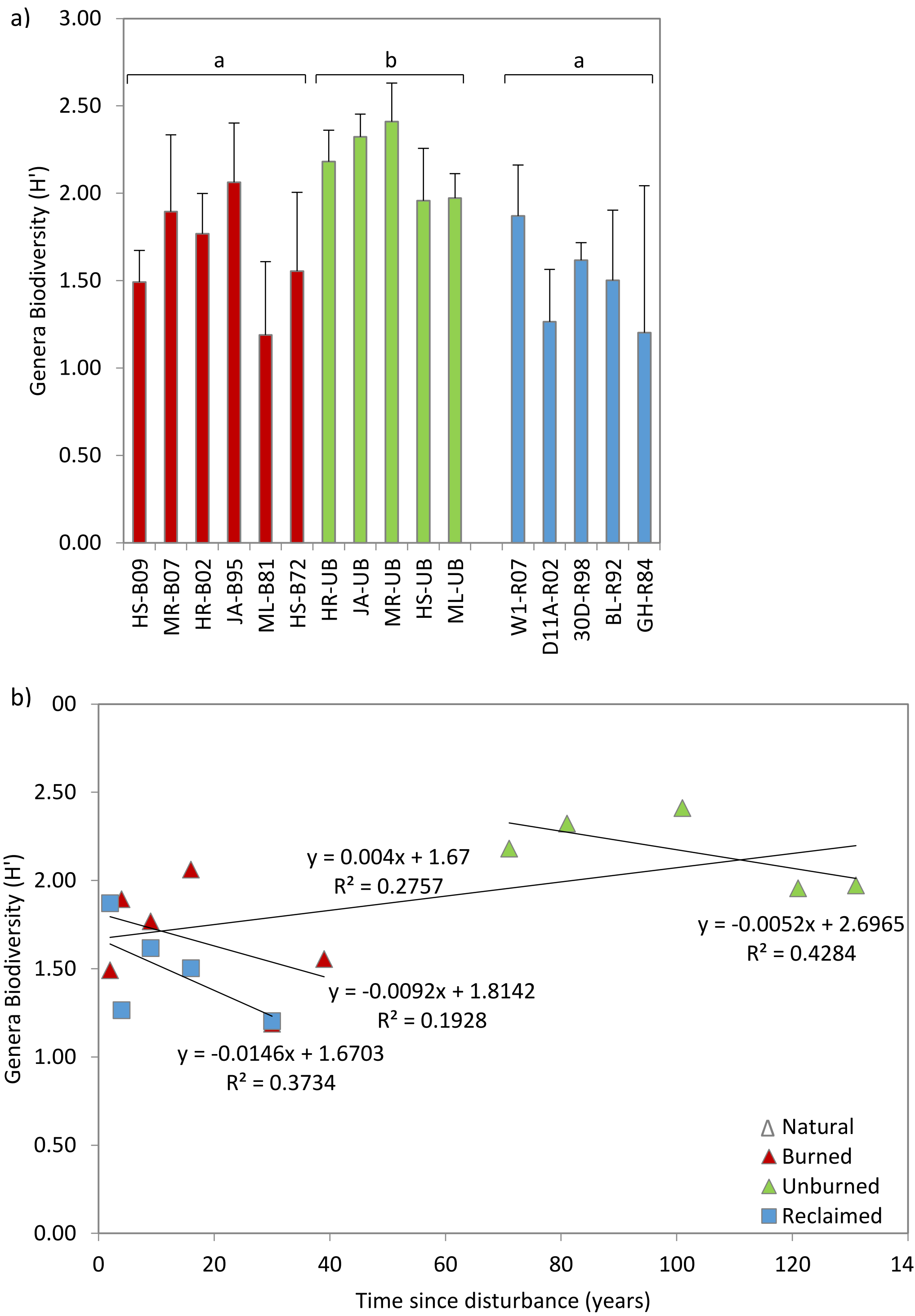


Figure 20. Genera Shannon-Weiner biodiversity index of vascular understory (a). Red bars indicate burned sites, green unburned, and blue reclaimed. Sites are arranged chronologically, by disturbance type. Error bars represent one standard deviation away from the mean. Different letters indicate statistically significant differences among disturbance type at α=0.05. Linear regression analysis of genera Shannon-Weiner biodiversity index with time since disturbance (b). Natural is combined burned and unburned sites.

