PLANT ABUNDANCE, DIVERSITY, AND COMPOSITION FOLLOWING RECLAMATION IN ALBERTA'S OIL SANDS.

By

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A Thesis Submitted in Fulfillment of the
Requirements for the Degree of Masters
of Science in Forestry

Faculty of Natural Resources Management

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September 2014

ABSTRACT

Sobey, T.M. 2014. Plant abundance, diversity, and composition following reclamation in Alberta's oil sands. 60 pp.

Key words: *boreal forest; community assembly; oil sands; overstory type; productivity; restoration; stand age; substrate; time since disturbance*

The Alberta oil sands have caused an economic boom in the Canadian economy in recent years. Identifying the best strategy for vegetation recovery after oil sands extraction is critical to restoring the biodiversity and functions of the pre-disturbed ecosystems. In this study, we examine how the dynamics of herbaceous and shrub vegetation abundance, diversity, and composition are affected by substrate, tree planting, and time since restoration. A total of 94 stands of 6 substrate materials (overburden, lean overburden, secondary overburden, clay overburden, and tailings), planted with conifer, mixed-wood, and broadleaf over-story ranging from 5 to 30 years old were studied. Substrate was a significant driver in vegetation cover, with overburden having the lowest average cover of 55.17 % (SE 6.83%) and clay overburden having the highest average of 78.85 % (SE4.41%). Over-story composition, however, was a more significant indicator of abundance within these anthropogenic ecosystems with broadleaf over-story dominated sites having a higher abundance. Total richness was primarily driven by substrate with secondary overburden, lean overburden, and clay overburden having the highest richness. Multivariate analysis indicated that plant communities were compositionally distinct across substrates, age, and over-story. Compositionally, herbaceous species were significantly affected by all independent variables with the exception of the three way interaction, while shrubs were significantly affected by substrate and age, as well as their interaction and age‟s interaction with over-story.

When examining the multivariate links between diversity and productivity in the reclaimed oil sand ecosystems, we used 70 reclaimed plots of varying stand ages, conifer cover, diversity, and substrate conditions (i.e., clay content and nitrogen content) through structural equation models. We show that over-story and total biomass was strongly positively influenced by stand age and Shannon‟s index. Conifer cover and total cover had large negative effects on understory aboveground biomass.

Our results demonstrate that plant communities‟ substrate has the strongest influence on abundance, richness, and composition within the oil sand restoration. Our results suggest that substrate is the most dominant factor in the ongoing restoration of the oil sands, particularly within the clay overburden and secondary overburden substrates. lastly, our results have shown understory biomass is limited by over-story composition. Overall, total biomass was shown to increase through time and tree diversity.

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ACKNOWLEDGEMENTS

I wish to give my sincere appreciation to my supervisor Dr. Han Chen for his assistance, support, and guidance throughout the development of my thesis. I would also like to thank my committee members Dr. Jian Wang and Dr. Brian Brassard, as well as my external reviewer Dr. Gordon Kayahara. I am grateful towards Eric Searle and Dr. Junlin Li for assisting me in the field and lab work. Without their efforts this study would not have been possible. I would also like to thank Suncor Energy Inc and Canadian Natural for their assistance in accommodating my research. Funding was provided by grants from the Natural Sciences and Engineering Research Council, and was greatly appreciated.

Finally, I would like to thank my parents Richard and Gail Sobey, as well as Thomas Mahoney for their support and encouragement throughout this work. Without their help I would not have accomplished as much as I have.

NOTE TO THE READER

While considerable effort has been made to integrate chapters 1 and 2, these chapters have been written and submitted for publication as distinct manuscripts, and as such, there is some overlap of term definitions and repetition of methods.

1) Chapter 1 – Plant abundance, diversity, and composition following reclamation in Alberta's oil sand.
2) Chapter 2 – Linking forest diversity and productivity in the oil sands of Fort McMurray, Canada.

GENERAL INTRODUCTION

Resource development and the subsequent degradation of forest ecosystems necessitate reclamation. Human disturbance through resource development varies in size and type, thus requiring site specific reclamation to ensure a sustainable future for degraded ecosystems (Aerts & Honnay 2011). This study defines reclamation as the goal to achieve equivalent land capacity. The goals of reclamation on degraded terrestrial sites include, but are not limited to, limiting soil erosion and remediating other soil structural issues, removing contaminants from the soil, and adjusting certain biological characteristics such as plant community structure, composition, and function (Ghose 2004; Ghose & Kundu 2004; Li 2004).

Reclamation of degraded ecosystems often requires active management to shift ecosystem structure towards a more desired trajectory (Choi 2004). One of the most successful management practices is tree planting (Chazdon 2008; Löf *et al.* 2014). Species, whether coniferous or broadleaf, could move a site towards a different reclaimed trajectory. Coniferous species are desired for their merchantability, but may limit the diversity and productivity of understory species on a site through limited light transmission, slow litter decomposition rates, and high pH (Hart & Chen 2008). Broadleaf species on the other hand have been shown to have the opposite effect: a high rate of nutrient release through more rapid forest litter decomposition and more light reaching the forest floor (Prescott *et al.* 2000). Thus, it is important to fully understand how different coniferous and broadleaf species perform within reclaimed ecosystems, and to examine if these species interacts with multiple substrates after reclamation takes place.

One of the most important interactions is between overstory composition and substrate. Substrate is responsible for many abiotic and biotic factors. One major abiotic factor which could limit the growth of vegetation is nutrient availability, particularly nitrogen (O'Brien *et al.* 2010). Nitrogen has been shown to promote the growth of vegetation, and is the limiting nutrient within the boreal forest; however, Alberta oil sands may not be as limited due to the deposition of NO_x compounds (Maynard *et al.* 2014). Another abiotic factor affecting the growth of vegetation is the percentage of clay within the soil particulates. Higher fractions of clay may allow nutrients to stick to the high surface area created by larger soil particles, allowing the vegetation to eventually obtain these nutrients more easily compared to a substrate with a higher sand content, which would have a higher drainage and potential loss of nutrients (Six *et al.* 2002).

The major biotic factor within the substrate is the propagules (Brekke Skrindo & Anker Pedersen 2004; Mackenzie & Naeth 2010; Rivera *et al.* 2012). The propagules within the top layer of the substrate are important for determining the presence of vegetation within an ecosystem. The likelihood of propagule germination into a plant can be attributed to many factors including species specific viability rates, nutrient and moisture availability, and competition from other vegetation (Rivera *et al.* 2012). While this study does not measure propagule success within the substrate, it should be noted as an important contributor which could explain the diversity and biomass patterns seen within reclaimed ecosystems.

Changes in ecosystem structure and function cannot solely be attributed to just anthropogenic inputs. Other factors such as age have an effect on ecosystems at the stand and even the individual level (Ryan *et al.* 1997). Changes of species through succession through facilitation and competition allow overstory and understory species to change through time as space and nutrient regimes shift (Turner *et al.* 1998; del Moral *et al.* 2007). Because age has shown to affect an ecosystem, it is important to demonstrate how age may also have an effect on novel ecosystems.

The current limited knowledge of how these factors separately and interactively drive the development of plant communities on oil sands mining sites following reclamation spawned the two objectives of this study. First, how substrate characteristics, i.e., the soil materials used to build the landforms, overstory composition, and time since reclamation affect plant abundance, richness, diversity, and composition. Secondly, examining the multiple relationships between aboveground biomass, species diversity, overstory composition, age, and substrate. Overall, the purpose of this study is how these relationships and metrics different between similar systems. Such an analysis is necessary for really establishing reclamation success and towards the merit of this study. This work will improve understanding of how reclaimed ecosystems after oil sands mining change through time, and will aid in establishing benchmarks for reclamation success in the Alberta oil sands.

CHAPTER ONE PLANT ABUNDANCE, DIVERSITY, AND COMPOSITION FOLLOWING RECLAMATION IN ALBERTA'S OIL SANDS.

INTRODUCTION

Increasing demand for resources has resulted in dramatic changes to many ecosystems. Resource exploitation has rendered many hitherto productive lands unproductive and uninhabitable. The development of oil sands reserves in Alberta, Canada for example, has resulted in the degradation of natural boreal ecosystems through the removal of vegetation and soils, i.e., overburden, in order to access the oil sands below. Following resource extraction, soils are placed to build desired landforms and sites are revegetated. Revegetating degraded land is a key mandate of oil sand reclamation on appropriate landforms. Despite its clear mandate, little is known about how alternative reclamation strategies affect vegetation recovery after oil sands mining. In this study, we examine how the dynamics of non-woody species (herbs, grasses, sedges, mosses, and lichens) and shrub vegetation abundance, diversity, and composition are affected by substrate, tree planting, and time since restoration.

Substrate characteristics, i.e., the soil materials used for landform construction, have been shown to affect vegetation recovery on reclaimed sites following oil sands mining. Substrate types with different structure and nutrients have been shown to have an important effect on plant growth and community development (Zhang & Dong 2010; Alday *et al.* 2011). In fact, soil moisture, organic matter, and nutrients play an important role in the vegetation recovery process (Kardol & Wardle 2010; O'Brien *et al.* 2010). These different soil conditions can also be induced by the vegetation and can also produce alternative states, due to positive feedbacks caused by dominant species (del Moral *et al.* 2007).

The success of certain species on particular substrates can be enhanced by manipulating soil fertility. On reclaimed sites, nutrients including nitrogen, potassium, and phosphorous are commonly added to promote the growth of high productivity species (Gaujour *et al.* 2012). Nitrogen and phosphorus are limited nutrients within an ecosystem, while additional nitrogen can be added to a system to assist this (Maynard *et al.* 2014). The addition of phosphorus may increase productivity and decrease species richness (amount of different species within a site) through competitive exclusion, while nitrogen favours the growth of grasses (Maynard *et al.* 2014), which may all assist the growth of vegetation within the oil sands vegetation species.

Not only does substrate provide a seed bank for potential re-growth, it also has imposes abiotic limitations such as moisture, nutrient lock up, and amount of organic matter that can affect plant growth and community diversity (Kardol & Wardle 2010; O'Brien *et al.* 2010). The soil seed bank comprises all viable seeds present in or on the soil, including both those that germinate within a year of initial dispersal and those that remain in the soil for longer periods (Gaujour *et al.* 2012). The potential of the seed bank to be a source of colonization depends on seed persistence in the soil, seed age, and soil conditions (mainly moisture content), on the depth of burial, and on seed abundance modulated by seed predation (Gaujour *et al.* 2012). Overall, richness may be most affected by storage of the original propagules within the ecosystem or through dispersal pathways from adjacent or nearby forests (Bremer & Farley 2010).

Substrate particulates can be one of the major indicators to distinguish substrates in order to understand how they affect the reclamation process. These particulates are composed of sand, silt, and clay fractions, each having a profound effect on the reclamation process. The size, quality and stability of these fractions reflect on aggregate forming factors such as organic matter, soil microorganisms, and soil fauna such as earthworms (Barrios 2007). As stated earlier, nutrients within an ecosystem is an important factor in the future diversity within a site, the aggregates within the soil further assist the growth of vegetation. Silt and clay have been shown to influence the stabilization of organic carbon and nitrogen within an ecosystem through small particles and high surface area, which would be beneficial for plant growth (Six *et al.* 2002). The increase in clay content in the surface sand layer also improves the soil water holding capacity and increases effective water available for shallower rooted herbaceous plants (Li 2005). Sand on the other hand is usually excessively drained, unstable, and subject to wind and water erosion (Mendez & Maier 2008). Therefore we hypothesize that clay and silt substrates should sustain the highest amount of plant diversity through their increased nutrient and water retention.

Changes in plant diversity and richness within noval ecosystems can be attributed to a number of factors including site preparation, exclusion of shade intolerant native species by plantation canopy cover, allelopathy, and physical barriers such as conifer litter (Bremer & Farley 2010). The structural complexity of the over-story has the potential to affect growth of understory, such as affecting the abundance of species within an ecosystem (Hart & Chen 2008). Gaps within the canopy as well as nutrient addition through leaf litter can assist in increasing the abundance of species; however, it does not necessarily affect species‟ richness (Bremer & Farley 2010; Harris *et al.* 2012). In addition, the over-story competes with the understory for initial nutrients, with these initial nutrients being fertilized treatments of nitrogen, phosphorous, and potassium as mandated through oil sand protocols. This competition may cause a slower growth of the over-story, while the younger highly competitive herbaceous understory dominates.

Similar to natural systems, anthropogenic ecosystems can contain a variety of coniferous and broadleaf tree species. Broad leaf dominated forests have been shown to have a higher amount of understory biodiversity than coniferous forests, as their leaves provide high nutrient inputs coupled with high light transmission (Barbier *et al.* 2008). Conifer forests, however, provide little light transmission and growing space due to their low canopy and dense needles (Messier *et al.* 1998). Not only does this stop light from reaching the soil surface, but the needles produced by conifer species typically have a lower decomposition rate than leaves produced by broad leaved species, leading to lower amount of available nutrients through mineralization of nutrients (Prescott *et al.* 2000). Richness appears to be higher in younger stands with high broadleaf cover suggesting that boreal understory communities are influenced more by plant tolerances for low resources than by competition (Hart & Chen 2008).

Age has a profound effect on the biodiversity of a reclaimed ecosystem, similar to natural ecosystems, as compositional diversity changes through time. A decrease in species evenness (how close in numbers each species in an environment are) through time is due to an increase in the relative dominance of certain species. (Zhang & Dong 2010). Species diversity is clearly related to species richness and evenness (Peet 1975). Species richness and evenness can therefore be used as indicators of the extent of reclamation success (Zhang & Dong 2010). Differences in community structure have also been shown to be effected by age, with older stands being more similar to naturally regenerating forests and younger stands having higher proportions of weedy species (Bremer & Farley 2010). However, confounding factors such as the functional characteristics of native understory species, and other environmental and site conditions including adequate seed sources and climate conditions, can further alter the diversity through time (Bremer & Farley 2010). Overall, age effects on species diversity is greatly varied in the restoration process, which means it could have a covariate effect in combination with other ecosystem factors such as substrate and over-story.

Little is known about the newly restored ecosystems of the Alberta oil sands, or the impact of the industry‟s restoration practises on species abundance, diversity, and composition. Also, little is known about the effects of multiple substrates using similar over-story compositions on diversity over time on novel ecosystems. Our primary objective is to examine the effects of these practises, namely the impact of substrate, tree species planted, and time since reclamation on understory plant species abundance, diversity, and composition. As ecosystem restoration cannot only be shown through diversity of a single group e.g. shrub species, as each functional group may be effected by an ecosystem trait in a different manor and in turn also effect the system, this paper acknowledges two distinct groups: woody (shrubs), and non-woody species (herbs, mosses, lichen, grasses, and sedges) (Aerts & Honnay 2011). This will allow us to properly investigate the driving factor of biodiversity in these novel anthropogenic ecosystems.

