Influence of Environmental and Site Factors and Biotic Interactions on Vegetation Development Following Surface Mine Reclamation Using Coversoil Salvaged From Forest Sites

By

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Abstract: Industrial activities such as surface mining are responsible for disturbing large areas of forest land. Reclamation methods must facilitate the development of soil, of a diverse natural understory plant community, and of a tree canopy. In my thesis research, I examined the response of vegetation diversity, cover and composition to constructed topography, tree seedlings planted at different densities, and coarse woody debris at a surface mine reclamation site in Alberta, Canada. These responses were studied in areas capped with coversoils salvaged from two forest types. Results suggested that seedling planting density and topographical aspect primarily influenced vegetation diversity, while coarse woody debris abundance primarily influenced vegetation cover. Diversity was higher on cooler, moister aspects and in areas with higher seedling planting density. Cover was negatively associated with coarse woody debris abundance. Studying characteristics of reclamation sites that reflect ecological processes can offer a deeper understanding than short term (often occurring in the first 1-5 years of vegetation development) surveys of vegetation composition. To better understand these processes, I explored the variation explained by environmental factors and by spatial patterns ('space,' representing biotic interactions such as competition or facilitation) at reclamation sites capped with coversoils salvaged from two forest types, and at two ages. For sites constructed with both material types and at both ages, space explained more variation than environmental factors, suggesting that competitive and facilitative interactions were the main structuring processes at these sites.

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Chapter 1: Introduction

1.1 Surface mining disturbance and reclamation

The boreal forest is a circumpolar biome covering over 10% of the Earth's terrestrial surface (Bonan and Shugart 1989). Boreal forests are typically characterized by a tree canopy dominated byfew species with a rich understory including shrubs, herbs, bryophytes and lichens; these forests, particularly their understory components, have received less attention from ecologists than temperate forests (Nilsson and Wardle 2005). The boreal forest landscape comprises a mosaic of different forest types, mostly driven by the parent soil material and topographical position of the site. Boreal forest landscapes are also shaped by natural disturbances such as fire, windthrow, insects and pathogens (McCullough et al. 1998; Rich et al. 2007; Malstrom et al. 2000). More recently anthropogenic disturbances in boreal forests, including severe disturbances such as surface mining, have increased over the last 200 years (Nilsson and Wardle 2005). Surface open-pit mining typically requires the removal of all vegetation and surface soil, as well as overburden material, severely disturbing soil structure, microbial communities and vegetation (Rowland et al. 2009; Shrestha and Lal 2011; Mummey et al. 2002).

Reclamation is needed to facilitate the development of soil properties, diverse natural understory communities and the tree canopy. In forested areas of Alberta, Canada, industrial operators must reclaim surface mine disturbances to 'equivalent land capability' to obtain a reclamation certificate; the target of reclamation activities is self-sustaining forests similar to local forest ecosystems (Powter et al. 2012; Naeth et al. 2013). Common methods used at forest reclamation sites to address the challenges of severely disturbed surface mine sites include landform reconstruction using overburden or post-mining materials, capping with coversoils including salvaged surface soil, forest floor material or other organic materials used to facilitate soil development, native tree seedling planting and application of coarse woody debris (Macdonald et al. 2015a). Prior to mining 'forest floor material' coversoil (litter, fermented litter and humic layers and surface mineral soil horizons) is required to be salvaged from sites scheduled for disturbance; this material can provide suitable soil material and a source of native plant propagules, which are not widely commercially available (Mackenzie and Naeth 2010; Naeth et al. 2013). Coversoils salvaged from forest sites can provide some of the only links to pre-disturbance conditions at severely disturbed reclamation sites (Mackenzie and Naeth 2010).

1.2 Landscape, topography, and soil re-construction

Landscape reconstruction, landforms and their topography, including slope and aspect, strongly influence vegetation community development; this effect is particularly strongly developed in northern and southern latitudes where solar angle is low (Bonan and Shugart 1989). In the northern boreal forest north facing aspects receive much less solar radiation and are typically cooler and moister than south facing aspects (Bonan and Shugart 1989). As a result, distinct vegetation communities and edaphic conditions have developed at these different topographical positions over long time scales (Desta et al. 2004). Reclamation sites provide a unique opportunity to study these processes, as similar soil materials are placed in different topographical positions; therefore, initial vegetation development will likely reflect only the immediate impact of differences in energy input among aspects, without being influenced by legacies such as the soil nutrient or propagule bank differences. In a reclamation context, slope aspect has been shown to affect growth of seeded cover crops (Gonzalez-Alday et al. 2008).

In natural forests, microtopographical variation (topographical variation one metre or less in height), often in the form of mounds and pits created by fallen trees, is common. This variation has been shown to drive patterns in understory vegetation, and different plant species may be associated with hummocks, pits and flat areas (Beatty 1984). Microtopography has been found to be an important driver of species composition and community richness in many ecosystem types; e.g., cliff faces (Kuntz and Larson 2006), boreal forests (Ulanova 2000), and forested wetlands (Okland et al. 2008). In a reclamation context, construction of microtopographical features has gained attention as a method of increasing heterogeneity (and thus diversity) (Biederman and Whisenant 2011). At a prairie site, Biederman and Whisenant (2011) found that in the first three years of development, constructed mounds improved growth of native prairie plants and drove the development of differing plant communities at the top and bottom of mound microsites. The effects of microtopography at reclamation sites appear to be maintained in the longer (up to 10 years) term; Hough-Snee et al. (2011) found that, 10 years after the creation of mound features at a grassland site, environmental factors such as soil moisture differed between mound tops and pits and that these differences drove the development of different plant communities.

Microtopographical variation has also been shown to be beneficial to natural regeneration of native tree species on reclamation sites (Schott et al. 2014). Like larger (landscape scale) topographical features, microtopographic variation will likely drive the development of differing vegetation communities at reclamation sites; however, understanding of the impact of constructed microtopography on vegetation communities, particularly at northern forest reclamation sites, is limited.

Coversoils salvaged from forest sites and placed on surface mining reclamation sites in many regions have been a viable source of native propagules and improved survival and growth of seeded native species, when compared to other soil materials (Rokich et al. 2000; Holmes 2001). In studies of boreal forest reclamation and restoration, coversoil salvaged from forest sites, as compared to other soil material, has been shown to facilitate establishment of forest understory species and to support vegetation communities more similar to surrounding native vegetation (Skrindo and Halvorson 2008; Macdonald et al. 2015b). At an Alberta boreal forest surface mine reclamation site, capping with coversoil salvaged from forest sites resulted in higher plant species richness and abundance than amendment with peat mineral mix, a mixture of organic and mineral soil salvaged from wetland areas (Mackenzie and Naeth 2010). Coversoils salvaged from different forest types will show different physical and chemical properties and host different species in the propagule bank. When placed on reclamation sites, coversoils salvaged from different forest types will likely, at least in the early establishment period, result in the development of different vegetation communities.

1.3 Vegetation establishment

Forest canopies exert a strong influence on the understory community. This influence can depend heavily on tree species; Strong (2011) found that in boreal forests *Populus* canopy trees exerted a much weaker influence on understory species than *Picea* canopy trees, and in a review of temperate and boreal forests, Barbier et al. (2008) suggested that understory species richness is generally higher in broadleaf than conifer dominated forests. Although the canopy is typically thought to have an inhibitory effect on the understory, it can sometimes have a beneficial role, particularly in heavily disturbed areas, by creating a more favourable growth environment for the shrub layer likely through soil nutrient enrichment and protection from harsh environmental conditions (Zvereva and Kozlov 2004). In turn, the understory can affect canopy development. In boreal forests, Nilsson and Wardle (2005) found that the understory shrub layer exerted a strong influence on tree seedling germination. At reclaimed surface mine sites, Franklin et al. (2012) showed that seeded groundcover vegetation could either facilitate or inhibit tree seedling growth, depending on the density of the groundcover and site factors. The effect of understory vegetation on the canopy is partially dependent on species characteristics; introduced grass species in particular can have inhibitory effects on tree seedling growth (Skousen et al. 2009).

Forest canopy development can drive shifts in the understory community at reclamation sites. Pensa et al. (2008) found that as forest canopies closed at European mine reclamation sites, the understory vegetation underwent a shift from light-demanding to shade tolerant species. Canopy development can also encourage growth of desirable species. Padilla and Pugnaire (2006) discussed the potential of using ‘nurse’ plants to promote the growth of desirable species at environmentally harsh reclamation sites and concluded that this strategy can be successful. Planted tree seedlings can also inhibit growth of undesirable species. For example, Tamang et al. (2008) used a combination of high density tree seedling planting and site preparation to successfully suppress an aggressive invasive grass and encourage growth of native species at a surface mine reclamation site in Florida. This suggests that planting of native trees could help accelerate development of diverse, natural understory communities at reclamation sites.

In natural forests, coarse woody debris, largely resulting from tree mortality, can provide habitat for animals, plants and invertebrates, a source of energy for bacteria and fungi, can play an important role in nutrient cycling, and can provide structural diversity (Harmon et al. 1986). Coarse woody debris also plays an important role in managed forests, where it has been shown to be positively associated with seedling regeneration (Beach and Halpern 2000). Reclaimed sites often lack the structural diversity present at natural sites; artificial addition of structural features such as coarse woody debris may be beneficial to plant establishment and attractive to wildlife (Larkin et al. 2008). At a reclamation site in the boreal forest, soil under coarse woody debris pieces had higher soil water content and a lower temperature range; vegetation cover was also higher in areas with woody debris. In addition, Brown and Naeth (2014) found that plant growth was sometimes higher near woody debris pieces, indicating that a microsite effect was occurring. The role of coarse woody debris in natural forests, as well as its demonstrated effects at forest reclamation sites, suggests that use of this material may increase plant establishment at environmentally harsh reclamation sites.

Environmental and site factors such as slope aspect, seedling planting density and coarse woody debris abundance will likely affect developing vegetation communities at reclamation sites both independently and through complex interactions. Environmental conditions (i.e. temperature extremes and water stress) are often harsher on south facing slopes (Bonan and Shugart 1989). Both coarse woody debris and planting density may provide a sheltering effect from harsh environmental conditions on these slopes and could interact with slope aspect to impact the vegetation developing in these areas (Strong 2000; Brown and Naeth 2014).

Ruderal species not associated with forest understory communities (often introduced) can become dominant at early-stage (i.e. in the first five years after construction) reclamation sites, and may suppress the development of a forest understory community through mechanisms such as allelopathy and resource competition (Ridenour and Callaway 2001). Introduced and non-forest associated species often have rapid growth, long-lived, easily dispersed seeds, annual or biennial life cycles, and are shade intolerant (van Kleunen et al. 2010; Baker 1974; Sutherland 2004); these characteristics may make these species very successful on reclamation sites. Many native, forest-associated species are much less successful on recently disturbed sites than in undisturbed forest, which makes these species less able to compete with introduced, non-forest species at reclamation sites (Djietror et al. 2011). However, in many cases the impact of these introduced or non-forest species on forest-associated species is not clear. Introduced species can provide benefits such as soil stabilization on reclamation sites in cases of severe disturbance where native species cannot establish (D’Antonio and Meyerson 2002). Additionally, introduced or non-forest species may be able to act as ‘nurse’ plants, directly benefiting native, forest associated species; these beneficial effects can be long term (Padilla and Pugnaire 2006; Gretarsdottir et al. 2004).

1.4 Spatial patterns and ecological processes

Ecological communities are spatially structured at a variety of scales (Borcard et al. 2004). This spatial structuring is typically driven by variation in environmental factors, biotic factors (such as competitive or facilitative interactions or dispersal limitations) or some combination of the two (Peres-Noto and Legendre 2010). Spatial patterns occur in natural communities at a variety of scales due to the varied processes driving them; understanding these patterns can provide important insight into the ecological processes structuring the community (Borcard et al. 2004). Spatial patterning varies over time during succession. For example, at arid sites in Israel, early successional stage communities exhibited primarily clustered patterns, while at later stage communities, the patterns were more regular; this was attributed to a shift from facilitative to competitive interactions (Malkinson et al. 2003).

In natural forests, a significant body of literature has attempted to separate the extent to which environmental factors and biotic factors explain spatial variation in the understory vegetation community. Biotic factors are typically accounted for using spatial pattern variables ('space'). Some studies have found environmental factors to be a stronger control than space (Gilbert and Lechowicz 2004; Karst et al. 2005), while others have found space to be the stronger driver (Gendreau-Berthiaume et al. 2015; Borcard et al. 1992). We have a limited understanding of processes driving variation in plant communities at reclamation sites.

1.5 The study sites

The research described in this thesis took place on two reclaimed areas at Syncrude Canada Ltd.'s Base Mine, which is located in the central mixedwood subregion, roughly 40 km north of Fort McMurray, Alberta, Canada. These sites were located in the Athabasca Oil Sands Region, an area containing approximately 4800 km^2 of surface mineable oil sands, of which 767 km^2 had been disturbed as of December 2012 (Government of Alberta 2016). The first research site was located in upland areas of a large scale experimental watershed (the Sandhill Watershed), which consisted of a wetland area surrounded by upland hummock features. The landforms at this site were constructed out of clean tailings sand on a former soft tailings pond. After landform construction a capping layer of coversoil was placed on the upland hummock landforms. The coversoil was salvaged from two donor sites representing the two forest types typical of upland sites within the region: upland forest sites that are nutrient poor, with xeric moisture regimes, coarse-textured soils, *Pinus banksiana* dominated canopies and sparse understories, and nutrient rich sites with mesic moisture regimes, fine-textured soils, *Populus tremuloides* and *Picea glauca* dominated canopies, and well-developed, lush and diverse understories. Coarse woody debris was placed on all of the hummocks after coversoil placement, and seedlings of three common boreal forest trees were planted in June 2012. The second field site (W1 Dump) was an experimental site constructed on a saline-sodic overburden landform, completed in early 2004 (Mackenzie 2006). Coversoil salvaged from a donor forest site similar to one used for the young site was placed in early 2004; in fall of 2005, native tree seedlings were planted at the site (Mackenzie 2006).

1.6 Objectives

The goals of the research presented in this thesis were to: 1) develop an understanding of how planted trees, topographic position (aspect), and coarse woody debris abundance influence vegetation development at reclamation sites constructed using coversoils salvaged from different forest types; and 2) quantify variation in spatial patterns of the forest understory community in these reclamation sites and determine the relative importance of environmental factors *versus* spatial variables (reflecting biotic interactions) in driving those.

In chapter 2 I explore the influence of density of planted tree seedlings, aspect and coarse woody debris abundance on vegetation diversity, cover and composition in areas capped with coversoils salvaged from two forest types.

In chapter 3 I determine how plant community complexity, spatial pattern complexity, and numbers of indicator species and species driving spatial patterns of different functional types differ between reclamation areas of different ages and capped using coversoils salvaged from two forest types. I also explore how much of the variation in the plant community is explained by environmental factors and by spatial variables (reflecting biotic interactions such as competition and dispersal limitations), and how this differs between the reclamation areas

In chapter 4 I present a synthesis of my work, suggestions for topics requiring further research and suggestions for incorporating the results of this research into reclamation practices.

Chapter 2: Factors affecting early vegetation development on sites reclaimed using coversoils salvaged from forest sites

2.1 Introduction

Industrial activities such as open pit mining are responsible for disturbing large areas of forest land. Reclamation methods, used in an effort to restore these areas to functioning forests, must facilitate the development of the soil, a diverse natural understory plant community and the tree canopy. Methods used to address these challenges include reconstructing appropriate topographical features; the salvage and placement of different soil materials, including forest surface material; amendment of the reclamation site with materials such as coarse woody debris; and the planting of trees to develop the required canopy (Macdonald et al. 2015a). However, few studies have examined the impacts of, and interactions between, these different operational practices on the early development of vegetation communities.

After surface mining, landscapes need to be rebuilt and surface soil reconstructed. While landscape reconstruction operations use relatively biologically inert materials, application of coversoil salvaged from nearby forest sites (typically including litter, fermented litter and humic layers and surface mineral soil horizons) provides some active link to pre-disturbance forest communities. This link can be stronger in materials that had been salvaged and directly (immediately) placed on a reclamation site, while these links can be weakened when material has been salvaged and stored for extended periods of time (Mackenzie 2013). Shortly after salvage, forest coversoils carry with them the soil properties and propagule banks of the upper soil horizons of the donor site; thus based on these legacies, the use of such materials can drive vegetation community development at reclamation sites. Placement of salvaged coversoils on reclamation sites has been shown to result in higher plant species richness and abundance than other soil materials (Mackenzie and Naeth 2010). In other studies in boreal forests, capping with coversoils salvaged from forest sites has been shown to facilitate establishment of forest understory species and to support vegetation communities more similar to surrounding native vegetation than other soil materials (Skrindo and Halvorson 2008; Macdonald et al. 2015b).

In natural forests, coarse woody debris provides structural diversity and habitat for both plants and animals, and strongly affects nutrient cycling (Beach and Halpern 2000). In some natural forests, nitrogen was found to be lower under coarse woody debris than in other areas, and similar effects have been shown experimentally using coversoils salvaged from forest sites (Hafner and Groffman 2005; Kwak et al. 2015). Application of coarse woody debris on reclamation sites can modify site conditions and influence vegetation development. At boreal forest reclamation sites, coarse woody debris application has been shown to increase vegetation cover (Brown and Naeth 2014) and improve soil quality (Kappes et al. 2007). However the influence of microsite and nutrient cycling effects associated with coarse woody debris application will likely differ with the forest type from which coversoil is salvaged due to the differences in soil properties and propagule banks, as well as the coarse woody material type and size.

As in natural forests, the canopy composition and closure are important factors that influence the understory vegetation. To establish and develop a canopy, tree seedlings are often planted at forest reclamation sites (Hart and Chen 2006; Padilla and Pugnaire 2006; Pensa et al. 2008). Achieving rapid canopy closure may prevent undesirable species such as aggressive rhizomatous grasses from becoming established and/or dominant in these early stage plant communities and canopy closure can promote a shift of the understory community towards shade tolerant, later successional plant species emerging from the coversoil propagule bank. High density planting of fast growing tree seedlings has been shown to suppress aggressive rhizomatous grass at a tropical reclamation site (Tamang et al. 2008); this suggests that tree seedlings planted at a higher than typical density at reclamation sites may result in rapid canopy closure and accelerated development of a diverse, forest understory community resembling more natural conditions. Depending on the forest type coversoil is salvaged from, the impact of the developing tree canopy may interact with the expression the propagule bank of these coversoil types.

Site topographic features are important drivers of forest composition. Slope and aspect of landscape features determine solar radiation levels, particularly in high latitude forests. At high latitudes the sun is at lower angles and north-facing slopes, which receive less solar radiation, are typically cooler and moister and often have lower soil nitrogen levels than south facing slopes; these resulting site characteristics could strongly influence ecological processes and vegetation community composition (Bonan and Shugart 1989; Small and McCarthy 2005). Topographic features also influence how vegetation communities respond to disturbance; in boreal forests, Astrom et al. (2007) showed that the effect of clearcutting on vegetation communities was stronger on south facing than north facing slopes. Constructed landscape features such as hills are thus expected to have a strong influence on vegetation communities developing at heavily disturbed reclamation sites. Development of the plant community, including species emerging from the coversoil propagule bank and species that arrived on the site in other ways (i.e. wind transport, transport on construction equipment), in response to material placement is likely to vary with topographic position. Species groupings (i.e. native *versus* introduced species, or functional types) in the community may respond differently to the environmental pressures present at different topographic positions. In natural communities, with lengthy histories of vegetation-environment interactions, it is impossible to separate the influence of vegetation on the environment from the influence of environment on vegetation. However, reclamation sites offer a rare opportunity to examine these relationships, on soil materials that have no history in their landscape position. Under these controlled conditions the vegetation community development in response to site characteristics such as aspect, the placement of salvaged coversoil, tree seedling planting density, and coarse woody debris application can be more closely examined. From this perspective it is possible to clarify and potentially separate the respective influence of physical site characteristics (such as aspect), remnant biological and structural legacies present in the coversoil, and site amendments on plant community development.

This chapter describes a study carried out at a large scale surface mine located in the Athabasca Oil Sands Region, Alberta, Canada. We tested the influence of planted tree seedling density, topographical aspect, and coarse woody debris abundance on the diversity, cover and composition of the colonizing vegetation derived from coversoil salvaged from two different forest types.

Objective:

Determine how diversity, cover and community composition of the colonizing vegetation is related to soil and plant propagule properties of coversoil salvaged from two forest types and how aspect, coarse woody debris volume, and the planting density of the associated tree species affects the outcome.

The following hypotheses were tested:

1. Vegetation diversity will be higher in areas planted with tree seedlings at higher densities; diversity will be higher on north-facing (cooler) slopes than south-facing (warmer) slopes
2. Due to greater energy inputs, vegetation cover will be higher on south-facing (warmer) slopes than north-facing (cooler) slopes and will be positively associated with coarse woody debris abundance.
3. Community composition will differ on north and south facing aspects, and will be affected by density of planted tree seedlings and abundance of coarse woody debris.

2.2 Materials and Methods

2.2.1 Research Area

This research took place on a reclaimed area at Syncrude Canada Ltd. (SCL)'s Base Mine, located roughly 40 km north of Fort McMurray, Alberta, Canada. The research area is situated within the central mixed-wood subregion of the boreal natural region; the climate in this region is characterized by very cold winters and short, warm summers (Natural Regions Committee 2006). The mean annual temperature in Fort McMurray is 1ºC (based on a 30 year average). The mean annual precipitation for the same time period was 418.6 mm, with 316.3 mm of that falling as rain. The coldest temperatures occur in January, with an average temperature of -17.4ºC, and the warmest month is July, with an average temperature of 17.1ºC (Environment Canada 2015). Temperature and precipitation were similar in the first two years of our study (2012 and 2013) although in 2013 much of the precipitation fell early in the growing season while in 2012 precipitation was more evenly distributed over the season (Table 2-1, Appendix figure B1). In 2015, temperature and total precipitation over the growing season was lower than in 2012 or 2013.

Soils in upland areas in this region are typically Grey Luvisols or Dystric and Eutric Brunisols, with Brunisolic soils associated with jack pine (*Pinus banksiana* Lamb.) dominated forests and Luvisolic soils associated with forests that are a mixture of broadleaf species (aspen (*Populus* *tremuloides* Michx.), poplar (*Populus balsamifera* L.) or birch (*Betula papyrifera* Marsh.)) with white spruce (*Picea glauca* Moench (Voss)). Wetlands, primarily forested or shrubby bogs or fens dominated by organic soils, are also an important component of the landscape (Natural Regions Committee 2006).

2.2.2 Field site

This research was conducted in the upland areas of a 57 ha experimental watershed which is a large collaborative research study (the Syncrude Sandhill Watershed). The research plots were located in upland areas (hummock or hill features) that surrounded roughly 17 ha of wetland area. The landforms at this site were constructed out of clean tailings sand placed at a depth of 10 m on top of a former soft tailings pond (Pollard et al. 2012). After placing a layer of salvaged subsoil over the tailings sand, a capping layer of coversoil was placed on the eight upland hummock landforms and one flat area. The coversoil was salvaged from two donor forest types typical of the region: 1) a 'rich-mesic' forest type, characterized by mesic moisture and nutrient regimes, Luvisolic soils, a *Populus tremuloides* and/or *Picea glauca* overstory, and a lush understory; and 2) a 'poor-xeric' forest type, characterized by xeric moisture regimes, nutrient poor Brunisolic soils, a *Pinus banksiana* overstory, and a sparse understory (Beckingham and Archibald 1996). Subsoil materials were chosen to be appropriate to the 'target' rich-mesic or poor-xeric forest type. In areas capped with coversoil from the rich-mesic forest type, a 30 cm layer of fine textured clay loam subsoil was placed below the coversoil, and in areas capped with coversoil from the poor-xeric forest type, a 40 cm layer of coarse textured sandy subsoil was placed below the coversoil. Six of the eight hummocks were capped with material salvaged from a poor-xeric forest site and two hummocks and one flat area were capped with material salvaged from a rich-mesic site (Figure 2-1). Coversoil from the rich-mesic site was placed at a thickness of 20 cm, and material from the poor-xeric site was placed at a thickness of 15 cm; both types of coversoil were salvaged at a depth of 20 cm (Syncrude Canada Ltd. 2008). Coarse woody debris was placed on all of the hummocks after coversoil placement; abundance varied widely within hummocks. Coarse woody debris originated from a mix of species, primarily *Populus balsamifera,* and was stored for less than one year before placement.

One-year-old seedlings (container stock) of three common boreal forest trees (*Populus tremuloides*, *Picea glauca* and *Pinus banksiana*) were planted in June 2012 in treatment areas to test the effects of planting density on understory vegetation development. A ‘high’ (10 000 stems per hectare), ‘medium’ (5 000 stems per hectare) and ‘no’ (0 stems per hectare) planting density treatment was established on each hummock. As with the coversoil and subsoil materials, the species composition of planted tree seedlings in areas capped with poor-xeric and rich-mesic coversoils was selected to be appropriate for the ‘target’ poor-xeric or rich-mesic forest type: hummocks capped with coversoil from a poor-xeric forest type were planted with a mixture of 80% *Pinus banksiana*, 10% *Populus tremuloides* and 10% *Picea glauca*, while hummocks capped with coversoil from a rich-mesic forest type were planted with a mixture of 80% *P. tremuloides*, 10% *P. banksiana* and 10% *P. glauca*. Height of planted seedlings was surveyed in August of 2012, 2013 and 2014; seedling height was not measured in the final year of the vegetation study (2015). Ten individuals from each planted species (*P. tremuloides, P. banksiana, P. glauca*) in each vegetation plot were measured; the same individuals were measured in each year. In 2012, in areas capped with both coversoil materials *P. tremuloides* individuals were on average taller than individuals of the other species (Appendix Table A1). Heights of all three species were similar between the two coversoils in 2012. In 2014, *P. tremuloides* individuals were still taller than the other species (44.94 cm in areas capped with poor-xeric coversoil and 89.63 cm in areas capped with rich-mesic coversoil), but individuals of all species were taller in areas capped with a rich-mesic than a poor-xeric coversoil.

Vegetation measurement plots (7 × 7 m) were established within each planting density treatment at each of the hummocks and kept free of any foot traffic over the experimental period. Depending on the size of the hummocks, between two and five vegetation plots were constructed per planting treatment. Across the site a total of 78 plots were established, 57 plots in areas covered with surface soil material salvaged from a poor-xeric site type and 21 plots in areas covered with surface soil material salvaged from a rich-mesic site type. Within a treatment, plots were located to capture the different aspects present on each hummock; north and south aspects, as well as flat areas, were well represented, while only a smaller number of plots were located on west aspects and none on east aspects. In each vegetation plot four 1 × 1 m subplots were laid out in the corners of the plot to assess vegetation cover.

2.2.3 Vegetation and Environmental Variable Measurements

In mid to late August of 2012, 2013 and 2015 vegetation community composition was surveyed. Plant species were identified and their percent cover was visually estimated. Cover by bare ground was also visually estimated. Covers were estimated to the nearest percentage up to 10% and to the nearest 5% after; if less than 1%, cover was either determined to be 0.5% or as a trace (0.05%). Each species was subsequently classified into functional types (forb, graminoid, shrub, (unplanted) tree and non-vascular) and vascular plants were classified as native or introduced (Moss 1994; USDA 2016). In 2012 coarse woody debris amount in each vegetation plot was assessed using an adapted line intercept method (Van Wagner 1982, Marshall et al. 2000). In each plot, a 36 m transect was laid out as an equilateral triangle with sides of 12 m. All woody debris pieces intersecting the transect were classified according to five diameter classes and volume of woody debris (m^3/ha) was estimated.

Heat load index was calculated by converting aspect into a linear value from 0 – 1, such that the warmest aspects (SW) were assigned a 1 and the coldest aspects (NE) a 0 (McCune and Keon 2002).

2.2.4 Statistical Analysis

All analyses were carried out in R version 3.1.2 (R Core Team 2014). Areas capped with coversoils salvaged from different forest types (rich-mesic and poor-xeric forest sites) were analyzed separately. Species richness and total vegetation cover per sample plot in areas capped with the two coversoils were compared using two sample t-tests; otherwise responses of the plant communities arising from the two different material types to the treatment variables were only qualitatively compared. Since we also expected significant variation between years due to colonization and climate differences between growing seasons, separate analyses were also run for each year. Alpha was set at 0.05 for all models.

Linear mixed effects models

Linear mixed-effects models were constructed to assess the effect of planting density, coarse woody debris volume and heat load index on univariate response variables describing vegetation cover and diversity. Measured response variables used to assess vegetation cover included total vegetation cover and cover by native, introduced, forb and graminoid species. Richness and cover of shrubs, non-planted tree species and non-vascular species were not analyzed statistically as these were very low across the site. Vegetation diversity was assessed using Hill's diversity numbers N_0 (species richness), N_1 (e^x, where x=Shannon's index) and N_2 (the inverse of Simpson's index). Hill's numbers measure effective numbers of species; rare species are weighted most heavily in N_0 and have decreasing weight in calculating N_1 and N_2 (Hill 1973). In addition to total species richness (Hill number N_0), richness of native, introduced, forb and graminoid species was modelled.

For all linear mixed effect models, seedling planting density, coarse woody debris volume (CWD) and heat load index (HLI) were used as independent variables. A random term was included (1|Hummock/Plot/Subplot). Scatterplots of residuals were assessed for all models to ensure that assumptions of linearity, homoscedasticity and normality were met. Statistically significant effects of continuous variables (coarse woody debris volume and heat load index) were determined to be either positive or negative. Statistically significant effects of the categorical variable (planting density) were followed up using pairwise comparisons of least squares means among the three planting densities. Interactions were removed from the model when non-significant. Statistically significant interactions were assessed by plotting the effect of one continuous variable on the response variable at different levels of the (continuous or categorical) moderating variable. When the moderating variable was also continuous, the response variable was plotted at the mean and at one standard deviation above and one standard deviation below the mean of the moderating variable. When the moderating variable was categorical (planting density), the response variable was plotted at the three levels of the treatment. To assess a three-way interaction between the categorical (planting density) and two continuous (coarse woody debris, heat load index) variables, the interaction between the continuous variables was plotted separately for each level of planting density.

Permutational multivariate analysis of variance models

Permutational multivariate analysis of variance (PERMANOVA) models were constructed to assess the effects of three independent variables (planting density, coarse woody debris, heat load index) and their interactions on community composition. A random term was included as in the linear mixed effects models. Interactions were removed from the model when non-significant. Statistically significant interactions between categorical (planting density) and continuous (coarse woody debris, heat load index) variables were assessed by creating models of the effect of the continuous variable separately for each level of the categorical variable and determining at which levels the continuous variable was significant. To assess interactions between the categorical (planting density) and two continuous (coarse woody debris, heat load index) variables, the interaction between the continuous variables was assessed separately for each level of planting density to determine significance.

NMDS ordinations

NMDS ordinations were used qualitatively to examine vegetation community change from 2012 to 2015 in the whole site and in each coversoil type.

2.3 Results

A total of 172 species were identified across the site, with 67 species identified in areas capped with coversoil from a poor-xeric site and 138 species identified in areas capped with coversoil from a rich-mesic site (adjusted for the unequal sample sizes in areas capped with the two coversoils) (Appendix Table A2). Species richness per vegetation subplot was significantly higher in areas capped with coversoil from rich-mesic than poor-xeric forest types (Table 2-2). Considering per subplot species richness, a greater proportion of species were native in areas capped with coversoil salvaged from a poor-xeric forest as compared to areas capped with coversoil from a rich-mesic forest. Relatively more species in the poor-xeric coversoil were graminoids and shrubs, while in the rich-mesic coversoil more species were forbs (Figure 2-2A). Vegetation cover per subplot was not significantly different between the two site types and followed a similar pattern to species richness, with proportionally greater cover by native species, graminoids and shrubs in areas capped with poor-xeric than rich-mesic coversoils (Figure 2-2B).