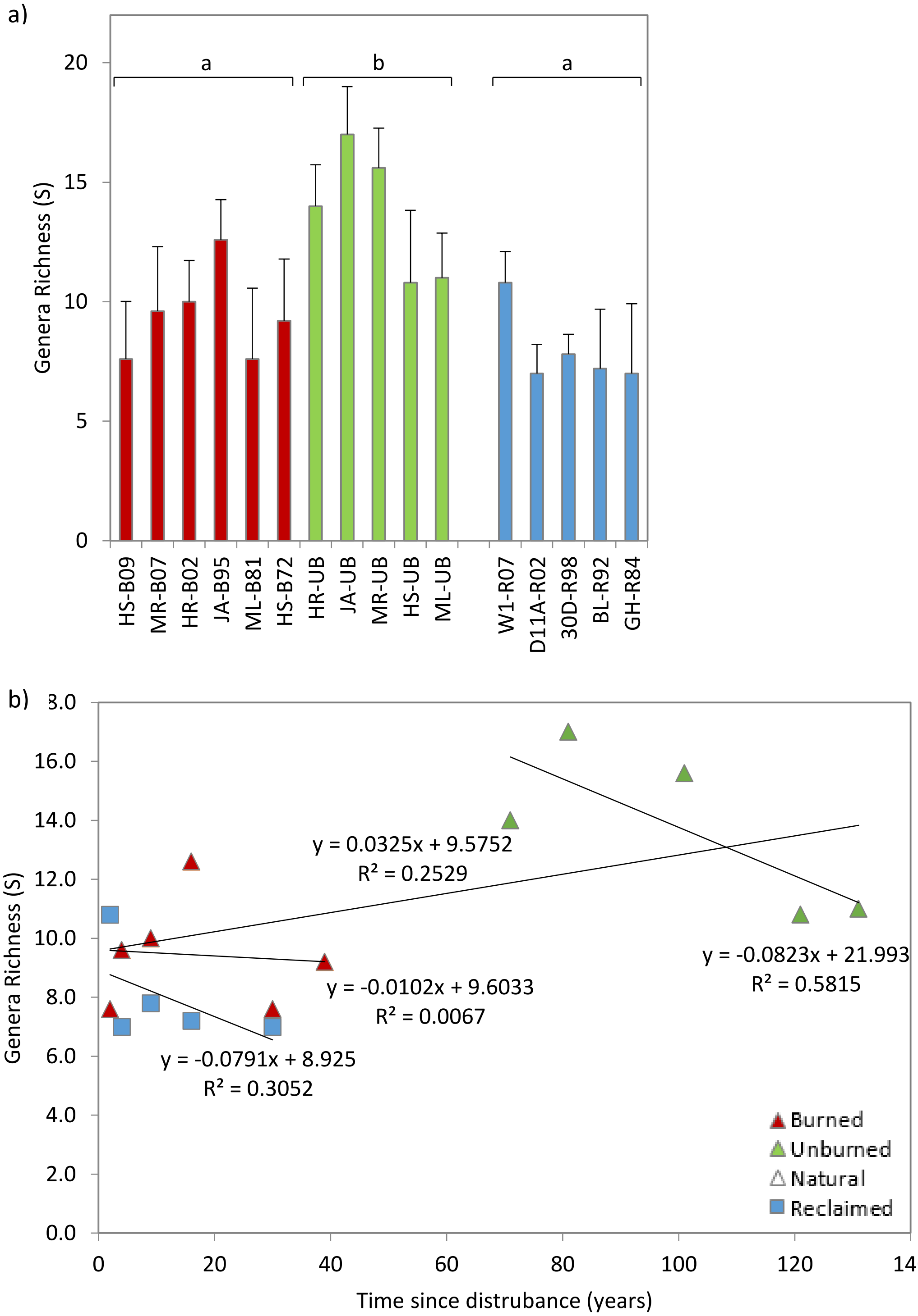


Figure 21. Genera richness of vascular understory (a). Red bars indicate burned sites, green unburned, and blue reclaimed. Sites are arranged chronologically, by disturbance type. Error bars represent one standard deviation away from the mean. Different letters indicate statistically significant differences among disturbance type at α=0.05. Linear regression analysis of genera richness with time since disturbance (b). Natural is combined burned and unburned sites.