METHODS

Study area

This study was conducted in the Regional Municipality of Wood Buffalo at Suncor Energy Inc.‟s Oil Sands (hereafter referred to as „Suncor‟), located approximately 30 km north of Fort McMurray, Alberta (59°39‟N, 111°13‟W). The climate of the study area is sub-humid with a mean annual precipitation of 418.6 mm and a mean daily average temperature of 1°C (Environment Canada 2010). The area is located in the boreal shield of western Canada. Wildfire is the dominant natural disturbance of the area, while oil sands development, in particular from surface mining and in-situ extraction, is the major anthropogenic disturbance. Mineral soils of the study area fall within the upland surface soil, with the exception of tailings (Alberta Environment and Water 2012). All sites were fertilized with Nitrogen, Phosphorous, and

Potassium to assist in concentrations of nutrients needed to establish desired plant community types (Alberta Environment and Water 2012).

Sampling design

In order to study the effects of substrate (i.e., the combination of soil materials used for landform construction), stand composition, and stand aging on forest diversity and productivity on reclaimed sites following oil sands mining, we select for study on Suncor"s lease from the Cumulative Environmental Management Association (CEMA) Long-Term Plot Network (Table 1.1), sites that varied in age from 5 to 30 years after reclamation (i.e., the point when tree planting occurs), with overstories ranging from mostly broadleaf composition to mostly coniferous composition. In addition, because reclamation practices have changed over the years, and are dependent on the availability of local soil materials, sites varied in substrate characteristics. A total of 94 stands of coniferous, mixedwood, and broadleaf overstory types, ranging in age from 5 to 30 years after reclamation (i.e., stand age), on six different substrate types were ultimately selected for study. The study substrates were: overburden, lean overburden, secondary overburden, clay overburden, and tailings.

Broadleaf and coniferous stands were classified as having an overstory by stem density of ≥ 70% broadleaf or coniferous tree species, respectively (Hart & Chen 2008). Mixedwood stands were defined as having mixtures of coniferous and broadleaf tree species in relatively equal proportions. Coniferous tree species found at the sites were white spruce (*Picea glauca* (Moench) Voss), jack pine (*Pinus banksiana* Lamb.), and lodgepole pine (*Pinus contorta* Douglas). Broadleaf tree species found were trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), and white birch (*Betula papyrifera* Marshall) (Table 1.1).

Overburden is the material (fine or coarse textured) that is removed after vegetation stripping, which exposes the oil sands below. Tailing are a mixture of sand, silt, clay, water, and residual hydrocarbons and metals, and are the material that remain following the separation of bitumen from oil sands. Tailings are left after the striping mining and extraction of bitumen from the oil sand deposits, which due to the salt associated with the ore itself may have increased concentrations of toxicity (Purdy *et al.* 2005). Due to the uneven nature of the caprock, the scrapers are unable to remove all of the overburden layer. Scrapers leave behind the overburden material in the concave pockets of the caprock, this is called secondary overburden. Lean overburden is oil sands that contain less than 6% bitumen by weight, and are therefore not commercially viable (Alberta Environment and Water 2012). Overburden, lean overburden, secondary overburden, clay overburden and tailings substrates all contained a cap of peat-mineral-mix (Table 1.1).

Every effort was made to produce three replicates for each stand age class-overstory type-substrate type combination. However, not every overstory type-substrate type combination could be found for every stand age class. As a result, stand age class was treated as a covariant in the analysis. In addition every effort was also made to avoid sampling stands of the same age class, overstory type, and substrate type in close proximity to one another, in order to avoid neighbourhood influences and unknown environmental influences that may be spatially correlated among sample stands. As a result, replicates were spaced at least 75 meters apart.

Reclaimed areas were scattered throughout Suncor‟s lease and varied greatly in size. Older reclaimed areas were mainly in the form of thin strips of land, while younger reclaimed areas covered larger, more uniform portions of land base.

Table 1.1 Characteristics (mean and 1 standard error of the mean in parenthesis) of the 94 study stands at Suncor Energy Inc.‟s Oil Sands, Alberta, Canada.

				Overstory composition (%)						
Substrate	Over story	N	Stand density (stems/ha)	Trembling aspen	White birch	White spruce	Jack pine	Lodgepole pine	Mountain maple	Balsam poplar
COO	CON	3	1920 (569)	8(4)		80(1)				12(3)
COO	MIX	4	3608 (904)	14 (8)	3 (2)	51 (7)				32 (12)
COO	BRO	2	13797 (1962)	30 (13)	5 (5)	9 (1)				56 (17)
PMMLO	CON	16	2261 (144)	8 (2)	1(1)	89 (3)				2 (1)
PMMLO	MIX	4	2776 (1035)	22 (7)	2 (2)	60 (6)				16 (14)
PMMLO	BRO	2	6753 (130)	8 (1)		25 (4)				67 (3)
PMMO	CON	13	2278 (244)	5 (2)	1 (1)	83 (8)	9 (7)	2 (2)		
PMMO	MIX	3	1970 (144)	38 (7)		51 (10)	2(2)			8(2)
PMMO	BRO	5	16247 (6035)	43 (16)	1(1)	8 (4)				48 (16)
PMMSO	CON	13	2527 (244)	8 (2)		87 (3)				5 (2)
PMMSO	MIX	6	2987 (645)	26 (7)	2 (1)	55 (4)				18 (5)
PMMSO	BRO	2	9805 (325)	21 (13)		23 (2)				56 (15)
PMMT	CON	15	1823 (134)	2 (1)		14 (5)	3 (3)	78 (7)	2 (2)	1 (1)
PMMT	MIX	5	3338 (683)	25 (11)	7 (4)	5 (5)	34 (11)	9 (8)	3 (3)	18 (10)
PMMT	BRO	1	5779 (0)	31 (0)		1 (0)		26 (0)		42 (0)

Notes: Substrate types are: COO- clay overburden, PMMLO- lean overburden, PMMO- overburden, PMMSO- secondary overburden, and PMMT- tailings. Overstory types are: CON- coniferous, BRO- broadleaf, and MIX- mixedwood.

Field measurements

Vegetation surveys occurred during July and August 2013, which is regarded as the annual timing of maximum vegetation cover for these ecosystems (Hart & Chen 2008). At each study site, a circular 154 m^2 plot was established to represent the stand. Within each plot, the diameter at breast height (DBH), taken 1.3 m above the root collar, of all trees ≥ 1.3 m in height were measured and recorded. Trees smaller than 1.3 m were measured for height only. Crown cover at each site was calculated by measuring the radius squared and multiplied by pi.

Shrub and herbaceous species sampling followed Canada‟s National Forest Inventory Ground Sampling Guidelines (Canadian Council of Forest Ministers 2008). The shrub layer was sampled within three 25 m^2 circular subplots. Each subplot was given a random distance from the plot centre and a random azimuth direction; however plots were not allowed to overlap with one another to avoid bias. Each species of shrub within a subplot was measured for percent cover using visual estimations (Dombois & Ellenberg 1974). Sampling of the herbaceous layer followed the same method as the shrub layer, with the exception that ten circular subplots of 1 m^2 were used instead. Since total percent cover for a plot is the summation of individual species percent covers, calculated percentages may be above 100, since plants often overlapped vertically.

Data analysis

Understory abundance is the sum of all species‟ percent cover in each sample plot. Understory species richness is the total number of species in each sample plot. Understory species evenness expresses how evenly the individuals in the community are distributed. Understory Shannon‟s index incorporates both richness and evenness to estimate diversity. Both

Shannon"s index and evenness formulas follow the equations within Peet (1975), and calculated using the "vegan" package in R3.0.2.

The effects of substrate type, overstory type, and stand age class on the dependant variables mentioned above were examined using a generalized linear model. Species richness was calculated using a generalized linear model with a Poisson distribution, while abundance and evenness used a Gaussian distribution with the link function of identity. The following generalized linear model equation was used in all instances:

$$Y_{ijkl} = \mu + A_i + S_j + T_k + S \times T_{jk} + \varepsilon_{(l)ijk} \qquad (1)$$

where $Y_{(ijkl)}$ is abundance, richness, Shannon"s index, evenness, or species composition separately analyzed by total, shrub and non-woody groups, μ is the overall mean, A is stand age as a continuous covariate, S is substrate (j= 1,2,...5), T is overstory (k= 1,2, 3), l is the sample size within each combination of stand age class, overstory type, and substrate type, and Ɛ is the error.

It should be noted that there is not an even number of plots among the treatment combinations of stand age, substrate, and overstory. For each generalized linear model, linearity and homogeneity assumptions were tested and met by using a standardized residuals plot and Bartlett"s test. The generalized linear model was conducted using R3.0.2. Significant results were compared using a Tukey"s post-hoc test using the *glht* function in the "multcomp" package in R3.0.2. Statistical significance was set at $\alpha = 0.05$.

We used permutational multivariate analysis of variance (PerMANOVA) to test the effects of substrate, overstory, and stand age on total, shrub, and non-woody species composition. PerMANOVA is a nonparametric, multivariate analysis that uses permutation techniques to test for compositional differences between more than one factor (Anderson 2001). It was run using the Bray-Curtis dissimilarity and 999 permutations of the compositional data. We then examined the trends in the compositional data using nonmetric multidimensional scaling (Kruskal 1964), which is an ordination method suitable for data that are non-normal or on discontinuous scales (McCune & Grace 2002) by specifying the Bray-Curtis distance measure.

Finally, indicator species analysis was performed using the “multipatt” function in R package “indicspecies”, using IndVal.g as the statistical value to identify species affinity for a particular substrate using species abundance. The P-value generated represents the probability that the calculated indicator value is greater than that found by chance. Only species of P-value less than 0.1 were considered an indicator species for a particular substrate in order to judge ecological significance (Hough *et al.* 2008).

RESULTS

General

We recorded a total of 89 understory plant species and 7 tree species among our sample plots. A total of 27 species were classified as shrubs, while 62 were classified as non-woody. The majority of plots contained shrubs, with the most commonly found species being beaked willow (*Salix bebbiana*), prickly wild rose (*Rosa acicularis*), and wild raspberry (*Rubus strigosus*). As for non-woody species, fireweed (*Chamerion angustifolium*), hawkweed (*Hieracium*), and strawberry (*Fragaria vesca*) were frequently found. It should be noted that there were no shrubs found within plots on the tailings substrate-broadleaf over-story combination.

Abundance

Total abundance was influenced by substrate (Pr(>Chisq)=0.005) and its interaction with overstory (Pr(>Chisq)=0.0001) (Table 1.2A, Fig. 1.1A). Clay overburden and secondary overburden had a greater abundance than tailings and overburden, while overburden was significantly less in abundance compared to clay overburden, lean overburden, and secondary overburden. Tailings and overburden had similar results and not significantly different from one another (Figure 1.1A). Broadleaf and mixed-wood stands on overburden along with broadleaf stands on tailings were shown to have to have the significantly least abundance compared to the rest of the sites, while the rest of the sites showed no difference in the effect of different overstory planted in particular substrates on abundance.

Shrub abundance was significantly influenced by overstory (Pr(>Chisq)=<0.001) and its interactions with substrate (Pr(>Chisq)=0.04) (Table 1.2A, Figure 1.1A). Shrub abundance was significantly distinguishable with coniferous stands having the lowest shrub abundance and broadleaf stands having the greatest, while mixed stands were not significantly different from either (Figure 1.1A). Conifer stands planted in both overburden and tailings and broadleaf stands planted in tailings were shown to have significantly less shrub abundance than broadleaf stands planted in overburden. Broadleaf stands within tailings were shown to have no shrubs located within them. The rest of the sites were not shown to have similar results.

Non-woody abundance was significantly influenced by substrate (Pr(>Chisq)=0.020), over-story (Pr(>Chisq)=0.008), and their interaction (Pr(>Chisq)=0.023) (Table 1.2A, Figure 1.1A). Overburden was shown to have significantly less abundance compared to the other substrates with the exception of tailings, while the other substrates were not significantly distinguishable from one another. Broadleaf stands were also shown to be significantly higher non-woody abundance than the other two substrates. The interaction effect between substrate and over-story showed broadleaf stands planted in overburden to be significantly less non-woody abundance compared to the majority of interactions with exception of broadleaf stands on tailings and mixed-wood on overburden (Figure 1.1A).

Richness

Unlike total abundance, total richness was strongly influenced by substrate only (Pr(>chisq) = <0.0001), which accounted for over 80% of total deviance (Table 1.2B), while the rest of the independent variables (overstory, age, and their interactions) had almost no effect on total richness. Clay overburden and secondary overburden had the highest total richness, overburden and lean overburden had the second highest, and tailings had the lowest total richness (Figure 1.1B).

Shrub richness was significantly influenced by only substrate (Pr(>chisq) = <0.0001), which accounted for over 60% of total deviance (Table 1.2B). Shrub richness on tailings was significantly lower than all other substrates, which were themselves indistinguishable from one another (Figure 1.1B).

Non-woody richness was significantly affected by only substrate (Pr(>chisq) = <0.002), which accounted for 68% of total deviance (Table 1.2B). Tailings and overburden had significantly lower non-woody richness compared to clay overburden and secondary overburden, while lean overburden was not significantly different from the other substrates (Figure 1.1B).

Shannon's index

Total Shannon"s index was shown to be significantly affected by substrate (Pr(>Chisq)= 0.0004), and its interaction with over-story (Pr(>Chisq)= 0.05) (Table 1.2C). Tailings was shown to be significantly lower Shannon's index than clay overburden, lean overburden, and secondary overburden, but not significantly differentiated from overburden. Overburden however, was significantly lower in Shannon's index than secondary overburden and clay overburden (Figure 1.1C). Conifer stands planted in tailings was shown to be significantly lower than the majority of combinations, with the exception of conifer stands in lean overburden and overburden, broadleaf stands planted in clay overburden, lean overburden, and tailings, and mixed-wood stands planted in lean overburden, overburden, and tailings. Mixed-wood stands in Clay overburden had the highest significant Shannon index.

Shrub Shannon's index was shown to be significantly affected by substrate (Pr(>Chisq)= >0.001), and over-story (Pr(>Chisq)= 0.01) (Table 1.2C). Tailings was shown to have the significantly least shrub Shannon's index compared to the other substrates, while the rest did not show a significant difference (Figure 1.1C). Coniferous over-story was shown to have the lowest significantly different Shannon's index, while broadleaf and mixed-wood stands showed no significant difference from one another.

Non-woody Shannon's index was shown to be significantly affected by substrate (Pr(>Chisq)= 0.001), and its interaction with over-story (Pr(>Chisq)= 0.05) (Table 1.2C). Tailings was shown to be significantly different producing less non- woody Shannon's index compared to clay overburden, lean overburden, and secondary overburden, while clay overburden and secondary overburden had the significantly highest Shannon's index compared to overburden and tailings. Mixed-wood stands planted in both clay overburden and secondary overburden were shown to have the highest significant Shannon's index, mixed-wood stands in overburden was shown to have the least (Figure 1.1C).