2.3.1 Coversoil and subsoil characteristics

Soil characteristics, including texture, conductivity and nutrient availability, differed between the two coversoils and the two subsoils. Coversoil salvaged from a poor-xeric forest site was largely composed of sand, while coversoil salvaged from a rich-mesic forest site had a larger clay component (Table 2-3). Total organic carbon, total nitrogen and total organic matter were greater in coversoils from rich-mesic than poor-xeric forest types. Available ammonium, nitrate, and potassium were higher in rich-mesic than poor-xeric coversoil, while available phosphorus was higher in poor-xeric coversoil. Soil pH, sodium and cation exchange capacity were higher in the rich-mesic than the poor-xeric coversoil. Characteristics of the sandy subsoil that underlay areas capped with the poor-xeric coversoil differed substantially from the clay loam subsoil that under lay areas capped with coversoil from a rich-mesic forest type. The sandy subsoil included much more sand and less clay and had a lower cation exchange capacity and lower levels of sodium, total organic carbon and organic matter than the clay loam subsoil. Both subsoils had few available nutrients; available ammonium, nitrate, and phosphorus were below the detectable limit. However, the clay loam subsoil had a fairly high level of available potassium while this nutrient was undetectable in the sandy subsoil.

2.3.2 Vegetation diversity and cover in areas capped with coversoil salvaged from a poor-xeric site

In sites capped with the poor-xeric coversoil planting density had no effect on the measured vegetation cover variables (data not shown); however, planting density significantly affected a number of diversity measures (total and native species richness, Hill numbers N_1 and N_2); in all cases, diversity was higher in the high and/or medium planting density compared to the unplanted treatment (Tables 2-4 & 2-5). Species richness (Hill number N_0) was only significantly affected in 2015 when N_0 (richness) was higher in the medium and high density treatments than in the unplanted treatment. Diversity measure N_1 (e^x, where x=Shannon’s index) was higher in 2012 for both the high and medium than the unplanted planting density treatments while in 2013, N_1 was only significantly higher in the high density planting treatment. The inverse of Simpson’s index (Hill number N_2) was significantly higher in 2012 in the medium density planting treatment than in the unplanted treatment; the high density treatment was intermediate between the two. In 2013, native species richness was significantly higher in the high density compared to the unplanted treatment, while the medium density treatment was intermediate. However, this effect was not detectable in 2012 or 2015.

In 2015, heat load index (HLI; reflecting aspect) had a significant negative relationship with Hill numbers N_1 and N_2 and a significant, positive relationship with introduced species richness; there were no effects of HLI in 2012 or 2013 (Tables 2-4 & 2-6).

Coarse woody debris affected measures of vegetation cover but not of diversity; the effects, when significant, were negative but in some cases also interacted with HLI (Tables 2-4 & 2-7). In both 2012 and 2015, coarse woody debris had significant, negative effects on total vegetation cover. In 2015, coarse woody debris also had significant, negative effects on cover by native species and graminoids. The negative effect of coarse woody debris on graminoid cover was also significant in 2013.

In two of the three years studied, the effect of heat load index on vegetation diversity and cover differed depending on coarse woody debris volume (HLI x CWD interaction; Table 2-4). In 2015 CWD and HLI influenced species richness; when coarse woody debris volume was low, species richness decreased as heat load index increased, but where coarse woody debris volume was high, species richness increased as heat load index increased (Appendix Figure B2). In 2013, there was a significant interaction between heat load index and coarse woody debris on total vegetation cover and on forb cover. In areas where coarse woody debris volume was low, total vegetation cover decreased strongly as heat load index increased (Appendix figures B3 and B4). Where coarse woody debris volume was moderate, total vegetation cover decreased less strongly with increasing heat load index, and where coarse woody debris volume was high, there was a slight increase in total vegetation cover as heat load index increased. The changes in total cover with HLI and CWD were likely driven by the forb cover as it followed a similar pattern in response to these factors.

In the first two years diversity measures were also affected by the interaction between coarse woody debris volume and heat load index and this interaction was further impacted by planting density (Table 2-4). In 2012, in unplanted areas total species richness, native species richness and forb species richness decreased strongly as heat load index increased and when coarse woody debris volume was high, while species richness decreased weakly when CWD volume was moderate and increased when volume was low (Appendix figures B5-7). In the medium density treatment, however, total and native species richness declined with heat load index regardless of woody debris cover, while forb species richness decreased more strongly with heat load index when coarse woody debris volume was lower. In the high density planting treatment, all three measures of richness increased with heat load index when coarse woody debris volume was high, increased more weakly when volume was moderate and either increased or decreased very weakly when volume was low. In 2013, there was a significant interaction of all three factors on total species richness. In the unplanted areas, species richness decreased as heat load index increased while coarse woody debris volume had very little impact (Appendix figure B8). In the medium density planting treatment, species richness again decreased as heat load index increased; however, this effect was stronger when coarse woody debris volume was high. In the high density treatment, species richness decreased as heat load index increased when coarse woody debris volume was low but increased with heat load index when coarse woody debris volume was high.

2.3.3 Vegetation diversity and cover in areas capped with coversoil salvaged from a rich-mesic forest site

In areas capped with coversoil salvaged from a rich-mesic forest site, planting density significantly affected both vegetation diversity (Hill numbers N_1 and N2, native species richness, forb species richness) and cover (native species cover) measures. Measures of diversity and cover were, in all cases, higher in the high and/or medium planting density than in the unplanted treatment (Table 2-5 & 2-8). In 2012, Hill number N_1, was significantly affected by planting density. N_1 was significantly higher in the high density treatment than the unplanted treatment, while the medium density treatment was intermediate. Hill number N_2 was significantly affected by planting density in 2015. N_2 was significantly higher in both the high and medium density treatments than in the unplanted treatment. Native species richness, forb species richness and native species cover were significantly affected by planting density in 2012. Native species richness was significantly higher in the high density treatment than in the medium or unplanted treatments. Forb species richness was significantly higher in the high density than the medium density treatment. Native species cover was significantly higher in the high density treatment than in the unplanted treatment, while cover in the medium density treatment was intermediate.

In 2015, heat load index (HLI; reflecting aspect) had a significant, negative effect on Hill numbers N_1 and N_2 (Tables 2-6 & 2-8). In 2012, heat load index had a significant, negative effect on native species richness and a significant, positive effect on introduced species richness, and in 2013, HLI had significant, negative effects on native species richness, introduced species richness and native species cover.

As in areas capped with coversoil from a poor-xeric forest site, coarse woody debris primarily affected vegetation cover, and the effects, when significant, were negative (Tables 2-7 & 2-8). Coarse woody debris also had a limited number of significant effects on diversity; in 2015 coarse woody debris had significant, positive effects on Hill numbers N_1 and N_2. In 2013, coarse woody debris had significant, negative effects on total vegetation cover, native species cover, introduced species cover and forb cover and in 2015 woody debris had significant, negative effects on total vegetation cover and native species cover.

In two of the years studied, diversity measures were affected by the interaction of planting density, coarse woody debris volume and heat load index (Table 2-8). In 2012 there was a significant interaction of the three factors on total and graminoid species richness, and in 2015 on native species richness. In unplanted areas, total, graminoid and native species richness responded similarly to coarse woody debris and heat load index; richness increased with heat load index when woody debris volume was high and decreased when volume was low (Appendix figures B9-B11). In the medium density treatment, total and graminoid species richness responded similarly; richness increased with heat load index when woody debris volume was high, decreased weakly when volume was moderate and decreased more strongly when volume was low (Appendix figures B9 & B10). Native species richness responded differently; richness increased with heat load index at all levels of woody debris volume and the increase was strongest when volume was high (Appendix figure B11). In the high density planting treatment, all three measures of richness responded similarly. Richness decreased with heat load index when coarse woody debris volume was high and increased when volume was low; richness was intermediate when volume was moderate.

2.3.4 Vegetation community composition

In areas that were capped with a poor-xeric coversoil, planting density, heat load index and coarse woody debris volume all significantly affected vegetation community composition in 2012 and 2013 (Table 2-9). In 2015, only coarse woody debris volume had a significant effect on community composition. There was also a significant interaction in 2013 between coarse woody debris and heat load index, and a significant three-way interaction between coarse woody debris, heat load index and planting density (Table 2-10). In the unplanted treatment, coarse woody debris and heat load index interacted significantly to affect community composition, while in the medium and high density planting treatments, coarse woody debris and heat load index both significantly affected composition but there was not a significant interaction between the two.

In areas capped with coversoil salvaged from a rich-mesic site, planting density, coarse woody debris and heat load index all had significant effects on community composition in 2012 (Table 2-9). There were also significant interactions between planting density and heat load index, and between planting density, coarse woody debris, and heat load index in 2012 (Table 2-10). In the unplanted treatment, both coarse woody debris and heat load index significantly affected community composition, but there was no significant interaction between these factors. In the medium density planting treatment, neither of the factors or the interaction was significant. In the high density treatment, only heat load index had a significant effect. In 2013, heat load index had a significant effect on the community, and there was a significant interaction between planting density and heat load index, and between planting density, heat load index and coarse woody debris. In the unplanted treatment, coarse woody debris and heat load index significantly affected community composition. In the medium density planting treatment, heat load index significantly affected community composition and there was a significant interaction between heat load index and coarse woody debris. In the high density planting treatment, neither of the factors significantly affected community composition. As in areas capped with coversoil from a poor-xeric forest site, in 2015 only coarse woody debris had a significant effect on community composition.

2.3.5 Vegetation community change from 2012 to 2015

An NMDS ordination including data from all plots showed a clear separation in community composition between areas capped with coversoil from poor-xeric versus rich-mesic forest types (Figure 2-3A). The species most strongly associated with the first ordination axis were a native lichen (*Cladonia mitis*) and an introduced forb (*Lepidium densiflorum*). The species most strongly associated with the second axis were a native grass (*Festuca rubra*) and an introduced forb (*Trifolium pratense*). There was some evidence of convergence between communities of the two coversoil types over time with greater similarity in 2015 than in the two earlier years, although PERMANOVA models showed that in all three years studied, community composition differed significantly between the two coversoil types (Table 2-11). An NMDS ordination of sites capped with coversoil from the poor-xeric site type showed greater similarity between 2012 and 2013 than 2015. Further, there was lower variability among plots in 2015 than in 2012 or 2013 (Figure 2-3B). In this material type, the species most strongly associated with the first axis were a native forb (*Achillea millefolium*) and a native moss (*Dicranum* sp.). The species most strongly associated with the second axis were two introduced forbs (*Chenopodium album* and *Lotus corniculatus*). In areas capped with coversoil salvaged from rich-mesic a forest site, an NMDS ordination showed that variability decreased over the three years studied (Figure 2-3C). The community in 2015 was more similar to the community in 2013 than in 2012. In this material type, the species most strongly associated with the first axis were a native shrub (*Amelanchier alnifolia*) and a native forb (*Astragalus canadensis*). The species most strongly associated with the second axis were a native forb (*Ranunculus scleratus*) and an introduced forb (*Polygonum convolvulus*).

2.4 Discussion

At the study site, seedling planting density, heat load index (reflecting topographical aspect), coarse woody debris volume as well as interactions between these three factors all impacted vegetation communities in areas capped with coversoils salvaged from poor-xeric and rich-mesic forest types. Planting density and heat load index primarily impacted vegetation diversity. Higher density planting treatments and cooler (north-facing) aspects were associated with increased diversity. Coarse woody debris volume primarily negatively impacted vegetation cover.

We hypothesized that vegetation diversity would be higher in areas planted with tree seedlings at higher densities; this hypothesis was generally supported. Planting density had significant effects on total species richness and metrics of diversity (Hill numbers N_1 and N_2) as well as native and forb species richness. In all of these cases diversity was positively associated with higher planting density. In areas capped with coversoil from a poor-xeric forest site, planting density significantly affected native species richness in two of the years studied. Native species were a greater proportion of the species assemblage in this coversoil than in the rich-mesic coversoil. This may explain the stronger response of these species to planting density in the poor-xeric coversoil. Similarly, in areas capped with coversoil from a rich-mesic site where forb species were a greater proportion of the species assemblage, forb species richness was significantly affected by planting density in 2012. Environmental modification stemming from seedling planting density treatments likely impacted vegetation diversity. Research in both natural and reclaimed forests has shown that canopy trees are able to modify the understory growth environment and drive shifts in species composition (Hart and Chen 2006; Padilla and Pugnaire 2006). Likewise, plants adapted to forest understory environments are often more successful in cooler, shaded environments than in open, disturbed areas (Watkins et al. 2003). Densely planted tree seedlings may accelerate forest succession by creating a microclimate more suitable for native, forest adapted species (Strong 2000). The higher density planting treatments, even at the early stage we studied, may have created an environment more conducive to forest plant growth, leading to greater emergence of forest species from the propagule bank present in the salvaged coversoil and the development of a more diverse community. Some research has shown that densely planted tree seedlings at reclamation sites can result in rapid canopy closure and successional development (Groninger et al. 2007). However, it is not clear if this initial acceleration of successional development will be maintained over the longer term (greater than 10 years after site construction) (Hodačová and Prach 2003). The effect of planting density on metrics of vegetation diversity (total, native, forb and graminoid species richness) was modified by both heat load index (reflecting aspect) and coarse woody debris volume. Measures of diversity impacted by this complex interaction responded differently in areas capped with coversoils from poor-xeric and rich-mesic forest types.

We found some support for our hypothesis that vegetation diversity would be higher on north-facing than south-facing slopes. The association between north facing slopes and higher diversity was stronger in areas capped with rich-mesic coversoil than in areas capped with poor-xeric coversoil. Heat load index (reflecting aspect) had significant effects on metrics of diversity (Hill numbers N_1 and N_2, introduced species richness) in both coversoil types and on native species richness in the rich-mesic coversoil. Diversity was higher on north facing slopes except in the case of introduced species richness. In the first year studied, introduced species richness was higher on south facing aspects in areas capped with coversoil from a rich-mesic site. In the final year studied, introduced species richness was higher on south facing aspects in areas capped with poor-xeric coversoil. Many introduced species are more successful in warm, dry, high light conditions (Parendes and Jones 2000). Therefore, south facing slopes, which receive more solar radiation than north facing slopes, may provide a more favourable environment for some introduced plant species. However, in areas capped with coversoil from a rich-mesic forest site, where proportionally more introduced species were present than in areas capped with coversoil from a poor-xeric forest site, introduced species richness was only higher on south facing slopes in 2012. In 2013, introduced species richness was higher on north-facing aspects. The success of introduced species on different aspects may be related to yearly climatic conditions; the later months of the 2013 growing season experienced less precipitation than in 2012, which may have resulted in increased water stress on south facing slopes. Although introduced species are often more tolerant of warm, dry conditions than native species, severe drought conditions at reclamation sites have been shown to reduce introduced species cover (Alday et al. 2010). During the later part of the 2013 season, potentially very dry conditions on south facing slopes may have negatively affected introduced species, leading to higher richness of these species on north facing slopes. Native species richness was likely also driven by differences in environmental conditions between north and south facing slopes. In two of the years studied, native species richness was higher on north than south facing slopes. Forest plants, adapted to cooler, moister environments, often experience lower growth vigor and higher mortality in open, heavily disturbed reclamation sites (Djietror et al. 2011) and so more of the forest adapted species present in the coversoil propagule bank may have been successful on north facing aspects, leading to higher diversity in these areas. In areas capped with coversoil from a poor-xeric forest site, the effect of aspect on species richness was modified by the volume of coarse woody debris present in the final year studied; species richness on south facing slopes was higher when coarse woody debris was abundant. Amendment with coarse woody debris can moderate soil temperature and result in increased soil moisture on reclamation sites (Brown and Naeth 2014); the presence of coarse woody debris in our study may have been modifying the harsher environmental conditions (heat and water stress) present on south facing slopes.

We hypothesized that vegetation cover in areas capped with both coversoils would respond to aspect differently than diversity, with higher cover expected on south facing than north facing slopes. We expected that this effect would be partially driven by ruderal, often introduced, species, many of which are more successful than forest adapted species in dry, high light environments (Parendes and Jones 2000; Djietror et al. 2011). However, we did not find support for this hypothesis. Heat load index had a significant effect on only one cover response variable (native species cover in areas capped with coversoil from a rich-mesic forest site) in one of the years studied. In this case, native species cover was higher on north than south facing slopes. Higher native species cover on north facing slopes may have been driven by cooler, moister conditions, which may have been more suitable for native, largely forest adapted species than typically warmer, drier south facing slopes (Djietror et al. 2011). Other measures of vegetation cover did not respond to aspect. This suggests that water stress on south facing slopes may have been more severe than we anticipated. Indeed, some research on herbaceous vegetation cover in arid regions has found cover to be lowest on south facing reclaimed slopes due to the influence of water stress (Cano et al. 2002). In addition, substantially different vegetation communities found on different slope aspects in natural boreal forests, are also driven, in part, by differences in soil properties on these aspects (Bonan and Shugart 1989; Desta et al. 2004). At our study site, similar coversoil material was recently placed on all aspects. Therefore, substantial differences in soil characteristics likely had insufficient time in which to develop. This may explain the weak response of vegetation cover to aspect. Although vegetation cover responded weakly to aspect, we found in 2013, in areas capped with coversoil from a poor-xeric forest site, that coarse woody debris volume modified the effect of aspect on vegetation cover measures. Similarly to the interaction between aspect and coarse woody debris on species richness, total cover and cover by forb species were higher on south facing slopes when coarse woody debris was abundant. This suggests that coarse woody debris may have been able to modify harsh environmental conditions on these slopes.

Our hypothesis that vegetation cover would be positively associated with coarse woody debris volume was not supported. Application of coarse woody debris at similar reclamation sites has been shown to increase vegetation cover (Brown and Naeth 2014). However, while most of the significant effects of coarse woody debris were on vegetation cover, in all cases the effect was negative. In this case the negative effect of coarse woody debris on vegetation cover can be explained by the fact that the CWD itself occupies growing space within the plot.

We found support for our hypothesis that coarse woody debris, density of planted tree seedlings and aspect would affect community composition. Community composition can be a better indicator of successional development and 'success' at reclamation sites than measures of diversity or cover (Jochimsen 2001; Alday et al. 2011). This suggests that composition may be a more sensitive indicator of vegetation response to site factors than diversity or cover. In mature forests, coarse woody debris, the tree canopy and slope aspect are all strong drivers of community composition (Scheller and Mladenoff 2002; Warren 2007; Bonan and Shugart 1989).

Likewise, all three factors anticipated by our hypothesis were found to affect community composition. However, in the final year studied, for both material types, only coarse woody debris had a significant effect. For all other years all three factors had a significant effect on composition. While canopy closure, which typically drives a shift in the understory community towards shade tolerant, later successional stage species (Hart and Chen 2006), had not occurred at the study site, tree planting density significantly influenced community composition. This may be partially due to the high planting densities tested. Tree seedlings planted at high densities can strongly influence the vegetation community and have been shown to quickly competitively exclude introduced species (Harrington et al. 2003). Aspect can also have a strong effect on community composition at reclamation sites. Alday et al. (2011) found that vegetation communities present on north, south and flat aspects at a reclaimed mine site developed on diverging successional trajectories. At our research site, the importance of aspect in driving community composition may increase with time.

Between 2012 and 2015, vegetation communities in areas capped with coversoils salvaged from poor-xeric and rich-mesic forest sites became more similar to each other. Because of the relatively short timescale of our study, it is not clear whether this trend of convergence will continue as the site develops. Other research at reclamation sites has shown that major shifts in the vegetation community often occur in the first few years following site construction. This suggests that the convergence we observed may be a short term shift (Prach and Pysek 2001). However, there is also evidence that initial post disturbance environmental conditions and species assemblages can determine the successional trajectory of the site and impact future colonizing species (del Moral and Lacher 2005). At reclamation sites, initial soil characteristics and propagule presence have been shown to strongly drive the vegetation community in the early stages of development and to be key determinants of successional trajectory (Moreno-de las Heras et al. 2008; Mackenzie and Naeth 2010). These studies suggest that coversoil type, with associated differences in propagule bank and soil characteristics, will strongly impact site successional trajectory. However, other research has shown that environmental factors such as aspect can be equally strong determinants of successional trajectory at reclamation sites, and that communities at nearby differently treated reclamation areas become more similar to each other over time (Alday et al. 2011; Baasch et al. 2012). Given the proximity of the treatments in this study, it is not clear whether, over longer time scales, the forest type that the coversoil is salvaged from will be the primary driver of vegetation communities, or if site features such as constructed topography, density of planted tree seedlings and coarse woody debris will be the stronger drivers of vegetation community development.

2.5 Conclusion

Use of coversoils salvaged from different forest types resulted in the development of vegetation communities composed of different proportions of native and introduced species and functional types. In areas capped with coversoil salvaged from a poor-xeric forest site, vegetation communities included a greater proportion of native species, graminoids and shrubs, while in areas capped with coversoil salvaged from a rich-mesic forest site, vegetation communities were composed of proportionally more introduced species and forbs.

Regardless of coversoil, vegetation diversity was primarily influenced by seedling planting density (canopy cover) and topographical aspect. In both coversoils metrics of diversity (Hill numbers N_1 and N_2, total, native and forb species richness) were highest in areas with north facing aspects and higher tree density. North facing aspects, which typically experience less heat and moisture stress, and treatments with higher densities of tree seedlings may have created an environment that was more favourable for emergence and growth of the largely forest adapted species present in the propagule banks of the coversoils, leading to a more diverse community. Complex interactions between planting density, aspect and coarse woody debris impacted metrics of diversity in both coversoils. In areas capped with coversoil from a poor-xeric forest site, the effect of aspect on diversity was modified by coarse woody debris abundance, suggesting that coarse woody debris may have moderated the harsher environmental conditions present on south facing slopes in areas capped with the poor-xeric material, where water may have been limiting

Vegetation cover was largely influenced by coarse woody debris. Where high, coarse woody debris volume had a negative effect on vegetation cover. This was likely because coarse woody debris occupied large areas of sample plots, reducing space for vegetation to establish. Application of very high volumes of woody debris may limit growth of early establishment vegetation. Several measures of vegetation cover in areas capped with coversoil from a poor-xeric forest site were impacted by interactions between aspect and coarse woody debris similarly to diversity, suggesting that the potentially moderating effect of coarse woody debris on south facing slopes also impacted vegetation cover.

Community composition in areas capped with coversoils from both forest types was influenced by all three factors, although only coarse woody debris had a significant effect in all three years studied, and in the final year.

Vegetation communities in areas capped with coversoils salvaged from poor-xeric and rich-mesic forest types became more similar to each other over the years studied. However, it is not clear from our study whether this trend of convergence will continue. It is possible that, on longer timescales, topographical position, density of planted tree seedlings and coarse woody debris will be more important drivers of vegetation community development than initial coversoil source. Alternatively, convergence of communities developing in areas capped with the two coversoils may not continue, leading to substantially different mature forests.

Tables

Table 2-1: Growing season (May 1 – September 30) mean temperature (ºC) and total precipitation (mm) for 2012, 2013 and 2015, collected at Mildred Lake, Alberta. Data from Environment Canada (2015).

Year	Mean Temperature (ºC)	Total Precipitation (mm)
2012	16.3	60.2
2013	16.2	64.1
2015	15.3	38.8

Table 2-2: Results of two sample t-tests of species richness and total vegetation cover per subplot between areas capped with a poor-xeric and a rich-mesic coversoil (see Appendix Table A2 for a complete species list). *P* values are bolded when significant.

	***P* value**
Species richness per subplot	**0.0146**
Total cover per subplot (%)	0.6447

Table 2-3: Characteristics of coversoils and subsoils placed at the Sandhill Watershed site. Coversoils were salvaged from two forest types, a nutrient poor site with a xeric moisture regime (poor-xeric) and a nutrient rich site with a mesic moisture regime (rich-mesic). The coversoil from a poor-xeric forest site was underlain by a sandy subsoil material, and the coversoil from a rich-mesic forest site was underlain by a clay loam subsoil material. Data (mean ± one standard deviation) were collected in 2013 (Syncrude Canada Ltd. 2014).

Soil Material	Poor-xeric coversoil	Sandy subsoil	Rich-mesic coversoil	Clay loam subsoil
Soil texture	Sand	Sand	Clay loam	Sandy clay loam
% Sand (by weight)	90.9±1.93	97.9±1.03	41.5±4.31	55.5±4.13
% Clay (by weight)	2.7±1.34	1.2±0.59	32.1±4.35	24.6±4.30
pH	6.3±0.67	7.4±0.15	6.9±0.40	7.5±0.26
Cation exchange capacity (meq/100 g)	7±1.38	undetectable	19±4.45	10±2.21
Sodium (mg/kg)	32±12.39	26±5.38	76±54.76	116±79.73
Total organic carbon (% dry weight)	1.6±0.48	0.2±0.11	4.3±4.52	1.4±0.28
Total nitrogen (%	0.08±0.02	0.03±0.00	0.28±0.36	0.04±0.02

dry weight)				
Organic matter (%)	3.3±0.95	0.4±0.20	8.5±9.04	2.8±0.55
Available Ammonium (µg/g)	0.8±0.56	undetectable	2.6±8.20	undetectable
Available Nitrate (µg/g)	undetectable	undetectable	5±2.75	undetectable
Available Phosphorus (µg/g)	9±3.42	undetectable	7±2.90	undetectable
Available Potassium (µg/g)	39±9.79	undetectable	100±27.28	69±24.79

Table 2-4: Results of linear mixed effects models testing for the effects of tree planting density (PD), heat load index (HLI; reflecting slope and aspect), and coarse woody debris amount (CWD) on vegetation diversity (overall species richness (Hill number N_0), Hill numbers N_1 (e^x, where x=Shannon's index) and N_2 (the inverse of Simpson's index), and native, introduced, forb and graminoid species richness) and cover (all species, native species, introduced species, forb species, and graminoid species) in areas capped with a poor-xeric coversoil (see Appendix Table A2 for a complete species list). *P* values are bolded when significant. Interaction terms are shown when significant; interactions were removed from models when not significant.

Response Variable	Planting Density	Heat load Index	Coarse Woody Debris	PD x HLI	PD x CWD	CWD x HLI	PD x CWD x HLI
Species richness 2012	0.0722	0.8678	0.2791	0.2929	0.8794	0.5439	**0.0021**
Species richness 2013	**0.0145**	0.2558	0.5401	0.6968	0.1240	0.1017	**0.0428**
Species richness 2015	**0.0374**	0.8234	0.1298			**0.0480**	
N_1 2012	**0.0387**	0.7549	0.1573				
N_1 2013	**0.0161**	0.0659	0.3053				
N_1 2015	0.3165	**0.0138**	0.1996				
N_2 2012	**0.0494**	0.6085	0.2393				
N_2 2013	0.0523	0.0522	0.3976				
N_2 2015	0.3283	**0.0047**	0.4138				
Native sp. richness 2012	**0.0463**	0.5528	0.3210	0.4290	0.7738	0.4710	**0.0062**
Native sp. richness 2013	**0.0209**	0.0923	0.9179				
Native sp. richness 2015	0.1024	0.1916	0.1281				
Introduced sp. richness 2012	0.5770	0.0889	0.6117				
Introduced sp. richness 2013	0.9475	0.1349	0.2998				

Introduced sp. richness 2015	0.3236	**0.0077**	0.6358				
Forb sp. richness 2012	0.5225	0.4410	0.4373	0.1537	0.6724	0.8870	**0.0195**
Forb sp. richness 2013	0.4496	0.7893	0.6960				
Forb sp. richness 2015	0.6204	0.1849	0.2799				
Graminoid sp. richness 2012	0.8322	0.4248	0.4274				
Graminoid sp. richness 2013	0.4142	0.5716	0.0900				
Graminoid sp. richness 2015	0.3359	0.7554	0.2266				
Total cover 2012	0.1456	0.8852	**0.0314**				
Total cover 2013	0.2275	0.3091	**0.0207**			**0.0432**	
Total cover 2015	0.3776	0.8030	**<0.0001**				
Native sp. cover 2012	0.7177	0.9742	0.2518				
Native sp. cover 2013	0.1905	0.3159	0.0512				
Native sp. cover 2015	0.3489	0.7276	**<0.0001**				
Introduced sp. cover 2012	0.2377	0.9337	0.2229				
Introduced sp. cover 2013	0.7748	0.9819	0.1779				
Introduced sp. cover 2015	0.3879	0.1278	0.0695				
Forb sp. cover 2012	0.1978	0.8702	0.1907				
Forb sp. cover 2013	0.6983	0.7727	0.9410			**0.0004**	
Forb sp. cover 2015	0.8296	0.0545	0.0687				
Gram. sp. cover 2012	0.8794	0.4972	0.2627				
Gram. sp. cover 2013	0.3967	0.2867	**0.0084**				
Gram. sp. cover 2015	0.8863	0.7763	**0.0453**				

Table 2-5: Summary of least squared means (± standard error) showing all significant effects of planting density on metrics of vegetation diversity for sites capped with coversoils from two different forest types. N_1 is e^x, where x=Shannon's index, and N_2 is the inverse of Simpson's index. Letters in rows indicate significant differences between treatments. Unplanted=0 stems per hectare, Medium Density=5 000 stems per hectare, High Density=10 000 stems per hectare. See also Table 4 and 8.

(a) Poor-xeric coversoil

Response Variable	**Year**	**Unplanted**	**Medium Density**	**High Density**
Species richness	2015	13.15±0.49 a	14.51±0.49 b	14.53±0.48 b
N_1	2012	4.32±0.25 a	5.19±0.25 b	4.92±0.25 b
N_1	2013	5.27±0.25 a	5.77±0.25 ab	6.33±0.25 b
N_2	2012	3.44±0.21 a	4.12±0.21 b	3.88±0.21 ab
Native sp. richness	2013	7.83±0.51 a	8.57±0.51 ab	9.88±0.51 b

(b) Rich-mesic coversoil

Response Variable	**Year**	**Unplanted**	**Medium Density**	**High Density**
N_1	2012	2.93±0.28 a	3.42±0.29 ab	3.97±0.27 b
N_2	2015	2.66± 0.26 a	3.49±0.27 b	3.89±0.25 b
Native sp. richness	2012	2.99±0.59 a	3.71±0.60 a	5.15±0.58 b
Forb sp. richness	2012	5.23±0.97 ab	4.21±0.98 a	6.21±0.97 b
Native sp. cover	2012	0.46±0.22 a	0.64±0.23 ab	1.26±0.22 b

Table 2-6: Summary of estimates (± standard error) showing all significant effects of heat load index on metrics of vegetation diversity for sites capped with coversoils from two different forest types. N_1 is e^x, where x=Shannon's index, and N_2 is the inverse of Simpson's index. See also Table 4 and 8.

(a) Poor-xeric coversoil

Response Variable	**Year**	**Heat load Index Estimate**
N_1	2015	-0.82±0.32
N_2	2015	-0.73±0.25
Introduced sp. richness	2015	1.08±0.39

(b) Rich-mesic coversoil

Response Variable	**Year**	**Heat load Index Estimate**
N_1	2015	-1.82±0.79
N_2	2015	-1.38±0.64
Native sp. richness	2012	-2.24±0.93
Native sp. richness	2013	-4.90±1.66
Introduced sp. richness	2012	2.14±0.90
Introduced sp. richness	2013	-0.57±0.77
Native sp. cover	2013	-8.89±3.03

Table 2-7: Summary of estimates (± standard error) showing all significant effects of coarse woody debris amount on metrics of vegetation diversity for sites capped with coversoils from two different forest types. N_1 is e^x, where x=Shannon's index, and N_2 is the inverse of Simpson's index. See also Table 4 and 8.