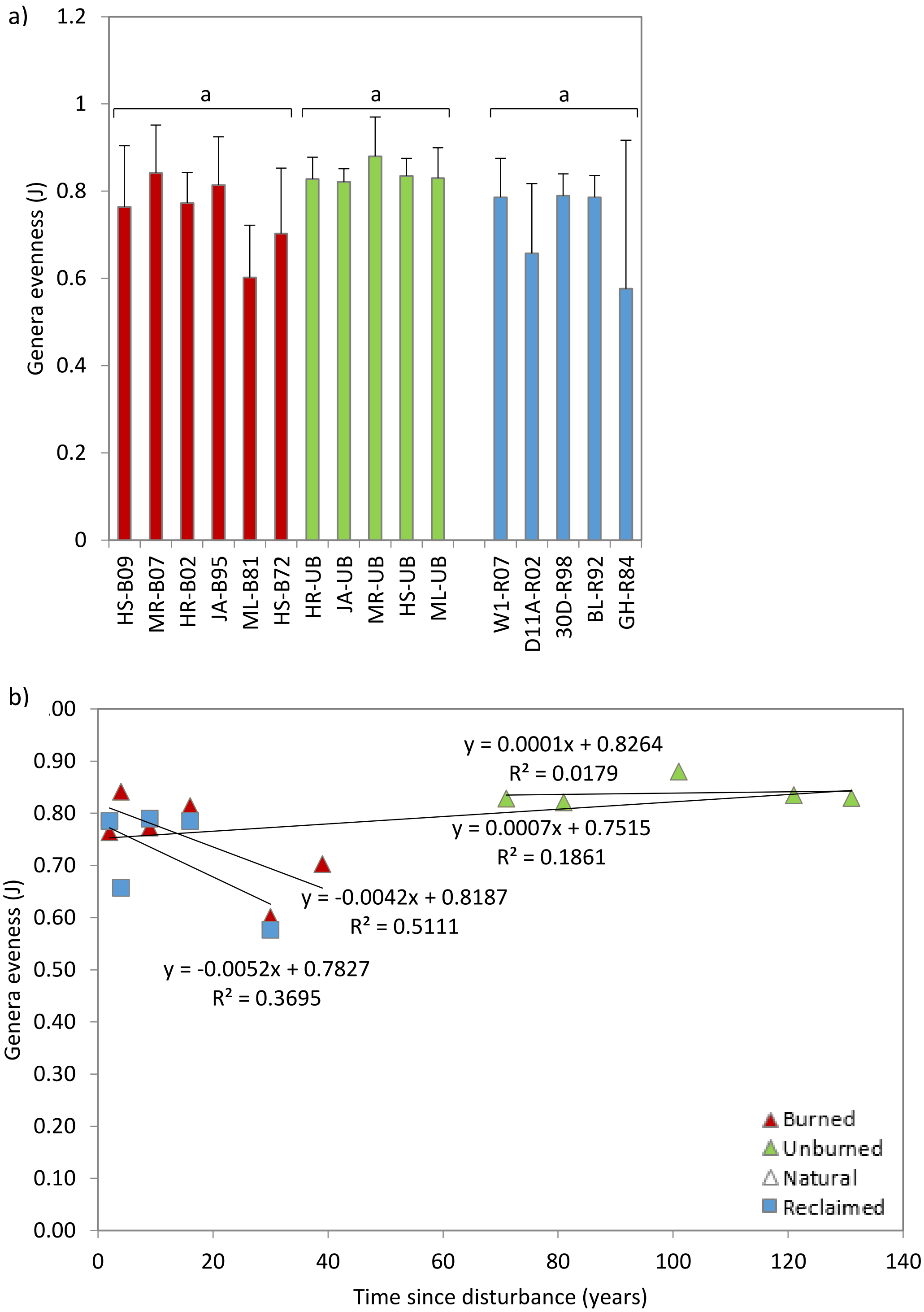


Figure 22. Genera evenness of vascular understory (a). Red bars indicate burned sites, green unburned, and blue reclaimed. Sites are arranged chronologically, by disturbance type. Error bars represent one standard deviation away from the mean. Different letters indicate statistically significant differences among disturbance type at α=0.05. Linear regression analysis of genera evenness with time since disturbance (b). Natural is combined burned and unburned sites.