Evenness

Total species evenness was shown to be significantly affected by substrate (Pr(>Chisq)= 0.0005) and its interaction with over-story (Pr(>Chisq)= 0.044) (Table 1.2D). Clay overburden and secondary overburden were shown to be significantly higher in evenness than overburden and tailings, while lean overburden was just significantly higher evenness than tailings. Mixed-wood stands in clay overburden was shown to have the highest significantly different evenness, while conifer stands in tailings was shown to have the lowest (Figure 1.1D).

Shrub species evenness was shown to be significantly affected by substrate (Pr(>Chisq)= 0.019) (Table 1.2D). Tailings were shown to have the least amount of evenness compared to the other substrates. All other substrates were not significantly different from one another.

Non-woody species evenness was shown to be significantly affected by substrates interaction with over-story (Pr(>Chisq)= 0.004) (Table 1.2D). Mixed-wood stands in overburden were shown to have the lowest evenness, while broadleaf stands in overburden were shown to have the highest (Figure 1.1D).

Species composition

Stands of different substrate (r^2= 0.278), over-story composition (r^2=0.030), their interaction (r2= 0.029), and age (r^2=0.026) differed significantly with a total of 52% variation explained (Table 1.3). Within these explained variables 53% of the variation can be attributed to substrate. When the trend in total vegetation species composition was visualized using nonmetric multidimensional scaling ordination, two particular trends occurred. First of all, there are two distinct groupings of substrates: Overburden and tailings, and lean overburden, secondary overburden, and clay overburden. Secondly, there is a large distinction in species composition according to age: younger stands are grouped apart from older stands (Figure 1.2).

Similar results were found within the woody species composition with the exception of the over-story variable and its interaction with substrate (Table 1.3). Substrate (r^2=0.250) was again the main contributing factor, explaining 53% of explained variation, while age was also a contributing significant factor ($r^2 = 0.028$). When visualized the substrate groups were in less prominent groups compared to total species composition (Figure 1.3). However, there is still a distinct pattern in separating tailings species composition compared to all other treatments.

Non-woody species composition was almost identical to total species composition in terms of significant variables, incorporating the majority of species found within plots (Table 1.3). Visual interpretation was similar in group distinctions of overburden and tailings, as well as lean overburden, secondary overburden, and clay overburden. Similarly, younger and older stands are grouped by age category (Figure 4).

Indicator species analysis revealed a number of plant species with common affinity for the substrates ($P<0.1$) (Table 1.4): clay overburden (30 species with 7 specific to the substrate), secondary overburden (25 species with 4 specific to the substrate), lean overburden (17 species with 3 specific to the substrate), overburden (17 species with 6 specific to the substrate), and tailings (10 species with 1 specific to the substrate).The number of indicator species for a given site gives an idea of the site‟s uniqueness. A high number of indicator species shared between sites may indicate that the species‟ shared functional traits are important as a descriptor of these sites, and also helps to distinguish these sites from others. For example, clay overburden and secondary overburden host a variety of functional groups (mosses/lichens, herbs, grasses/sedge, and shrubs), suggesting they are very diverse ecosystems. Lean overburden and overburden, while having a similar amount of species, had a limited number of grass/sedge indicator species. Tailings had the fewest indicator species, and lacked any shrub indicator species.

Table 1.2 Analysis of deviance of the effects of stand age (Ai, continuous), substrate type (Sj, j = 1, 2…5), and overstory type (Tk, k = 1, 2, 3) on abundance of vegetation.

A		Total cover		Woody cover		Non-Woody cover	
Source	Df	LR Chisq	Pr(>Chisq)	LR Chisq	Pr(>Chisq)	LR Chisq	Pr(>Chisq)
S_j	4	14.9	0.005	4.3	0.366	11.4	0.023
T_k	2	4.0	0.134	16.6	<0.001	9.6	0.008
A_i	1	0.1	0.678	0.9	0.344	0.005	0.941
$S_j \times T_k$	8	31.5	<0.001	16.5	0.036	41.1	<0.001
B		Total Richness		Shrub Richness		Non-Woody richness	
S_j	4	31.5	<0.001	26.6	<0.001	17.0	0.002
T_k	2	0.7	0.688	6.3	0.419	2.3	0.314
A_i	1	1.2	0.266	3.0	0.083	0.1	0.800
$S_j \times T_k$	8	4.5	0.805	6.7	0.566	5.7	0.678
C		Total α-diversity		Shrub α-diversity		Non-Woody α-diversity	
S_j	4	20.6	<0.001	25.0	<0.001	18.1	0.001
T_k	2	4.3	0.118	9.1	0.011	1.1	0.562
A_i	1	0.3	0.557	3.6	0.057	1.0	0.307
$S_j \times T_k$	8	15.5	0.049	5.4	0.709	15.0	0.058
D		Total evenness		Shrub evenness		Non-Woody evenness	
S_j	4	19.8	<0.001	11.7	0.020	1.7	0.782
T_k	2	4.0	0.133	1.6	0.439	3.5	0.173
A_i	1	0.4	0.550	2.5	0.110	2.9	0.088
$S_j \times T_k$	8	15.9	0.044	4.6	0.796	22.4	0.004

Notes: The columns give the degrees of freedom, LR Chisquare, and PR(>Chisquare) which is used for significance.

Table 1.3. Results of permutation multivariate analysis of variance test (PERMANOVA) testing the effects of substrate type, stand age, overstory type, and interactions on (A) total species composition, (B) woody composition, and (C) non-woody composition.

	Source	Df	Sums of sqs	Mean sqs	F.Model	R^2	Pr(>F)
(A) Total	Substrate	4	8.98	2.24	9.51	0.28	0.001
	Over-story	2	0.96	0.48	2.02	0.03	0.006
	Age	1	0.85	0.85	3.61	0.03	0.001
	Substrate × Overstory	8	3.13	0.39	1.66	0.10	0.002
	Residuals	78	18.41	0.24	[redacted]	0.57	[redacted]
	Total	93	32.32	[redacted]	[redacted]	1	[redacted]
(B) Shrub	Substrate	4	6.86	1.72	7.63	0.25	0.001
	Overstory	1	0.54	0.27	1.21	0.02	0.254
	Age	2	0.51	0.51	2.25	0.02	0.028
	Substrate × Overstory	8	2.04	0.26	1.14	0.07	0.218
	Residuals	78	17.53	0.22	[redacted]	0.64	[redacted]
	Total	93	27.48	[redacted]	[redacted]	1.00	[redacted]
(C) Non-woody	Substrate	4	9.31	2.33	10.18	0.29	0.001
	Over-story	1	0.99	0.50	2.17	0.31	0.002
	Age	2	0.87	0.87	3.80	0.03	0.001
	Substrate × Overstory	8	3.19	0.40	1.74	0.10	0.001
	Residuals	78	17.84	0.23	[redacted]	0.55	[redacted]
	Total	93	32.21	[redacted]	[redacted]	1.00	[redacted]

Notes: the columns give the degrees of freedom, sum of squares, mean squares, f.model, r^2 value, and Pr(>F) which is used for significance.

Table 1.4. Indicator values and randomized indicator values for species that are indicators of substrate type. Only indicator species with P < 0.10 are reported.

Origin	Species	P-value	Index	Statistic	Functional group
COO	*Bromus tectorum*	0.005	8	0.606	G
	Carex prairea	0.005	1	0.604	G
	Agrophyron repens	0.01	6	0.475	G
	Carex argyrantha	0.01	9	0.483	G
	Carex bebbii	0.015	1	0.441	G
	Hordeum jubatum	0.015	8	0.575	G
	Poa palustris	0.015	28	0.641	G
	Chamerion angustifolium	0.005	17	0.935	H
	Crepis tectorum	0.005	17	0.758	H
	Equisetum arvense	0.005	17	0.947	H
	Fragaria ovalis	0.005	26	0.919	H
	Glycyrrhiza lepidota	0.005	1	0.577	H
	Hieracium canadense	0.005	17	0.902	H
	Potentilla norvegica	0.005	17	0.665	H
	Sonchus arvensis	0.005	8	0.633	H
	Taraxacum officinale	0.005	7	0.805	H
	Vicia americana	0.005	8	0.839	H
	Trifolium hybridum	0.02	1	0.446	H
	Trifolium repens	0.035	7	0.526	H
	Achillea millefolium	0.055	17	0.693	H
	Aralia nudicaulis	0.09	1	0.333	H
	Gentianella amarell	0.09	1	0.333	H
	Galium boreale	0.095	28	0.522	H
	Cladina mitis	0.02	20	0.485	M
	Cornus sericea	0.005	7	0.568	S
	Rubus strigosus	0.005	26	0.788	S
	Salix bebbiana	0.005	17	0.739	S
	Prunus virginiana	0.01	1	0.471	S
	Potentilla fruticosa	0.03	17	0.513	S
	Caragana arborescens	0.035	8	0.482	S
	Salix scouleriana	0.04	8	0.472	S
PMMLO	*Agrophyron repens*	0.01	6	0.475	G
	Poa palustris	0.015	28	0.641	G
	Chamerion angustifolium	0.005	17	0.935	H
	Crepis tectorum	0.005	17	0.758	H
	Equisetum arvense	0.005	17	0.947	H

	Fragaria ovalis	0.005	26	0.919	H
	Hieracium canadense	0.005	17	0.902	H
	Potentilla norvegica	0.005	17	0.665	H
	Erigeron philadelphicus	0.045	2	0.441	H
	Achillea millefolium	0.055	17	0.693	H
	Petasites frigidus	0.08	11	0.403	H
	Galium boreale	0.095	28	0.522	H
	Urtica dioica	0.095	2	0.424	H
	Rubus strigosus	0.005	26	0.788	S
	Salix bebbiana	0.005	17	0.739	S
	Salix drummondiana	0.005	2	0.598	S
	Potentilla fruticosa	0.03	17	0.513	S
PMMO	*Bromus inermis subsp. inermis*	0.005	14	0.816	G
	Fragaria ovalis	0.005	26	0.919	H
	Medicago sativa	0.005	14	0.724	H
	Pyrola asarifolia	0.005	3	0.488	H
	Taraxacum officinale	0.005	7	0.805	H
	Melilotus officinalis	0.025	14	0.463	H
	Trifolium repens	0.035	7	0.526	H
	Packera paupercula	0.04	3	0.436	H
	Astragalus cicer	0.075	3	0.356	H
	Pleurozium schreberi	0.005	3	0.755	M
	Polytrichum piliferum	0.01	25	0.638	M
	Cladina mitis	0.02	20	0.485	M
	Cladonia grascilis	0.065	3	0.356	M
	Cornus sericea	0.005	7	0.568	S
	Rubus strigosus	0.005	26	0.788	S
	Chamaedaphne calyculata	0.015	3	0.501	S
	Amelanchier alnifolia	0.04	13	0.517	S
PMMSO	*Bromus tectorum*	0.005	8	0.606	G
	Poa pratensis	0.01	4	0.576	G
	Hordeum jubatum	0.015	8	0.575	G
	Poa palustris	0.015	28	0.641	G
	Calamagrostis canadensis	0.05	4	0.422	G
	Carex brunnescens	0.055	4	0.449	G
	Chamerion angustifolium	0.005	17	0.935	H
	Crepis tectorum	0.005	17	0.758	H
	Equisetum arvense	0.005	17	0.947	H
	Fragaria ovalis	0.005	26	0.919	H
	Hieracium canadense	0.005	17	0.902	H
	Potentilla norvegica	0.005	17	0.665	H

	Sonchus arvensis	0.005	8	0.633	H
	Vicia americana	0.005	8	0.839	H
	Rhinanthus minor	0.035	4	0.378	H
	Achillea millefolium	0.055	17	0.693	H
	Petasites frigidus	0.08	11	0.403	H
	Galium boreale	0.095	28	0.522	H
	Polytrichum piliferum	0.01	25	0.638	M
	Rubus strigosus	0.005	26	0.788	S
	Salix bebbiana	0.005	17	0.739	S
	Potentilla fruticosa	0.03	17	0.513	S
	Caragana arborescens	0.035	8	0.482	S
	Amelanchier alnifolia	0.04	13	0.517	S
	Salix scouleriana	0.04	8	0.472	S
PMMT	*Bromus inermis subsp. inermis*	0.005	14	0.816	G
	Festuca rubra	0.005	5	0.535	G
	Carex argyrantha	0.01	9	0.483	G
	Festuca saximontana	0.015	5	0.436	G
	Poa palustris	0.015	28	0.641	G
	Medicago sativa	0.005	14	0.724	H
	Melilotus officinalis	0.025	14	0.463	H
	Galium boreale	0.095	28	0.522	H
	Polytrichum piliferum	0.01	25	0.638	M
	Cladina mitis	0.02	20	0.485	M

Notes: functional group categories are: g = grass/sedge species, m=moss/lichen species, h= herbaceous species, and s= shrub species. P-value is used for significance, index is the grouping factor (appendix I), and the statistic.