(a) Poor-xeric coversoil

Response Variable	**Year**	**Coarse Woody Debris Estimate**
Total cover	2012	-0.13±0.06
Total cover	2015	-0.81±0.17
Native sp. cover	2015	-0.78±0.17
Graminoid sp. cover	2013	-0.11±0.04
Graminoid sp. cover	2015	-0.07±0.04

(b) Rich-mesic coversoil

Response Variable	**Year**	**Coarse Woody Debris Estimate**
N_1	2015	0.03±0.01
N_2	2015	0.03±0.01
Total cover	2013	-0.43±0.14
Total cover	2015	-0.84±0.23
Native sp. cover	2013	-0.14±0.05
Native sp. cover	2015	-0.65±0.23
Introduced sp. cover	2013	-0.30±0.14
Forb sp. cover	2013	-0.41±0.14

Table 2-8: Results of linear mixed effects models testing for the effects of tree planting density (PD), heat load index (HLI; reflecting slope and aspect), and coarse woody debris amount (CWD) on vegetation diversity (overall species richness (Hill number N_0), Hill numbers N_1 (e^x, where x=Shannon's index) and N_2 (the inverse of Simpson's index), and native, introduced, forb and graminoid species richness) and cover (all species, native species, introduced species, forb species, and graminoid species) in areas capped with a rich-mesic coversoil (see Appendix Table A2 for a complete species list). *P* values are bolded when significant. Interaction terms are shown when significant; interactions were removed from models when not significant.

Response Variable	**Planting Density**	**Heat load Index**	**Coarse Woody Debris**	**PD x HLI**	**PD x CWD**	**CWD x HLI**	**PD x CWD x HLI**
Species richness 2012	**0.0025**	0.9943	**0.0362**	0.8379	0.7805	0.7187	**0.0288**
Species richness 2013	0.1447	0.1834	0.2057				
Species richness 2015	0.1719	0.3756	0.7302				
N_1 2012	**0.0430**	0.5855	0.9906				
N_1 2013	0.3179	0.1072	0.3352				
N_1 2015	0.0991	**0.0362**	**0.0066**				
N_2 2012	0.1711	0.6257	0.9570				
N_2 2013	0.4581	0.1878	0.4943				
N_2 2015	**0.0444**	**0.0477**	**0.0052**				
Native sp. richness 2012	**0.0027**	**0.0298**	0.5149				
Native sp. richness 2013	0.1420	**0.0099**	0.2644				
Native sp. richness 2015	0.0524	0.1708	0.7682	0.1827	0.9067	0.6202	**0.0417**
Introduced sp. richness 2012	0.3608	**0.0319**	0.0843				
Introduced sp. richness 2013	0.4971	**0.0167**	0.7110				
Introduced sp. richness	0.8314	0.6694	0.1759				

2015							
Forb sp. richness 2012	**0.0152**	0.5803	0.1483				
Forb sp. richness 2013	0.3044	0.0808	0.3036				
Forb sp. richness 2015	0.3567	0.2008	0.3159				
Graminoid sp. richness 2012	0.4588	0.9002	0.5427	0.9832	0.8237	0.9099	**0.0359**
Graminoid sp. richness 2013	0.6909	0.7433	0.8180				
Graminoid sp. richness 2015	0.3225	0.6215	0.9823				
Total cover 2012	0.3734	0.3100	0.1280				
Total cover 2013	0.0929	0.5711	**0.0041**				
Total cover 2015	0.6044	0.7983	**0.0005**				
Native sp. cover 2012	**0.0474**	0.9618	0.6680				
Native sp. cover 2013	0.3521	**0.0102**	**0.0215**				
Native sp. cover 2015	0.4763	0.8049	**0.0074**				
Introduced sp. cover 2012	0.4263	0.2859	0.1469				
Introduced sp. cover 2013	0.2313	0.5219	**0.0292**				
Introduced sp. cover 2015	0.7986	0.2826	0.2283				
Forb sp. cover 2012	0.3904	0.2985	0.1326				
Forb sp.	0.1187	0.6402	**0.0059**				

cover 2013			
Forb sp. cover 2015	0.8667	0.9070	0.0984
Gram. sp. cover 2012	0.1732	0.5730	0.1966
Gram. sp. cover 2013	0.9045	0.4124	0.0530
Gram. sp. cover 2015	0.4928	0.7551	0.1558

Table 2-9: Results of permutational multivariate analysis of variance (PERMANOVA) models testing for the effects of tree planting density (PD), heat load index (HLI; reflecting slope and aspect) and coarse woody debris (CWD) amount on community composition in areas capped with coversoil from a poor-xeric (PX) and a rich-mesic (RM) forest site. *P* values are bolded when significant. Interaction terms are shown when significant; interactions were removed from models when not significant.

Coversoil Type	**Response year**	**Planting Density**	**Heat load Index**	**Coarse Woody Debris**	**PD x HLI**	**PD x CWD**	**CWD x HLI**	**PD x CWD x HLI**
PX	2012	**0.001**	**0.008**	**0.001**				
PX	2013	**0.052**	**0.002**	**0.001**	0.364	0.071	**0.012**	**0.004**
PX	2015	0.218	0.246	**0.001**				
RM	2012	**0.017**	**0.039**	**0.026**	**0.023**	0.265	0.690	**0.022**
RM	2013	0.522	**0.021**	0.242	**0.005**	0.124	0.205	**0.041**
RM	2015	0.173	0.098	**0.001**				

Table 2-10: Results of permutational multivariate analysis of variance (PERMANOVA) models testing for the effects of coarse woody debris (CWD) amount, heat load index (HLI; reflecting slope and aspect) and an interaction between the two (CWD x HLI) on community composition at each level of planting density treatment, when a significant interaction of planting density, coarse woody debris and heat load index was found (see Table 9) in areas capped with coversoil from a poor-xeric and a rich-mesic forest site. *P* values are bolded when significant. Interaction terms are shown when significant; interactions were removed from models when not significant. Unplanted=0 stems per hectare, Medium Density=5 000 stems per hectare, High Density=10 000 stems per hectare.

Coversoil Type	**Year**	**Planting Density**	**CWD**	**HLI**	**CWD x HLI**
Poor-xeric	2013	Unplanted	**0.006**	**0.025**	**0.001**
		Medium	**0.006**	**0.030**	
		High	**0.001**	**0.022**	
Rich-mesic	2012	Unplanted	**0.031**	0.051	
		Medium	0.371	0.286	
		High	0.203	**0.025**	

Rich-mesic	2013	Unplanted	**0.043**	**0.005**	**0.025**
		Medium	0.142	**0.031**	
		High	0.710	0.259	

Table 2-11: Results of permutational multivariate analysis of variance (PERMANOVA) models testing for the effects of coversoil type on community composition in areas capped with coversoil from a poor-xeric and a rich-mesic forest site. *P* values are bolded when significant.

Year	Coversoil type
2012	**0.001**
2013	**0.001**
2015	**0.001**

Figures

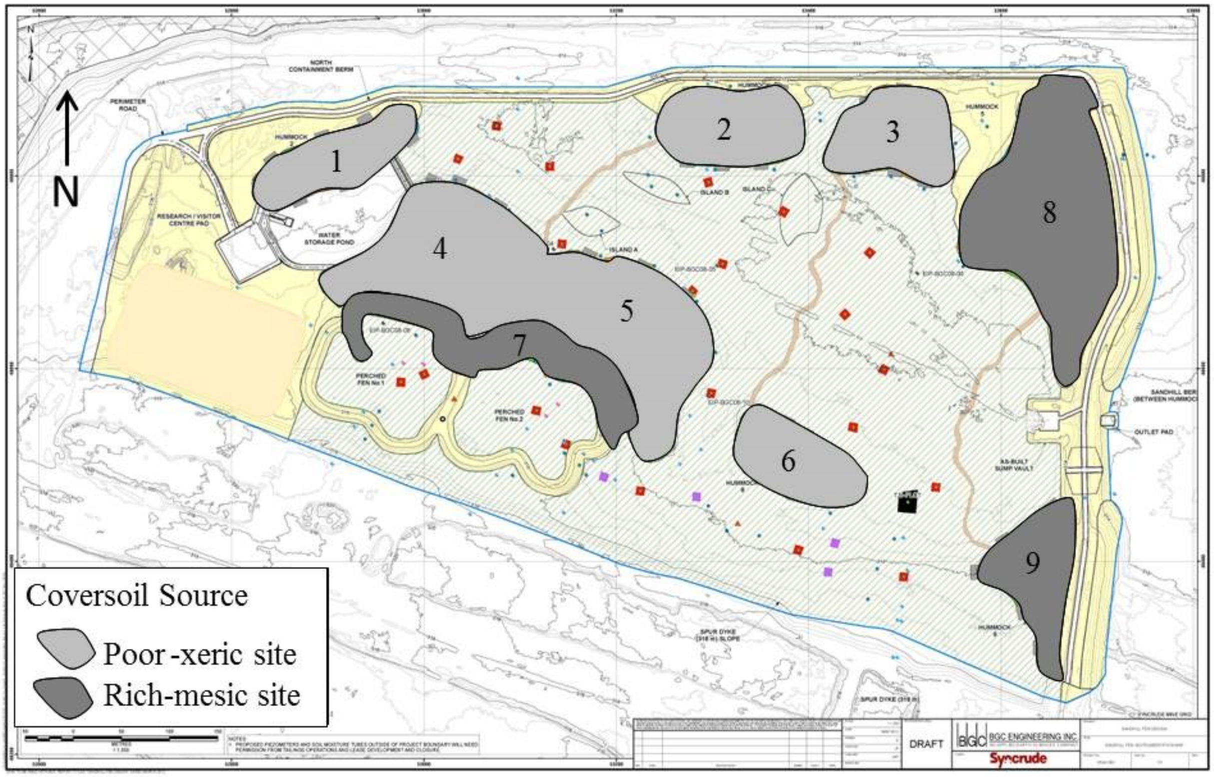

Figure 2-1: Overview of research site showing upland hummocks capped with coversoils from a poor-xeric and a rich-mesic forest site. Hummocks 1 – 6 were capped with coversoil salvaged from a poor-xeric site; a flat area (7) and hummocks 8 and 9 were capped with coversoil from a rich-mesic site. (Map produced by BGC Engineering Inc. for Syncrude Canada Ltd.; modified by Fran Leishman and Elizabeth Hoffman).

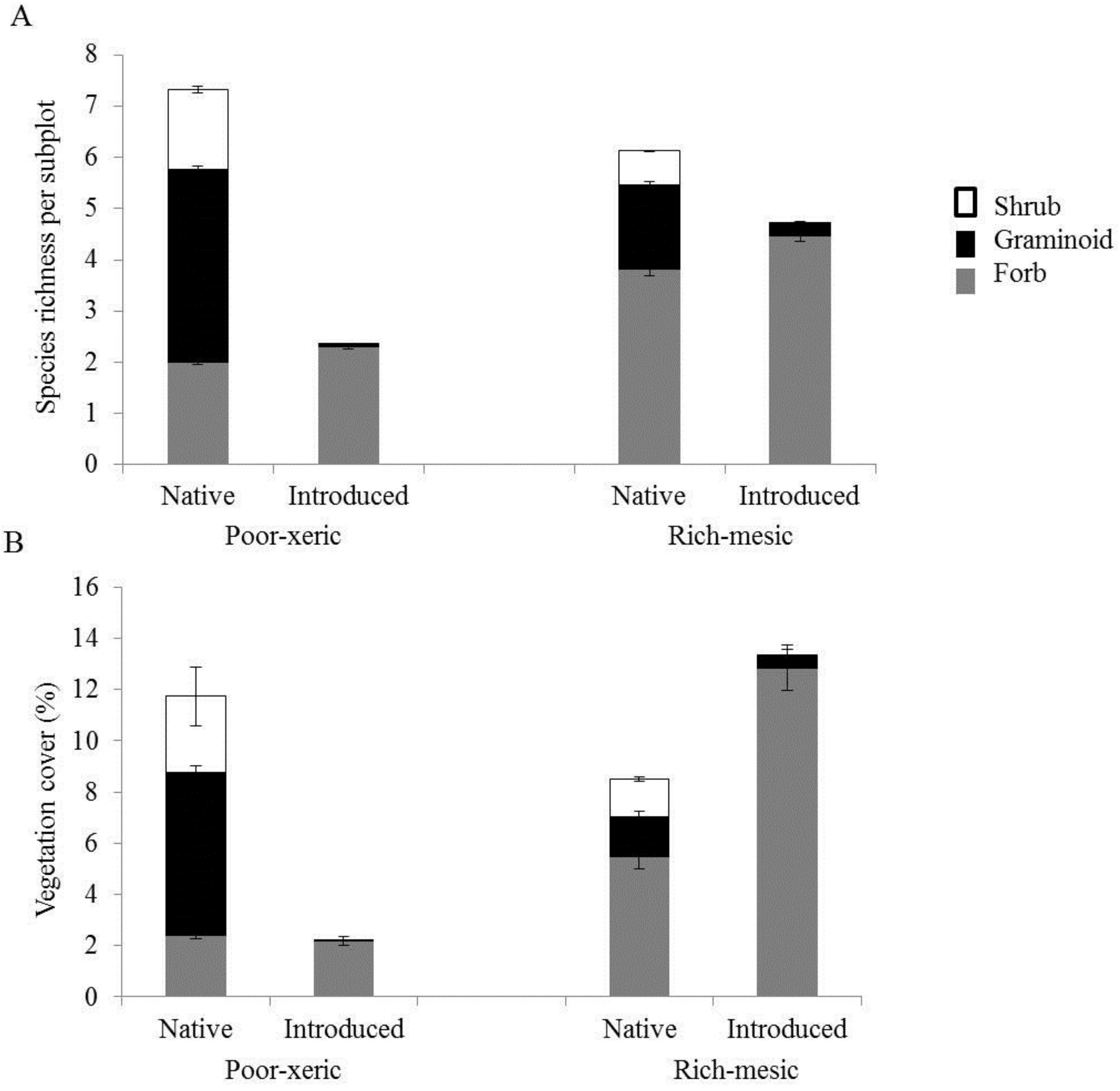

Figure 2-2: Vegetation cover (%) (A) and species richness per vegetation subplot (B) of native and introduced forb, graminoid and shrub species per subplot in areas capped with cover soil salvaged from poor-xeric and rich-mesic forest sites. Error bars show one standard error.

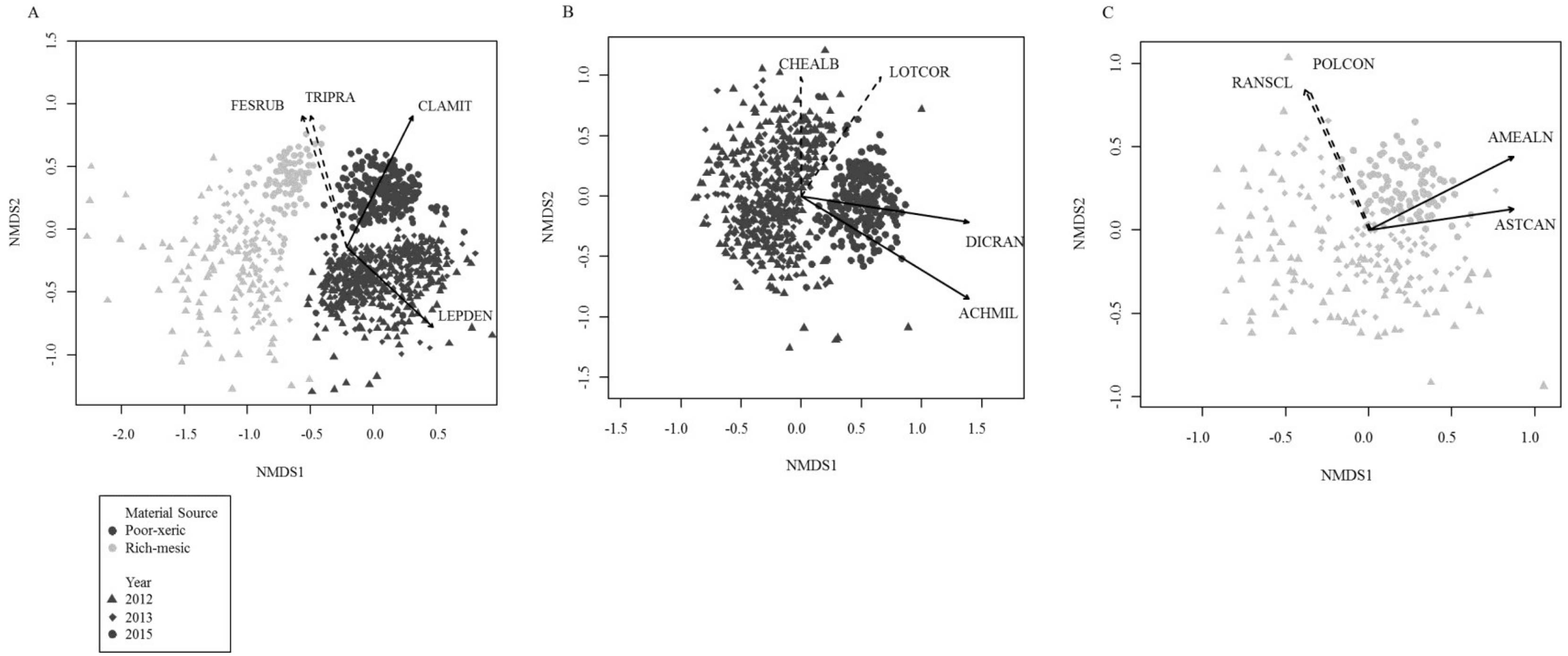

Figure 2-3: NMDS ordinations of (A) areas capped with coversoils salvaged from poor-xeric and rich-mesic forest sites in 2012, 2013 and 2015; (B) only areas capped with a poor-xeric coversoil over the same three years; and (C) only areas capped with a rich-mesic coversoil over the same three years. The two species most positively associated with the first two ordination axes are shown in each panel. Species strongly associated with the first axis (NMDS 1) are shown with solid arrows, and species strongly associated with the second axis (NMDS 2) are shown with dashed arrows. CLAMIT=*Cladonia mitis*, LEPDEN=*Lepidium densiflorum*, TRIPRA=*Trifolium pratense*, FESRUB=Festuca rubra, ACHMIL=*Achillea millefolium*, DICRAN=*Dicranum* sp., CHEALB=*Chenopodium album*, LOTCOR=*Lotus corniculatus*, ASTCAN=*Astragalus canadensis*, AMEALN=*Amelanchier alnifolia*, POLCON=*Polygonum convolvulus*, RANSCL=*Ranunculus scleratus*.

Chapter 3: Spatial variation in early vegetation community development on forest reclamation sites

3.1 Introduction

Plant communities exhibit spatial structure (i.e. non-random spatial organization) across multiple spatial scales (Borcard et al. 2004; Peres-Noto and Legendre 2010). This spatial structure is driven by both abiotic (e.g. climatic or resource variation) and biotic factors (e.g., competition or dispersal) (Peres-Noto and Legendre 2010). Spatial patterns, the interpretation of spatial structure based on selected variables, are found in natural communities across multiple scales (Peres-Noto and Legendre 2010); understanding the spatial patterns present in a community provides important insight into the ecological processes structuring the community (Borcard et al. 2004).

Disturbances, such as fire, insect or pathogen outbreaks, play an important role in structuring natural ecosystems, and shaping the recovery of plant communities that are adapted to these disturbances (Malmstrom and Raffa 2000; Bergeron et al. 2002; Chazdon 2003). The recovery process, including development of spatial structure, is impacted by the disturbance regime, biological legacies (including remnant species and propagules, structural components, and soil organisms), environmental abiotic and biotic conditions (such as climate, soil nutrient and moisture regimes and species interactions) present at the site (Franklin et al. 2000; Suding et al. 2004; Ledger et al. 2006; Cuddington 2011). Notably, biological legacies such as the propagule bank and soil characteristics are determined by the pre-disturbance forest type. Thus, spatial patterns which develop as communities recover from disturbance are strongly influenced by patterns and processes present in the pre-disturbance community (Franklin et al. 2002).

Compared to natural disturbances, some anthropogenic disturbances create site and environmental conditions that are dramatically changed and biological legacies that can be severely reduced. Thus the connections between pre- and post-disturbance conditions are greatly limited. Such disturbances, therefore, will have post-disturbance plant communities and spatial patterns that are weakly associated with the pre-disturbance conditions. The result is that recovery of communities proceeds very differently (similarly to primary succession) than communities after natural disturbances (secondary succession). This provides a unique opportunity to study the ecological processes of community development in reclaimed ecosystems, as well as the development of spatial patterns in communities where historical legacy effects have been severely reduced. While successional processes within natural communities have been studied extensively, there is limited information on these processes at reclamation and restoration sites. Walker and del Moral (2009) suggest that the study of succession at restoration and reclamation sites has important contributions to make in understanding succession at natural sites.

The severity of the disturbance caused by open-pit surface mining requires extensive reclamation and restoration efforts including topographic reconstruction, surface soil placement, and revegetation. These restoration activities will have a strong influence on the recovery of the vegetation, including development of spatial patterns. Placement of coversoil salvaged from nearby forest sites (including litter, fermented litter and humic layers and surface mineral horizons) can provide a rich source of biological legacies in the form of suitable soil material and plant propagules. Application of this material at reclamation sites can result in higher plant species richness and abundance than other soil materials and facilitate establishment of forest understory species and a community more similar to surrounding native vegetation (Skrindo and Halvorson 2008; Mackenzie and Naeth 2010; Macdonald et al. 2015b).

The propagule bank placed on the site will subsequently be filtered through site conditions such as microtopography. Beatty (1984) found that microtopographical variation can drive understory vegetation patterns. Microtopography, created at reclamation and restoration sites to increase site heterogeneity, facilitates plant establishment and results in the development of differing communities at mound tops and bottoms (Biederman and Whisenant 2011). Similarly, coarse woody debris (CWD) provides structural diversity and habitat for animals, plants and invertebrates and plays an important role in nutrient cycling in natural forests (Beach and Halpern 2000). At reclamation sites, the placement of CWD has been used to increase structural diversity and resulted in greater vegetation cover (Brown and Naeth 2014). Other variables such as tree canopy composition and density strongly influence understory plant communities and edaphic conditions in natural and reclaimed forests (Barbier et al. 2008; Strong 2011; Sorenson et al. 2011). Plant functional types play different roles in natural communities and interactions between species types are important in maintaining diversity (Chesson 2000). The importance of different functional types in plant communities at reclamation sites is not well understood, but some research has shown that aggressive or introduced species can have both negative and positive impacts on establishment of native, forest associated species, and thus on the success of reclamation efforts (Gretarsdottir et al. 2004; Tamang et al. 2008).

At many reclamation and restoration sites, some fast growing ruderal species present management concerns. If these species become dominant for an extended period of time, they may suppress or alter the development of forests and their understory communities and structure (Ridenour and Callaway 2001). However, ruderal species can also prove beneficial at reclamation sites, by stabilizing soil and/or acting as 'nurse' plants (D'Antonio and Meyerson 2002; Padilla and Pugnaire 2006, Macdonald et al. 2015b). Studying spatial patterns, particularly in cases where severe disturbance has reduced biological legacies, may aid in determining the importance and role of site characteristics and species composition (e.g. forest and non-forest associated species) in the development of plant communities at reclamation sites.

Traditional assessment of reclamation 'success' has focused on short term (typically occurring in the first 1-5 years after construction) surveys of vegetation community composition and thus has provided limited insight into ecological processes occurring at reclamation sites (Herrick et al. 2006). The result may be incorrect predictions of 'success' or 'failure' of reclamation treatments. Studying characteristics that reflect ecological processes, such as complexity of community composition and spatial pattern, may provide a better predictor of long term reclamation site 'success' than species composition surveys alone (Herrick et al. 2006). In natural forests, research has attempted to quantify variation in vegetation communities explained by environmental factors and by spatial patterns (reflecting biotic interactions such as competition or dispersal limitations) (Borcard et al. 1992; Gilbert and Lechowicz 2004; Gendreau-Berthiaume et al. 2015). At reclamation sites, where little research has explored the relative importance of environmental factors and biotic interactions in structuring the vegetation community, the proportion of variation explained by these factors is likely influenced by both the forest type from which coversoils were salvaged (which impacts environmental conditions such as soil nutrient regime, water holding capacity and propagule bank) and by site age.

This chapter describes a study carried out at a large scale surface mine located in the Athabasca Oil Sands Region, Alberta, Canada. Plant communities at an older (10 years since construction) and a younger (2 years since construction) reclamation area, constructed with different salvaged soil materials, were compared and the complexity of communities, spatial patterning, and some factors potentially driving community development were analyzed.

Objectives

1. Determine how: i) plant community complexity; ii) the complexity of spatial patterns (spatial complexity) in the plant community; and iii) how the proportions of different functional types for indicator species and species driving spatial patterns differ between: reclamation areas of different ages, and constructed using soil material salvaged from different donor forest types.
2. Determine how much of the variation in the plant community is explained by environmental factors *versus* by spatial variables (which reflect biotic interactions such as competition and dispersal limitations) and how this differs between reclamation areas of different ages, and constructed using soil material salvaged from different donor forest types.

The following hypotheses were tested:

1. Plant community complexity (the number of unique community types present and complexity within these types) will be higher at older reclamation sites and community complexity will be higher in soil salvaged from nutrient rich, mesic forest types compared with nutrient poor, xeric forest types.
2. Spatial pattern complexity in the plant community will show similar responses as predicted for community complexity (higher at an older site than a younger site and higher at a site constructed with richer, mesic material than with poorer, xeric material).
3. Introduced and non-forest associated species will be more dominant as indicator species and drivers of spatial patterns in young sites *versus* older sites, and in richer, mesic sites *versus* poorer, xeric sites.

4. Environmental factors (microtopography, coarse woody debris abundance, canopy cover) and space (accounting for biotic interactions including competition and facilitation) will explain a greater amount of variation at a site constructed with richer, mesic material than with poorer, xeric material. At a younger site, environmental factors will explain a greater proportion of the total variation than space; at an older site, space will explain a greater proportion of total variation than environmental factors.

3.2 Materials and Methods

3.2.1 Research Area

This research took place on a large reclamation area at Syncrude Canada Ltd. (SCL)'s Base Mine, located roughly 40 km north of Fort McMurray, Alberta, Canada. The mine operation is situated within the central mixed-wood subregion of the boreal natural region (Natural Regions Committee 2006). The climate in this region is characterized by very cold winters and short, warm summers (Natural Regions Committee 2006). The mean annual temperature in Fort McMurray is 1ºC (based on a 30 year average). The mean annual precipitation for the same time period was 418.6 mm, with 316.3 mm falling as rain and 133.8 mm as snow. The coldest temperatures occur in January, with an average temperature of -17.4ºC, and the warmest month is July, with an average temperature of 17.1ºC (Environment Canada 2015).

The overall landscape in the region is rolling and contains a mosaic of upland and lowlands. Soils in upland areas in this region are typically Dystric and Eutric Brunisolic soils associated with jack pine (*Pinus banksiana*) dominated forests or Grey Luvisolic soils associated with forests that contain a mixture of broadleaf species (aspen (*Populus tremuloides*), poplar (*Populus balsamifera*) or birch (*Betula papyrifera*)) and white spruce (*Picea glauca*). Wetlands are dominated by organic soils and are primarily forested or shrubby bogs or fens (Natural Regions Committee 2006).

3.2.2 Field sites

Two large reclamation sites were selected for this research study. Both sites were set up to test questions related to operational-scale reclamation approaches using different cover material types. The sites were approximately 8 km apart. Reclamation involved capping with coversoil salvaged prior to mining from one of two different forest types (‘rich-mesic’ and ‘poor-xeric’). The ‘rich-mesic’ coversoil originated from a mature forest dominated by a mixture of *Populus tremuloides* and *Picea glauca* with a lush understory and a fine textured Luvisolic soil with a mesic moisture and rich nutrient regime. The ‘poor-xeric’ coversoil originated from a mature forest dominated by *Pinus banksiana* with a sparse understory and a coarse textured Brunisolic soil with a xeric moisture and poor nutrient regime. After the removal of the trees from the donor sites, coversoil was salvaged in the winter using a D10 Caterpillar bulldozer. Surface soil was salvaged including the entire organic L, F and H soil horizons as well as the upper 5-20 cm of underlying mineral A and part of the B soil horizon(s).

Young field reclamation site

The young field site was located on upland areas of a 57 ha collaborative experimental watershed study (the Sandhill Watershed, construction completed in 2012). The landforms at this site were constructed out of tailings sand, which was placed to a depth of >10 m on a former soft tailings pond (Pollard et al. 2012). Upland (hummocks) surrounding the lowland (wetland) were capped with either the poor-xeric or the rich-mesic coversoil. Both were underlain by a layer of salvaged subsoil material. The poor-xeric coversoil areas had a 40 cm layer of sandy subsoil capped with a 15 cm layer of salvaged coversoil, while the rich-mesic areas had a 30 cm layer of clay loam subsoil placed below a 20 cm layer of salvaged coversoil. Throughout the site, upland areas received various amounts of coarse woody debris (CWD) consisting of residual woody material salvaged on the harvested sites. As part of the larger study tree seedlings native to the surrounding forests (*Populus tremuloides, Pinus banksiana* and *Picea glauca*) were planted in most areas of the site while some areas remained unplanted. Only unplanted areas were sampled for this study.

Older field reclamation site

The second field site (W1 Dump) was an experimental site constructed on a landform built with saline-sodic overburden (Clearwater formation origin). The site was completed in early 2004 (Mackenzie 2006). Coversoil salvaged from a rich-mesic donor forest site, similar to the one used for the young site, was placed in early 2004 at a depth of 20 cm, underlain by 90 cm of fine textured subsoil (Mackenzie 2006). After salvage and prior to placement, the coversoil material was stored in windrows for three months (November 2003-February 2004) (Mackenzie and Naeth 2010). In the fall of 2005, seedlings of *Picea glauca* and *Populus tremuloides* were planted at a density of 1200 stems ha^{-1} at the site. No coarse woody debris was placed at this site, although small amounts were included with the salvaged coversoil when it was placed. Initial vegetation community composition on this site was surveyed during the first and second growing season after site construction (Mackenzie 2006), and the early community was found to have a species composition very similar to the one we found on the young field site constructed with the rich-mesic coversoil.

3.2.3 Experimental Design

Five grid plots were established in each of the three site types (young – poor-xeric, young – rich-mesic and older – rich-mesic). Grid plots were located in areas representative of the site that were generally flat, although some micro-topographical variation was present in plots. Each grid plot was a 5 × 5 m square composed of 100 contiguous 50 × 50 cm quadrats. The grid plots were 50 to 800 m apart within a site.

3.2.4 Vegetation and Environmental Variable Measurements

Data on several variables describing vegetation communities and environmental factors were collected from each grid plot. Within each quadrat, individual vascular plant species were identified and their percent cover visually estimated. Total cover of bryophytes, coarse woody debris (CWD), and bare soil were also determined at the quadrat level. Cover by bryophytes was divided into 'mature' and 'immature' mosses; mature mosses had well developed vegetative and reproductive structures while immature mosses did not. Covers were estimated to the nearest percentage up to 10% and to the nearest 5% after; if less than 1%, cover was either determined to be 0.5% or as a trace (0.05%). To ensure consistency of the cover estimates, researchers performing the task calibrated estimate assessments several times a day, and used coroplast cut-outs (1% and 5% of the plot size) to help estimate cover more accurately.