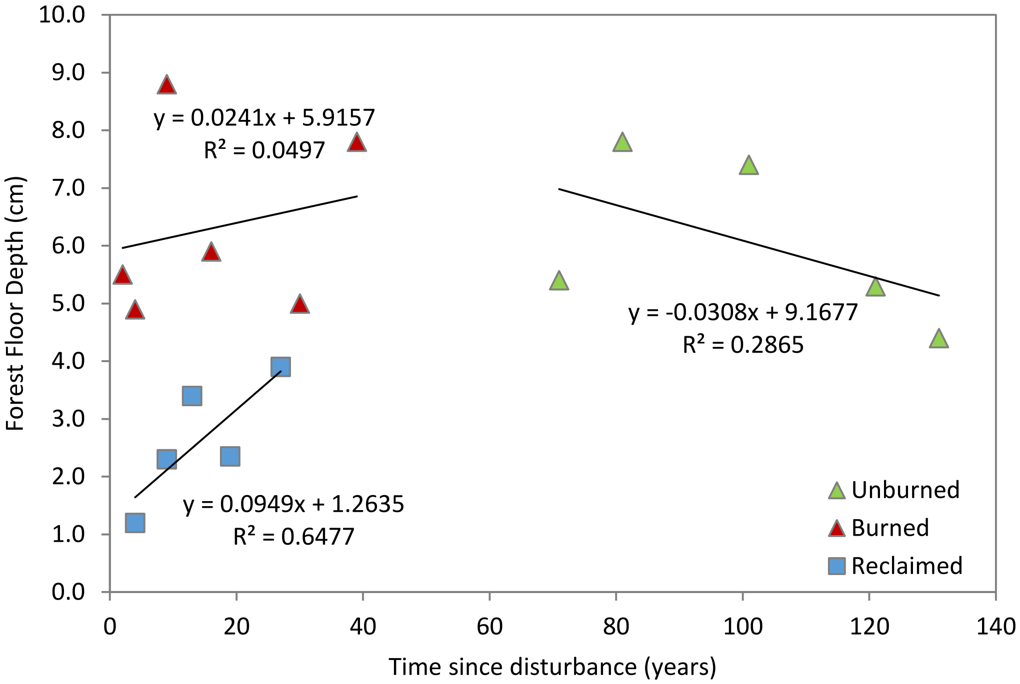


Figure 23. Linear regression analysis of forest floor depth with time since disturbance.

CHAPTER 4 DISCUSSION

4.1 Ecosystem Function

Ecosystem function is the framework of biological, geochemical, and physical processes and components that take place or occur within an ecosystem. The goal of reclamation is to re-create self-sustaining forests with similar ecosystem function as the natural landscape. MacDonald et al. (2012) list examples of soil quality criteria used to assess sustainability in reconstructed soils of the ASOR. These include variables of nutrient supply, organic matter quality, and microbial community.

Traditional agronomic productivity indicators such as total soil C and N, C:N, pH, and fertility (NPKS) have previously been used as benchmark indicators for reclamation success. They are baseline characteristics that can show how soils are different. While appropriate in an agricultural setting, agronomic indicators are not ideal in a forest landscape or for measuring reclamation success. Productivity indicators, like their name indicates, are designed to indicate growth and yield of single agronomic plants. These indicators are static and can be artificially enhanced with amendments and fertilization. They often relate to soil pedological development which may take centuries to develop following reclamation (Bradshaw, 2000). Whereas microbial community processes and nutrient cycling can develop over several decades (Bradshaw, 2000). Measuring the ecosystem function is therefore more appropriate.

We measured several traditional agronomic productivity indicators, including pH, soil texture, total soil C and N (Figure 6 a, b), and C:N. Overall, we did not find these variables to predict future health of the sites studied. Similarly, vegetation measurements such as tree density, tree species, tree height, DBH, and canopy cover, did not indicate ecosystem function and provided no clear trends or insight into reclamation or post-fire trends on the sites.