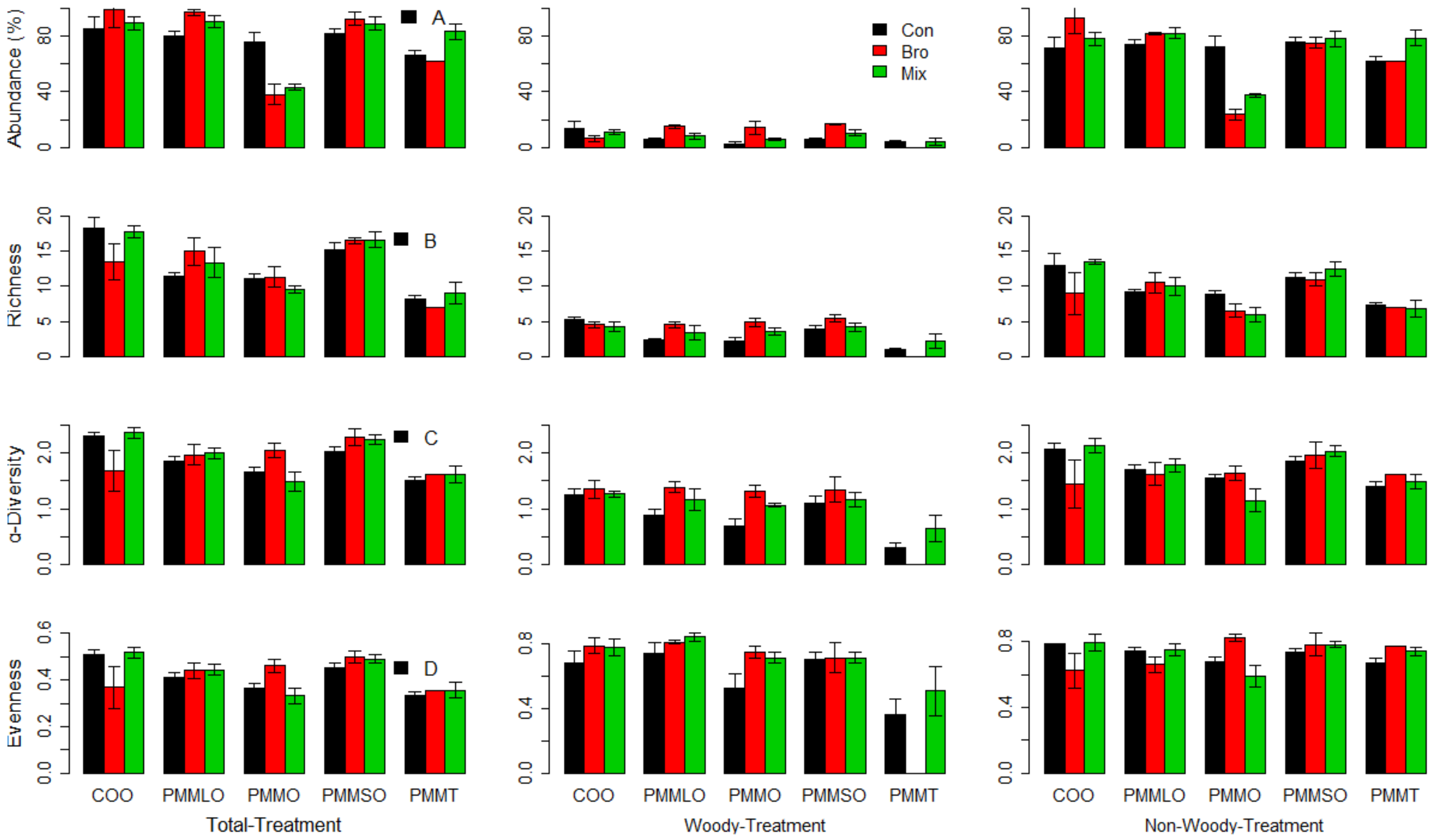

Figure 1.1 (A)Total abundance, woody abundance, and non-woody abundance (mean +SE) in relation to over-story and substrate with cover (%) as the y axis and substrate as the x axis. (B) Total richness, woody richness, and non-woody richness (mean +SE) in relation to over-story and substrate with cover (%) as the y axis and substrate as the x axis. (C) Total α-diversity, woody α-diversity, and non-woody α-diversity (mean +SE) in relation to over-story and substrate with cover (%) as the y axis and substrate as the x axis. (D) Total evenness, woody evenness, and non-woody evenness (mean +SE) in relation to over-story and substrate with cover (%) as the y axis and substrate as the x axis. With conifer over-story symbolized as black, broadleaf over-story symbolized as red, and mixed-woody over-story symbolized as green. COO- clay overburden, PMMLO - lean overburden, PMMO- overburden, PMMSO- secondary overburden, and PMMT- tailings.

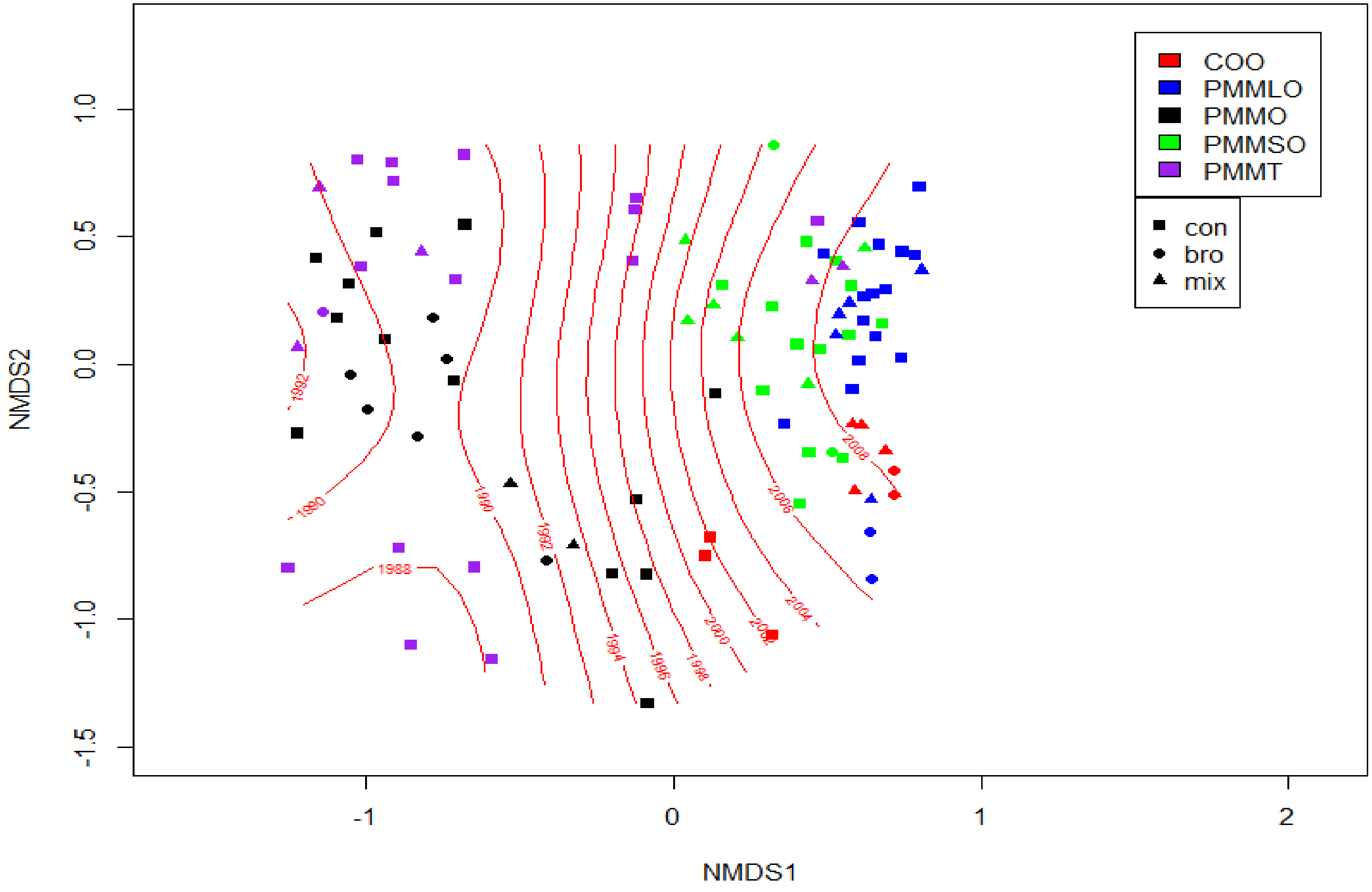

Figure 1.2. Nonmetric multidimensional scaling ordination of total species composition for broadleaf (triangle), conifer (square), and mixed-wood (circle) stands of substrate material PMMLO, PMMSO, PMMO, COO, and PMMT. Stands nearest each other in ordination space have similar floristic assemblages, whereas those located farther apart are less similar.

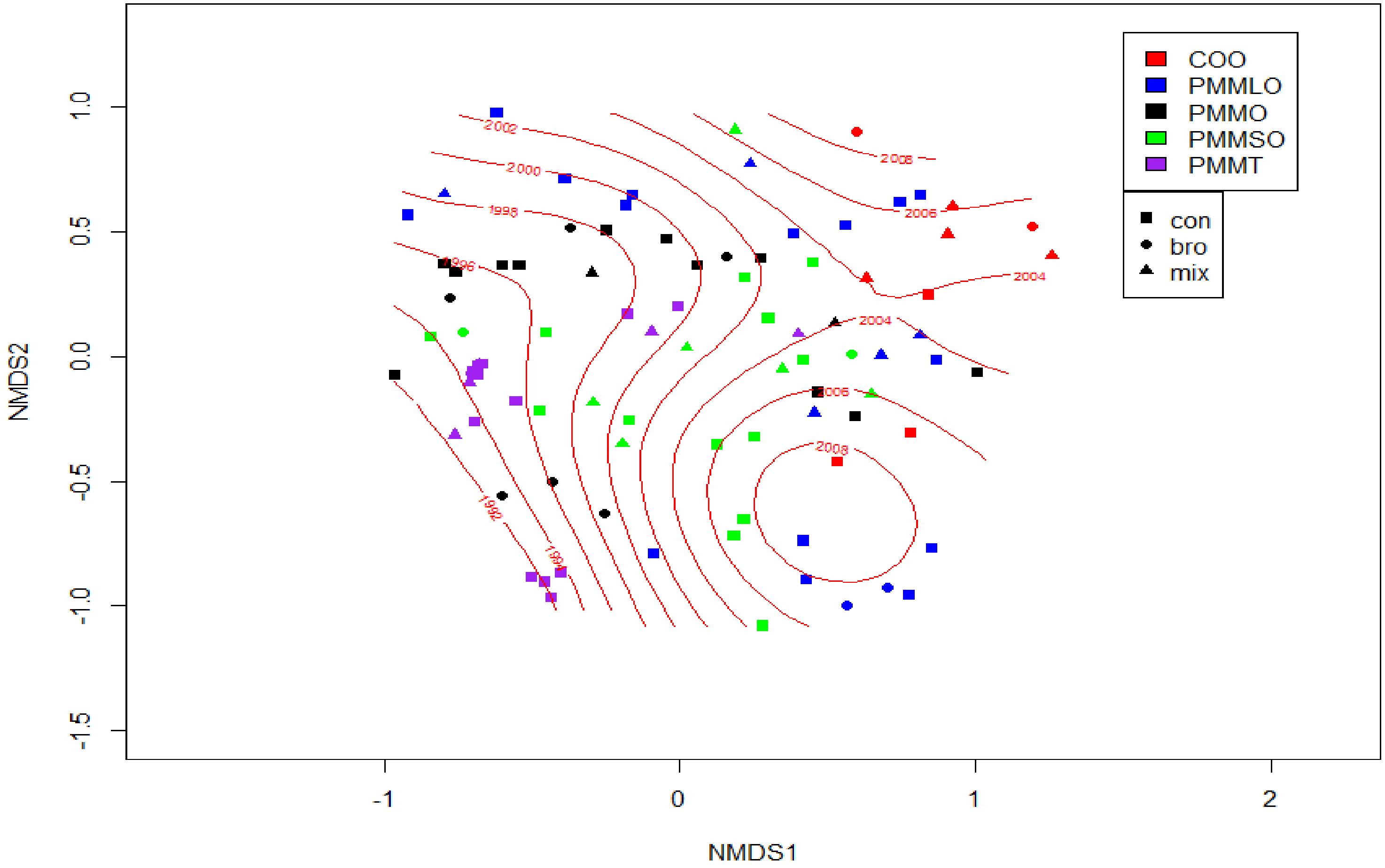

Figure 1.3. Nonmetric multidimensional scaling ordination of woody species composition for broadleaf (triangle), conifer (square), and mixed-wood (circle) stands of substrate material PMMLO, PMMSO, PMMO, COO, and PMMT. Stands nearest each other in ordination space have similar floristic assemblages, whereas those located farther apart are less similar.

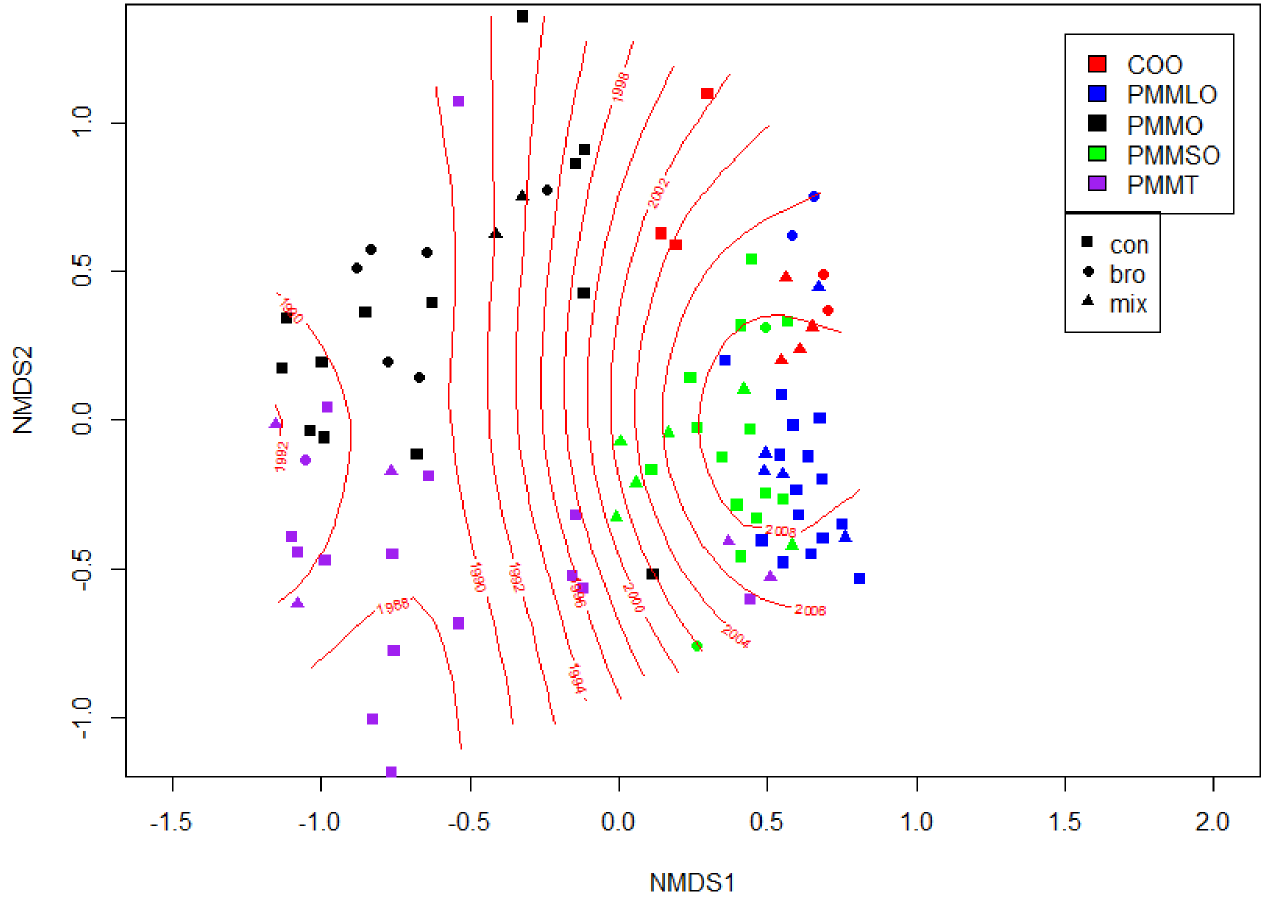

Figure 1.4. Nonmetric multidimensional scaling ordination of non-woody species composition for broadleaf (triangle), conifer (square), and mixed-wood (circle) stands of substrate material PMMLO, PMMSO, PMMO, COO, and PMMT. Stands nearest each other in ordination space have similar floristic assemblages, whereas those located farther apart are less similar.