Grid plot microtopography was mapped using the individual quadrats as guides to hand-draw an overlay of various features onto the grid plot. These maps included high and low areas in the plots, as well as features such as ridges, mounds and depressions, along with approximate heights of some of those features. For each grid, the map of topographical features was converted into a matrix of binary 'dummy variables' indicating whether a feature – for example, a ridge –

was present or absent within each quadrat in the grid. Additionally, for the older – rich-mesic site type, the area of the plot covered by the crown of a planted *P. tremuloides* or *P. glauca* individual was measured. For all trees for which the crown was covering the grid plot we recorded: species, stem location (according to grid plot coordinates), height, and crown radius. The data on tree crown dimensions were then overlain onto the grid plot using ArcGIS 10.2.2 (ESRI 2014). The Fishnet tool was used to create a reference grid, onto which the tree stem locations were mapped. Each stem location was then buffered by the crown diameter measurement of that tree. Using the Intersect tool, the area of each quadrat covered by tree canopies was calculated, and then converted into values for percent cover by each tree species.

To estimate differences in available nutrients between the site types, leaf samples of *Populus tremuloides* were collected in grid plots in late July, as aspen was present on all sites. At the two young site types 20 *P. tremuloides* leaves were collected from five seedlings adjacent to each grid plot, as no planted seedlings were present within the plots; values for the five seedlings per grid plot were pooled. The leaf samples were oven dried at 70ºC for three days and then ground to pass through a #40 (0.4 mm) mesh using a Wiley Mini-Mill (Thomas Scientific, New Jersey, USA). The samples were then analyzed for a selection of common elements (N, P, K, S, Al, B, Ca, Cu, Fe, Mg, Mn and Zn) measured using microwave digestion followed by ICP-OES (optical emission spectrometry). N was measured by combustion using a Costech Model EA 4010 Elemental Analyzer (Costech International Strumatzione, Florence, Italy, 2003). All analyses were carried out at the University of Alberta Natural Resources Analytical Laboratory.

Differences between site types in concentrations of selected nutrients were analyzed using one-way ANOVA followed by post-hoc Tukey HSD tests. The similar percentage of Nitrogen and concentrations of Phosphorus, Potassium, Manganese and Sulphur in *P. tremuloides* leaves at the older and young rich-mesic site type suggest that available soil nutrients at these sites were similar (Table 3-1, Appendix Table A3). Although not significantly different, concentrations of Nitrogen and Potassium were lower at the young – poor-xeric site type than at either rich-mesic site type. Concentrations of Manganese and Sulphur were significantly higher for the young – poor-xeric site type than the older – rich-mesic site type; concentrations for the young – rich-mesic site type were intermediate. These differences suggest that available soil nutrients in the poor-xeric material were likely different than in the rich-mesic material.

3.2.5 Statistical Analyses

All analyses were carried out in R version 3.1.2 (R Core Team 2014). Analyses were conducted for each of the 15 grid plots separately; community and spatial complexity were determined for each grid and these measures were compared between the three site types.

Complexity of plant community composition was measured as the number of unique community types within a grid, the total number of indicator species for each grid, the mean number of quadrats per community type and the mean number of indicator species per community type.

Cluster analysis was used to classify vegetation communities within each grid plot. The Average (UPGMA) method was selected as the best clustering method based on examination of the Cophenetic correlation and Gower distance (Borcard et al. 2011). The R function `hclust()` was used for the cluster analysis. The optimal number of clusters to be interpreted for each grid plot was selected using silhouette widths; this is a measure of how well an object 'fits' with its assigned cluster (in this case the objects are quadrats within a grid plot) (Borcard et al. 2011). The R function `silhouette()` was used to determine silhouette widths for each quadrat within a grid (Maechler et al. 2014).

Indicator Species Analysis was used to identify indicator species for each community type that was identified by the cluster analyses. The analysis was done using the R function `multipatt()`, which compares combinations of input clusters to the species in the input vegetation matrix, selects species with the highest association value, and tests for statistical significance (De Caceres and Legendre 2009). The total number of indicator species selected for each grid was interpreted as a measure of community complexity at the grid level. The mean number of indicator species selected for each community type within a grid was interpreted as a measure of complexity at the within-grid level. The species identified in each grid as indicator species were subsequently categorized by four functional types: forbs, graminoids, shrubs and non-vascular (moss classified as 'mature' and 'immature'). Species were then classified as either native or introduced, and as either 'forest' or 'non-forest' species. Forest species were native species commonly found in the understory of the target forest types. Proportions of indicator species of each functional type and original range or forest association were compared between the three site types; these proportions were calculated as the number of indicator species of a functional type and original range or forest association (i.e. forb and native) as a proportion of all indicator species selected for the site type.

To assess complexity of spatial pattern we used principal coordinates of neighbour matrices (PCNM) analysis. The technique used a truncated matrix of sampling locations (quadrats) within a grid plot to generate a large number of spatial pattern variables; these were then used as explanatory variables in a redundancy analysis (RDA) (Borcard and Legendre 2002). The R function `PCNM()` was used to create the spatial pattern variables used in the analysis (Legendre et al. 2013).

Spatial complexity was quantified as the number of significant axes produced during the RDA and the number of significant PCNM variables; for both, higher values indicated greater complexity. Additionally, PCNM analysis was used to identify which species were important in driving spatial patterns; a greater number of species driving the patterns was interpreted as greater spatial complexity. This gave insight into both complexity present in the grid plots and spatial relationships among species. Species with scores on RDA axis 1 (the first axis explained the most variation) greater than or equal to 0.1 were considered to be drivers of spatial pattern. As in the community complexity analysis, the species identified as drivers of spatial patterns in each grid were categorized by functional type, original range and forest association and proportions were compared between the site types (see above).

Variation partitioning was used to assess the relative influence of different environmental and site factors on vegetation community composition in the grid plots. The variation partitioning was performed using the R function `varpart()` (Oksanen et al. 2015). This function partitioned variation in a vegetation community composition response matrix with respect to a series of explanatory environmental variable components: microtopography, CWD abundance, tree canopy (at the older – rich-mesic site type only), PCNM patterns (a surrogate for space to represent dispersal limitations and competition), and a linear trend component, which accounted for variation explained by trends at scales larger than the grid plots. At the young – rich-mesic and young – poor-xeric site types, microtopography and CWD variables were considered together as one ‘environmental variable’ component. For each explanatory component, a matrix containing all possible variables was constructed; the PCNM matrix included all positively spatially correlated PCNM variables, the tree canopy matrix included variables for cover by *P.*

tremuloides, *P. glauca* and both species combined, and the microtopography matrix included all microtopography variables created from the microtopography field maps. Forward selection (using R function `forward.sel()` (Miller and Farr 1971)) was used to select the variables from each initial component matrix to be used in the variation partitioning analysis. In grid 6, none of the environmental variables were selected, and in grid 11 none of the tree canopy variables were selected; these components were excluded from the analyses.

Differences between site types in mean values for the results of the community complexity, spatial complexity and variation partitioning analyses were analyzed using one-way ANOVA followed by post-hoc Tukey HSD tests, except in cases where the results for one site type had no variation. In these cases, results for the remaining two site types were analyzed using Wilcoxon signed-rank tests because of non-normality. Differences between site types of proportions of indicator species and species driving spatial patterns of species types (native and introduced, forest associated and non-forest associated species) were analyzed using Fisher's exact tests.

3.3 Results

The young – poor-xeric site type had an average of two community types per grid plot, while the young rich-mesic site type had an average of 2.4 community types and the older – rich-mesic site type had an average of 7.8 community types. In addition, for the young – poor-xeric site type an average of 50 quadrats per grid represented each community type while the community types were represented by 45 and 14 grid plots on average for the young and old rich mesic site types, respectively. Because there was no variation among grid plots in number of community types and number of quadrats per community type for the young – poor-xeric site type this site type was not included in the statistical analysis for these measures (Table 3-2, Appendix tables A4 and A5 and figures B12-B14). The number of indicator species per grid and per community type did not differ between the two young site types, but was significantly greater at the older site type than at either young site type.

The number of significant RDA axes, and of PCNM variables, was significantly lower at the young – poor-xeric site type than at the young and older - rich-mesic site types, which did not differ from one another (Table 3-2 (see also Appendix Table A5 and A6)). The average number of species that drove spatial patterns was significantly greater at the older site type than at either of the young site types, which did not differ from one another.

Proportions of native *versus* introduced and forest associated *versus* non-forest associated species selected as indicator species and as drivers of spatial pattern, and that were present in the community, did not show significant differences between the site types (Table 3-3; see Appendix Table A7). When compared to the young – rich-mesic site type, however, relatively more of both the indicator species and drivers of spatial pattern were native and forest-associated for the young – poor-xeric site type, and relatively fewer were non-forest grass and non-forest forb species (Figure 3-1). In the community, more introduced and non-forest associated species were present at the young – rich-mesic than the young – poor-xeric site type (Figure 3-2). For the older – rich-mesic site type, relatively more indicator species and species driving spatial pattern were forest-associated and native than at the young – rich-mesic site type. Relatively more of the non-forest species selected as indicator species and drivers of spatial patterns at the older – rich-mesic site type were grasses, and relatively fewer were forbs, when compared to the young – rich-mesic site type. More native and forest-associated species were present in the community at the older than the young – rich-mesic site type (Figure 3-2).

For all three site types the variance partitioning showed that the vast majority of the explained variation was explained by space. Significantly more variation was explained by space at the young – rich-mesic site type than at the young – poor-xeric site type (Table 3-2, Appendix tables A5 and A8 and figures B15-B24). The amount of variation explained by the environmental component was not different between the two young site types.

Due to the different site conditions at the older site type (i.e. tree cover, greater variability in topography) the variation was partitioned into a slightly different set of components than at the young site types. The components used were: the PCNM (space) component, a microtopography component, a tree canopy component and a linear trend component. Coarse woody debris and size of large ant hills were also considered but were not selected during the variable selection process. At the older rich-mesic site, as at the two young site types, space explained a much greater proportion of total variation than environmental variables (Table 3-2, Appendix figures B25-B29). The majority of the variation explained by environmental factors at the older site type was explained by microtopography, with a smaller amount explained by the tree canopy.

3.4 Discussion

The forest type that coversoils are salvaged from affected the structure of the developing vegetation communities. In this study coversoil materials salvaged from different forest types had different impacts on vegetation complexity, the types of species selected as indicator species for the communities and as drivers of spatial patterns, and the amount of variation explained by environmental factors and by space (e.g. spatial variables that most likely reflect initial propagule distribution and competitive interactions). Coversoil materials salvaged from similar forest types, measured at an early and a later stage of development, also differed in measures of complexity, types of species dominant in the community and variation explained by environment and by space.

Both complexity of plant community composition (number of community types per grid, quadrats per community type, indicator species per grid and per community type) and complexity of spatial patterns in the plant community (number of RDA axes, PCNM variables, species driving spatial pattern) were higher at rich-mesic than at poor-xeric sites of the same age, which supported our stated hypothesis that the difference in complexity between the two sites was likely driven by differences in coversoil materials, their edaphic properties, and their legacy of vegetative propagules. At the young – rich-mesic site type, a lusher vegetation community (including many native and non-native non-forest forb and grass species) developed, likely in response to water holding capacity (and thus soil moisture) and nitrogen availability, which were probably higher at this site type. This coversoil material was salvaged from a forest with an overstory dominated by *P. tremuloides*. The material was fine textured and had somewhat higher levels of available soil nitrogen than the poor-xeric coversoil material. The availability of nitrogen, often a limiting nutrient in boreal forests, is determined by the extent of nitrogen mineralization which is, in turn, controlled by interactions between soil moisture, temperature, and litter type (Cassman and Munns 1980; Vitousek and Howarth 1991; Agehara and Warncke 2005).

We also hypothesized that the proportion of introduced and non-forest associated species selected as indicator species and drivers of spatial pattern would be greater in the young – rich-mesic than the young – poor-xeric site type; this hypothesis was somewhat supported by our results. At the young – rich-mesic site type, the likely higher levels of moisture and available nitrogen may have contributed to the dominance of introduced species and non-forest grasses, potentially suppressing native forest species that were present in the coversoil propagule bank. On the other hand, at the young – poor-xeric site type, the native forest species were more dominant, likely a result of their adaptation to the dry, nutrient poor conditions and the overall lower competition. Competition driven by greater nutrient availability can impact the establishment and success of native forest species on reclamation sites during the early successional stage (Djietror et al. 2011; Macdonald et al. 2015b).

The greater importance of competitive interactions at the young – rich-mesic than at the young – poor-xeric site type was further supported by the variation partitioning analysis, which indicated that space explained a greater amount of variation at the young – rich-mesic than at the young – poor-xeric site type. Variation explained by the environmental component was small and did not differ between the two young site types. This suggests that interactions driven by space, which have been attributed to autogenic processes such as competition and aggregation (Borcard et al. 1992; Gilbert and Lechowicz 2004), may have been more important in the structuring of these early successional plant communities than environmental factors. In mature forests, some research has found the most variation in understory plant communities is explained by space (Borcard et al. 1992; Gendreau-Berthiaume et al. 2015), while other studies have found that environmental factors were a stronger control of species distributions (Gilbert and Lechowicz 2004). Some authors also attribute variation explained by space partially to unmeasured environmental effects (Borcard et al. 1992), while others argue that these unmeasured environmental components are accounted for as unexplained variation (Jones et al. 2008). At both young sites, a large amount of variation was unexplained, which may indicate that some driving variables were not measured or that uncaptured random and stochastic events were driving the variation. Regardless, the amount of variation unaccounted for by our measurements was similar to that found in comparable research done in natural forests (Borcard et al. 1992; Jones et al. 2008).

Older reclamation sites had higher community complexity than younger sites; this supported our hypothesis that community complexity increases with age. However, we had also hypothesized that spatial complexity would be higher at the older site, but this was not the case on our reclamation site; spatial complexity was the same between the older and young – rich-mesic site types. This suggests that spatial complexity may develop more slowly at reclamation sites than community complexity; the development of unique community types within a larger vegetation community may be a slower process than the development of complex patterns of vegetation distribution. While there are large bodies of research examining vegetation community structure and spatial patterns in natural communities, little research has explored the time frames under which vegetation community structures develop at reclamation sites. However, research exploring temporal changes in non-structural aspects of reclamation site vegetation communities (i.e. community composition) may offer insight into structural development. Major shifts in the vegetation community often occur at reclamation sites in the first few years after site construction (Prach and Pysek 2001). Although vegetation communities at the reclamation sites we studied are likely still undergoing changes, these communities will eventually stabilize. However, neither the processes driving stabilization nor the timing of stabilization are well understood; some research has shown that environmental factors such as water table level can have a greater impact on successional trajectory than time (Rehounkova and Prach 2006).

For the older – rich-mesic site type, where the vegetation community had more time to develop, we hypothesized that introduced and non-forest associated forb and graminoid species would be less abundant as indicator species and drivers of spatial patterns than at the young – rich-mesic site type; this hypothesis was partially supported. Many of the non-forest species at the older site had likely been outcompeted by native, forest associated species, which had become dominant in the older community. Long-term studies of reclaimed areas show that naturalization and the development towards mature communities of native species occurs over time (Gretarsdottir et al. 2004; Tischew et al. 2014).

Additionally, we found some evidence suggesting that grass species that are not generally associated with forests may be more persistent in the community than non-forest associated forb species. Although differences were not statistically significant, relatively more non-forest associated grass species were indicator species for the communities and were driving spatial patterns at the older than at the young – rich-mesic site; conversely, relatively fewer non-forest forbs were indicator species or drivers of spatial patterns at the older than the young site. In natural forest communities, perennial, often rhizomatous, native forest grasses can establish and persist after disturbance, however, at reclamation sites aggressive introduced grass species can have negative effects on the growth of planted tree seedlings and the establishment of a native plant community (D'Antonio and Meyerson 2002; Cabin et al. 2002; Tamang et al. 2008). However, the effect of these species on native forest species is not always negative; many native bunch grasses can act as 'nurse' plants, improving establishment of desirable native species (Maestre et al. 2001; Maestre et al. 2003). The positive effects of early grass species presence on native species may be maintained over longer timescales, even when the grass species do not persist in the community (Gretarsdottir er al. 2004). In our study, we found some evidence that non-forest associated grass species were important in the community at the older site, but we were not able to determine the magnitude or direction of their influence on forest associated species. The importance of these species at the older site, and their effects on other species, may change as the sites age.

We had hypothesized that space would explain a greater proportion of total variation than environmental factors at the older – rich-mesic site type, while at the young – rich-mesic site type the reverse would be true. Our analysis partially supported this hypothesis; the spatial component explained similar, large proportions of the total variation at the young and older – rich-mesic site types. This makes sense as levels of spatial complexity were similar at the young and older site types. Variation explained by space can represent biotic processes such as competitive and facilitative interactions and dispersal limitations (Borcard et al. 1992; Gilbert and Lechowicz 2004). Gendreau-Berthiaume et al. (2015) showed that, in natural forests, dispersal limitations become more important with time as later successional species, which reproduce vegetatively, increase in abundance; this appeared to be linked with canopy closure and might occur over longer time scales than we examined in this study. At the sites we studied, the communities were largely composed of early successional species and competitive and facilitative interactions were likely the major structuring processes.

At both rich-mesic site types the proportion of variation explained by environment was much less than the proportion explained by space; at the older site type, environmental factors explained significantly more variation than at the young site type. This was likely at least in part because the environment at the young – rich-mesic site type was less heterogeneous than at the older site type. Variability in microtopography at the older site was actually greater and the features were much larger than at the young site due to both biological activity (such as forest ants) and the residual effects of construction equipment (ruts and scrapes). Microtopographic feature size, which affects the strength of the environmental gradients created, can impact plant species establishment and growth on these features (Kuntz and Larson 2006); larger features may therefore explain more variation. As well, coarse woody debris, which was included in the environmental component at the young site, may not have been abundant or large enough to be a strong driver of vegetation patterns, although other research has shown an association between a higher abundance of coarse woody debris and increased cover of forest understory plants (Santiago 2000; Bartels and Chen 2013; Brown and Naeth 2014).

At the older site, the developing tree canopy also explained a significant amount of variation. This amount may increase with future canopy closure. Canopy closure and composition will cause shifts in the understory vegetation community development and soil edaphic conditions (Pensa et al. 2008; Sorenson et al. 2011). Conifers may exert a stronger influence on the understory community than broadleaf species, because of differences in their effects on light availability and quality and litter type; in our study most *P. glauca* individuals present at the older site were much smaller than the *P. tremuloides* individuals, thus more variation might be explained as the conifer cover increases with time (Barbier et al. 2008; Strong 2011).

Some research has found that the influence of the environment as a driver of variation in vegetation communities is dominant at large and meso scales, and argued that biotic interactions may be more important at fine scales where the environment is less heterogeneous (Gilbert and Lechowicz 2004; Karst et al. 2005). Processes occurring at finer scales than those at which measurements are taken cannot be quantified, and may contribute to the amount of unexplained variation (Jones et al. 2008). Much of the research on spatial patterns has been conducted with fairly large distances between sampling points (i.e. 100 – 3000 m) (Gilbert and Lechowicz 2004; Jones 2008) or occasionally at finer scales (i.e. 5 m x 5 m contiguous quadrats) (Gendreau-Berthiaume et al. 2015). Our study utilized a finer scale than these examples from the literature, allowing us to capture very fine-scale spatial variation; our study is unique both in exploring variation explained by space and environmental factors at a very fine scale, and in doing so in a reclamation context.

3.5 Conclusion

Use of different coversoil materials, with the accompanying remnant biological legacies of plant propagules, led to clear differences in spatial and community complexity of the developing plant communities. Older reclamation areas had higher community complexity, while spatial complexity was similar to young sites; this suggests that these properties may develop at different time scales. The older site type (as compared to the young – rich-mesic site type) had higher numbers of indicator species and species driving spatial patterns and relatively greater abundance of forest associated species; this suggests that some naturalization is occurring.

Overall, space explained much more variation than environmental variables at all three site types, which is consistent with other studies, particularly at fine spatial scales. The relative homogeneity of the environment and early successional stage at all three site types suggest that competitive and facilitative interactions were likely the main structuring processes; competitive interactions may have been in large part driven by ruderal species. As these sites age and as the tree canopies close, shifts in the understory community will occur. At that time dispersal limitations may become more important.

To our knowledge, this study is the first to quantify variation explained by environment and space in a reclamation context and the results thus contribute significantly to filling a research gap in this area. The limited biological legacies inherent to the reclamation sites we studied offer a unique opportunity to examine how environmental factors and biotic interactions structure early successional stage vegetation communities. Understanding how these processes structure communities at reclamation sites is important in designing and managing successful reclamation, and may allow managers to determine which environmental factors drive variation in vegetation communities, as well as the role biotic interactions play in the community.

Tables:

Table 3-1: Mean concentrations of selected nutrients in *Populus tremuloides* leaves from each of three site types. All concentrations are µg/g except Nitrogen, which is a percentage. Letters indicate significant differences between site types (α= 0.05) (n=5). Significant differences were determined using one-way ANOVA followed by Tukey HSD tests.

	Young – poor-xeric	**Young – rich-mesic**	**Older – rich-mesic**
Nitrogen (%)	1.95 **a**	2.24 **a**	2.18 **a**
Phosphorus	1404.83 **a**	1357.16 **a**	1545.74 **a**
Potassium	7964.20 **a**	8418.84 **a**	8486.97 **a**
Manganese	131.80 **a**	59.61 **ab**	56.94 **b**
Sulphur	3044.40 **a**	2332.75 **ab**	1922.64 **b**

Table 3-2: Mean values (±SD) of variables describing community complexity (number of community types, number of indicator species per grid, number of quadrats per community type, number of indicator species per community type), spatial complexity (number of significant RDA axes, PCNM variables, and PCNM drivers (number of species driving spatial patterns)), and variation partitioning (proportion variation explained by the PCNM/spatial component, environmental variable component, tree canopy component, microtopography component, linear trend component, and residual component). At the two young site types, the environmental variables consisted of coarse woody debris and microtopography and at the older – rich-mesic site type, of microtopography and tree canopy cover. Letters indicate significant differences between site types (α= 0.05) (n=5). Significant differences were determined using one-way ANOVA followed by Tukey HSD tests except in cases (indicated by *) where one site type had no variation; in these cases, non-parametric Wilcoxon signed-rank tests were used to compare the remaining two site types.

	Young – poor-xeric	**Young – rich-mesic**	**Older – rich-mesic**
Community Types (CT)*	2.0±0 **-**	2.4±0.8 **a**	7.8±1.9 **b**
Indicator species (IS) per grid	1.8±1.2 **a**	3.4±1.0 **b**	9.8±1.6 **b**
Quadrats per CT*	50.0±0 -	45.0±10 **a**	13.8±3.9 **b**
IS per CT	0.9±0.6 **a**	1.6±0.3 **a**	4.2±1.3 **b**
Significant RDA Axes	7.2±0.7 **a**	11.2±1.9 **b**	11.4±0.8 **b**
Significant PCNM Variables	19.6±2.2 **a**	27.6±4.8 **b**	26.6±4.6 **b**
PCNM Drivers (# species)	4.6±2.3 **a**	5.2±1.7 **a**	9.6±2.3 **b**
PCNM (Space)	0.34± 0.020 **a**	0.52± 0.065 **b**	0.58± 0.025 **b**
Environmental Variables	0.053±0.020 **a**	0.051±0.050 **a**	0.16±0.027 **b**
Tree Canopy	-	-	0.055± 0.0046
Microtopography	-	-	0.14±0.021
Linear Trend	0.066± 0.019 **a**	0.12± 0.045 **ab**	0.16± 0.056 **b**
Residuals	0.64± 0.040 **a**	0.47± 0.065 **b**	0.41± 0.022 **b**

Table 3-3: Results (*P* values) of Fisher's exact tests comparing the three site types (young – poor-xeric, young – rich-mesic and older – rich-mesic) in terms of the proportions of forest associated *versus* non-forest associated and native *versus* introduced species that were indicator species or drivers of spatial patterns.

	P value
Proportion of forest associated to non-forest associated indicator species	0.539
Proportion of native to introduced indicator species	0.4
Proportion of forest associated to non-forest associated drivers of spatial pattern	0.783
Proportion of native to introduced drivers of spatial pattern	0.5

Figures:

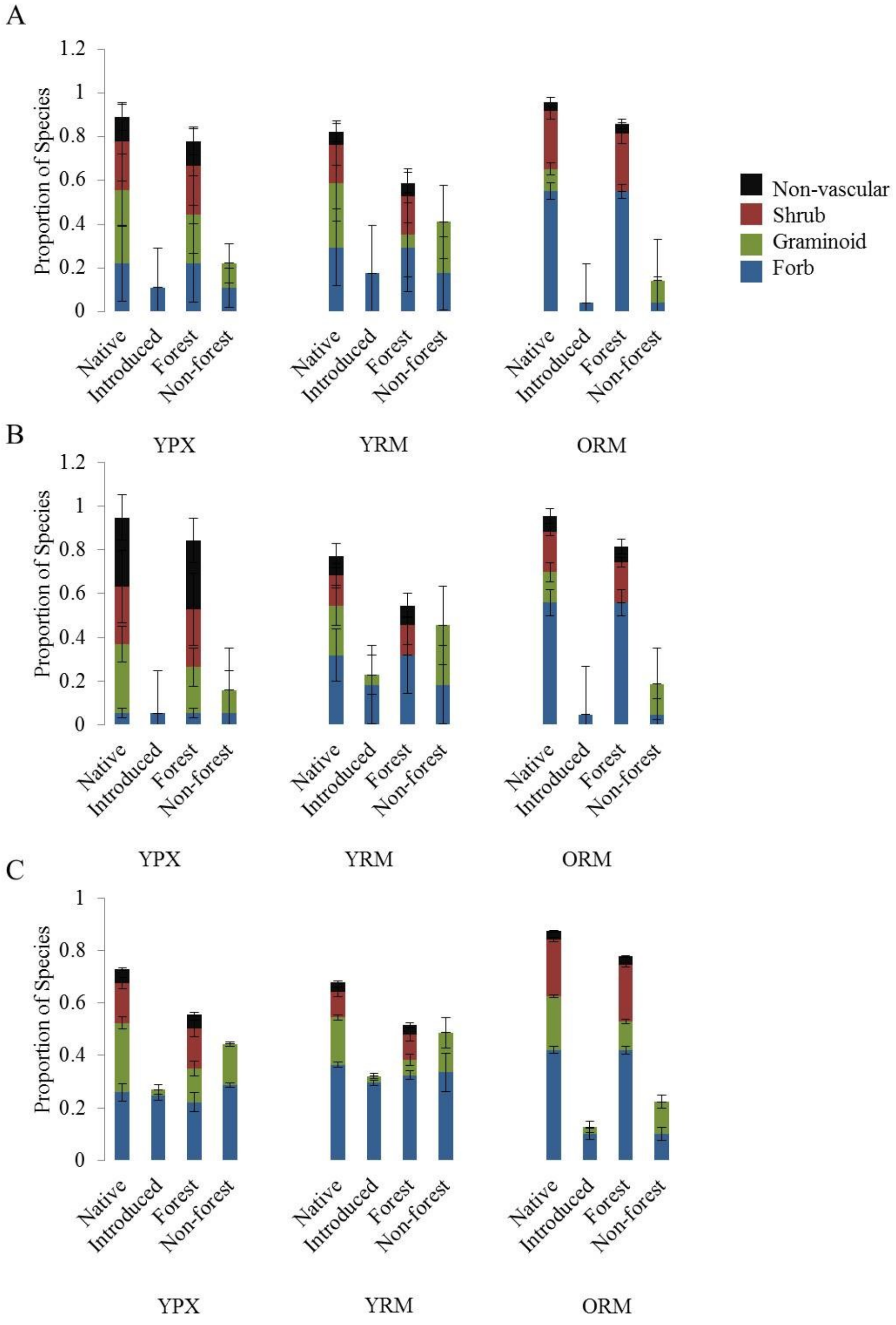

Figure 3-1: Proportions of four functional types (forb, graminoid, shrub, non-vascular (moss) of native and introduced and forest associated and non-forest associated species at the three site types (YPX: young – poor-xeric, YRM: young – rich-mesic, ORM: older – rich-mesic). Plots show proportions of: A) indicator species; B) species driving spatial patterns; and C) total species of each functional type. Error bars show one standard error.

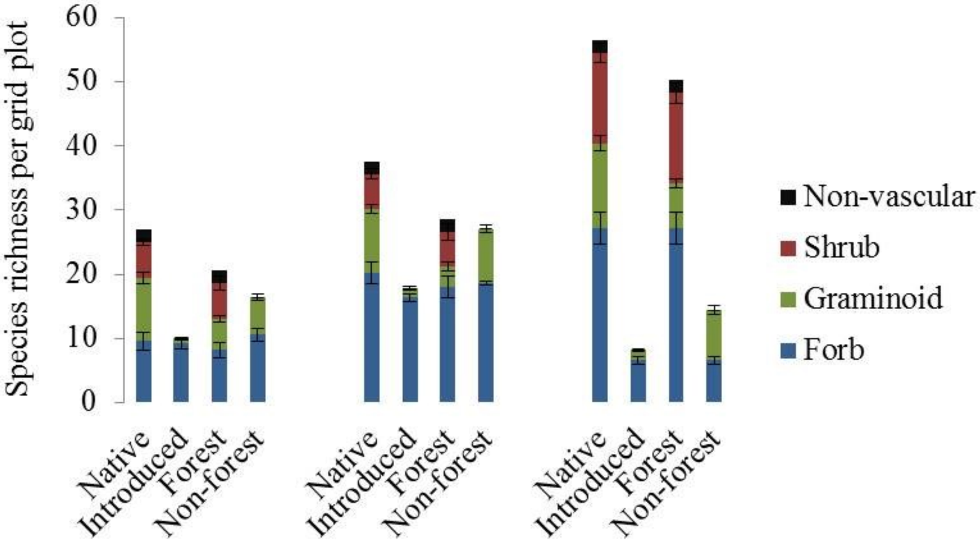

Figure 3-2: Mean numbers of species per grid plot by four functional types (forb, graminoid, shrub, non-vascular (moss) that were native *versus* introduced or forest associated *versus* non-forest associated for the three site types (YPX: young – poor-xeric, YRM: young – rich-mesic, ORM: older – rich-mesic). Error bars show one standard error.

Chapter 4: General conclusions

4.1 Research summary:

Industrial activities such as surface mining have resulted in increasing areas of disturbed forest land. Reclamation methods, including topography construction, use of coversoils salvaged from forest sites, native tree seedling planting, and application of coarse woody debris, are used to facilitate development of self-sustaining forest communities with diverse, natural understories. My research objectives were to examine: 1) the influences of reclamation treatments and their interactions on vegetation communities at a site capped with coversoils salvaged from a nutrient poor forest site with a xeric moisture regime (poor-xeric) and from a nutrient rich forest site with a mesic moisture regime (rich-mesic); and 2) the relative importance of environmental factors and spatial variables (reflecting biotic interactions such as competition and dispersal limitations) in driving variation in the vegetation community in areas reclaimed with both coversoil types at the first study site, and at a second, 10 year old study site reclaimed with coversoil from a rich-mesic site type. To meet these objectives I carried out two studies; both studies were conducted at operational scale reclamation sites.

In the first study, vegetation development in areas capped with the two coversoils was influenced by seedling planting density, slope aspect and coarse woody debris abundance, as well as by interactions between these factors. Vegetation diversity was influenced largely by seedling planting density and slope aspect. Higher vegetation diversity was associated with north facing slopes and with higher densities of planted trees. Vegetation communities on the cooler, wetter north facing slopes and in areas planted with tree seedlings at high densities may have experienced less heat and water stress than on south facing slopes; these conditions may have been more conducive to emergence and growth of native understory species present in the coversoil propagule bank. Many forest understory plant species are less successful in open, unshaded, highly disturbed environments such as early reclamation sites than in more sheltered forest environments that experience less temperature extremes (Parendes and Jones 2000; Djietror et al. 2011).