4.1.1 Available Nitrogen

In terms of ecosystem function, we measured *in situ* resin available N, potentially available N, microbial biomass and activity, and microbial community structure. For *in situ* resin available N, the expected post fire N availability trend (Figure 4) reported in previous chronosequence studies (Choromanska and DeLuca, 2002; DeLuca and Sala, 2006; Hart et al., 2005; MacKenzie and DeLuca, 2006; MacKenzie, et al., 2004, 2006) in temperate ecosystems was not observed. While NO_3^- was found to be higher in the most recently burned sites following the spring melt (Figure 8a, 9a), none of the other resin data support a significant trend. These earlier studies were conducted in temperate pine forests with a dead understory, very different from the Alberta boreal forest aspen-spruce ecosystem and its living forest floor and more diverse understory. This suggests that because of this living forest floor and understory on the sites, N dynamics are much different, with plants possibly playing a larger role in N cycling.

Ammonium concentrations were found to be higher than NO_3^-, contrary to what has been previously observed in the area (Hemsley, 2013). The Richardson fire burned over 700,000 hectares of forest in the AOSR throughout the summer of 2011. Large scale biomass burning produces pollution and deposition rich in NH_4^+ (Karlsson et al, 2013). If the Richardson fire resulted in large scale NH_4^+ deposition, it may explain the high NH_4^+ levels found and why there were no trends over time as deposition from the fire may have masked any trends that may have been present. It is possible that the winter resins were removed too quickly following the spring thaw and that the system had not drained and was still anaerobic. Nitrification by aerobic bacteria would have not yet occurred, possibly explaining the higher NH_4^+ levels in the winter in the absence of wildfire deposition. Site ML-UB had extremely high NH_4^+ levels during winter 2011 (107.23 ug/capsule), likely from the deposition of automobile emissions due to the sites proximity to a major highway. Overall, NH_4^+ was higher than reported by previous studies (Hemsley, 2013), possibly due to the reasons listed above. The summer resins had lower available N than the winter data set. This would be expected as the spring melt results in a flush of available N. There was also low precipitation in summer 2011, possibly inhibiting microbial transformations. The average monthly precipitation for the 2011 summer months compared to the normals are as follows; June, 51mm vs 74.8mm normal; July, 3mm vs 81.3mm normal; and August, 61.5mm vs 72.7mm normal (Environment Canada, 2015).

Previous work by Hemsley (2013) and Sorensen et al. (2011) on reclaimed AOSR sites indicate canopy cover to be a good indicator for N availability. Comparing available N with canopy cover rather than time did not highlight any further trends. Potentially mineralizable N in the forest floor increased sharply on reclaimed sites (Figure 10) to fall within the natural variability of the burned natural sites. However, it is uncertain if it will plateau as seen on the natural sites.

4.1.2 Microbial Dynamics

The microbial biomass and activity (respiration) measurements obtained were not found to be useful ecosystem function indicators on the studied sites, with essentially no significant difference between disturbance types or trends with time. Microbial community structure on the reclaimed sites was drastically different from natural microbial communities, as expected due to the drastic differences in the two types of soil materials present on the reclaimed and natural sites. Differences could be a consequence of the relic microbial community in the PMM. These would have been anaerobic communities from a wetland ecosystem, drastically different from what is present in the aspen-spruce upland forests these sites are made to mimic.

4.1.3 Understory vegetation

The diversity of the vegetation on the reclaimed sites was found to be similar to that on the naturally disturbed burned sites (Figure 21). This is positive for ongoing reclamation in the oil sands. While the negative trajectory of vegetation diversity on the reclaimed sites may seem to be of concern, the same trend is observed on naturally disturbed sites and, like on the natural sites, may begin to increase with time. Initially, disturbed sites, naturally or anthropogenically, are colonized by numerous ruderal species. This causes an increase in the diversity of the understory, which decreases and certain species begin to dominate, but as more woody species establish with time diversity increases once again.