DISCUSSION

Our study represents one of the first attempts to examine how oil sands reclamation practices affect the vegetation dynamics of reclaimed sites. Contrasting substrate, overstory, their interaction, and stand age effects on abundance, richness, evenness, Shannon"s index, and composition resulted in the following trends: (1) substrate pays a pivotal role in determining diversity, (2) overstory was only significant in determining abundance, (3) stand age is not a significant factor in differentiating between sites, (4) the interaction effect between substrate and overstory is significant, and (5) overburden and tailings substrates tend to have similar plant species, while secondary overburden, lean overburden, and clay overburden had similar plant.

Substrate, while a significant driver of abundance alone, did not affect abundance as greatly as the overstory-substrate interaction. Many studies from both natural and disturbed forests have shown that overstory characteristics are key drivers for patterns of plant abundance, as it may create micro-environments depending on the canopy composition (Hart & Chen 2008; Chávez & Macdonald 2012). Resource demanding, shade intolerant species may do best in mixed-stand or broadleaf stands due to increased canopy closer, while more shade tolerant species may thrive better within conifer stands (Chávez & Macdonald 2012) . In general, this study has shown that clay overburden as well as secondary overburden has the highest overall abundance for woody and non-woody species, while overburden has the lowest. Substrate interactions with overstory revealed that the highest abundances were combinations of these substrates with broadleaf stands, although broadleaf stands on overburden had the lowest abundance. This pattern does not follow the literature, as mixed-woods would normally produce higher understory abundance (Hart & Chen 2006). Broadleaf planted within overburden was shown to have the highest stem density (16247) with a high error (6035) because a few of the plots were shown to cover the entire plot through planted and reproductive vegetation. Because of this increase in overstory density understory species may have been limited to light resources to the point where only shade tolerant species may persist (Canham *et al.* 1994).

Woody abundance was shown to have the most variability; however it generally followed the pattern of broadleaf stands having the highest abundance of shrub species with the exception of its combination with tailings where shrubs were absent. This would suggest that shrubs can establish and grow the best in broadleaf stands on the overburden substrate types (overburden, secondary overburden, and lean overburden), while having lower abundances in clay overburden and tailings. It also suggests that shrubs may not be able to persist on sites with tailings sand substrates, regardless of overstory type.

Richness seems to be driven by substrate, which can be used as the best indicator of optimal substrate conditions for plant growth. Thus, understanding what makes these substrates unique is the key to understanding how some can obtain higher richness than others. Tailings for example was shown to have lower abundance, richness, Shannon"s index, and evenness compared to the other substrate types. As previously stated, tailings sand is fine-grained and drains rapidly, is unstable and subject to wind and water erosion, contains very few nutrients, and is high in salinity (Mendez & Maier 2008). Concentrations of certain ions, in particular sodium and sulphate, in the tailings sand may be high enough to influence plant establishment and performance, as only a few native species to the area would likely be able to tolerate the high salinity of tailings sand (Greenway & Munns 1980). Excessive salt in the soil can also adversely affect physiological activity and cause plant injury and reduced water availability (Renault *et al.* 1998), further restricting the types of plants that can establish and grow successfully on tailings sand in the Alberta oil sands.

Overburden and tailings substrates were shown to have lower richness in comparison to secondary overburden and lean overburden substrates. One possible explanation is that sites with lean overburden and secondary overburden substrates have similar compositions and a higher richness, as they are located in areas with no ecological barriers to plant dispersal (e.g. roads, excavation pits, tailings ponds, etc), while both tailings and overburden sites were fragmented and more isolated from the influences of outside sources (MacArthur 1967; Gaujour *et al.* 2012). Because I do not have any supporting data within this study, it is purely speculation and warrants further study.

Here, we show that clay overburden, secondary overburden, and lean overburden are the optimal substrates for achieving high diversity, at least early in stand development. Changing the size of reclamation areas may help solve problems of low initial propagule availability for some site types. Finally, it is clear tailings sand is a poor substrate that leads to low diversity and poor conditions for plant growth. These should be avoided if possible when building landforms assigned for productive forest.

CHAPTER 2 LINKING PLANT DIVERSITY AND PRODUCTIVITY IN THE OIL SANDS OF FORT MCMURAY, CANADA.

INTRODUCTION

The effect of human disturbance on the biodiversity and function of ecosystems has been emphasized in multiple studies throughout the past decade (Aerts & Honnay 2011; Tilman *et al.* 2012; Mendoza-Hernandez *et al.* 2013). With the oil sands being one of the largest disturbances to ecosystems (Mackenzie & Naeth 2010), it is important to understand how the biodiversity reclaimed within these ecosystems along a variety of experimental treatments affects the productivity within the anthropogenic reclaimed ecosystems. Anthropogenic reclaimed ecosystems lands have direct human inputs including, but not limited to, limiting erosion, adjusting for soil structure issues, contamination limitation, and adjusting for biological characteristics such as future structure, composition and function of these new ecosystems. The underlying effects of these disturbances on ecosystems are often poorly understood (Isbell *et al.* 2013). Furthermore, it should be noted that although there is already some knowledge on the effects of tree diversity on forest productivity, it is not known how understory shrub diversity, and even herbaceous species, affect forest productivity or other ecosystem functions (Aerts & Honnay 2011).

Productivity changes within an anthropogenic ecosystem can occur due to many parameters: particularly time since disturbance and substrate conditions (Chapín III *et al.* 1996; Isbell *et al.* 2013). These parameters affect reclamation of ecosystems in both direct and indirect manners. After ecosystem disturbance has occurred, primary succession occurs, involving an initial period of ecosystem development leading to a maximal biomass stage. The build-up phase has been studied and is characterized by broadly predictable changes in ecosystem productivity, biomass, and productivity (Walker & Del Moral 2003).

Over-story species has been shown to affect the future productivity of an ecosystem (Reich *et al.* 2001). Broadleaved forests have been shown to have a higher productivity compared to conifer forests (Gower *et al.* 2001). Broadleaf species allow for more canopy openings and increased light availability allowing for advanced regeneration (Barbier *et al.* 2008). Since species are planted within anthropogenic ecosystems, successional phases are initially based off of managerial decisions. These decisions are critical, as tree diversity has also been shown to effect the productivity of an ecosystem (Erskine *et al.* 2006), with higher diversity driving higher productivity.

A common problem on degraded ecosystems is lack of nutrients, particularly nitrogen (Bradshaw 1996). The deficiencies of these vital nutrients within degraded ecosystems is mainly due to weathered subsoil‟s or deeper unweathered overburdens (Bradshaw 1997). Natural nitrogen within an ecosystem may be impossible to obtain due to the nutrients being within minerals; therefore it may be necessary to add nutrients fertilizers. Within the oil sands, ecosystems are fertilized three times in order to replace missing or few nutrients; however, uptake and leeching of these nutrients within these ecosystems have not been fully explored (O'Brien *et al.* 2010). Nutrient availability is also related to the extent and intensity of the soil disturbed, as there is the potential for nitrogen leeching as disturbance increases (Maynard *et al.* 2014). Clay has been shown to influence the stabilization of organic carbon and nitrogen within an ecosystem through small particles and high surface area, which can be beneficial for plant growth (Six *et al.* 2002).

As little is known about the effects of multiple substrates using similar over-story compositions on productivity over time on novel ecosystems, we aim to examine the multiple relationships between above ground biomass, species diversity, over-story composition, age, and substrate in the anthropogenic ecosystems of the Alberta oil sands by using structural equation models (SEM). Specifically, we test the following paths: (1) Nitrogen, clay content, total cover (m^2), proportion conifer cover, Over-story Shannon‟s index and stand age influences total above ground biomass, over-story above ground biomass, and understory above ground biomass and (2) testing the effects of stand age, total cover (m^2) and proportion conifer cover on Shannon‟s index.

METHODS

Study area

This study was conducted in the Regional Municipality of Wood Buffalo at Suncor Energy Inc.‟s Oil Sands (hereafter referred to as „Suncor‟), located approximately 30 km north of Fort McMurray, Alberta (59°39‟N, 111°13‟W). The climate of the study area is sub-humid with a mean annual precipitation of 418.6 mm and a mean daily average temperature of 1°C (Environment Canada 2010). The area is located in the boreal shield of western Canada. Wildfire is the dominant natural disturbance of the area, while oil sands development, in particular from surface mining and in-situ extraction, is the major anthropogenic disturbance. Mineral soils of the study area fall within the upland surface soil, with the exception of tailings (Alberta Environment and Water 2012). All sites were fertilized with Nitrogen, Phosphorous, and Potassium to assist in concentrations of nutrients needed to establish desired plant community types (Alberta Environment and Water 2012).

Sampling design

Due to limitations in availability of randomly allocated spatially interspersed plots, sites were chosen from the CEMA plot network (Table 1). A total of 70 stands of conifer, mixed-wood, and broadleaf over-story types ranging from 5 to 30 years old were studied. An effort was also made to avoid sampling stands of the same age in close proximity to one another. As a result, replicates were spaced at least 75 meters apart. Substrates within the area included overburden, secondary overburden, lean overburden, and tailings all with a peat mineral mix cap, and clay over overburden. Overburden is the material (fine or coarse textured) that is removed after vegetation stripping, which exposes the oil sands below. Tailing are a mixture of sand, silt, clay, water, and residual hydrocarbons and metals, and are the material that remain following the separation of bitumen from oil sands. Tailings are left after the striping mining and extraction of bitumen from the oil sand deposits, which due to the salt associated with the ore itself may have increased concentrations of toxicity (Purdy *et al.* 2005). Secondary overburden are the layer below the original overburden, lean overburden are unprocessed raw-state oil sands with less than 6% oil by weight, usually rejected due to high clay content (Alberta Environment and Water 2012). Reclaimed areas were scattered throughout Suncor‟s lease and varied greatly in size. Older reclaimed areas were mainly in the form of thin strips of land, while younger reclaimed areas covered larger, more uniform portions of land base.

Field measurements

Vegetation surveys occurred during July and August 2013, which is regarded as the timing of maximum vegetation cover for these ecosystems (Hart & Chen 2008). At each site, a circular 154 m^2 plot was established to represent the stand. Within each plot, the diameter at breast height (DBH), taken 1.3 m above the root collar, of all trees ≥ 1.3 m in height were measured and recorded. Trees smaller than 1.3 m were measured for height only. Crown cover at each site was calculated by measuring the radius squared and multiplied by pi.

We measured total aboveground biomass (AGB, g.m^2) as a surrogate for aboveground stand productivity. Aboveground biomasses of individual live trees ≥ 1.3 m in height were determined using DBH and height measurements and species-specific allometric equations that were developed for Canadian boreal tree species (Miao & Li 2007). Trees smaller than 1.3 m in height were based off of local boreal forest allometric equations using height as the indicator of estimated biomass, within Thunder Bay, ON. Each species was cut at ground level categorized into 10 cm height groupings up to 1.3m, with at least 10 samples within each group to account for variation. Each sample was measured for height (cm) and oven dried for 48 hours at 75°C or until completely dry. Once dried the samples (dependant variable) were plotted against height (independent variable) using a scatter plot and a regression line. The height of trees smaller than 1.3m in height sampled within the research site was then placed within the regression equation to estimate its biomass.

Shrub and herbaceous species sampling followed Canada"s National Forest Inventory Ground Sampling Guidelines. The shrub layer was sampled within three 25 m^2 circular subplots. Each subplot was given a random distance from the plot centre and a random azimuth direction; however, plots were not allowed to overlap with one another to avoid bias. Each species of shrub within a subplot was identified and clipped at the soil surface. Herbaceous layer sampling followed the same method as the shrub layer, with the exception that five 0.5 m^2 subplots were used instead. Shrubs and non-woody vegetation that were removed from a site were dried at 75°C for 24 hours and weighed. Averages among the 3, 5, and whole plots, respectively, were taken at each site for the shrub, herbaceous, and tree layer characteristics. Then expressed all biomass estimates on a g/m2 basis by scaling appropriately.

We chose Shannon‟s index as a measure of tree diversity because it accounts for both species richness and evenness, two of the most important factors in productivity studies (Whittaker 2010; Zhang *et al.* 2012). While richness and evenness are both important indicators on their own, Shannon‟s index reaches a maximum when the tree ranges widely in diameter in this case and are evenly distributed (Brassard *et al.* 2008). Because these sites were species poor consisting of less than 5 species with different diameter classes and evenness, it is important to show how that effect can shift productivity. Shannon‟s index utilized the percent cover of tree species measured within the plot.

Stand age (years) for each plot was assumed to be the year that tree planting occured. Stand ages ranged from 4 to 30 years after reclamation. Substrate nitrogen was sampled as it is a important nutrient in the boreal forest (Magnani *et al.* 2007). Nutrient concentration (total nitrogen) at each site were determined by taking three randomly selected 10 cm deep soil samples using a soil corer. Soil samples were air dried and sent to the Forest Resources and Soils Testing Laboratory (FoReST) at Lakehead University in Thunder Bay, Ontario for analysis. Soil structure (particle-size analysis), was taken through similar sampling as nitrogen, with the exception of clay, silt, and sand percentage being analyzed using the particle-size analysis using the Bouyoucho hyrdrometer method outlined by Kalra and Maynard (1991).

The canopy cover (m^2) of each tree was found by multiplying a trees radius by pi. Individual tree canopy covers were then summed to give the total canopy cover of each plot. Total conifer cover was calculated by measuring canopy cover of coniferous species only within the plot. Conifer species found at our sites included: white spruce (*Picea glauca* (Moench) Voss), jack pine (*Pinus banksiana* Lamb.), and lodgepole pine (*Pinus contorta* Douglas).