Vegetation cover was primarily impacted by coarse woody debris abundance. The influence of coarse woody debris on vegetation cover was negative and this was likely due to the fact that coarse woody debris reduced vegetation cover by occupying much of the available growing space. However, coarse woody debris abundance did significantly modify the effect of aspect on several metrics of vegetation diversity and cover in areas capped with coversoil from a poor-xeric forest site. These metrics of diversity and cover were higher on south facing than north facing slopes when coarse woody debris was abundant, while the opposite was true when coarse woody debris was scarce. This suggests that coarse woody debris may have moderated the harsher environmental conditions (i.e. temperature extremes and water stress) on these south-facing slopes.

Ordinations showed that over the time period we studied, vegetation communities in areas capped with coversoils salvaged from the two forest types became more similar to each other; however, due to the brief timescale of our study, it was not clear whether this convergence was a short term shift (common in the first 1-5 years of development) on reclamation sites (Prach and Pysek 2001)) or a longer term trend towards homogenization between the two coversoil treatments.

Our second study showed that in level areas of all three reclamation sites, fine-scale patterns of variation in the developing plant community were more strongly related to space (likely reflecting mostly competitive and/or facilitative interactions) than to measured environmental parameters. This suggests that space was more important than the environmental parameters in structuring these early successional communities. Although environmental factors explained much less variation than space, they did explain significant variation in all three site types. Microtopographical features drove variation in vegetation communities, particularly at the older site type. Planted trees also influenced the variation in the vegetation community at the older site, although trees explained less variation than microtopography. More variation mightbe explained by trees at this site type once canopy closure, which often drives a shift in understory vegetation composition, occurs (Pensa et al. 2008). Environmental factors, including microtopography but excluding trees, explained more variation at the older than the young – rich-mesic site type; however, it was not clear whether this was an effect of site age or whether it was due to the larger size of microtopographic features at the older site type.

In addition to differences in explained variation, the three site types also differed in the types of indicator species and species driving spatial patterns. Comparing the two young site types, the community at the young – rich-mesic site type was driven more by introduced and non-forest associated species than at the young – poor-xeric site type. This was likely in large part due to potentially greater soil nutrients and lower water stress at the young – rich-mesic site type, as well as the different propagule banks present in the two materials. These factors might have created an environment more conducive to growth of introduced and non-forest species at the young – rich-mesic site type, while at the young – poor-xeric site type, conditions were more appropriate for native, forest-associated species.

Comparing the two ages of rich-mesic site types, at the older one spatial patterns were driven by many more forest-associated species and fewer non-forest forbs than at the young – rich-mesic site type. Forest-associated species at the older site had likely outcompeted many of the non-forest forbs, suggesting that some naturalization had occurred. We found some evidence that non-forest grass species may have been more persistent in the community than non-forest forbs but the effect of these species on forest-associated species was not clear.

Results from both studies showed that topographical features at large and small scales are important in structuring vegetation communities at reclamation sites. Thus creation of topographic variation at different scales could result in more complex vegetation communities and higher heterogeneity at reclamation sites. Both studies also showed that planted trees impacted the vegetation community. In the first study, vegetation diversity was associated with higher density tree seedling planting, suggesting that tree seedlings may have modified the understory growth environment, making it a more suitable environment for the species contained in the coversoil propagule bank. In the second study, planted trees explained a significant amount of variation in the vegetation community at the older site.

At the older site, we found evidence suggesting that some naturalization had occurred, leading to a community more dominated by native, forest-associated species. Although I studied the Sandhill Watershed site only four years after construction, some of our results (higher vegetation diversity in high density planting treatments and on north facing slopes) suggest that the reclamation methods examined in this study may be effective for accelerating development of a 'naturalized' diverse understory community.

4.2 Future research and limitations:

In future, studies should explore the longer term (greater than 10 years of development) influence of coversoil source and site design and amendments in structuring the developing forest community. Similar, but longer term, studies to my first study, or resampling of the Sandhill Watershed site later in development (particularly after canopy closure has occurred), will allow exploration of the longer term impact of factors such as capping with coversoil salvaged from different forest types, seedling planting density, slope aspect and coarse woody debris abundance on vegetation development.

Conclusions about vegetation community characteristics later in development in areas capped with coversoil salvaged from a poor-xeric forest site, as well as about convergence of communities in areas constructed with the two coversoil types, were limited by the lack of a suitable older – poor-xeric site type. Future research should include examination of a site capped with coversoil from a poor-xeric forest at an older stage; resampling of the young – poor-xeric site type used in my second study would accomplish this.

Our conclusions about the role of microtopography in driving vegetation patterns were limited by the fact that microtopography at the older – rich-mesic site type was larger in scale than at the young site types. This meant that it was not possible to determine whether the greater variation explained by this component at the older site type was due to the larger scale microtopography or to the greater time since material placement. Future research should examine the role of microtopographical feature size in driving vegetation communities.

In both studies, trees were planted in mixed species plantings. Natural forest studies have shown that different canopy species impact the understory community differently (Strong 2011), but this has not been explored in a reclamation context. Future research should explore the impact of planting of different tree species on understory vegetation development at reclamation sites.

Further research on the roles of non-forest grass species would also be beneficial. We found some evidence that these grasses may be more persistent than introduced forbs in vegetation communities at some reclamation sites, but the effect of these grasses on forest associated species was not clear. Further research could clarify the role of these species in the community and their persistence on longer timescales.

4.3 Management implications

Our results suggest that managers should create variation in topography at different scales from the microtopographical (one metre or less in height) level to the landscape level to achieve greater heterogeneity in vegetation communities at reclamation sites. More heterogeneous landscapes may be more resilient to disturbances. Tree seedlings should be planted at high densities to increase diversity of native and forest associated species at reclamation sites. Coarse woody debris should be placed, particularly on environmentally harsh sites (such as south facing slopes capped with coarse textured coversoils), to increase diversity and cover of native and forest associated vegetation. Using coversoils salvaged from different forest types will, at least early in site development, result in differing vegetation communities. Use of these coversoils in different reclamation areas may also increase landscape scale heterogeneity. Application of these coversoils in patches of varying sizes, or mixed together, will likely drive the development of differing communities than when these materials are applied separately. As spatial patterns at reclamation sites change over time, introduced species in the community may decline in importance. However, the long term effects of both non-forest grasses and forbs on forest associated species are not clear. Therefore, until the effects of these species types on forest-associated species are better understood, management interventions such as herbicide use on early establishment vegetation may be premature.

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Appendices

Appendix A Tables

Table A1: Mean height (cm) of tree seedlings of three species (*Populus tremuloides*, *Pinus banksiana*, *Picea glauca*) in areas capped with the two coversoil materials in 2012, 2013 and 2014 (seedling height was not measured in 2015).

(a) Poor-xeric coversoil

Species	2012	2013	2014
Populus tremuloides	36.63	39.43	44.94
Pinus banksiana	25.96	31.60	46.93
Picea glauca	29.83	33.50	32.53

(b) Rich-mesic coversoil

Species	2012	2013	2014
Populus tremuloides	34.37	65.59	89.63
Pinus banksiana	22.34	39.81	76.44
Picea glauca	29.03	32.54	45.65

Table A2: Species found at the Sandhill Watershed and W1 Dump research sites, including areas capped with coversoil from poor-xeric and rich-mesic sites. Species were identified and classified according to original range (native or introduced) and functional type (Tree, Shrub, Forb, Graminoid or Non-vascular) according to Moss (1994) and USDA (2016).

Species	Original Range	Functional Type
Achillea millefolium L.	Native	Forb
Achillea sibirica Ledeb.	Native	Forb
Actaea rubra (Ait) Willd.	Native	Forb
Agropyron trachycaulum var. glaucum (Pease & Moore) Matte	Native	Graminoid
Agropyron trachycaulum var. trachycaulum (Link) Malte	Native	Graminoid
Agropyron trachycaulum var. unilaterale (Cassidy) Malte	Native	Graminoid
Agrostis scabra Willd.	Native	Graminoid
Alnus crispa (Ait) Pursh	Native	Shrub
Alnus tenuifolia Nutt.	Native	Shrub
Alopecurus aequalis Sobol.	Native	Graminoid
Amelanchier alnifolia Nutt.	Native	Shrub
Apocynum androsaemifolium L.	Native	Forb
Apocynum cannabinum L.	Native	Forb
Aquilegia brevistyla Hook.	Native	Forb

Arabis lyrata ssp. kamchatica (Fisch.) Hult.	Native	Forb
Aralia nudicaulis L.	Native	Forb
Arctostaphylos uva-ursi (L.) Spreng.	Native	Shrub
Arnica chamissonis Less.	Native	Forb
Aster ciliolatus Lindl.	Native	Forb
Aster puniceus L.	Native	Forb
Aster sp. L.	Native	Forb
Astragalus canadensis L.	Native	Forb
Astragalus cicer L.	Introduced	Forb
Astragalus sp. L.	Native	Forb
Aulacomnium palustre (Hedw.) Schwaegr.	Native	Non-vascular
Beckmannia syzigachne (Steud.) Fern.	Native	Graminoid
Betula papyrifera Marsh.	Native	Tree
Betula pumila L.	Native	Shrub
Bidens cernua L.	Native	Forb
Brachythecium sp. BSG.	Native	Non-vascular
Bromus ciliatus L.	Native	Graminoid
Bromus inermis Leyss.	Introduced	Graminoid
Bromus sp. L.	Native	Graminoid
Bryum argenteum Hedw.	Native	Non-vascular
Calamagrostis canadensis spp. canadensis (Michx.) Beauv.	Native	Graminoid
Calamagrostis inexpansa A. Gray	Native	Graminoid
Campanula rotundifolia L.	Native	Forb
Carex aenea Fern.	Native	Graminoid
Carex atherodes Spreng.	Native	Graminoid
Carex aurea Nutt.	Native	Graminoid
Carex bebbii Olney ex. Fern.	Native	Graminoid
Carex deflexa Hornem.	Native	Graminoid
Carex lasiocarpa Ehrh.	Native	Graminoid
Carex praticola Ryed.	Native	Graminoid
Carex rossii Boott.	Native	Graminoid
Carex rostrata Stokes	Native	Graminoid
Carex siccata Dewey	Native	Graminoid
Carex spp. L.	Native	Graminoid
Carex trisperma Dewey	Native	Graminoid
Carex umbellata Schk.	Native	Graminoid
Ceratodon purpureus (Hedw.) Brid.	Native	Non-vascular
Chamaesaracha grandifolia (Hook.) Fern.	Native	Forb
Chenopodium album L. (berlandieri)	Introduced	Forb
Chenopodium capitatum (L.) Aschers.	Native	Forb
Chenopodium gigantospernum Aellen	Native	Forb
Chenopodium rubrum L.	Native	Forb
Circium arvense (L.) Scop.	Introduced	Forb
Cladonia mitis Sandst.	Native	Non-vascular

Cladonia sp. P. Browne	Native	Non-vascular
Comandra umbellata (L.) Nutt.	Native	Forb
Cornus canadensis L.	Native	Forb
Cornus stolonifera Michx.	Native	Shrub
Corydalis aurea Willd.	Native	Forb
Corydalis sempervirens (L.) Pers.	Native	Forb
Corylus cornuta Marsh.	Native	Shrub
Crepis tectorum L.	Introduced	Forb
Danthonia spicata (L.) Beauv.	Native	Graminoid
Dicranum sp. Hedw.	Native	Non-vascular
Dracocephalum parviflorum Nutt.	Native	Forb
Drepanocladus uncinatus (Hedw.) Warnst.	Native	Non-vascular
Elymus canadensis L.	Native	Graminoid
Elymus innovatus ssp. Innovatus Beal.	Native	Graminoid
Epilobium angustifolium L.	Native	Forb
Epilobium ciliatum Raf.	Native	Forb
Equisetum arvense L.	Native	Forb
Equisetum hymale L.	Native	Forb
Equisetum pratense Ehrh.	Native	Forb
Equisetum scirpoides Michx.	Native	Forb
Equisetum sylvaticum L.	Native	Forb
Equisetum variegatum Schleich.	Native	Forb
Erigeron canadensis L.	Native	Forb
Erysimum cheiranthoides L. *ssp. Altum* Ahti.	Introduced	Forb
Festuca rubra L.	Native	Graminoid
Festuca saximontana Rydb.	Native	Graminoid
Fragaria vesca L.	Native	Forb
Fragaria virginiana Duchesne	Native	Forb
Fumaria hygrometrica Hedw.	Native	Forb
Galeopsis tetrahit L.	Introduced	Forb
Galium aparine L.	Native	Forb
Galium boreale L.	Native	Forb
Galium trifidum L.	Native	Forb
Galium triflorum Michx.	Native	Forb
Geranium bicknellii Britt.	Native	Forb
Geum aleppicum Jacq.	Native	Forb
Geum macrophyllum Willd.	Native	Forb
Glyceria pulchella (Nash) K. Schum	Native	Graminoid
Halenia deflexa (Sm.) Griseb.	Native	Forb
Hieracium umbellatum L.	Native	Forb
Hierochloe odorata (L.) Beauv.	Native	Graminoid
Hippophae rhamnoides L.	Introduced	Forb
Hordeum jubatum L.	Native	Graminoid
Hylocomium splendens (Hedw.) BSG	Native	Non-vascular
Impatiens capensis Meerb.	Native	Forb

Juncus (c.f.) balticus Willd.	Native	Graminoid
Larix laricina (Du Roi) K. Koch	Native	Tree
Lathyrus ochroleucus Hook.	Native	Forb
Lathyrus venosus Muhl.	Native	Forb
Lepidium densiflorum Schrad.	Introduced	Forb
Lilium philadelphicum L.	Native	Forb
Lonicera dioica L.	Native	Forb
Lotus corniculatus L.	Introduced	Forb
Lysimachia thrysiflora L.	Native	Forb
Maianthemum canadense Desf.	Native	Forb
Matricaria matricarioides (Less.) Porter	Introduced	Forb
Medicago sativa L.	Introduced	Forb
Melilotus alba Desr.	Introduced	Forb
Melilotus officinalis (L.) Lam.	Introduced	Forb
Melilotus sp. Mill.	Introduced	Forb
Mentha arvensis L.	Native	Forb
Mertensia paniculata (Ait.) G. Don	Native	Forb
Moehringia lateriflora (L.) Fenz.	Native	Forb
Oryzopsis asperifolia Michx.	Native	Graminoid
Oryzopsis pungens (Torr.) A.S. Hitchc.	Native	Graminoid
Peltigera sp. Willd.	Native	Non-vascular
Petasites palmatus (Ait) A. Gray	Native	Forb
Petasites sagittatus (Pursh) A. Gray	Native	Forb
Phalaris arundinacea L.	Native	Graminoid
Phleum pratense L.	Introduced	Graminoid
Picea glauca (Moench) Voss	Native	Tree
Pinus banksiana Lamb.	Native	Tree
Plantago major L.	Introduced	Forb
Pleurozium schreberi (Brid.) Mitt.	Native	Non-vascular
Poa palustris L.	Native	Graminoid
Poa pratensis L.	Introduced	Graminoid
Poa sp. L.	Native	Graminoid
Polygonum arenastrum Jord. ex. Bor.	Introduced	Forb
Polygonum convolvulus L.	Introduced	Forb
Polygonum erectum L.	Native	Forb
Polygonum lapathifolium L.	Introduced	Forb
Polygonum spp. L.	Introduced	Forb
Polytrichum juniperinum Hedw.	Native	Non-vascular
Polytrichum pilferum Hedw.	Native	Non-vascular
Populus balsamifera L.	Native	Tree
Populus tremuloides Michx.	Native	Tree
Potentilla norvegica L.	Introduced	Forb
Potentilla tridentata Ait.	Native	Forb
Prunus pensylvanica L.f.	Native	Shrub
Prunus virginiana L.	Native	Shrub
Puccinella pauciflora (Presl.) Munz	Native	Graminoid

Pyrola sp. L.	Native	Forb
Ranunculus abortivus L.	Native	Forb
Ranunculus macounii Britt.	Native	Forb
Ranunculus sceleratus L.	Native	Forb
Ranunculus spp. L.	Native	Forb
Ribes cf. triste Pall.	Native	Shrub
Ribes glandulosum Grauer	Native	Shrub
Ribes lacustre (Pers.) Poir.	Native	Shrub
Ribes oxyacanthoides L.	Native	Shrub
Rorippa palustris ssp. hispida (L.) Besser	Native	Forb
Rosa acicularis Lindl.	Native	Shrub
Rosa woodsii Lindl.	Native	Shrub
Rubus acaulis Michx.	Native	Forb
Rubus arcticus L.	Native	Forb
Rubus idaeus L.	Native	Shrub
Rubus pubescens Raf.	Native	Forb
Salix cf. planifolia Pursh	Native	Shrub
Salix cf. bebbiana Sarg.	Native	Shrub
Salix lucida ssp. lasiandra Muhl. (Benth)	Native	Shrub
Salix sp. L.	Native	Shrub
Salsola kali L.	Introduced	Forb
Schizachne purpurascens ssp. purpurascens (Torr.) Swallen	Native	Graminoid
Scutellaria galericulata L.	Native	Forb
Senecio pauperculus Michx.	Native	Forb
Shepherdia canadensis (L.) Nutt.	Native	Shrub
Sisyrinchium montanum Greene	Native	Forb
Sium suave Walt.	Native	Forb
Solidago canadensis L.	Native	Forb
Solidago sp. L.	Native	Forb
Solidago spathulata DC.	Native	Forb
Sonchus arvensis L.	Introduced	Forb
Sonchus asper L.	Introduced	Forb
Sonchus uliginosus Bieb.	Introduced	Forb
Stachys palustris L.	Introduced	Forb
Stellaria longifolia Muhl.	Native	Forb
Stellaria longipes Goldie.	Native	Forb
Symphoricarpos albus (L.) Blake	Native	Shrub
Symphoricarpos occidentalis Hook.	Native	Shrub
Taraxicum officinale Weber	Introduced	Forb
Tragopogon dubius Scop.	Introduced	Forb
Trientalis borealis Raf.	Native	Forb
Trifolium hybridum L.	Introduced	Forb
Trifolium pratense L.	Introduced	Forb
Trifolium repens L.	Introduced	Forb
Trifolium sp. L.	Introduced	Forb

Typha latifolia L.	Native	Graminoid
Urtica dioica L.	Native	Forb
Vaccinium myrtilloides Michx.	Native	Shrub
Vicia americana Muhl.	Native	Forb
Viola adunca J.E. Smith	Native	Forb
Viola canadensis L.	Native	Forb
Unidentifiable vascular plant sp.		
Unidentifiable moss sp.		

Table A3: Results (*P* values) of (a) one-way ANOVA testing differences in concentrations of Nitrogen, Phosphorus, Potassium, Manganese and Sulphur between the three site types and (b) post hoc Tukey HSD tests of differences in Manganese and Sulphur concentrations between the three site types (YPX = young – poor-xeric, YRM = young – rich-mesic, ORM = older – rich-mesic). *P* values are shown in bold when significant (α= 0.05).

(a)

Nutrient	***P* value**
Nitrogen (%)	0.0777
Phosphorus	0.0820
Potassium	0.5380
Manganese	**0.0123**
Sulphur	**0.0286**

(b)

Nutrient	**Young – poor-xeric *versus* older – rich-mesic**	**Young – rich-mesic *versus* older – rich-mesic**	**Young – poor-xeric *versus* young – rich-mesic**
Manganese	**0.0098**	0.6182	0.0729
Sulphur	**0.0369**	0.9847	0.0519

Table A4: Number of community types per grid, indicator species per grid, quadrats per community type and indicator species per community type for each grid plot. Site types are indicated using abbreviations: young – rich-mesic site type (YRM), young – poor-xeric site type (YPX) and older – rich-mesic site type (ORM). There were five grid plots per site type.

Site-Type	**Grid**	**Number of community types**	**Number of indicator species per grid**	**Mean number of quadrats per community type**	**Mean number of indicator species per community type**
YPX	**1**	2	1	50.0	0.5
YPX	**2**	2	1	50.0	0.5

YPX	**3**	2	2	50.0	1.0
YPX	**4**	2	4	50.0	2.0
YPX	**5**	2	1	50.0	0.5
YRM	**6**	4	5	25.0	1.8
YRM	**7**	2	3	50.0	1.5
YRM	**8**	2	2	50.0	1.0
YRM	**9**	2	4	50.0	2.0
YRM	**10**	2	3	50.0	1.5
ORM	**11**	5	11	20.0	4.6
ORM	**12**	6	9	16.7	2.5
ORM	**13**	10	11	10.0	6.1
ORM	**14**	9	7	11.1	2.8
ORM	**15**	9	11	11.1	4.8

Table A5: Results (*P* values) of pairwise comparisons among site types for mean values of response variables resulting from community complexity, spatial complexity and variation partitioning analyses. Significant differences between site types are shown in bold (alpha = 0.05). Variables were analyzed using one-way ANOVA followed by Tukey HSD tests, except in cases (indicated by *) in which no variation was present in one site type; in these cases a Wilcoxon signed-rank test was used to analyze the remaining two site types.

	Young – poor-xeric *versus* older – rich-mesic	**Young – rich-mesic *versus* older – rich-mesic**	**Young – rich-mesic *versus* young – poor-xeric**
Number of community types*	**-**	**0.0095***	-
Number of quadrats per community type*	**-**	**0.0095***	-
Number of indicator species	**<0.0001**	**<0.0001**	0.2243
Number of indicator species per community type	**0.0005**	**0.0030**	0.5546
Number of significant PCNM variables	**0.0349**	0.9782	**0.0498**
Number of significant RDA axes	**0.0010**	0.8016	**0.0029**
Number of species driving spatial patterns	**0.0164**	**0.0333**	0.9181
Variation explained by space	**<0.0001**	0.2590	**0.0004**
Variation explained by environment	**0.0023**	**0.0032**	0.9980

Variation explained by linear trend	**0.0282**	0.5296	0.1849
Residuals	**<0.0001**	0.2440	**0.0005**

Table A6: Number of significant RDA axes, PCNM variables, and species driving spatial patterns per grid are shown for each grid plot. Site types are indicated using abbreviations: young – rich-mesic site type (YRM), young – poor-xeric site type (YPX) and older – rich-mesic site type (ORM).

Site-Type	Grid	Significant RDA Axes	Significant PCNM Variables	PCNM Drivers
YPX	**1**	8	18	3
YPX	**2**	7	18	3
YPX	**3**	8	24	5
YPX	**4**	6	19	3
YPX	**5**	7	19	9
YRM	**6**	10	24	5
YRM	**7**	10	30	2
YRM	**8**	15	35	6
YRM	**9**	11	28	6
YRM	**10**	10	21	7
ORM	**11**	10	19	13
ORM	**12**	12	28	9
ORM	**13**	12	33	9
ORM	**14**	12	28	6
ORM	**15**	11	25	11

Table A7: Indicator species (identified using indicator species analysis during analysis for community complexity) for each community type (identified using cluster analysis) of each grid plot. Vascular plant species were identified according to Moss (1994). There were five grid plots for each site type: young-rich-mesic (YRM), young-poor-xeric (YPX) and older-rich-mesic (ORM). See Appendix Table A1 for a complete species list.

Grid & Site Type	Community Type	Indicator Species
1 (YPX)	1	None
	2	*Petasites palmatus*
2 (YPX)	1	None
	2	*Oryzopsis pungens*
3 (YPX)	1	None
	2	*Carex siccata, Rosa acicularis*

4 (YPX)	1	None
	2	*Agropyron trachycaulum var. trachycaulum, Epilobium angustifolium, Mature moss, Taraxacum officinale*
5 (YPX)	1	None
	2	*Prunus pensylvanica*
6 (YRM)	1	None
	2	*Calamagrostis canadensis, Mature moss, Trifolium* sp.
	3	*Rubus idaeus*
	4	*Calamagrostis canadensis, Ribes glandulosum, Trifolium* sp.
7 (YRM)	1	None
	2	*Hordeum jubatum, Melilotus alba, Typha latifolia*
8 (YRM)	1	*Fragaria virginiana*
	2	*Aster ciliolatus*
9 (YRM)	1	*Epilobium angustifolium*
	2	*Medicago sativa, Sisyrinchium montanum, Ribes glandulosum*
10 (YRM)	1	None
	2	*Agrostis scabra, Calamagrostis canadensis, Urtica dioica*
11 (ORM)	1	*Agropyron trachycaulum var. trachycaulum, Epilobium angustifolium, Rubus idaeus*
	2	*Epilobium angustifolium,* Immature moss
	3	*Agropyron trachycaulum var. trachycaulum, Petasites palmatus, Rubus idaeus, Vicia americana*
	4	*Agropyron trachycaulum var. trachycaulum, Epilobium angustifolium,* Immature moss, *Rubus idaeus, Vicia americana*
	5	*Agropyron trachycaulum var. trachycaulum, Aster ciliolatus, Equisetum sylvaticum, Lathyrus ochroleucus,* Immature moss, *Rosa acicularis, Rubus idaeus, Rubus pubescens, Vicia americana*
12 (ORM)	1	None
	2	*Equisetum arvense*
	3	*Hieracium umbellatum, Equisetum arvense, Halenia deflexa, Lathyrus ochroleucus, Salix sp. Vicia americana*
	4	*Equisetum arvense,* Mature moss
	5	*Equisetum arvense, Lathyrus ochroleucus, Petasites palmatus, Rubus idaeus, Vicia americana*
	6	*Rubus idaeus*
13 (ORM)	1	*Epilobium angustifolium, Lathyrus ochroleucus, Rubus idaeus, Sonchus arvensis, Taraxacum officinale*

	2	*Epilobium angustifolium, Mertensia paniculata, Rosa acicularis, Rubus idaeus, Sonchus arvensis, Taraxacum officinale*
	3	*Elymus innovatus, Epilobium angustifolium, Lathyrus ochroleucus, Sonchus arvensis, Taraxacum officinale*
	4	*Elymus innovatus, Epilobium angustifolium, Lathyrus ochroleucus, Mertensia paniculata, Rosa acicularis, Rubus idaeus, Sonchus arvensis, Taraxacum officinale, Trientalis borealis*
	5	*Epilobium angustifolium, Rosa acicularis, Rubus idaeus, Sonchus arvensis, Taraxacum officinale*
	6	*Epilobium angustifolium, Lathyrus ochroleucus, Rubus idaeus, Sonchus arvensis, Taraxacum officinale, Trientalis borealis*
	7	*Mertensia paniculata, Sonchus arvensis, Taraxacum officinale*
	8	*Epilobium angustifolium, Lathyrus ochroleucus, Mertensia paniculata, Rosa acicularis, Rubus idaeus, Sonchus arvensis, Taraxacum officinale, Trientalis borealis*
	9	*Epilobium angustifolium, Lathyrus ochroleucus, Mertensia paniculata, Petasites palmatus, Rosa acicularis, Rubus idaeus, Taraxacum officinale, Vaccinium myrtilloides*
	10	*Elymus innovatus, Epilobium angustifolium, Lathyrus ochroleucus, Petasites palmatus, Rosa acicularis, Rubus idaeus*
14 (ORM)	1	None
	2	*Rosa acicularis*
	3	*Calamagrostis canadensis, Rubus pubescens, Rubus idaeus, Rosa acicularis, Epilobium angustifolium*
	4	*Salix sp., Rubus idaeus, Epilobium angustifolium*
	5	*Rubus pubescens, Equisetum arvense, Rosa acicularis, Epilobium angustifolium*
	6	*Rubus idaeus, Equisetum arvense, Rosa acicularis, Epilobium angustifolium*
	7	*Rosa acicularis*
	8	*Rubus pubescens, Rubus idaeus, Equisetum arvense, Rosa acicularis, Epilobium angustifolium*
	9	*Equisetum arvense, Epilobium angustifolium*
15 (ORM)	1	*Achillea millefolium, Vicia americana*, Bare ground
	2	*Achillea millefolium, Lathyrus ochroleucus, Rubus idaeus, Vicia americana*, Bare ground
	3	*Achillea millefolium, Galium boreale, Lathyrus ochroleucus, Vicia americana*, Bare ground
	4	*Elymus innovatus, Lathyrus ochroleucus, Petasites palmatus, Rosa acicularis, Vicia americana*
	5	*Achillea millefolium, Ribes oxyacanthoides, Lathyrus ochroleucus, Petasites palmatus, Rosa acicularis, Vicia americana*, Bare ground
	6	*Achillea millefolium, Lathyrus ochroleucus, Petasites palmatus,*

	Vicia americana
7	*Achillea millefolium, Lathyrus ochroleucus, Mertensia paniculata, Petasites palmatus, Rubus idaeus, Vicia americana*
8	*Calamagrostis canadensis, Elymus innovatus*, Bare ground
9	*Achillea millefolium, Calamagrostis canadensis, Elymus innovatus, Vicia americana*, Bare ground

Table A8: The percent variation explained by each component in the variation partitioning analysis for each grid plot. Site types are indicated using abbreviations: young – rich-mesic site type (YRM), young – poor-xeric site type (YPX) and older – rich-mesic site type (ORM). Dashes (-) indicate that component was not considered for the site type or was not chosen during the forward selection process. The environmental variable component at the young – poor-xeric and young – rich-mesic site types included microtopography and coarse woody debris; at the older – rich-mesic site type this component included microtopography and the tree canopy.