While diversity is similar, the understory genera colonizing the reclaimed and fire disturbed sites are different. The N profiles of the soils they are colonizing are completely different. Following wildfire, the forest floor is generally mostly consumed and pioneer species establish themselves on exposed mineral soil or the small amount of remaining forest floor. Natural mineral soil is low in nutrition, with low C and N supply (Figure 7). There are also very different microbial communities in PMM compared to forest floor. PMM which is used as mineral soil substitute is just the opposite, with relatively high levels of C and N (Figure 6). Pioneer species present on neighbouring sites are blown onto the newly constructed sites. There is no seed bank of upland species in the soil/PMM. There is lack of seeds from woody shrubs and species that would commonly colonize as the sites matured. First, there is lack of neighbouring species to be transported to the sites as there are no mature stands bordering the reclaimed site. Dispersal of woody species such as *vaccinium* sp. is primarily by dispersal of berries by bears. There are no bears on site to disperse the seeds. There is a large difference in canopy cover. The natural sites reach partial canopy very quickly, within a couple years it is close to 50 %, while it take more than 10 years for a similar cover to form on the reclaimed sites (Figure 20a).

The lack of woody species seed dispersal may also explain the decreasing understory cover on the reclaimed sites. As the canopy closes the sun loving ruderal species die but there are no shade tolerant shrubs to replace them. On the reclaimed sites there is an increase in non-vascular species present and much more bare ground on the older sites. The declining understory may also be a result of the pattern of seedling planting, lack of heterogeneity, or lack of gaps.

4.2 Reclamation Trajectory

Reclamation trajectory is the development route of the reclaimed ecosystem function over time. The goal of reclamation is to create a reclamation trajectory where the ecosystem function of the reclaimed sites eventually falls within the natural variability of the natural landscape. Previous work measuring reclamation trajectory in the AOSR (Turcotte et al., 2009; Rowland et al., 2009; Dimitriu et al., 2010) has used mature boreal forest sites to establish natural variability and found little similarities between reclaimed and mature sites. Quideau et al. (2013) included middle aged (as young as 48 years since fire) natural boreal stands as comparison and still found little similarities between reclaimed and natural sites. Rowland et al. (2009) and Sorenson (2011) did find an evolution of the reclaimed sites over time, with respect to plant community composition, nutrient availability and organic matter.

Like the previous work mentioned above, we found microbial and vegetation communities, and nutrient profiles, on the reclaimed sites differ from those on mature undisturbed forest sites. There was an observed shift over time with microbial community structure (Figure 15) and potentially mineralizable N (Figure 10). Potentially mineralizable N in the forest floor increased sharply over time (Figure 10) and it is uncertain if it will plateau as seen on the natural sites. Unlike previous work, we also used young natural sites recently (2-30 years since disturbance) disturbed by wildfire. The reclaimed sites are beginning to show some similarities with the burned sites. They are on a reclamation trajectory where the oldest reclaimed sites are beginning to fall within the natural variability of these naturally disturbed sites (Figure 10, 14, 18). More work is required to see if the C substrate is causing the microbial shift. It could in part be to the system shifting from peat, which is anaerobic to upland aerobic community, and because of the plant community shift.

This highlights the importance of using an appropriate natural comparison when evaluating trajectory success. No previous work compares the reclamation trajectory of reclaimed ASOR soils to natural soils coming back from disturbance in the same time frame as the young reclaimed sites. Reclaimed sites may not be emulating mature stands, but they may be on a trajectory that is in some aspect comparable to natural disturbance recovery. This work shows that young disturbed sites are a more appropriate comparison/benchmark than mature stands.

4.3 Functional similarity

For a reclaimed ecosystem to be successful it must be self-sustaining, have a reclamation trajectory that falls within natural variability, and similar ecosystem functioning to the natural sites. We want to create functional similarity between the reclaimed and natural landscape. To determine reclamation success, ecosystem processes occurring following reclamation are compared to the same processes on the natural landscape.

Mukhoppadhyay (2014) used principal component analysis (PCA) to create a ‘mine soil quality index’ to be used for assessing reclamation success. The index uses both ecosystem processes and traditional agronomic soil productivity measurements to quantify the stage of recovery of a reclaimed site, and for wildland ecosystems this is inappropriate as discussed earlier. Using this framework, a similar index could be created for reclaimed ecosystems in the AOSR using measurements of ecosystem function to compose the index, and naturally disturbed soils as a reference ecosystem. An 'ecosystem functional similarity index' would be ideal from a management perspective as the health of a reclaimed area and time required for the development of self-sustaining forest cover can be quantified.