Data analysis

Structural equation models were used to analyze the data, as it analyzes the connections between empirical data and theoretical ideas. In this case it uses exogenous (variables with no causal links (arrows) leading to them from other variables in the model, which are usually measured variables) to find the effect on endogenous (variables with causal links (arrows) leading to them from other variables in the model. In other words, endogenous variables have explicit causes within the model). To aid in the construction of structural equation models (SEMs) and interpretation of results, we first examined the relationships between each hypothesized casual paths. We visually inspect how the relationship between each relationship appears graphically. Then fit the most appropriate equations and use the model that had the best fit (e.g. linear regressions or polynomial regressions (if quadratic term and/or cubic term were significant)). Normality was tested for all variables using the Shapiro-Wilk goodness-of-fit test ($P > 0.05$). Non-normal continuous variables, including total and understory aboveground biomass were natural-logarithm transformed to mitigate departure from normality and linearity as recommended by Grace *et al.* (2010) and Byrne (2013), while stand age and total cover were log transformed for their regressions with Shannon"s index of tree species. No excessive multivariate skewness and kurtosis were found in the data using Mardia"s multivariate tests, indicating that the maximum likelihood estimation for SEM was valid. It should be noted that total cover was not included in the total and overstory aboveground biomass SEMs, as it skews the models towards determinism (Supplementary information I). It should be noted that Shannon"s index and biomass directional paths were both measured to demonstrate, which factor is affecting which. Because biomass seems to not be significantly affecting Shannon‟s index, the directional pathway goes from Shannon‟s to biomass.

We used the *chi*-square test, Tucker-Lewis index (TLI), standardized root mean square (SRMS), and comparative fit index (CFI) to evaluate the model fit of all SEMs (Sharma *et al.* 2005). Root mean square error (RMSEA) of approximation was mentioned within the results; however, it tends to over reject true population models at small sample sizes (<200 cases), and thus it is not a preferred index for this study (Hu & Bentler 1999).

A *chi*-square value of $P > 0.05$ indicates that the observed and expected covariance matrices are not statistically different; TLI and CFI have a cut off value close to 0.95; SMRS has a cut off value close to 0.08; and a cut-off value close to 0.06 for RMSEA, respectively are needed before conclusions can be made that there is a relatively good fit between the hypothesized model and the observed data (Hu & Bentler 1999; Rosseel 2012). Depending on how far the values are from the cut off values it will determine how well the fit of the model is, higher departures may indicate a poor fit and therefore either more values are needed or the observed values are statistically different from the expected covariance matrix. The significant path coefficient for directional paths (single-headed arrows) indicates that the represented causal relationship is statistically significant. Furthermore, the path coefficient, standardized for comparison between pathways, can be a measure for the sensitivity of a dependent variable to the predictor (Grace & Bollen 2005). To facilitate the interpretation of our SEM results, the total effect of a given exogenous variable on aboveground biomass was estimated by adding the direct standardized effect and the indirect standardized effect (Grace & Bollen 2005). The SEM was implemented using the *lavaan* package (Rosseel 2012) in R 3.0.2 (R Development Core Team 2013).

Above ground biomass‟ relationship with total cover and Shannon‟s index could not be normalized. Three outliers were removed, as they were not representative of the anthropogenic ecosystems as a whole having more than three standard deviations from the mean of total above ground biomass. Their representation within the oil sands were limited to their 3 replicates of the same overstory type, no other plots of the same overstory were as dense or have as a high of tree biomass. Because these values were much greater they skewed the model and produced results which may not be representative of the entire area.

RESULTS

Our analysis revealed that total aboveground biomass increased with stand age, conifer cover, nitrogen concentration, and Shannon‟s index of tree species, whereas total aboveground biomass decreased with clay content (Figs. 2.1A, B, C, D, and E). Shannon‟s index of tree species was positively related to stand age (Fig. 2.1F), while there was no significant relationship between Shannon‟s index of tree species and conifer cover (Fig. 2.1G). Overstory aboveground biomass was positively related to all factors except for nitrogen concentration and clay content, which had an insignificant relationship, and negative relationship, with respectively (Fig. 2.2). Understory aboveground biomass, however, was negatively related to stand age, Shannon‟s index of tree species, total cover, and conifer cover (Figs. 2.3A, D, E, and F). By contrast, understory aboveground biomass had a positive relationship with clay content (Fig. 3C), while there was no significant relationship detected between nitrogen concentration and understory aboveground biomass (Fig. 3B).

The SEM for total aboveground biomass had good fit with the data ($\chi^2 = 8.90$, d.f. = 2, $P = 0.012$; RMSEA = 0.222; SRMR = 0.05; TLI = 0.80; CFI = 0.96) (Table 2.1A, Fig. 2.4). Stand age and Shannon's index of tree species had positive effects on total aboveground biomass.

Shannon's index of tree species was shown to be influenced positively by stand age, while being negatively influenced by proportion conifer cover. By contrast, total aboveground biomass was not significantly affected by nitrogen concentration, clay content, or conifer cover (Fig. 2.4). Model including total cover was shown to have a high correlation instead of causation; because of this we removed it from the equation, as well as the overstory above ground biomass SEM (Supplementary information I).

The SEM for overstory aboveground biomass had poor fit with the data (χ^2 = 12.09, d.f. = 4, P = 0.017; RMSEA = 0.170; SRMR = 0.041; TLI = 0.89; CFI = 0.96) (Table 2.1B, Fig. 2.5). Overstory aboveground biomass was positively influenced by stand age and Shannon"s index of tree species. Shannon's index of tree species was positively influenced by stand age, while being negatively influenced by conifer cover. Similar to total aboveground biomass, overstory aboveground biomass was not affected significantly by nitrogen concentration, clay content, or conifer cover (Fig. 2.5).

The understory aboveground biomass SEM also had poor fit with the data (χ^2 = 19.33, d.f. = 5, P = 0.002; RMSEA = 0.202; SRMR = 0.04.; TLI = 0.584; CFI = 0.84) (Table 2.1C, Fig. 2.6). However, only a couple of factors significantly affected understory aboveground biomass and Shannon"s index of tree species. The SEM showed that conifer cover and total cover both had negative effects on understory aboveground biomass and Shannon"s index (Fig. 2.6).

Table 2.1. Direct, indirect, and total standardized effects on total aboveground biomass based on structural equation models (SEMs). Significant effects are at P < 0.05 (*), < 0.01 (**), < 0.001 (***).

SEM model	Predictor	Pathway to aboveground biomass	Effect
(**A**) Total above ground biomass	Shannon's index	Direct	0.19*
		Indirect	-
		Total	0.19
	Stand age (years)	Direct	0.81***
		indirect through α-diversity	0.15*
		Total	0.96
	Proportion conifer cover (%)	Direct	-0.05
		indirect through α-diversity	-0.04
		Total	-0.09
	Nitrogen concentration (%)	Direct	0.09
		Indirect	-
		Total	0.09
	Clay (%)	Direct	0.11
		indirect	-
		Total	0.11
(**B**) Overstory aboveground Biomass	Shannon's index	Direct	0.28***
		Indirect	-
		Total	0.28
	Stand age (years)	Direct	0.70***
		indirect through α-diversity	0.22***
		Total	0.92
	Proportion conifer cover (%)	Direct	-0.01
		indirect through α-diversity	-0.07***
		Total	-0.08
	Nitrogen concentration (%)	Direct	0.00
		Indirect	-
		Total	0.00
	Clay (%)	Direct	-0.09
		indirect	-
		Total	-0.09
(**C**) Understory aboveground Biomass	Shannon's index	Direct	-0.30
		Indirect	-
		Total	-0.30
	Stand age (years)	Direct	0.45

	indirect through α-diversity	-0.24*
	Total	0.21
Proportion conifer cover (%)	Direct	-0.31*
	indirect through α-diversity	0.07
	Total	-0.24
Total cover (m^2)	Direct	-0.65**
	indirect through α-diversity	-
	Total	-0.65
Nitrogen concentration (%)	Direct	0.14
	Indirect	-
	Total	0.14
Clay (%)	Direct	-0.07
	indirect	-
	Total	-0.07

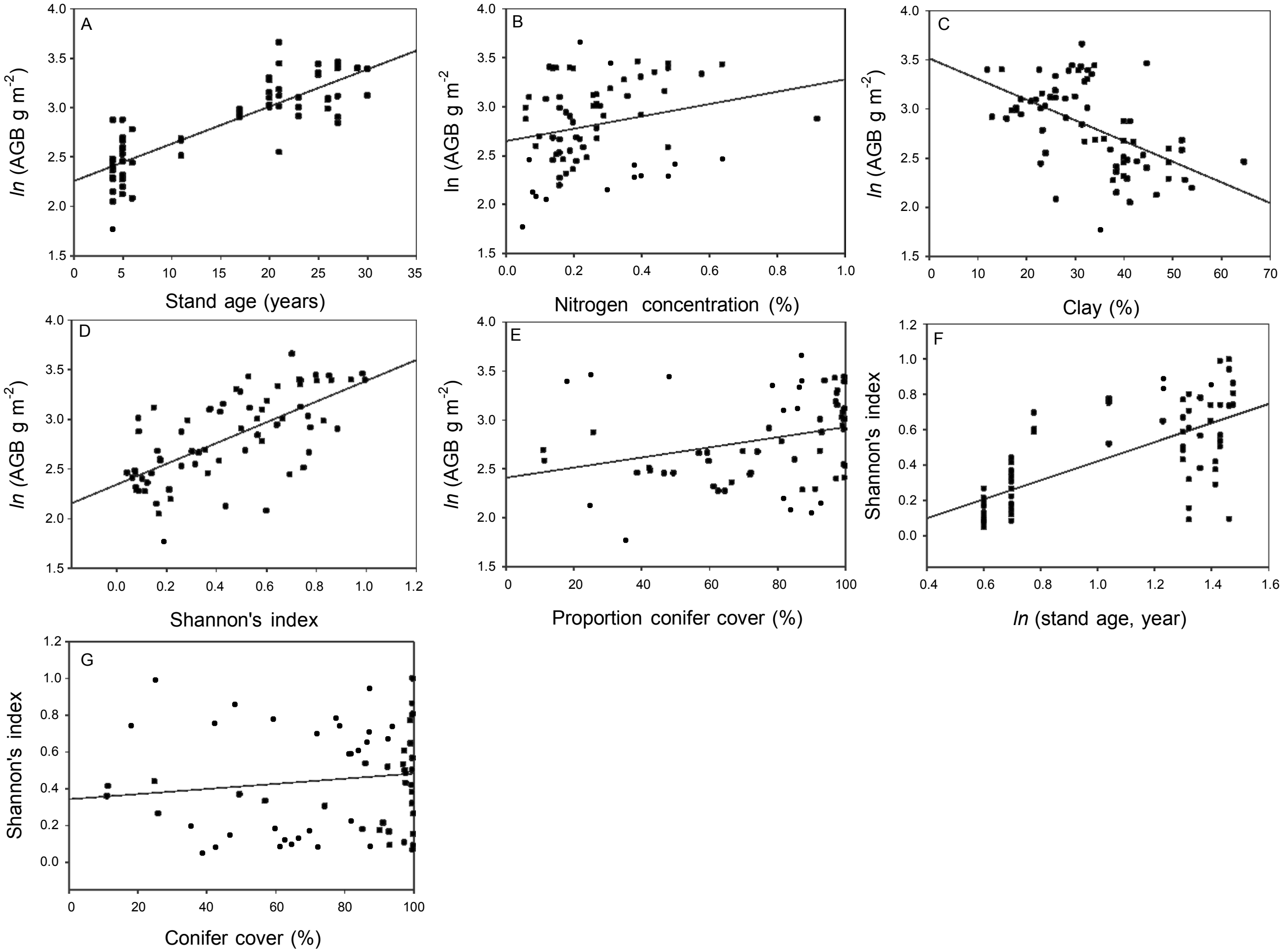

Figure 2.1. Univariate relationships between endogenous (dependent) and exogenous (independent) variables (n =70). Significant regression lines were plotted using a linear regression. Parametric assumptions were checked. (a) y= 2.26 + 0.04x, r^2= 0.72, (b) y = 2.648 + 0.6299x, r^2= 0.04, (c) y = 3.51 – 2.10, r^2= 0.28, (d) y = 2.34 +1.05x, r^2= 0.44, (e) y = 2.41 + 0.005x, r^2 = 0.08, (f) y = -0.12 + 0.54x, r^2= 0.46, and (g) Non-significant. The assumptions of normality and homogeneous variance were validated for all fitted regressions (P≤ 0.05), with exception of g.

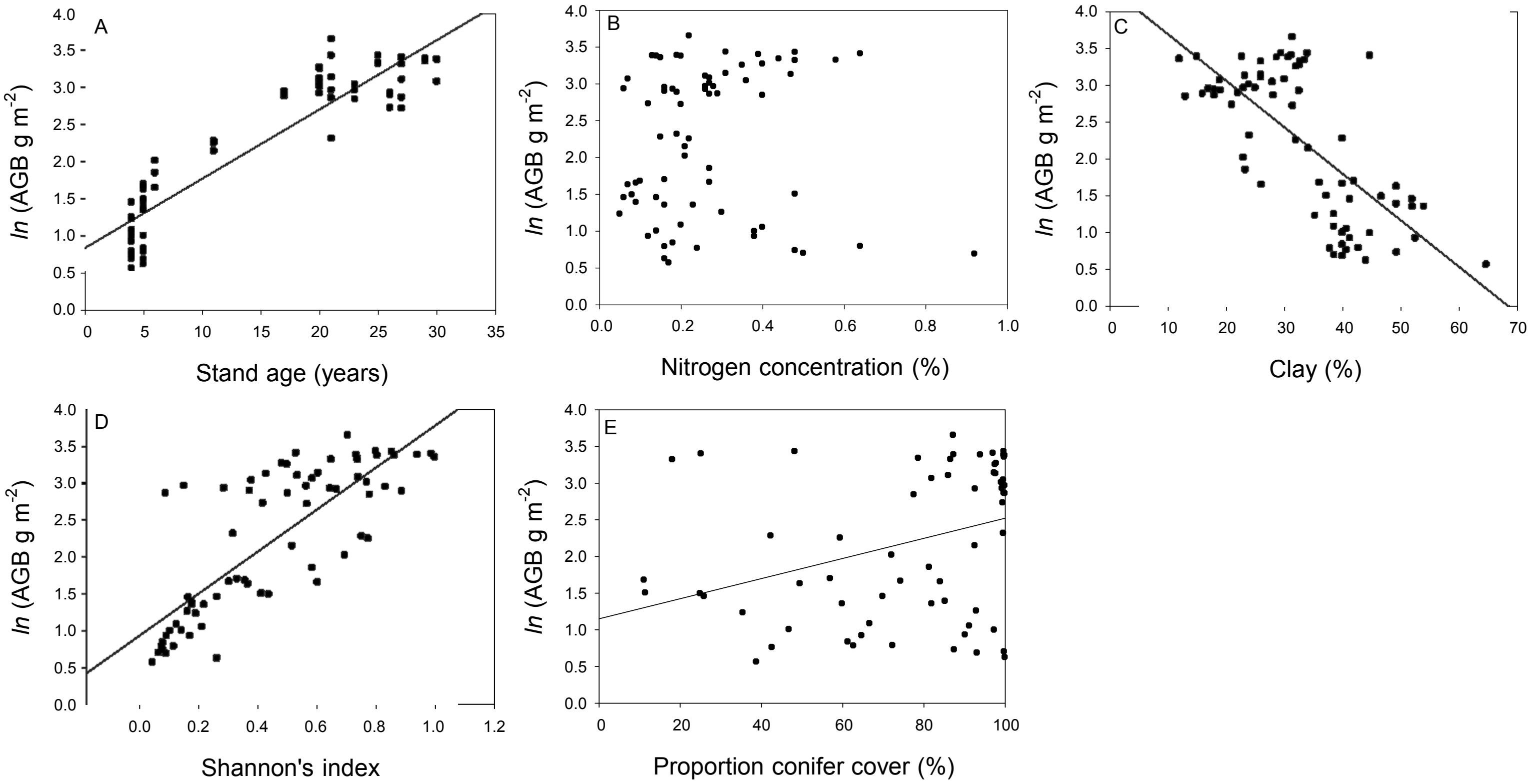

Figure 2.2. Univariate relationships between endogenous (dependent) and exogenous (independent) variables (n =70). Significant regression lines were plotted using a linear regression. Parametric assumptions were checked. (a) y= 0.94 + 0.09x, r^2= 0.77, (b) non-significant, (c) y = 4.33 - 0.632x, r^2= 0.51, (d) y = 1.41 + 2.03x, r^2= 0.36, and (e) y = 1.45 + 0.01x, r^2 = 0.64. The assumptions of normality and homogeneous variance were validated for all fitted regressions (P≤ 0.05).