Site Type	Grid	PCNM (Spatial)	Environmental Variables	Tree Canopy	Microtopography	Linear Trend	Residuals
YPX	**1**	0.36	0.052	-	-	0.065	0.63
YPX	**2**	0.31	0.031	-	-	0.040	0.69
YPX	**3**	0.41	0.088	-	-	0.090	0.57
YPX	**4**	0.33	0.035	-	-	0.052	0.66
YPX	**5**	0.31	0.058	-	-	0.085	0.67
YRM	**6**	0.52	-	-	-	0.15	0.48
YRM	**7**	0.52	0.0041	-	-	0.11	0.47
YRM	**8**	0.54	0.051	-	-	0.11	0.46
YRM	**9**	0.62	0.13	-	-	0.19	0.40
YRM	**10**	0.42	0.018	-	-	0.061	0.57
ORM	**11**	0.59	0.12	-	0.12	0.26	0.40
ORM	**12**	0.56	0.19	0.062	0.17	0.097	0.44
ORM	**13**	0.55	0.15	0.056	0.11	0.14	0.43
ORM	**14**	0.57	0.15	0.050	0.14	0.12	0.42
ORM	**15**	0.62	0.19	0.052	0.16	0.17	0.38

Appendix B Figures

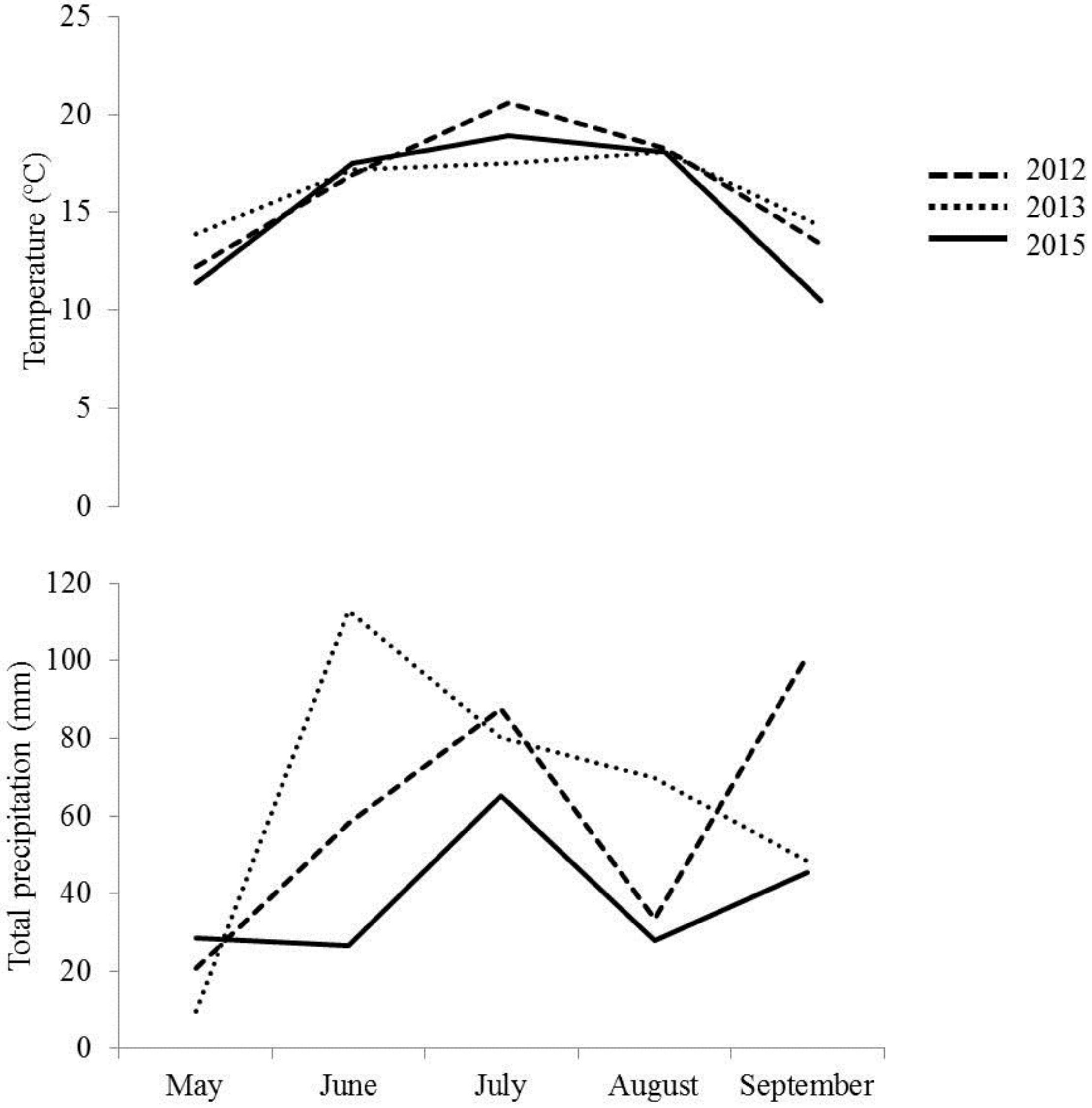


Figure B1: Growing season (May 1 – September 30) mean monthly temperature (ºC) and total monthly precipitation (mm) for 2012, 2013 and 2015, collected at Mildred Lake, Alberta. Data from Environment Canada (2015).

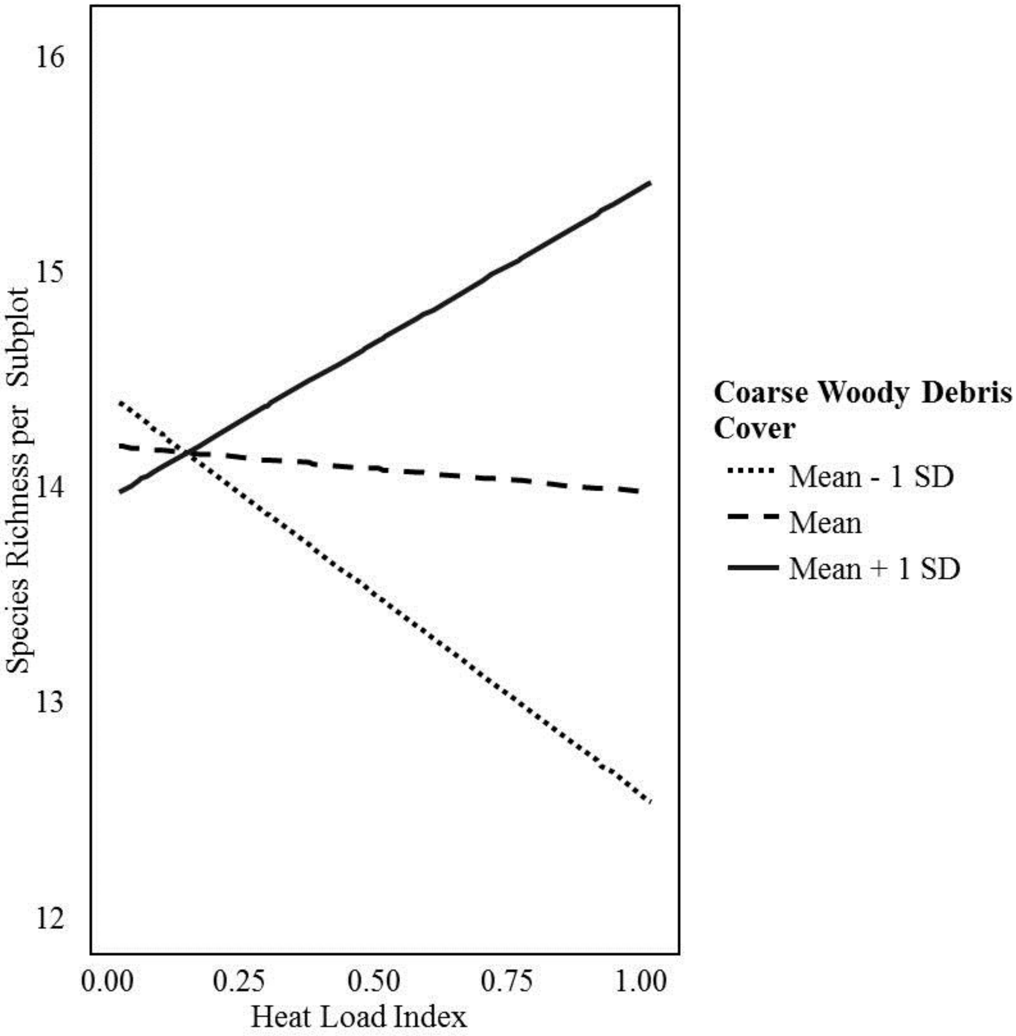


Figure B2: Interaction of heat load index (HLI; reflecting slope and aspect) and coarse woody debris volume on species richness per vegetation subplot in 2015 in areas reclaimed with coversoil salvaged from a poor-xeric site. The influence of HLI on vegetation cover is shown at three levels of coarse woody debris cover (mean, mean – 1 standard deviation and mean + 1 standard deviation). See also Table 2-4.

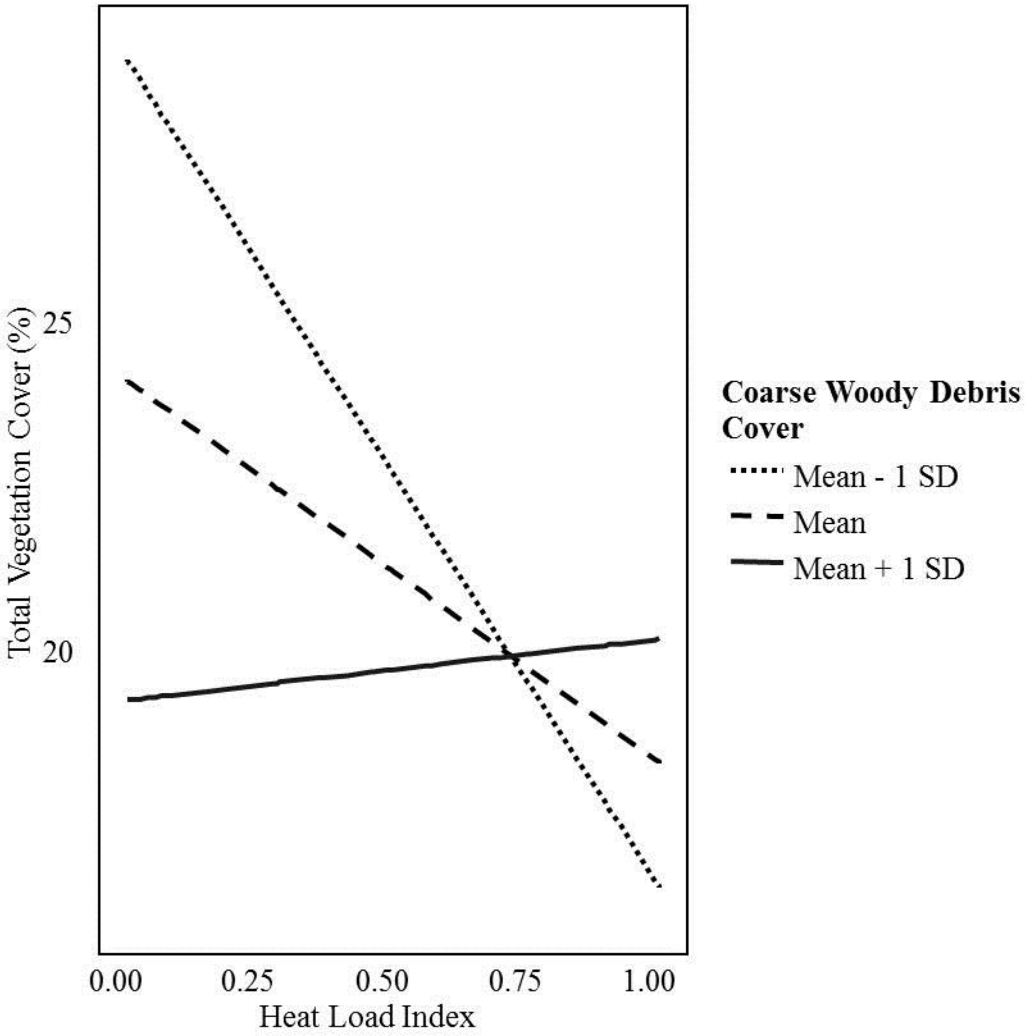


Figure B3: Interaction of heat load index (HLI; reflecting slope and aspect) and coarse woody debris volume on total vegetation cover (%) in 2013 in areas reclaimed with coversoil salvaged from a poor-xeric site. The influence of HLI on vegetation cover is shown at three levels of coarse woody debris cover (mean, mean – 1 standard deviation and mean + 1 standard deviation). See also Table 2-4.

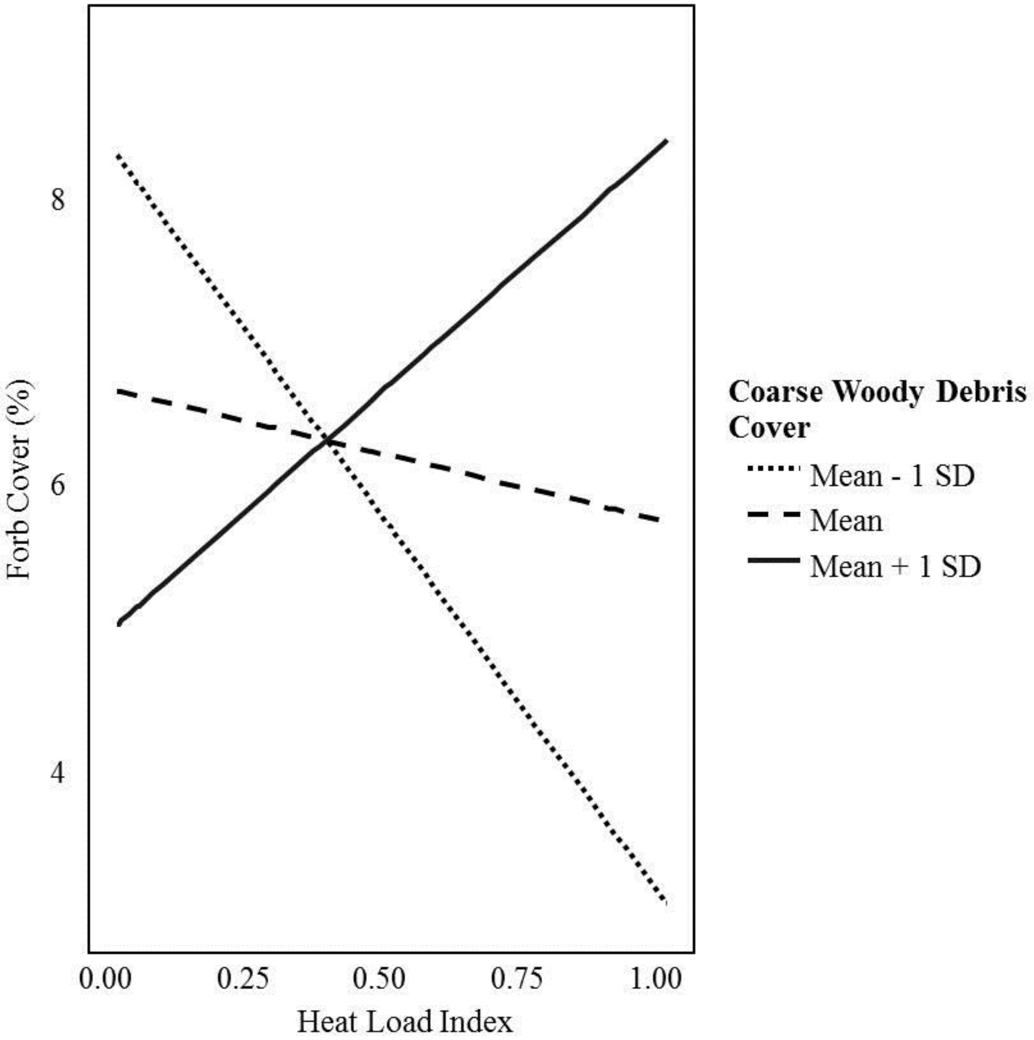


Figure B4: Interaction of heat load index (HLI; reflecting slope and aspect) and coarse woody debris volume on cover by forb species (%) in 2013 in areas reclaimed with coversoil salvaged from a poor-xeric site. The influence of HLI on vegetation cover is shown at three levels of coarse woody debris cover (mean, mean – 1 standard deviation and mean + 1 standard deviation). See also Table 2-4.

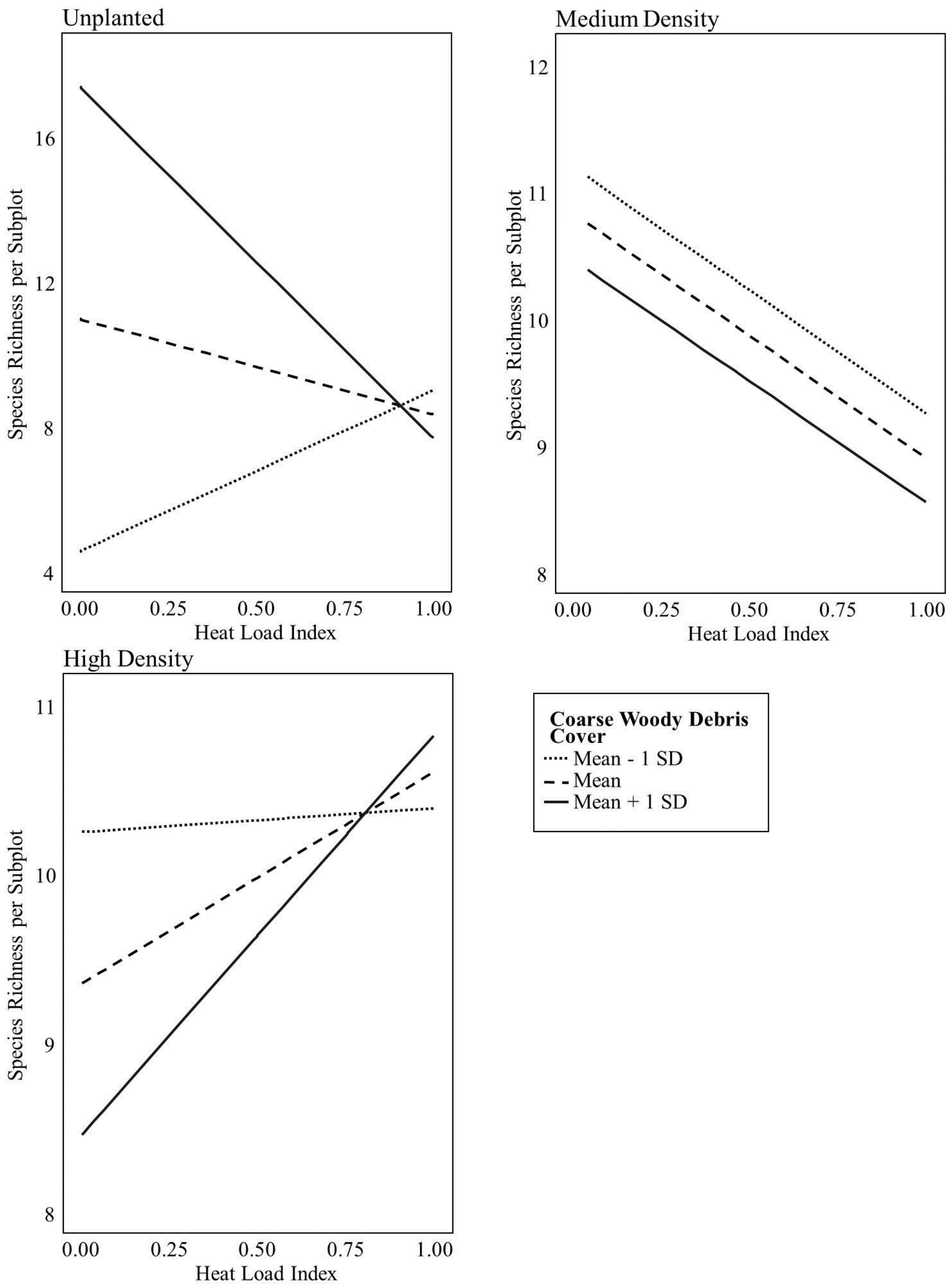


Figure B5: Interaction of planting density, heat load index (HLI; reflecting slope and aspect) and coarse woody debris volume on species richness per vegetation subplot in 2012 in areas reclaimed with coversoil salvaged from a poor-xeric site. In each of the three planting density treatments (unplanted = 0 stems per hectare (sph), medium density = 5 000 sph, high density = 10 000 sph) the influence of heat load index on species richness is shown at three levels of coarse woody debris cover (mean, mean – 1 standard deviation and mean + 1 standard deviation). See also Table 2-4.

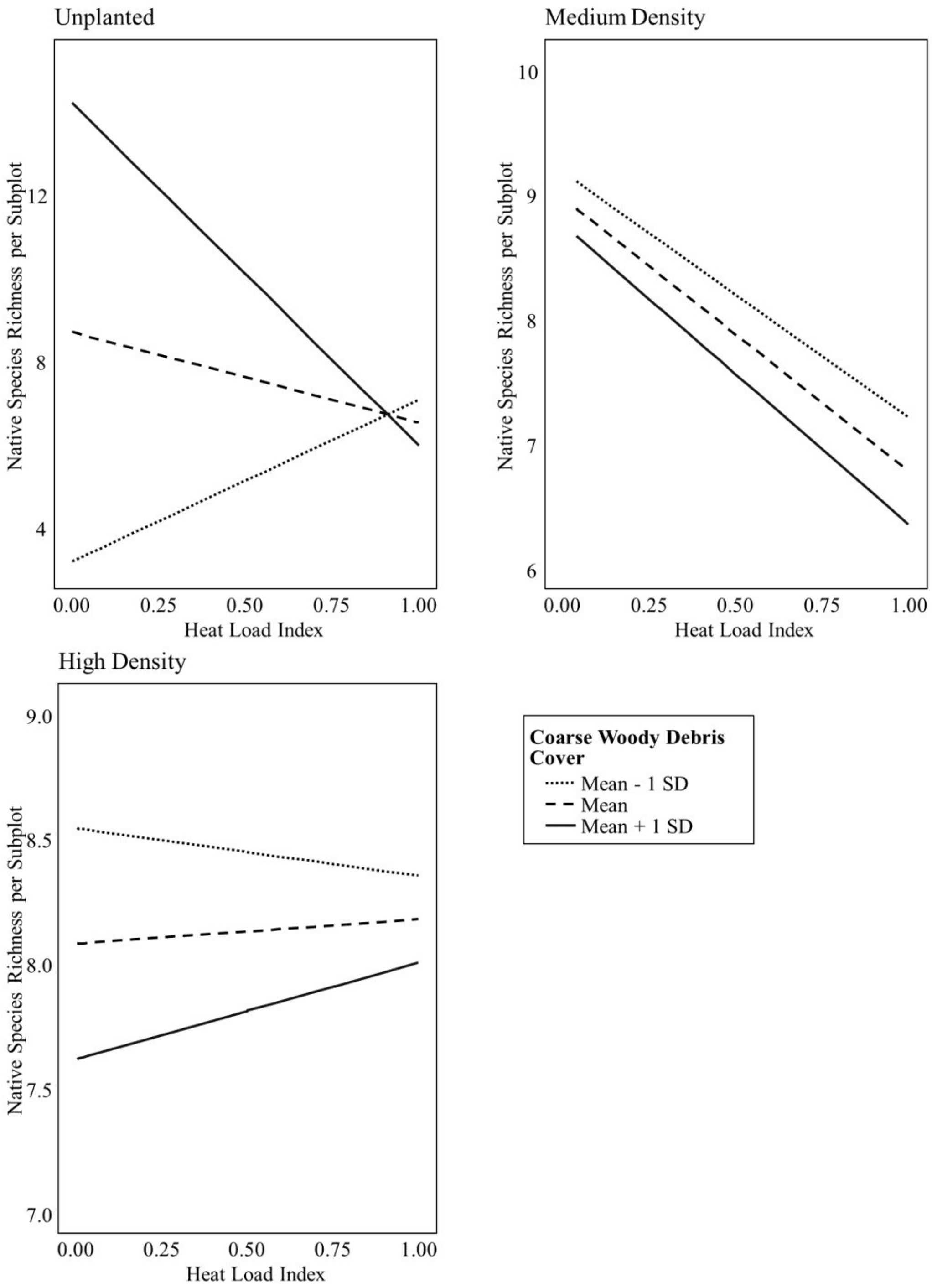


Figure B6: Interaction of planting density, heat load index (HLI; reflecting slope and aspect) and coarse woody debris volume on native species richness per vegetation subplot in 2012 in areas reclaimed with coversoil salvaged from a poor-xeric site. In each of the three planting density treatments (unplanted = 0 stems per hectare (sph), medium density = 5 000 sph, high density = 10 000 sph) the influence of heat load index on species richness is shown at three levels of coarse woody debris cover (mean, mean – 1 standard deviation and mean + 1 standard deviation). See also Table 2-4.

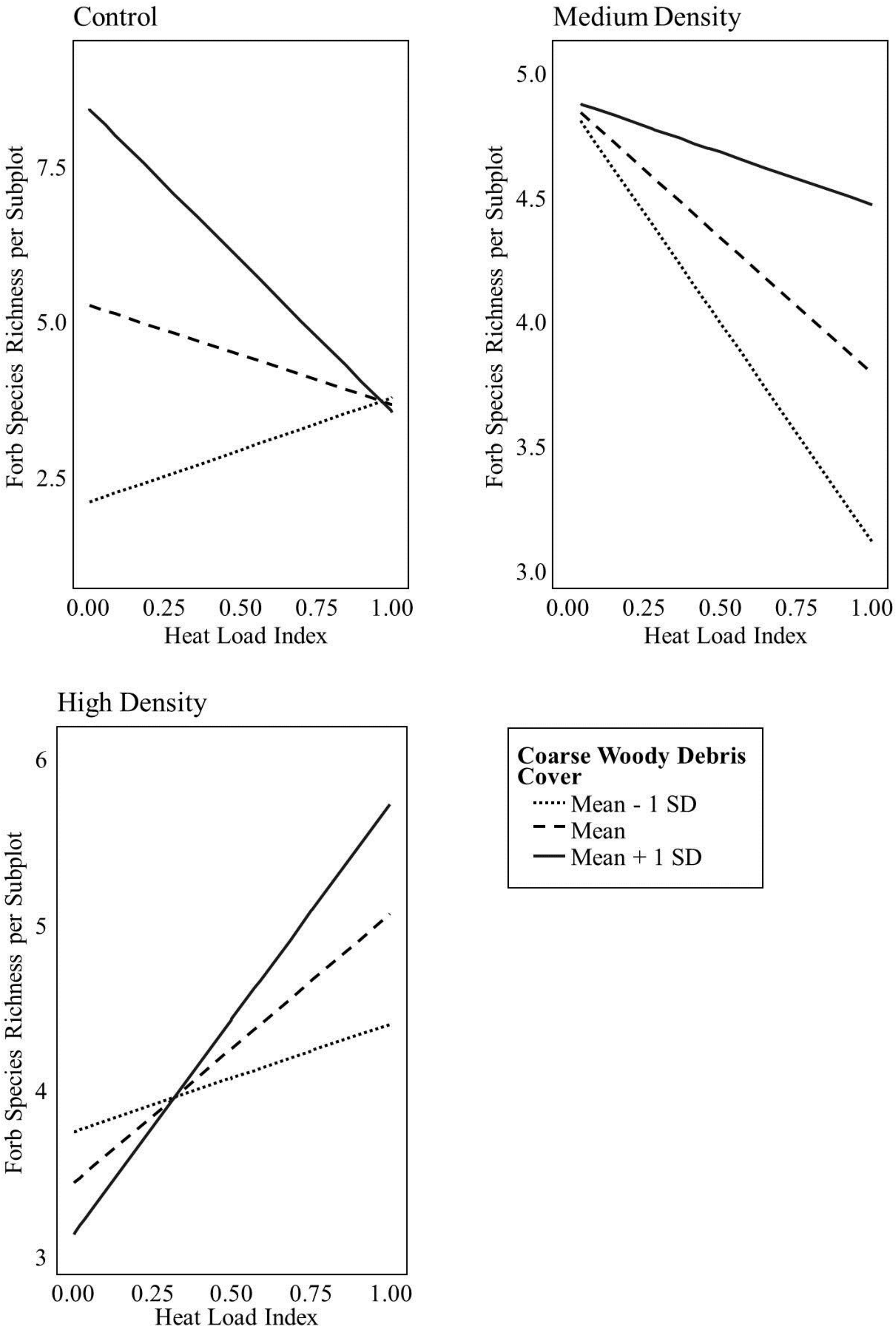


Figure B7: Interaction of planting density, heat load index (HLI; reflecting slope and aspect) and coarse woody debris volume on forb species richness per vegetation subplot in 2012 in areas reclaimed with coversoil salvaged from a poor-xeric site. In each of the three planting density treatments (unplanted = 0 stems per hectare (sph), medium density = 5 000 sph, high density = 10 000 sph) the influence of heat load index on species richness is shown at three levels of coarse woody debris cover (mean, mean – 1 standard deviation and mean + 1 standard deviation). See also Table 2-4.

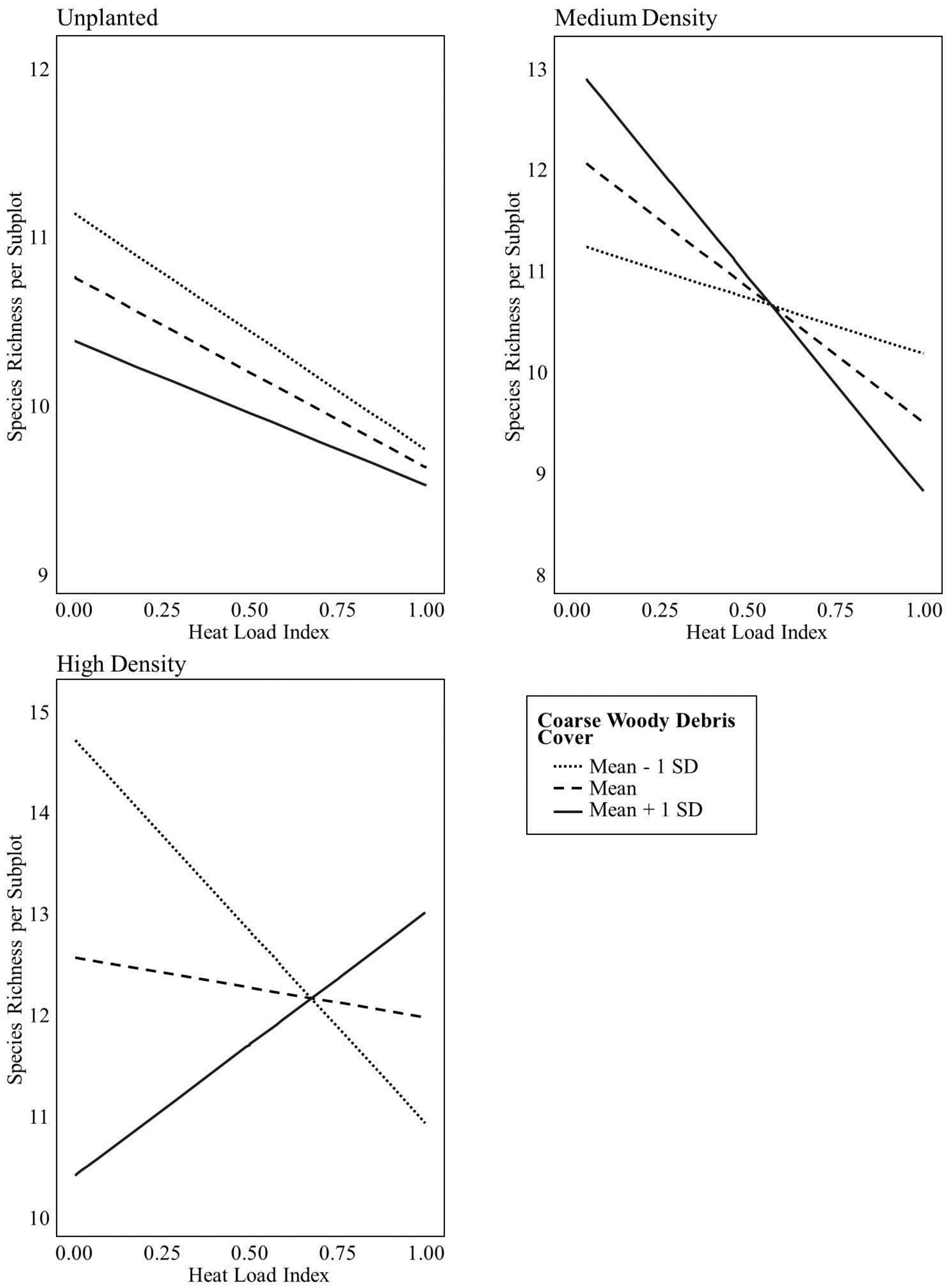


Figure B8: Interaction of planting density, heat load index (HLI; reflecting slope and aspect) and coarse woody debris volume on species richness per vegetation subplot in 2013 in areas reclaimed with coversoil salvaged from a poor-xeric site. In each of the three planting density treatments (unplanted = 0 stems per hectare (sph), medium density = 5 000 sph, high density = 10 000 sph) the influence of heat load index on species richness per subplot is shown at three levels of coarse woody debris cover (mean, mean – 1 standard deviation and mean + 1 standard deviation). See also Table 2-4.