Ordination can express the similarities and dissimilarities between reclaimed and natural sites. We used ordination to represent the microbial and understory vegetation communities and highlight the similarities between the disturbance type (Figure 14 and 18). Both these ecosystem functions would be ideal to incorporate into an 'ecosystem functional similarity index'. The MRPP analysis of the microbial community data highlights the potential of ordination to express these dissimilarities. When excluding one disturbance type, the similarity/dissimilarity between the other two can be quantified. The reclaimed and unburned sites were the most dissimilar (T=-19.11, A=0.097, p=0.00), the burned and reclaimed sites were slightly less dissimilar (T=-16.64, A=0.072, p=0.00), and the burned and unburned quite similar (T=-2.33, A=0.0099, p=0.027), with a very low A-value. The goal of reclamation would be to create more similar microbial communities to natural sites, so lower A-values when comparing to burned and unburned. Potentially, something in the range of the burned and unburned (A=0.0099).

CHAPTER 5 CONCLUSIONS

The expected post-disturbance available nitrogen trends measured by the resin cap analysis were not observed on either the natural or reclaimed sites. This does not mean it is not present in the Alberta boreal forest, just not this stand type. Similar work needs to be conducted to determine what the post-fire nitrogen trend is on jack pine sites.

Aspen spruce reclaimed sites have different nutrient profiles, microbial communities, soil characteristics and vegetation than mature boreal stands. However, similarities exist when comparing them to naturally wildfire disturbed sites of similar age. The microbial community of the oldest reclaimed sites are most similar to naturally disturbed sites. Potentially mineralizable N of the forest floor on the reclaimed sites appears to be on a trajectory to become more like naturally disturbed sites. The understory vegetation community on the reclaimed sites is similar to that on some of the wildfire sites. These trends need to be monitored further as the sites age to see if they do in fact develop to be similar to what is observed in the natural forest floor.

The PMM had few similarities to natural soil. However, if it can provide enough nutrition for a planted stand to grow that stand will begin to naturally develop its own forest floor. With these microbial communities becoming more similar to those on natural sites, perhaps a more natural soil nutrition source for plants will develop.

A successfully reclaimed ecosystem must be self-sustaining, have a reclamation trajectory that falls within natural variability, and similar ecosystem functioning to similar natural forest sites. Appropriate soil quality criteria to assess ecosystem function and sustainability in reconstructed soils of the ASOR include variables of nutrient supply, organic matter quality, microbial and vegetation community. These are more suitable than traditional soil productivity indicators. This work shows that young naturally disturbed sites may be a more relevant comparison when evaluating reclamation trajectory than mature stands, which have previously been used. There is potential to create an ‘ecosystem functional similarity index’, using the previously mentioned measurements of ecosystem function. An index could quantify the health of a reclaimed area and time required for the development of self-sustaining forest.

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APPENDIX

Table A1. GPS locations of sample sites.

Site	Code	Age	Latitude	Longitude
Hangingstone	HS-B09	2	56.27175422	-111.55057881
Hangingstone	HS-B72	39	56.25506988	-111.49068793
Hangingstone	HS-UB	121	56.27065904	-111.54717810
Makay River	MR-B07	4	56.96078070	-111.88794337
Makay River	MR-UB	101	56.95778458	-111.83030731
House River	HR-B02	9	55.75233598	-112.21698068
House River	HR-UB	71	55.75360592	-112.21725158
JACOS	JA-B95	16	56.31005935	-111.66168555
JACOS	JA-UB	81	56.30738209	-111.66342865
Mariana Lake	ML-B81	30	55.96471212	-112.00608898
Mariana Lake	ML-UB	131	55.94135410	-112.04247633
W1-Dump	W1-R07	4	57.01944388	-111.72837515
Dyke-11A	D11A-R02	9	56.89997845	-111.40638703
30-Dump	30D-R98	13	56.99598913	-111.62057357
Bison Lake	BL-R92	19	56.99958706	-111.60943419
Gateway Hill	GH-R84	27	56.99101036	-111.56327345

Table A2. Reclamation prescription descriptions of reclaimed sample sites.