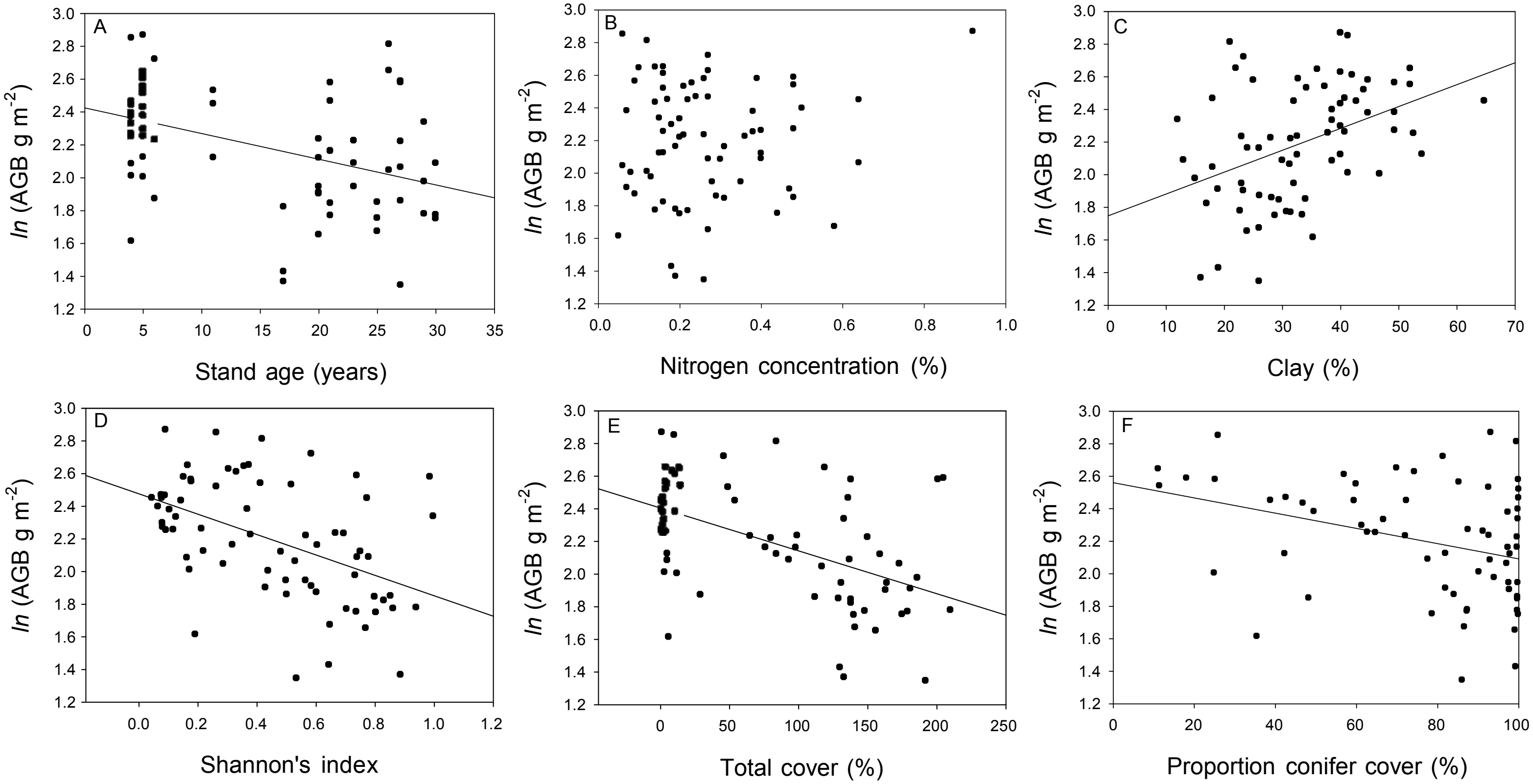

Figure 2.3. Univariate relationships between endogenous (dependent) and exogenous (independent) variables (n =70). Significant regression lines were plotted using a linear regression. Parametric assumptions were checked. (a) y= 2.43 - 0.02x, r^2= 0.17, (b) Non-significant (c) y= 1.75 + 1.34, r^2= 0.16, (d) y= 2.48 – 0.62, r^2= 0.22 , (e) y = 2.40 - 0.002x, r^2 = 0.25, and (f) y= 2.56 – 0.005x. r^2= 0.10. The assumptions of normality and homogeneous variance were validated for all fitted regressions ($P \leq 0.05$).

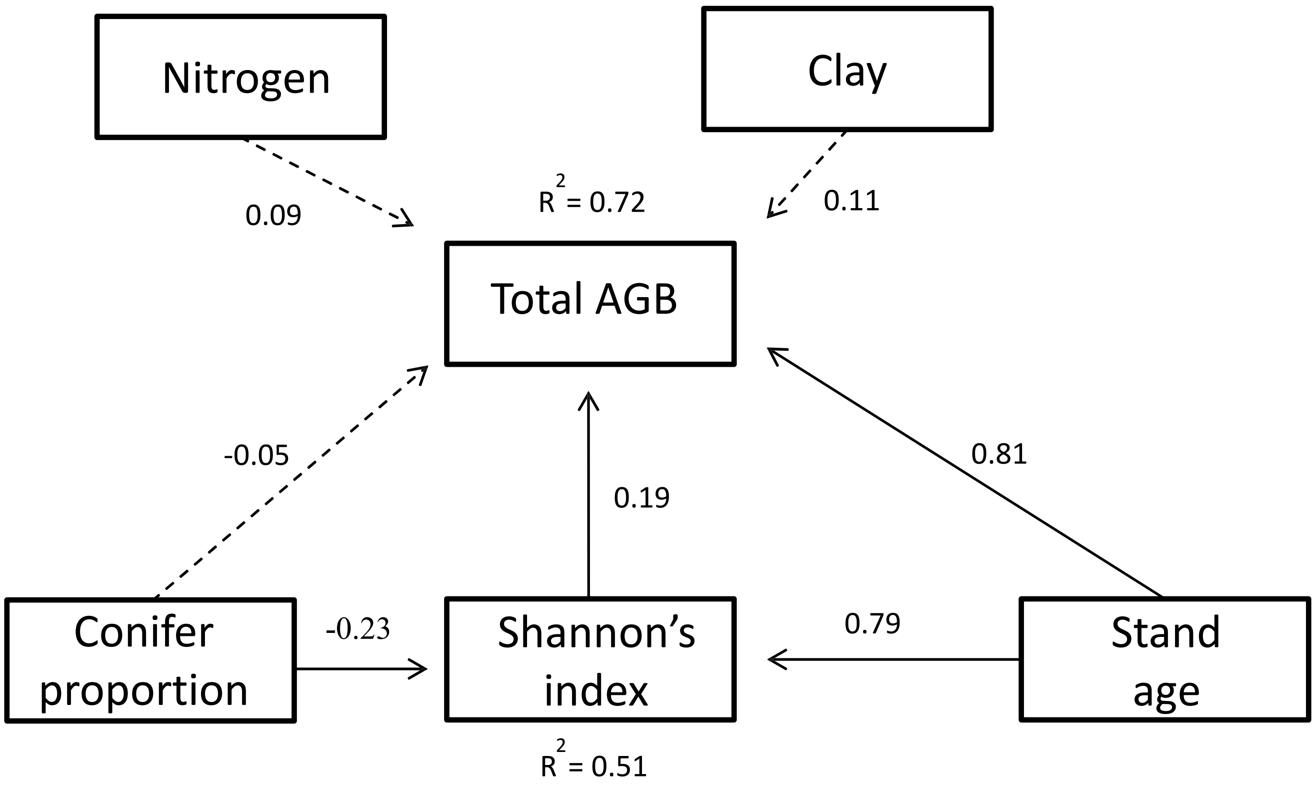

Figure 2.4. Structural equation models linking total aboveground biomass (AGB) and species diversity. Demonstrating the effects of (a) stand age (years), (b) clay content (%), (c) conifer cover (%), (d) nitrogen concentration (%), and (e) Shannon"s index of tree species on total aboveground biomass. With (f) natural log stand age, (g) natural log total cover, and (h) conifer cover on Shannon"s index of tree species. The coefficients are standardized prediction coefficients for each causal pathway. Solid lines represent significant paths ($P \leq 0.05$) and dashed lines insignificant paths ($P > 0.05$).

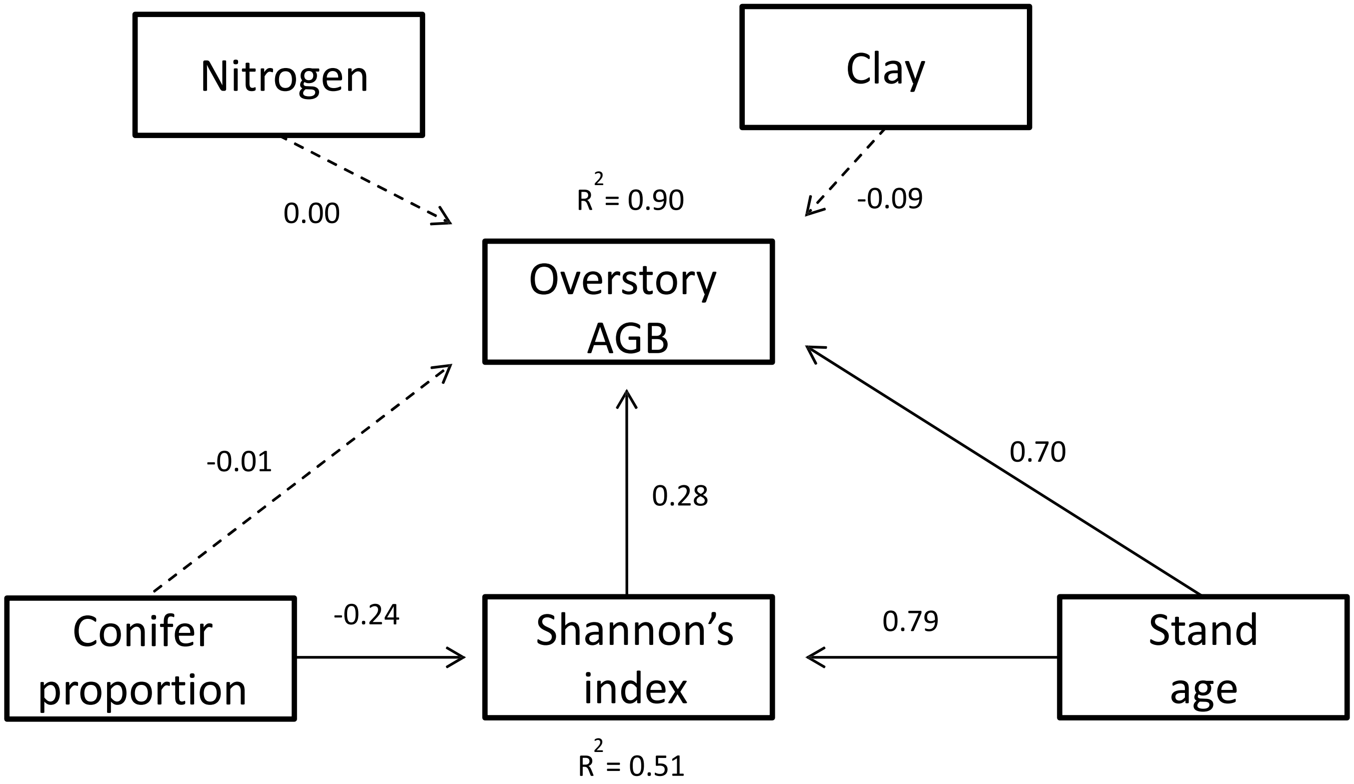

Figure 2.5. Structural equation models linking overstory aboveground biomass (AGB) and species diversity. Demonstrating the effects of (a) stand age (years), (b) clay content (%), (c) conifer cover (%), (d) nitrogen concentration (%), and (e) Shannon"s index of tree species on overstory aboveground biomass. With (f) natural log stand age, (g) natural log total cover and (h) conifer cover on Shannon"s index of tree species. The coefficients are standardized prediction coefficients for each causal pathway. Solid lines represent significant paths ($P \leq 0.05$) and dashed lines insignificant paths ($P > 0.05$).