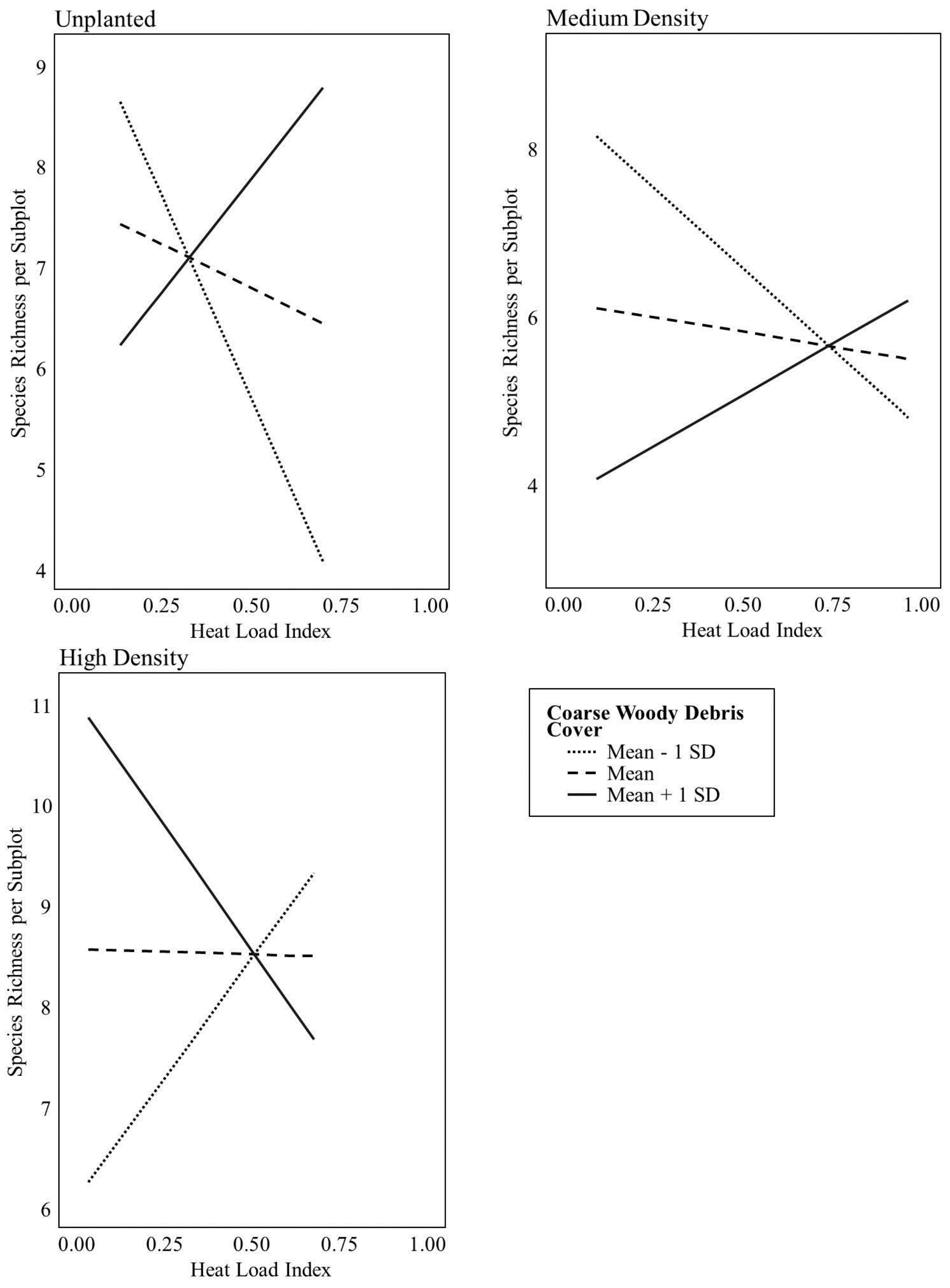


Figure B9: Interaction of planting density, heat load index (HLI; reflecting slope and aspect) and coarse woody debris volume on species richness per vegetation subplot in 2012 in areas reclaimed with coversoil salvaged from a rich-mesic site. In each of the three planting density treatments (unplanted = 0 stems per hectare (sph), medium density = 5 000 sph, high density = 10 000 sph) the influence of heat load index on species richness is shown at three levels of coarse woody debris cover (mean, mean – 1 standard deviation and mean + 1 standard deviation). See also Table 2-8.

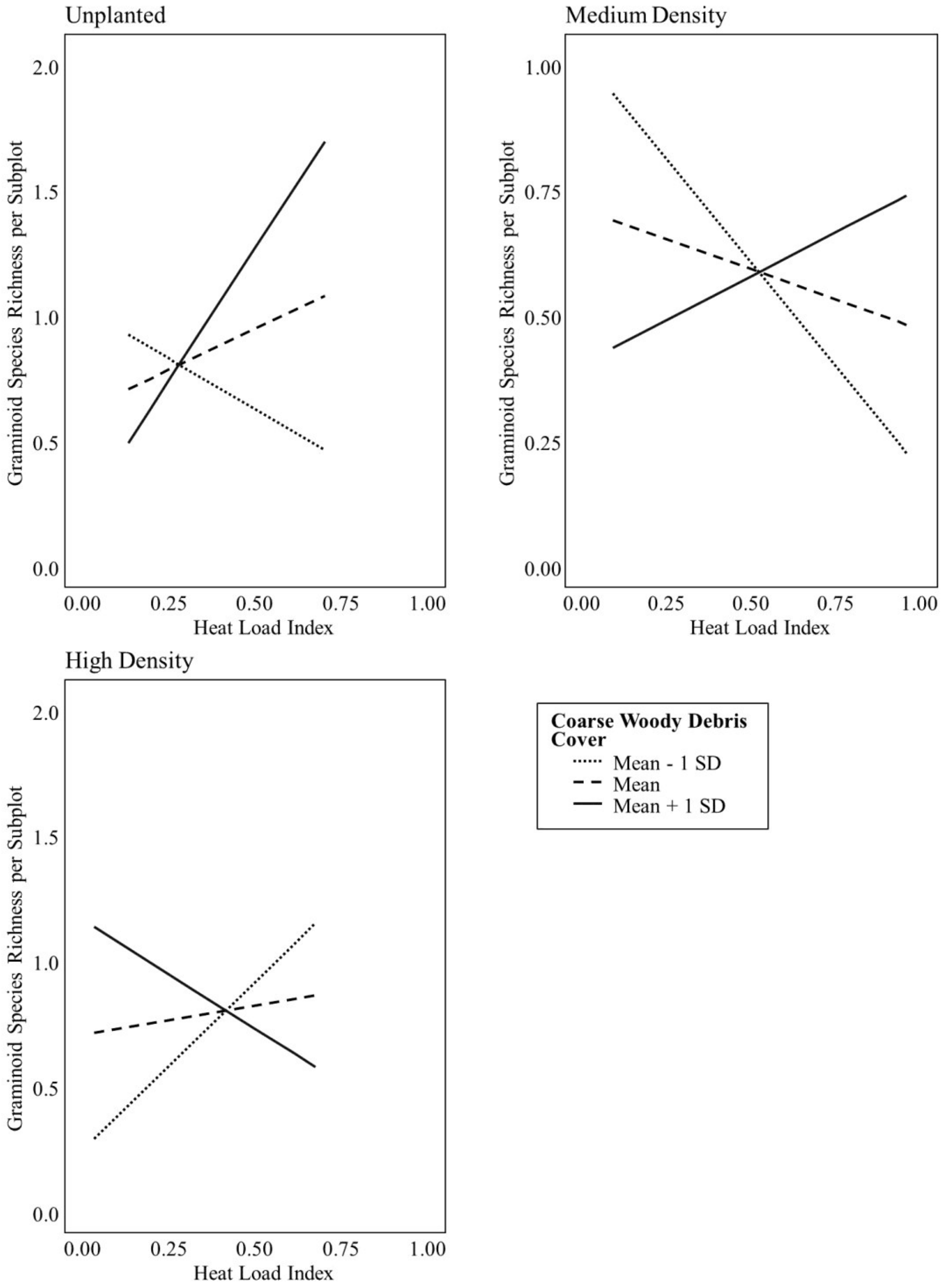


Figure B10: Interaction of planting density, heat load index (HLI; reflecting slope and aspect) and coarse woody debris volume on graminoid species richness per vegetation subplot in 2012 in areas reclaimed with coversoil salvaged from a rich-mesic site. In each of the three planting density treatments (unplanted = 0 stems per hectare (sph), medium density = 5 000 sph, high density = 10 000 sph) the influence of heat load index on species richness is shown at three levels of coarse woody debris cover (mean, mean – 1 standard deviation and mean + 1 standard deviation). See also Table 2-8.

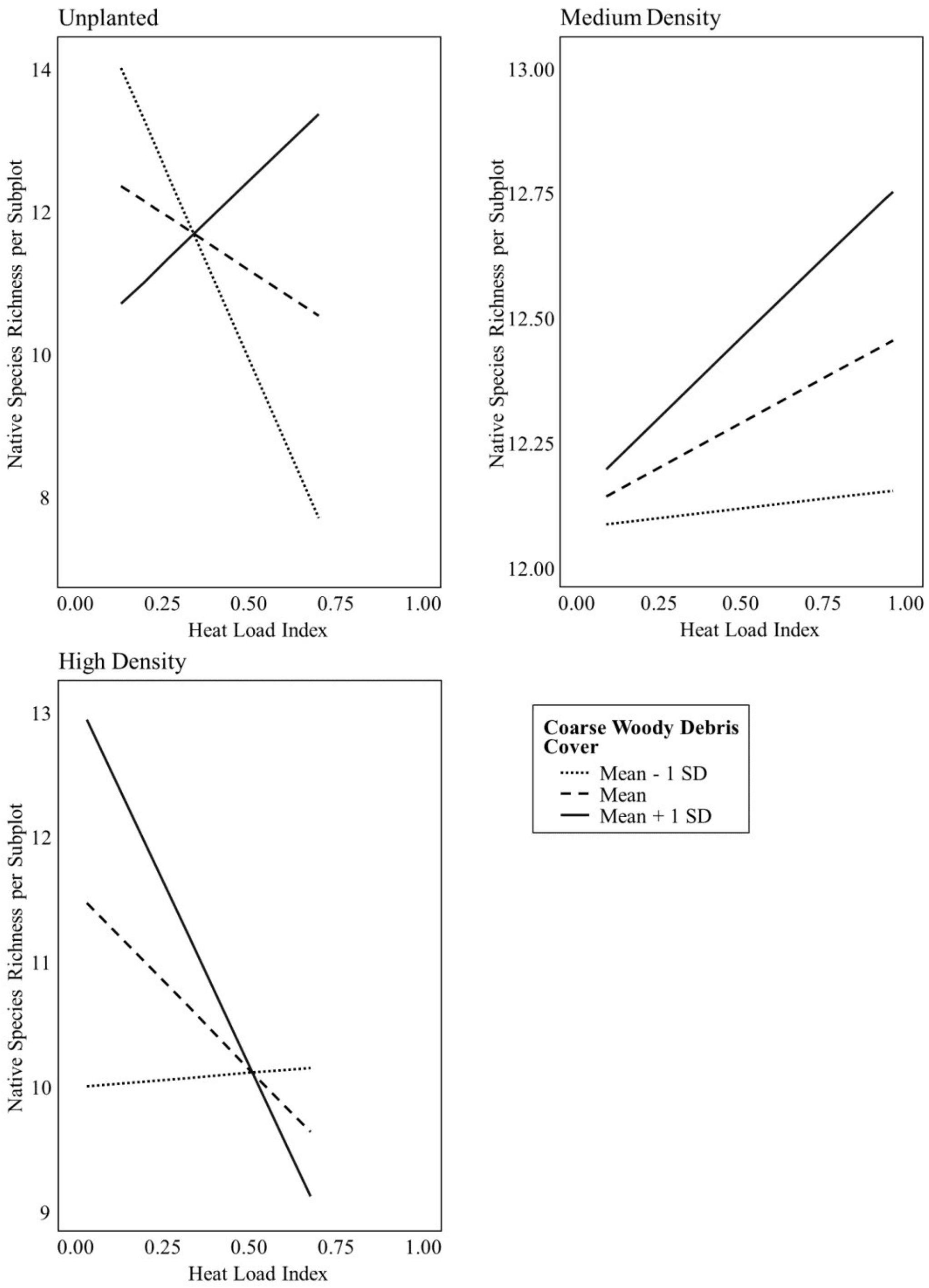


Figure B11: Interaction of planting density, heat load index (HLI; reflecting slope and aspect) and coarse woody debris volume on native species richness per vegetation subplot in 2015 in areas reclaimed with coversoil salvaged from a rich-mesic site. In each of the three planting density treatments (unplanted = 0 stems per hectare (sph), medium density = 5 000 sph, high density = 10 000 sph) the influence of heat load index on species richness is shown at three levels of coarse woody debris cover (mean, mean – 1 standard deviation and mean + 1 standard deviation). See also Table 2-8.

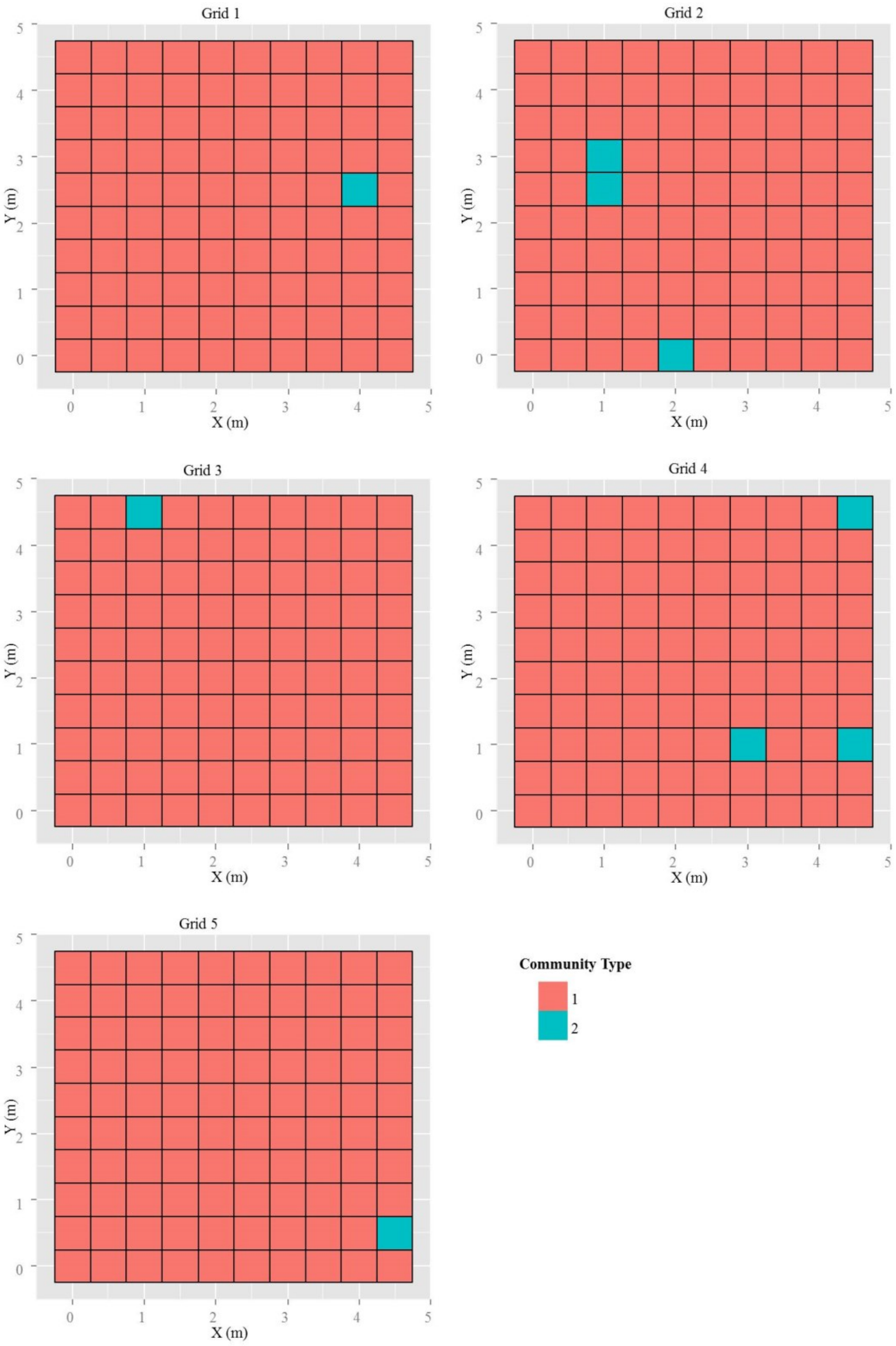


Figure B12: Results of cluster analysis of young – poor-xeric site type grids (1-5) showing community types for each quadrat in the grid plot.

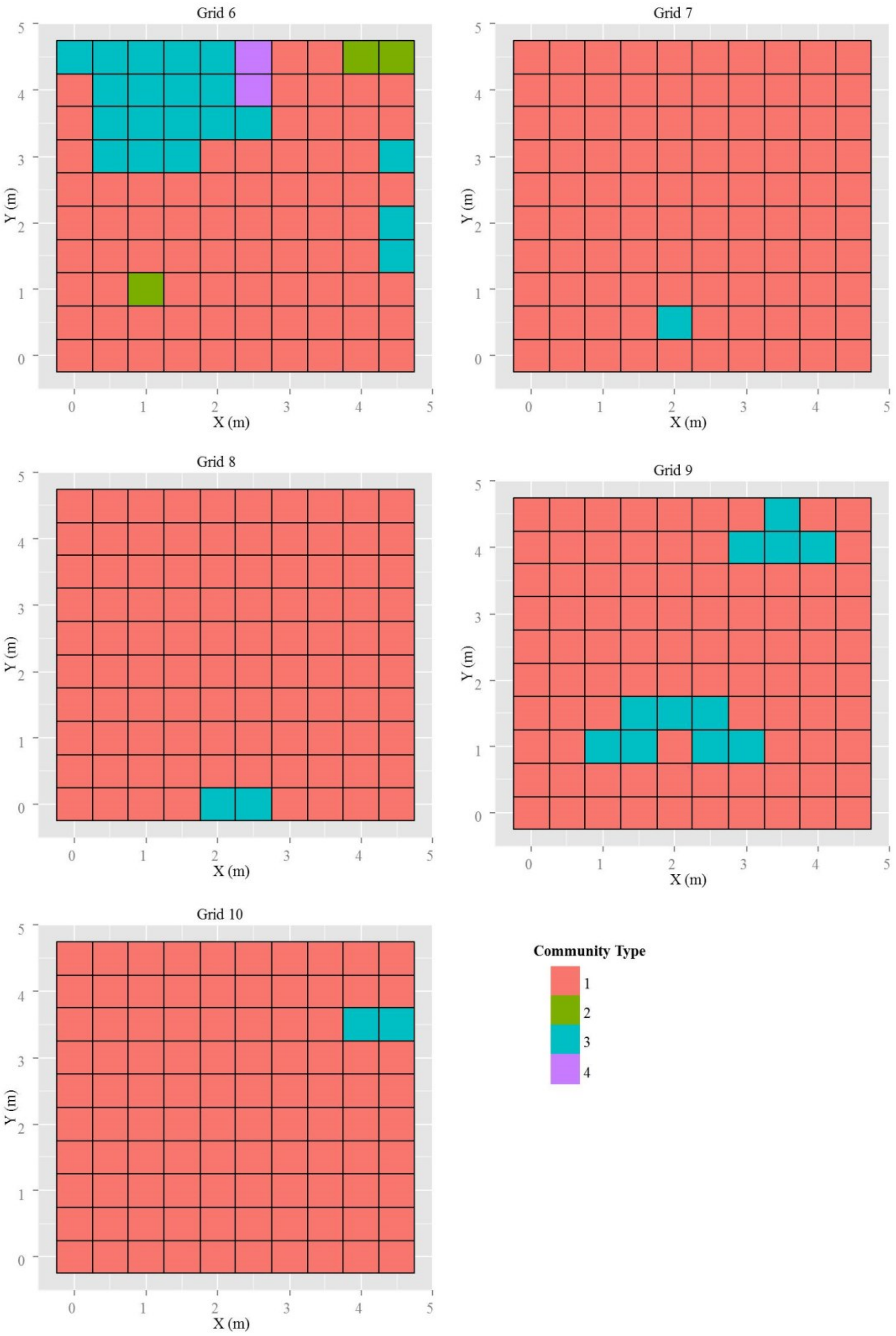


Figure B13: Results of cluster analysis of young – rich-mesic site type grids (6-10) showing community types for each quadrat in the grid plot.

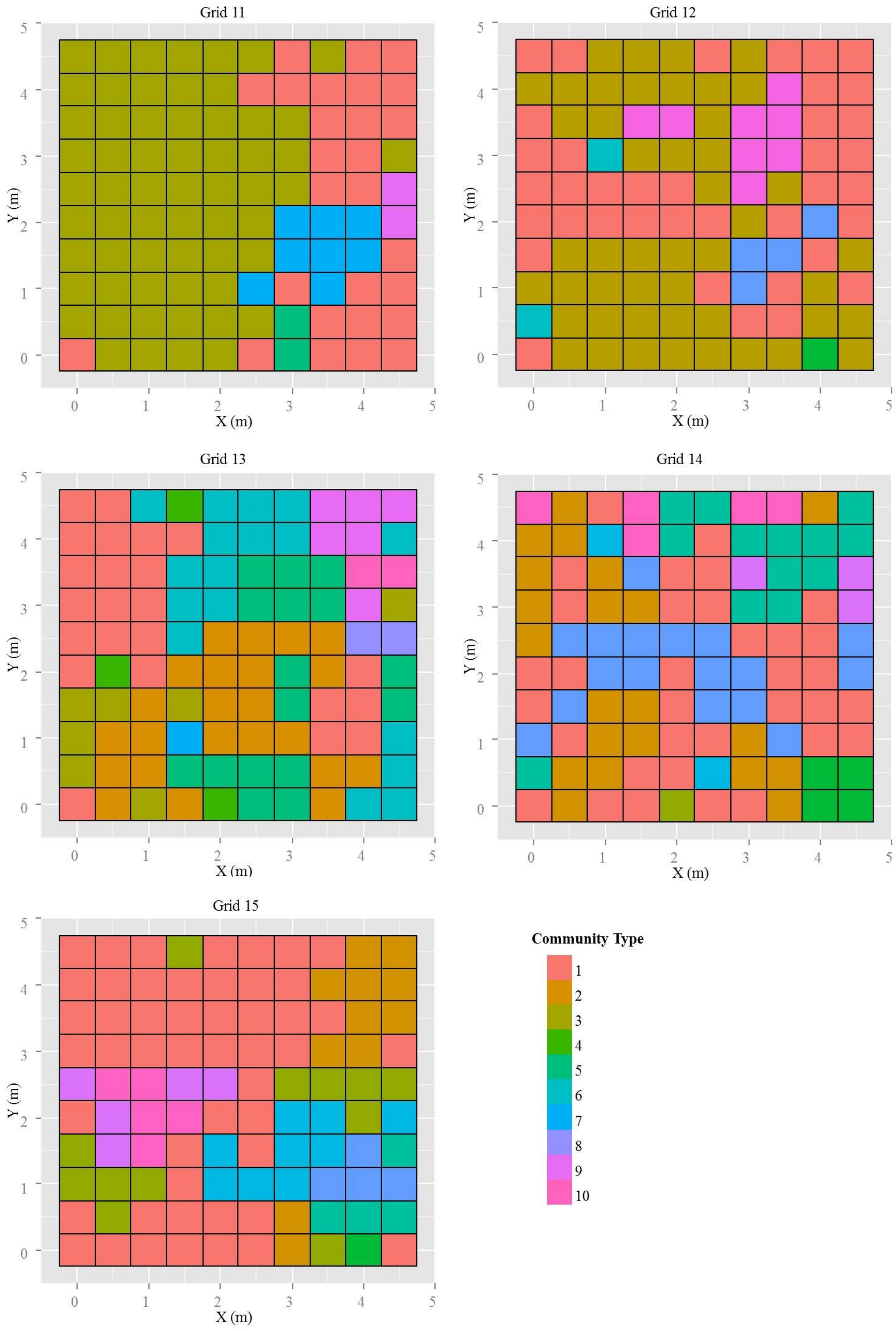


Figure B14: Results of cluster analysis of older – rich-mesic site type grids (11-15) showing community types for each quadrat in the grid plot.

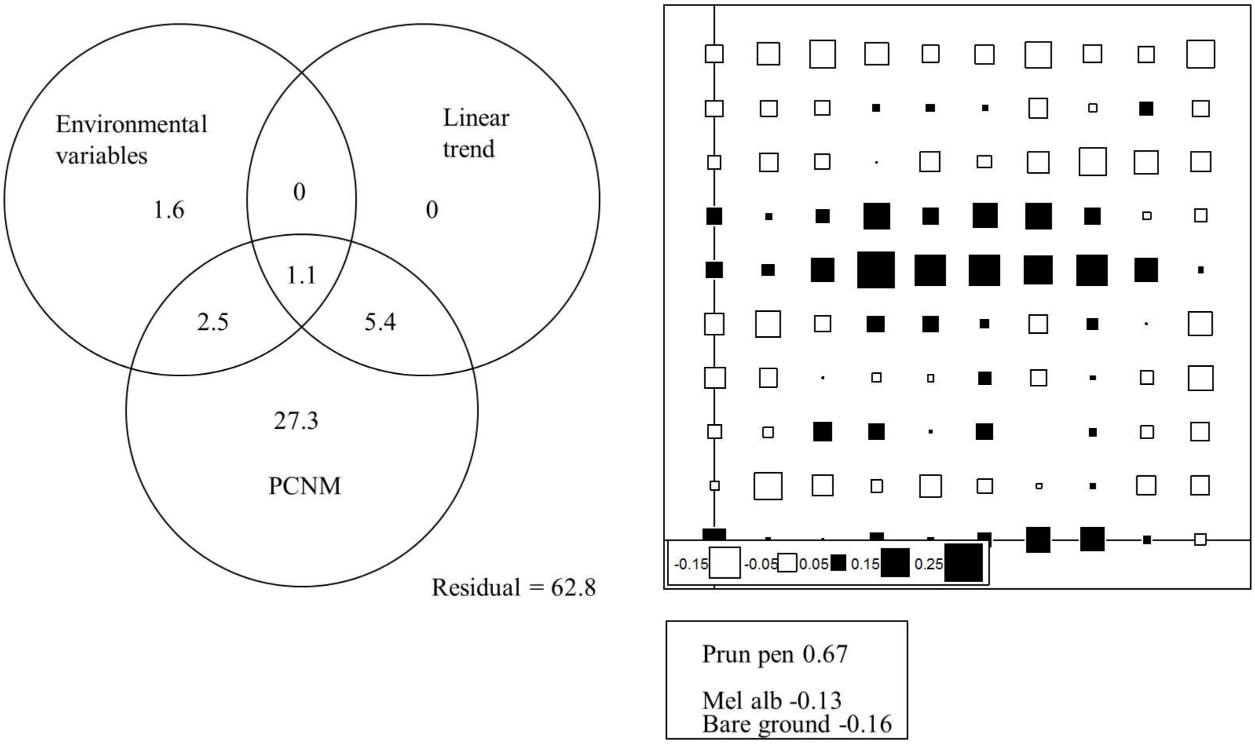


Figure B15: Results of PCNM analysis (right) and variation partitioning (left) for grid 1, which was a young – poor-xeric site type. The variation partitioning included linear trend, PCNM (spatial) and environmental variable components; the percent variation for each is given and the value in overlapping sections of the diagram indicates the percent of variation shared by the two. Residual indicates the unexplained variation. The PCNM diagram shows the results for correlation of species with the first RDA axis; the diagram is representative of the layout of the grid plot. Species driving the spatial pattern are shown below it (Prun pen = *Prunus pensylvanica*, Mel alb = *Melilotus alba*). Species with positive scores were associated with the positive (black) pattern and species with negative scores are associated with the negative (white) pattern. The magnitude of the species score, indicating the strength of the association, is shown by the symbol size.