Site	Code	Disturbance Type	Location	Age	Prescription Description
W1-Dump	W1-R07	Reclaimed	Syncrude	4	100cm of secondary material/ 25cm of muskeg, over overburden
Dyke-11A	D11A-R02	Reclaimed	Suncor	9	20 cm of muskeg/ 80 cm of secondary material, over lean oils sands
30-Dump	30D-R98	Reclaimed	Syncrude	13	90cm of secondary material/10cm of muskeg, over overburden
Bison Lake	BL-R92	Reclaimed	Syncrude	19	20cm of secondary material / 15cm of muskeg, over overburden
Gateway Hills	GH-R84	Reclaimed	Syncrude	27	80cm of secondary material/ 30cm of muskeg, over overburden

Table A3. Natural site average soil characteristics.

Site	Code	Age	Disturbance Type	pH (in $CaCl_2$)		MS Texture	Db (g/cm)		FF Depth (cm)
				MS	FF		FF	MS	
Hangingstone	HS-B09	2	Burned	5.2	3.7	loam	0.16	1.30	5.5
Makay River	MR-B07	4	Burned	5.6	4.0	loam	0.16	1.59	4.9
House River	HR-B02	9	Burned	5.6	5.3	sandy loam	0.09	1.34	8.8
JACOS	JA-B95	16	Burned	4.8	4.2	loam	0.11	1.43	5.9
Mariana Lake	ML-B81	30	Burned	4.3	3.9	loam	0.19	1.46	5.0
Hangingstone	HS-B72	39	Burned	3.8	3.8	loam	0.19	1.37	7.8
House River	HR-UB	71	Unburned	4.9	4.1	sandy loam	0.23	1.20	5.4
JACOS	JA-UB	81	Unburned	4.8	4.2	loam	0.12	1.27	7.8
Makay River	MR-UB	101	Unburned	4.8	3.8	loam	0.12	1.19	7.4
Hangingstone	HS-UB	121	Unburned	4.3	3.8	loam	0.25	1.32	5.3
Mariana Lake	ML-UB	131	Unburned	4.5	3.8	loam	0.16	0.95	4.4

Table A4. Average site vegetation characteristics.

Site	Code	Age	Disturbance Type	Canopy Cover (%)	Vascular Understory Cover (%)	Shrub Cover (%)	Forb Cover (%)	Grass Cover (%)	Non-vascular (%)	Ericoid Cover (%)	DBH (cm)	Tree Height (cm)	Number of trees
Hangingstone	HS-B09	2	Burned	46.9	76.4	14	55	25	38	4.2	2.1	123.3	31.2
Makay River	MR-B07	4	Burned	47.8	127.7	33	63	25	18	5.6	3.5	155.9	22
House River	HR-B02	9	Burned	30.7	108.9	51	31	60	0	0.4	10.4	203.9	5.8
JACOS	JA-B95	16	Burned	80.4	154.7	56	59	10	17	42.7	9.1	291.1	35.4
Mariana Lake	ML-B81	30	Burned	90.6	68.8	28	59	0	28	2.2	4.7	688.6	12.6
Hangingstone	HS-B72	39	Burned	89	126.2	70	34	19	60	78.2	5.7	711	7.4
House River	HR-UB	71	Unburned	91.1	151.7	41	52	3	6	3.7	5.3	534.5	5.4
JACOS	JA-UB	81	Unburned	91	138.5	49	64	20	21	9.6	12.1	1305.6	3.6
Makay River	MR-UB	101	Unburned	83.6	222	57	64	7	9	9.9	7.3	739.7	3.2
Hangingstone	HS-UB	121	Unburned	85.3	111.5	61	52	14	38	34.2	4.5	457.3	6.8
Mariana Lake	ML-UB	131	Unburned	71.1	175.3	59	36	52	14	7.8	5.3	487.2	1.8
W1-Dump	W1-R07	4	Reclaimed	0.2	121.5	5	49	49	34	0.1	2.3	102.9	1.6
Dyke-11A	D11A-	9	Reclaimed	12.7	130.5	31	27	77	2	0	2.4	151.5	6.4
30-Dump	30D-R98	13	Reclaimed	44.3	138.9	41	49	29	16	2	4.3	297.4	8.4
Bison Lake	BL-R92	19	Reclaimed	87	84.5	19	33	21	16	6.1	6.4	479.7	3.4
Gateway Hill	GH-R84	27	Reclaimed	88.8	70.7	24	27	16	38	0.3	11.6	909.4	1.6