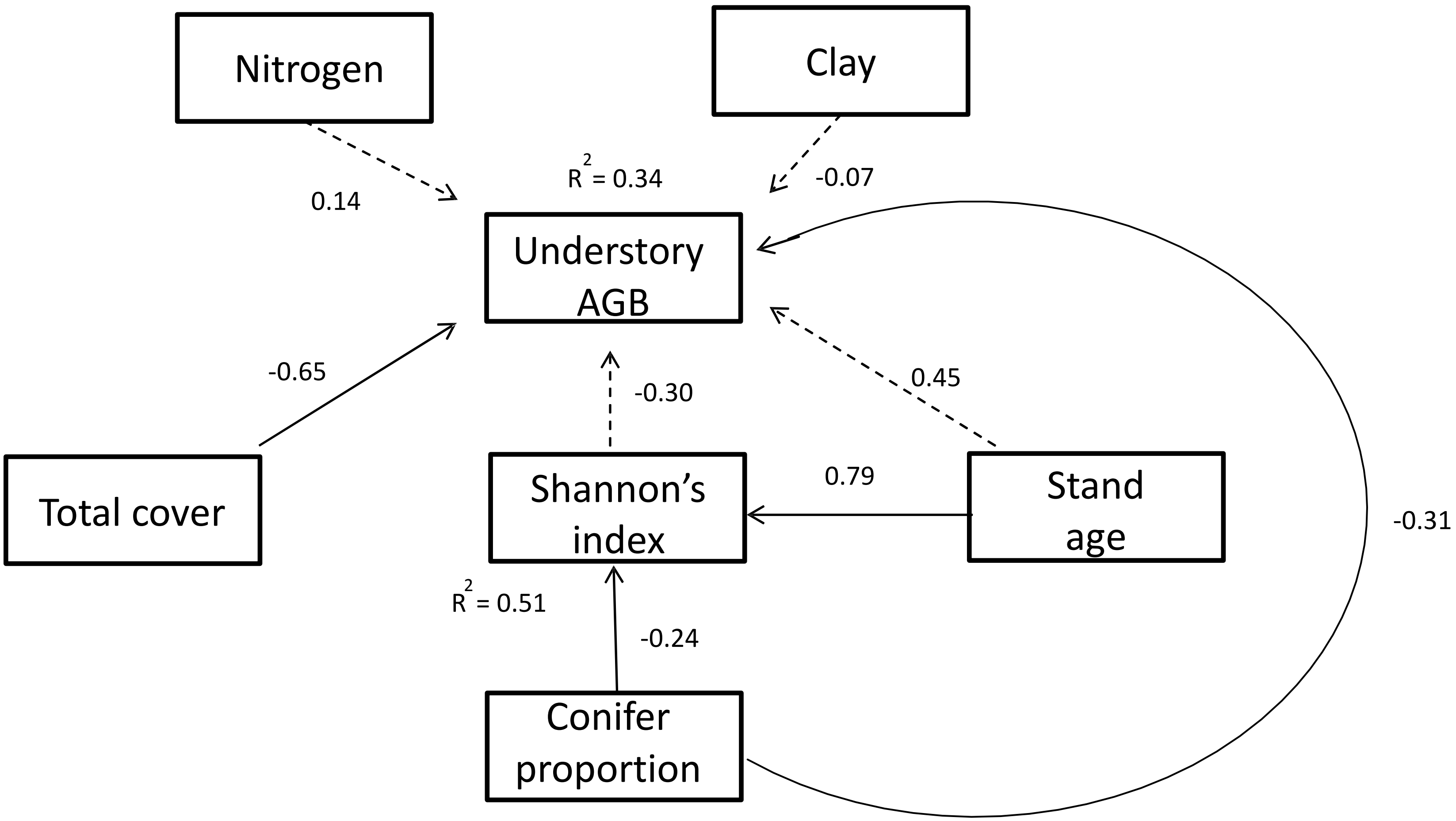

Figure 2.6. Structural equation models linking understory aboveground biomass (AGB) and species diversity. Demonstrating the effects of (a) stand age (years), (b) clay content (%), (c) conifer cover (%), (d) nitrogen concentration (%), (e) total cover (m^2), and (f) Shannon‟s index of tree species on understory aboveground biomass. With (g) natural log stand age, (h) natural log total cover and (i) conifer cover on Shannon‟s index of tree species. The coefficients are standardized prediction coefficients for each causal pathway. Solid lines represent significant paths ($P \leq 0.05$) and dashed lines insignificant paths ($P > 0.05$).

DISCUSSION

Biotic influences have been shown to be the main driver of aboveground biomass within reclaimed ecosystems after oil sands mining, particularly stand age and stand composition. Tree establishment is one of the predominant drivers at the beginning of reclamation of stand dynamics (Aerts & Honnay 2011; Löf *et al.* 2014), and we have shown it to effect the productivity and recovery of aboveground biomass within these ecosystems. Typically, tree species may facilitate understory plant establishment by creating micro-sites of reduced radiation and increased soil resources (Brooker *et al.* 2008). While tree species affect the productivity of the understory, they also account for the majority of stand biomass. Tree biomass can primarily be attributed to stand age and species composition (Hüttl & Weber 2001; Löf *et al.* 2014; Maynard *et al.* 2014). Since the study stands were a maximum of 30 years of age, age-related decline in forest growth had yet to occur (Ryan *et al.* 1997)**.** Aboveground net primary production should eventually start to decline as the stands become older due to an altered balance between photosynthetic and respiring tissue, decreased soil nutrients, and stomatal constraint (Gower *et al.* 1996). However, due to the short legacy of reclamation in the Alberta oil sands, it is unknown if stand dynamics will follow similar patterns on these reclaimed sites as their natural analogues.

Total cover had a negative effect on understory aboveground biomass. This can be attributed to lower light availability and soil temperatures and higher soil moisture in stands with higher total cover versus lower total cover, which restricts the growth of understory species (Aerts & Honnay 2011; Harris *et al.* 2012). Similar trends can be found with understory species decreased presence under coniferous trees, thus demonstrating why there was a high negative effect on understory biomass through increased coniferous cover (Prescott *et al.* 2000)

The negative effect from Shannon"s diversity does not agree with the findings of previous studies from natural forests, which show that mixed stands usually have higher productivity at similar stages of stand development as conifer and broadleaf stands due to better niche exploitation (Kelty 2006; Whittaker 2010; Zhang *et al.* 2012).

Coniferous cover within these reclaimed ecosystems had a negative impact on understory aboveground biomass, which is similar to trends found for natural forest ecosystems (Messier *et al.* 1998). Within conifer dominated stands, conifer trees covered a larger proportion of the stand and reached higher total biomass than broadleaf trees in broadleaf dominated stands. Consequently, conifer stands provide poor light transmission and growing space on the forest floor due to their low canopies and dense needles (Messier *et al.* 1998). Not only does this stop light from reaching the forest floor, but the needles produced by coniferous species typically have a lower decomposition rate than leaves produced by broad leaved species, leading to lower nutrient inputs (Prescott *et al.* 2000). Reduced native seed source caused by conifer-induced soil acidity and site conditions may also affect the total regenerative capacity of the understory (Harris *et al.* 2012). All of these factors lead to lower understory biomass in conifer versus broadleaf stands.

Conifer cover had a negative effect within the SEMs on Shannon's index. While higher conifer cover is linked to higher aboveground tree biomass, it limits other tree species presence through inter and intra specific competition. This is due to sucessional patterns as well as limiting niche space by conifers lower decomposition foliar litter rates and dense canopy cover may limit the potential of other tree species entering the ecosystem.

Nutrient concentration did not have an effect on aboveground biomass, which suggests nutrient concentration supply has little effect on plant production within these reclaimed ecosystems. While other nutrients within an ecosystem can be vital to plant production such as phosphorus and potassium, they were not included in the modelling due to their poor estimates within the model. Substrate composition, particularly clay content, did not have a significant effect on aboveground biomass within the SEMs either.

In summary, we show in this study that stand age and Shannon's index have positive effects on total aboveground biomass. Understory aboveground biomass is highly correlated with canopy cover within reclaimed ecosystems, where greater cover promotes lower understory aboveground biomass. While conifer cover has a positive effect on total aboveground biomass, it negatively influences understory aboveground biomass.

SUPPLEMENTARY INFORMATION

Direct, indirect, and total standardized effects on overstory aboveground biomass based on structural equation models (SEMs) including total cover. Significant effects are at $P < 0.05$ (*), <0.01 (**), <0.001 (***).

SEM model	Predictor	Pathway to aboveground biomass	Effect
(**B**) Overstory Biomass	α-diversity	Direct	0.20***
		Indirect	-
		Total	0.20
	Stand age (years)	Direct	0.34***
		indirect through α-diversity	0.01
		Total	0.35
	Conifer cover (%)	Direct	0.02
		indirect through α-diversity	-0.03**
		Total	-0.01
	Total cover (m^2)	Direct	0.48***
		indirect through α-diversity	0.16**
		Total	0.63
	Nitrogen (%)	Direct	-0.04
		Indirect	-
		Total	-0.04
	Clay (%)	Direct	-0.03
		Indirect	-
		Total	-0.03

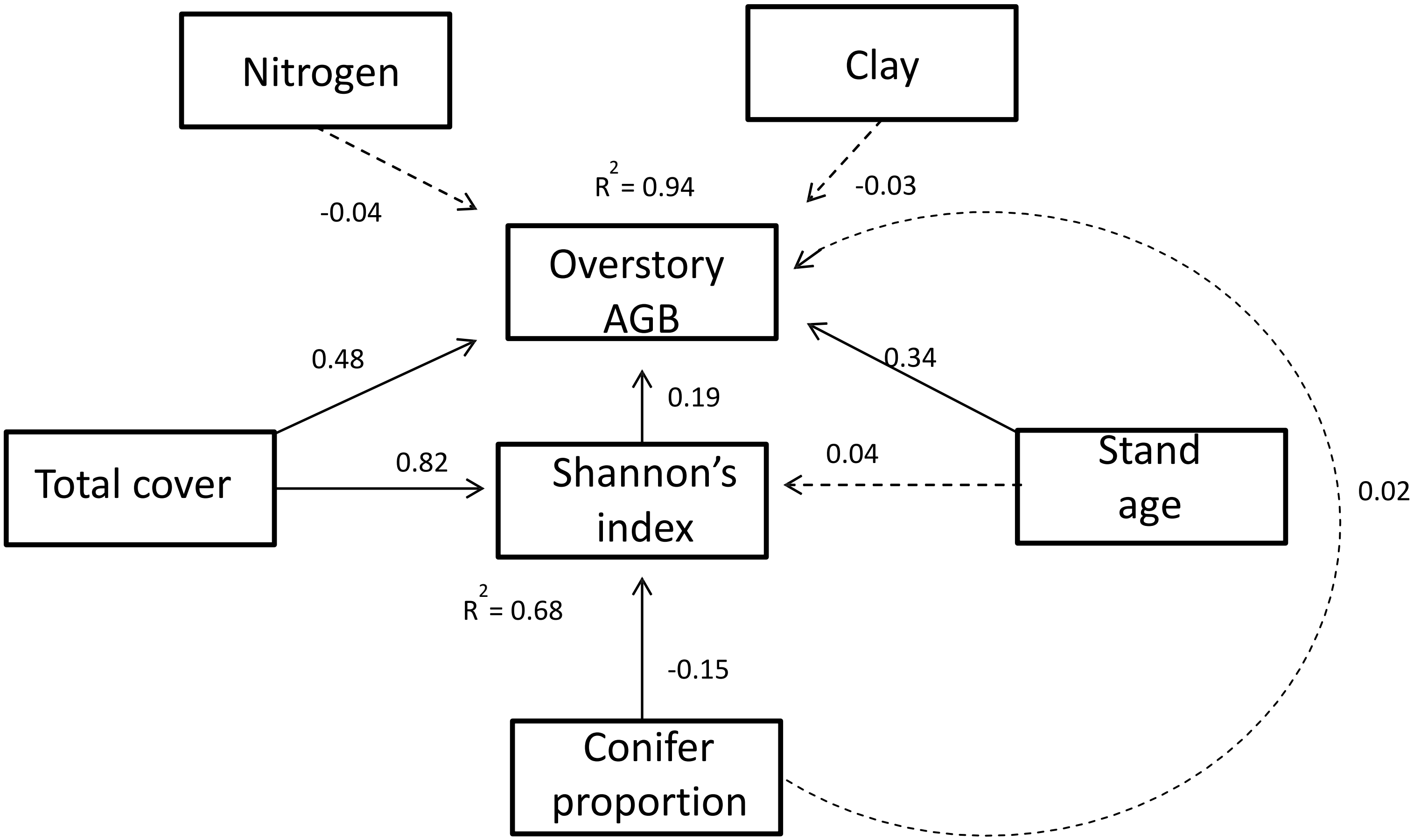

Figure 1. Structural equation models linking over-story aboveground biomass (AGB) and species diversity. Demonstrating the effects of (a) stand age (years), (b) clay content (%), (c) conifer cover (%), (d) nitrogen content (%), (e) total cover (m^2) (f) Shannon‟s index of tree species on total aboveground biomass. With (g) natural log stand age, (h) natural log total cover and (i) conifer cover on Shannon‟s index of tree species. The coefficients are standardized prediction coefficients for each causal path. Solid lines represent significant paths ($P \leq 0.05$) and dash lines for non-significant paths ($P > 0.05$).

GENERAL CONCLUSION

The findings of my thesis confirm that biodiversity and biomass vary with stand age, over-story composition, and substrate. A summary of my research findings and conclusions and management implications and recommendations are as follows:

(1) Abundance was driven by substrate, as well its interaction with over-story composition. Clay overburden and secondary overburden were shown to have the most prominent abundance. Overburdens as well as tailings were shown to have the lowest abundance. Broadleaf"s combination with clay overburden produced the significantly highest abundance. Richness was driven mainly by substrate. Similar to abundance, richness was most abundant in clay and secondary overburden. Compositionally, tailings and overburden had similar species, while clay overburden, secondary overburden, and lean overburden had similar species. Overall, these results may be explained by the potential of the propagules to expand and take over resources. Thus, a larger reclaimed area would allow for a higher chance of propagule success.

(2) Increased tree biomass, particularly coniferous biomass, leads to minimal understory biomass. Relative coniferous cover has been shown to limit the growth of these understory species through shading and limiting the propagule potential. Nutrients and clay proportion were not shown to limit the biomass growth.

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Appendices

Index catagories of the indicator values found in Table 1.4.

Index	Origin
1	COO
2	PMMLO
3	PMMO
4	PMMSO
5	PMMT
6	COO/PMMLO
7	COO/PMMO
8	COO/PMMSO
9	COO/PMMT
10	PMMLO/PMMO
11	PMMLO/PMMSO
12	PMMLO/PMMT
13	PMMO/PMMSO
14	PMMO/PMMT
15	PMMSO/PMMT
16	COO/PMMLO/PMMO
17	COO/PMMLO/PMMSO
18	COO/PMMLO/PMMT
19	COO/PMMO/PMMSO
20	COO/PMMO/PMMT
21	COO/PMMSO/PMMT
22	PMMLO/PMMO/PMMSO
23	PMMLO/PMMO/PMMT
24	PMMLO/PMMSO/PMMT
25	PMMO/PMMSO/PMMT
26	COO/PMMLO/PMMO/PMMSO
27	COO/PMMLO/PMMO/PMMT
28	COO/PMMLO/PMMSO/PMMT
29	COO/PMMO/PMMSO/PMMT
30	PMMLO/PMMO/PMMSO/PMMT
31	COO/PMMLO/PMMO/PMMSO/PMMT

Notes: COO- clay overburden, PMMO-overburden, PMMSO- secondary overburden, PMMLO-lean overburden, PMMT- tailings.