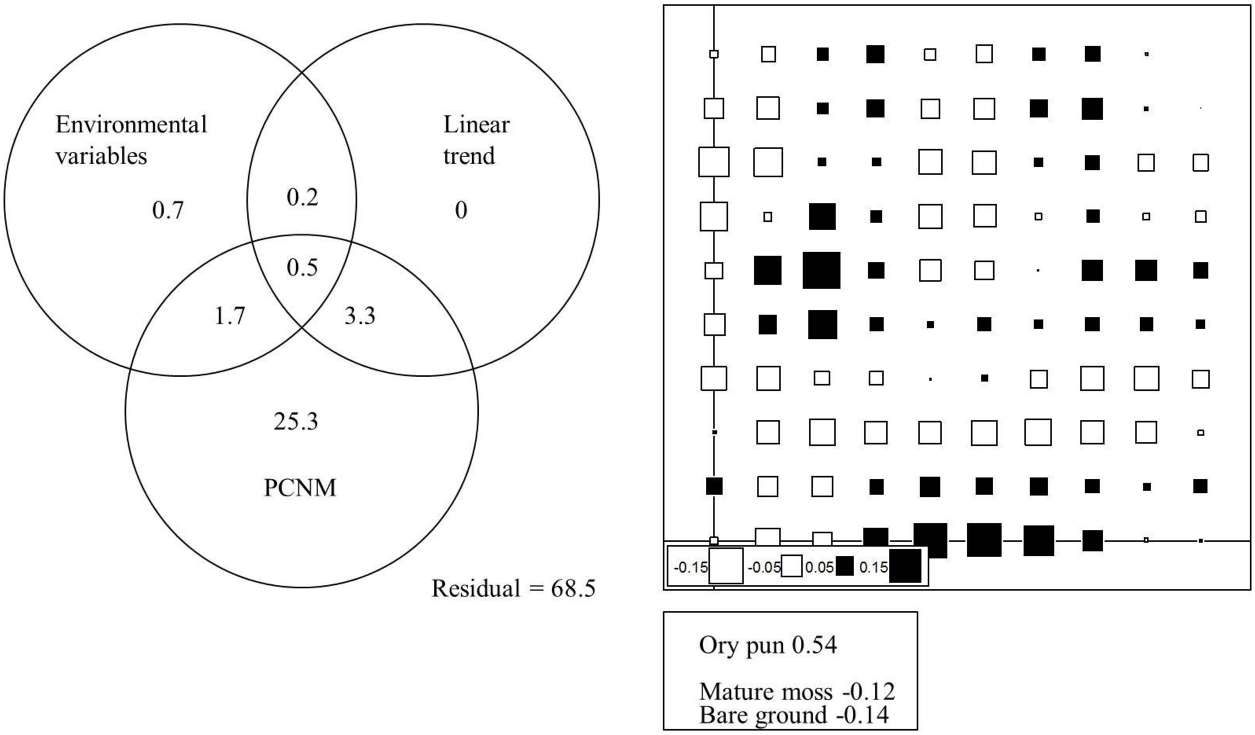
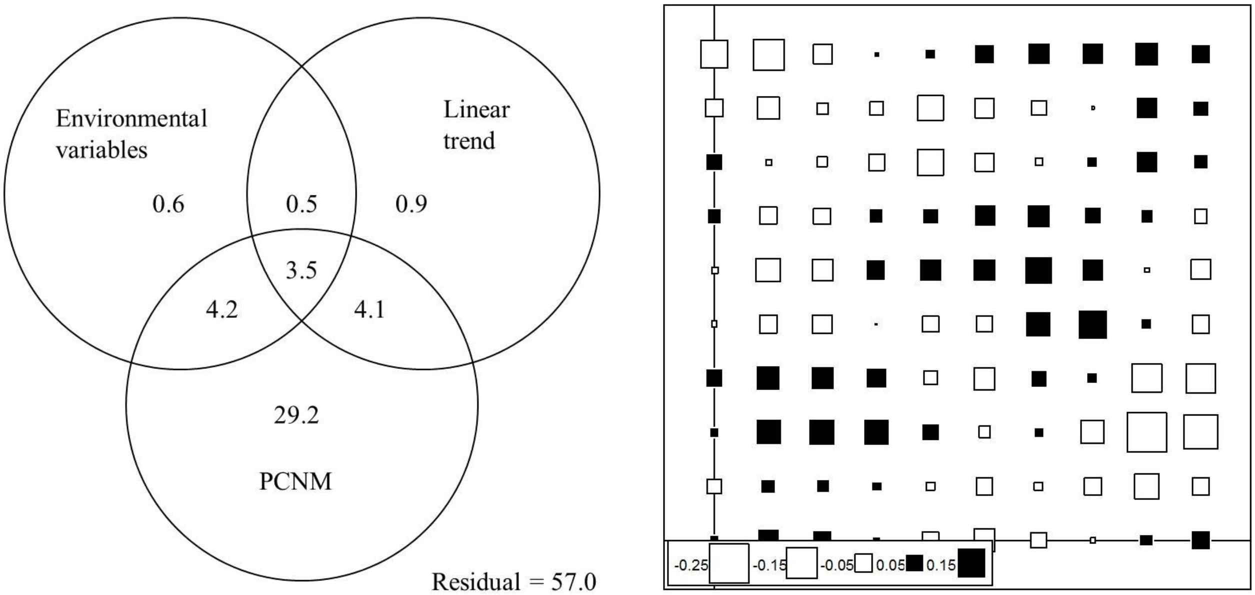


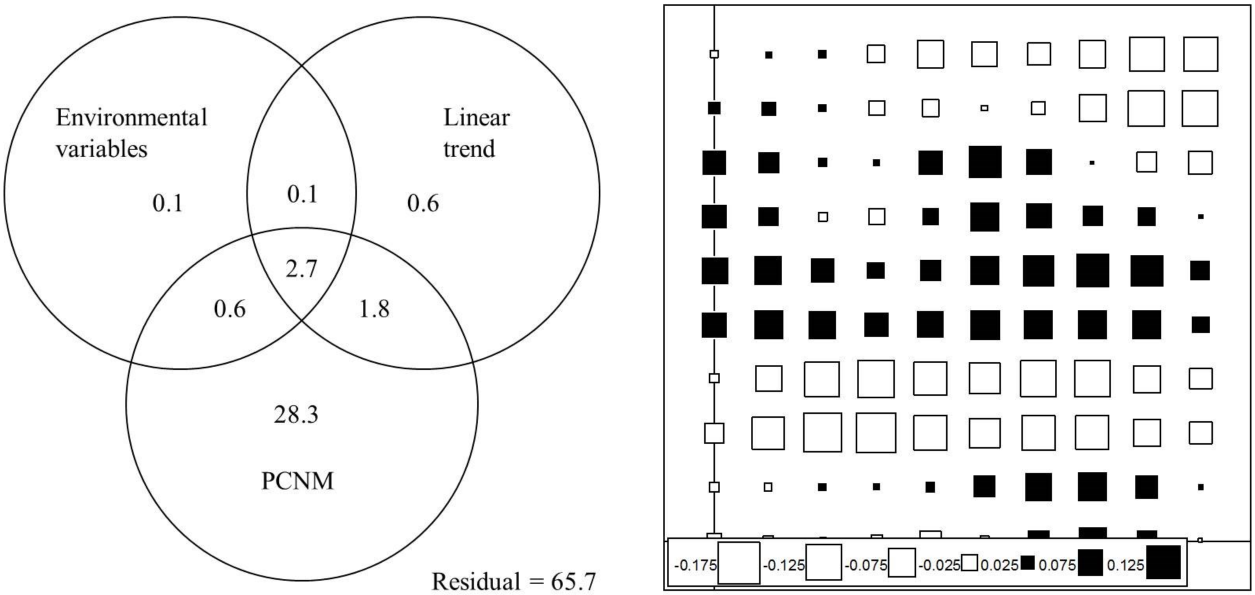
Figure B16: Results of PCNM analysis (right) and variation partitioning (left) for grid 2, which was a young – poor-xeric site type. The variation partitioning included linear trend, PCNM (spatial) and environmental variable components; the percent variation for each is given and the value in overlapping sections of the diagram indicates the percent of variation shared by the two. Residual indicates the unexplained variation. The PCNM diagram shows the results for correlation of species with the first RDA axis; the diagram is representative of the layout of the grid plot. Species driving the spatial pattern are shown below it (Ory pun = *Oryzopsis pungens*). Species with positive scores were associated with the positive (black) pattern and species with negative scores are associated with the negative (white) pattern. The magnitude of the species score, indicating the strength of the association, is shown by the symbol size.



Hor jub 0.10
Bare ground 0.28

Agr sca -0.13
Immature moss -0.40
Pru pen -0.48

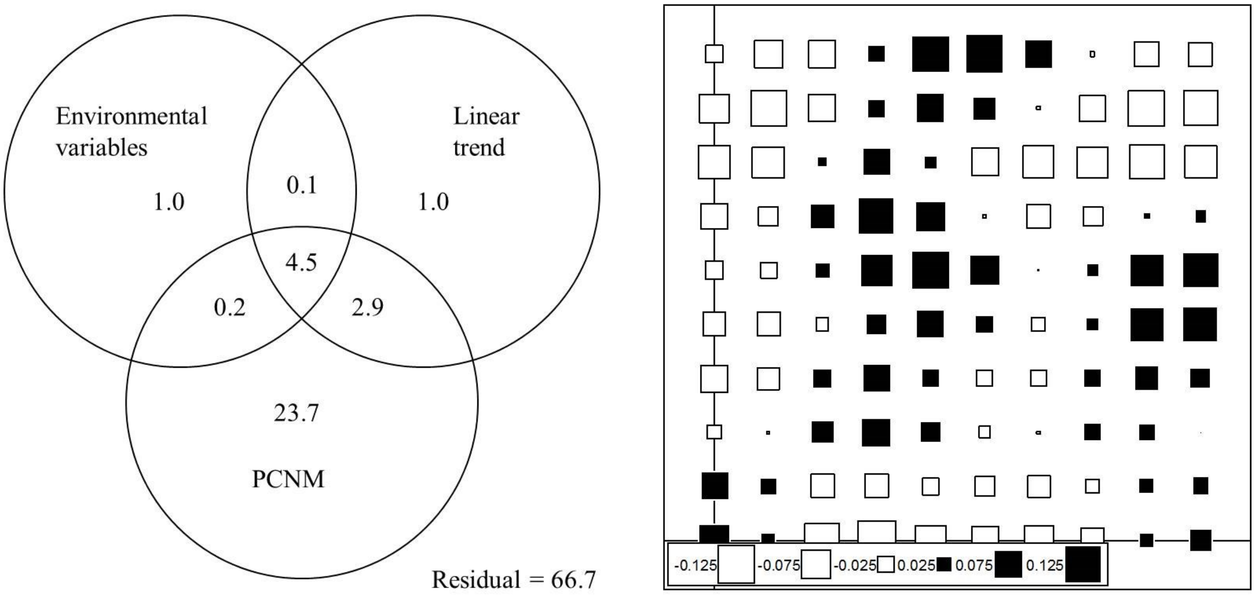
Figure B17: Results of PCNM analysis (right) and variation partitioning (left) for grid 3, which was a young – poor-xeric site type. The variation partitioning included linear trend, PCNM (spatial) and environmental variable components; the percent variation for each is given and the value in overlapping sections of the diagram indicates the percent of variation shared by the two. Residual indicates the unexplained variation. The PCNM diagram shows the results for correlation of species with the first RDA axis; the diagram is representative of the layout of the grid plot. Species driving the spatial pattern are shown below it (Hor jub = *Hordeum jubatum,* Agr sca = *Agrostis scabra*, Pru pen = *Prunus pensylvanica*). Species with positive scores were associated with the positive (black) pattern and species with negative scores are associated with the negative (white) pattern. The magnitude of the species score, indicating the strength of the association, is shown by the symbol size.



Car sic 0.28
Immature moss 0.16

Mature moss -0.63

Figure B18: Results of PCNM analysis (right) and variation partitioning (left) for grid 4, which was a young – poor-xeric site type. The variation partitioning included linear trend, PCNM (spatial) and environmental variable components; the percent variation for each is given and the value in overlapping sections of the diagram indicates the percent of variation shared by the two. Residual indicates the unexplained variation. The PCNM diagram shows the results for correlation of species with the first RDA axis; the diagram is representative of the layout of the grid plot. Species driving the spatial pattern are shown below it (Car sic = *Carex siccata*). Species with positive scores were associated with the positive (black) pattern and species with negative scores are associated with the negative (white) pattern. The magnitude of the species score, indicating the strength of the association, is shown by the symbol size.



Arc uva 0.16
Com umb 0.17
Immature moss 0.10
Mature moss 0.13
Ory pun 0.36
Pru pen 0.31
Vac myr 0.11

Car sic -0.25
Bare ground -0.18

Figure B19: Results of PCNM analysis (right) and variation partitioning (left) for grid 5, which was a young – poor-xeric site type. The variation partitioning included linear trend, PCNM (spatial) and environmental variable components; the percent variation for each is given and the value in overlapping sections of the diagram indicates the percent of variation shared by the two. Residual indicates the unexplained variation. The PCNM diagram shows the results for correlation of species with the first RDA axis; the diagram is representative of the layout of the grid plot. Species driving the spatial pattern are shown below it (Arc uva = *Arctostaphylos uva-ursi*, Com umb = *Commandra umbellata*, Ory pun = *Oryzopsis pungens*, Pru pen = *Prunus pensylvanica*, Vac myr = *Vaccinium myrtilloides*, Car sic = *Carex siccata*). Species with positive scores were associated with the positive (black) pattern and species with negative scores are associated with the negative (white) pattern. The magnitude of the species score, indicating the strength of the association, is shown by the symbol size.

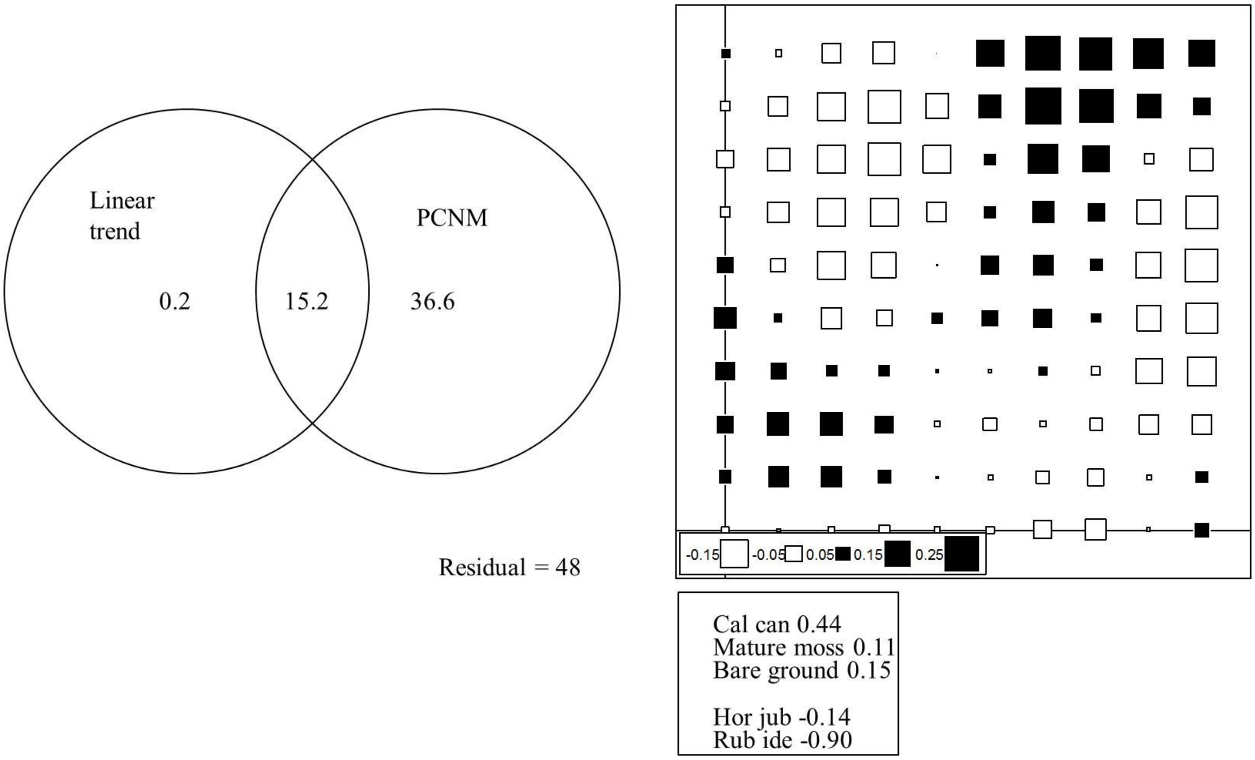
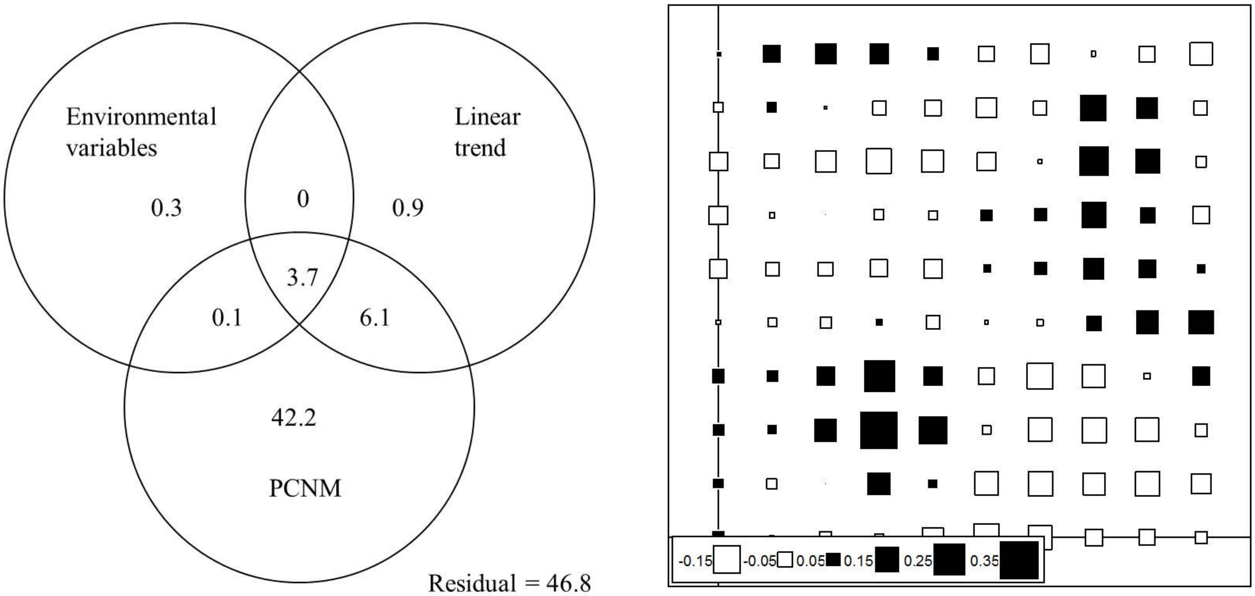


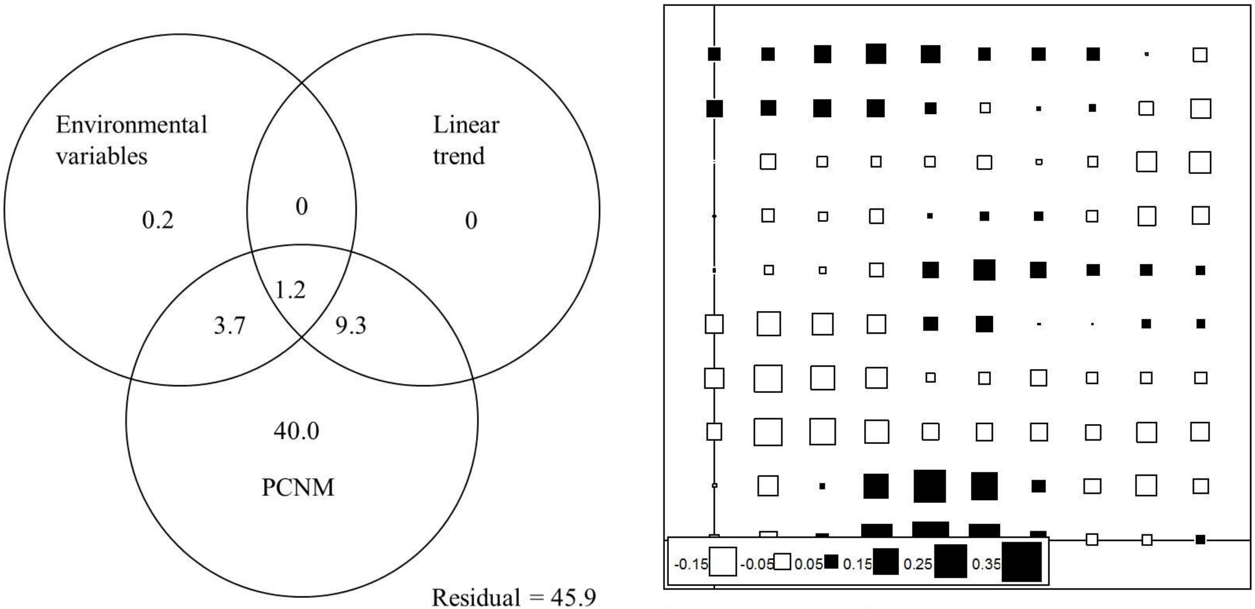
Figure B20: Results of PCNM analysis (right) and variation partitioning (left) for grid 6, which was a young – rich-mesic site type. The variation partitioning included linear trend and PCNM (spatial) components; the percent variation for each is given and the value in overlapping sections of the diagram indicates the percent of variation shared by the two. None of the environmental variables were chosen in the forward selection process so were not included in the variation partitioning. Residual indicates the unexplained variation. The PCNM diagram shows the results for correlation of species with the first RDA axis; the diagram is representative of the layout of the grid plot. Species driving the spatial pattern are shown below it (Cal can = *Calamagrostis canadensis,* Hor jub = *Hordeum jubatum,* Rub ide = *Rubus idaeus*). Species with positive scores were associated with the positive (black) pattern and species with negative scores are associated with the negative (white) pattern. The magnitude of the species score, indicating the strength of the association, is shown by the symbol size.



Lot cor 0.78

Bare ground -0.45

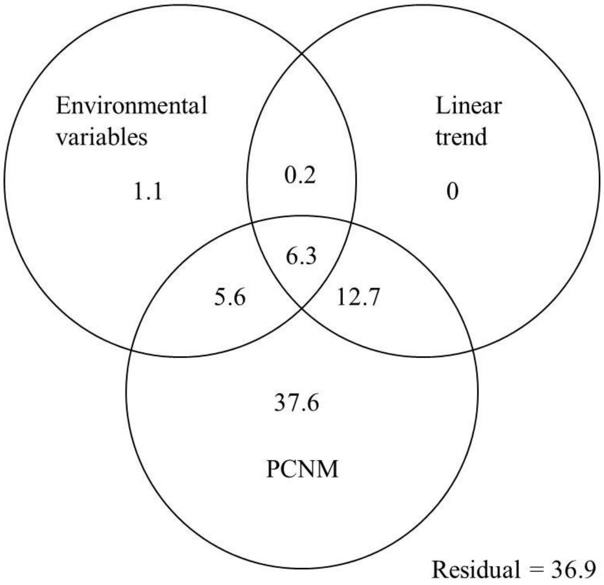
Figure B21: Results of PCNM analysis (right) and variation partitioning (left) for grid 7, which was a young – rich-mesic site type. The variation partitioning included linear trend, PCNM (spatial) and environmental variable components; the percent variation for each is given and the value in overlapping sections of the diagram indicates the percent of variation shared by the two. Residual indicates the unexplained variation. The PCNM diagram shows the results for correlation of species with the first RDA axis; the diagram is representative of the layout of the grid plot. Species driving the spatial pattern are shown below it (Lot cor = *Lotus corniculatus*). Species with positive scores were associated with the positive (black) pattern and species with negative scores are associated with the negative (white) pattern. The magnitude of the species score, indicating the strength of the association, is shown by the symbol size.

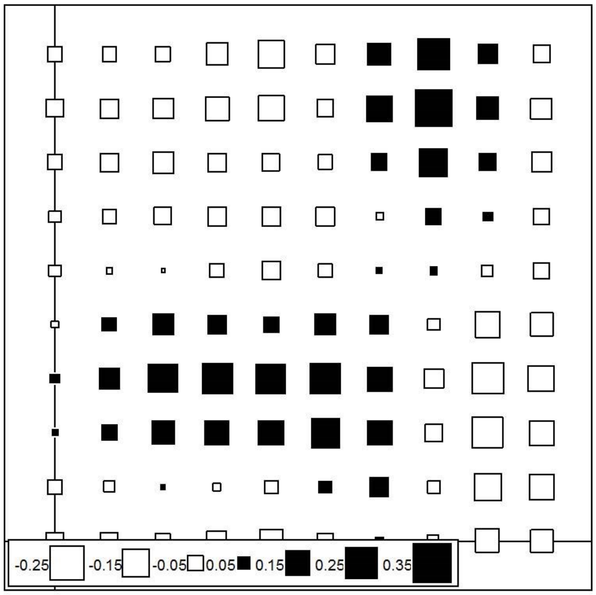


Ag tra 0.18
Ast cil 0.49

Cal can -0.26
Eri can -0.15
Fra vir -0.41
Vic ame -0.17

Figure B22: Results of PCNM analysis (right) and variation partitioning (left) for grid 8, which was a young – rich-mesic site type. The variation partitioning linear trend, PCNM (spatial) and environmental variable components; the percent variation for each is given and the value in overlapping sections of the diagram indicates the percent of variation shared by the two. Residual indicates the unexplained variation. The PCNM diagram shows the results for correlation of species with the first RDA axis; the diagram is representative of the layout of the grid plot. Species driving the spatial pattern are shown below it (Ag tra = *Agropyron trachycaulum* var. *trachycaulum*, Ast cil = *Aster ciliolatus*, Cal can = *Calamagrostis canadensis*, Eri can = *Erigeron canadensis*, Fra vir = *Fragaria virginiana*, Vic ame = *Vicia americana*). Species with positive scores were associated with the positive (black) pattern and species with negative scores are associated with the negative (white) pattern. The magnitude of the species score, indicating the strength of the association, is shown by the symbol size.

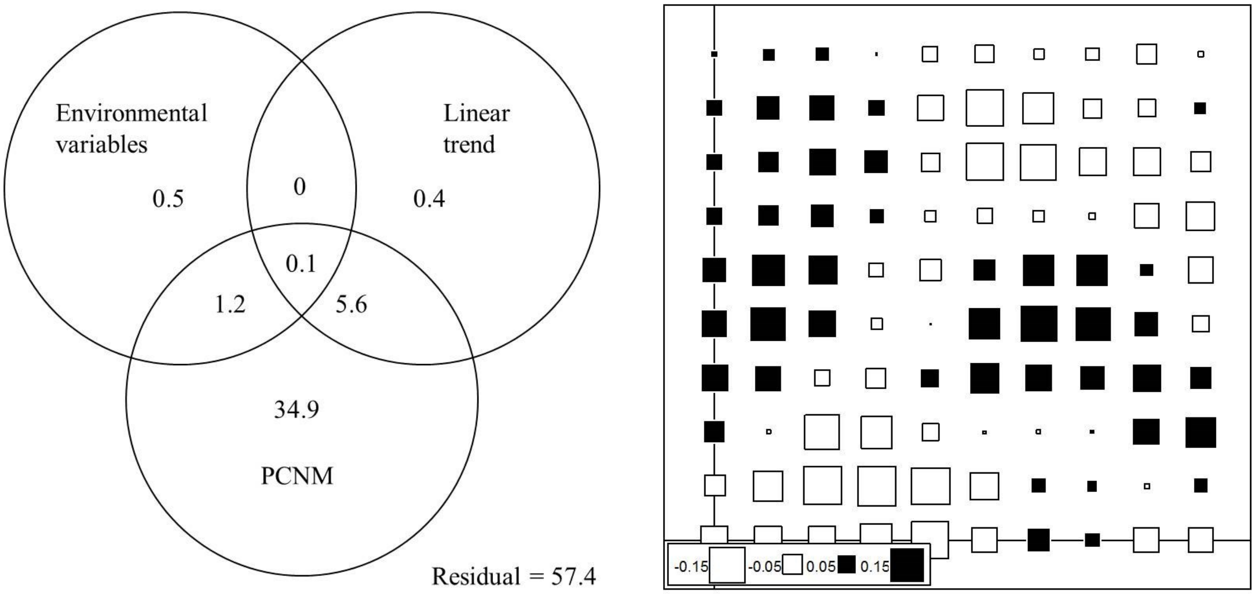




Med sat 0.93
Mature moss 0.12

Epi ang -0.28
Fra vir -0.10
Rub ide -0.19
Bare ground -0.37

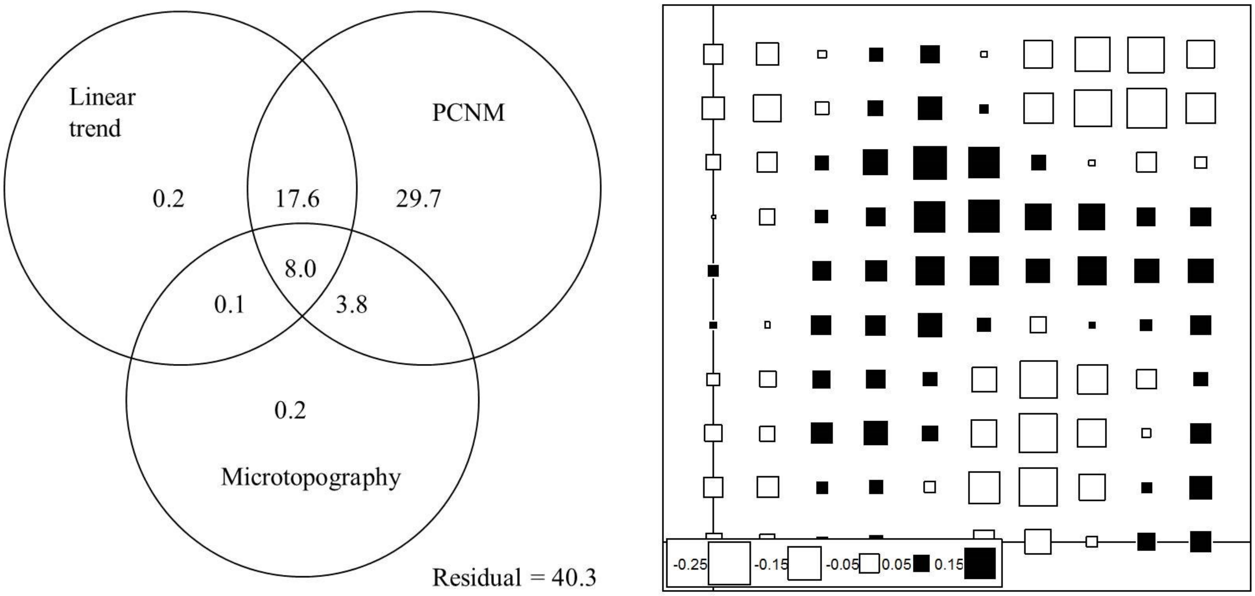
Figure B23**:** Results of PCNM analysis (right) and variation partitioning (left) for grid 9, which was a young – rich-mesic site type. The variation partitioning included linear trend, PCNM (spatial) and environmental variable components; the percent variation for each is given and the value in overlapping sections of the diagram indicates the percent of variation shared by the two. Residual indicates the unexplained variation. The PCNM diagram shows the results for correlation of species with the first RDA axis; the diagram is representative of the layout of the grid plot. Species driving the spatial pattern are shown below it (Med sat = *Medicago sativa*, Epi ang = *Epilobium angustifolium*, Fra vir = *Fragaria virginiana*, Rub ide = *Rubus idaeus*.). Species with positive scores were associated with the positive (black) pattern and species with negative scores are associated with the negative (white) pattern. The magnitude of the species score, indicating the strength of the association, is shown by the symbol size.



Bro ine 0.15
Rub ide 0.71
Stellaria sp. 0.13

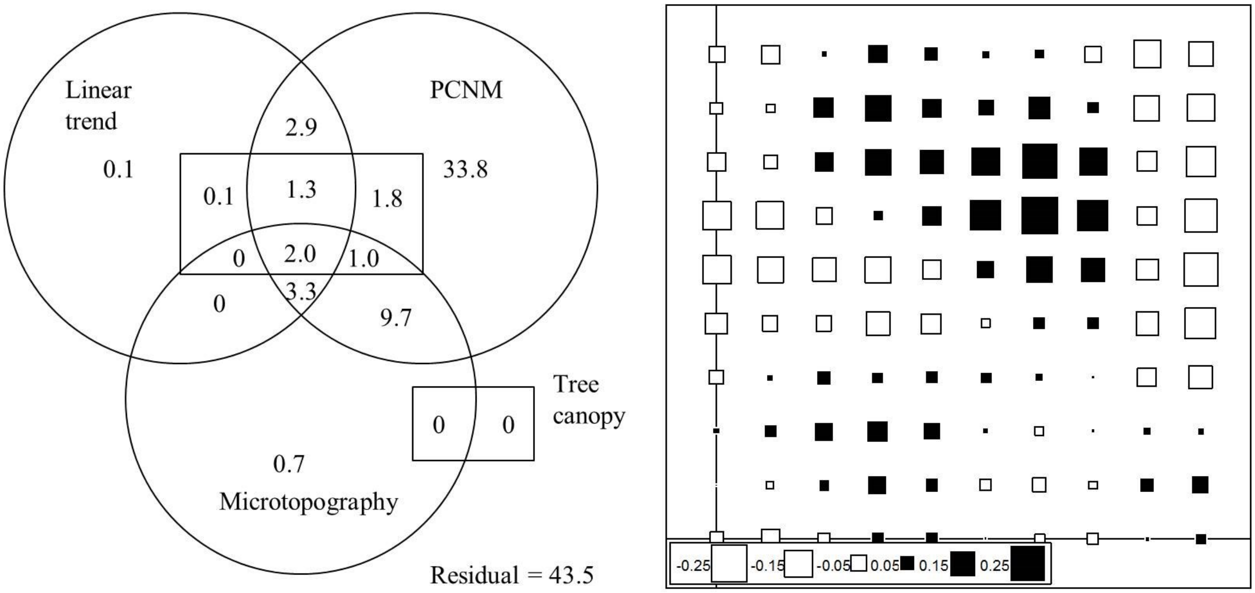
Cal can -0.10
Epi ang -0.24
Son arv -0.11
Bare ground -0.22

Figure B24: Results of PCNM analysis (right) and variation partitioning (left) for grid 10, which was a young – rich-mesic site type. The variation partitioning included linear trend, PCNM (spatial) and environmental variable components; the percent variation for each is given and the value in overlapping sections of the diagram indicates the percent of variation shared by the two. Residual indicates the unexplained variation. The PCNM diagram shows the results for correlation of species with the first RDA axis; the diagram is representative of the layout of the grid plot. Species driving the spatial pattern are shown below it (Bro ine = *Bromus inermis*, Rub ide = *Rubus idaeus*, Cal can = *Calamagrostis canadensis*, Epi ang = *Epilobium angustifolium*, Son arv = *Sonchus arvensis*). Species with positive scores were associated with the positive (black) pattern and species with negative scores are associated with the negative (white) pattern. The magnitude of the species score, indicating the strength of the association, is shown by the symbol size.



Arc uva	0.11
Equ arv	0.12
Equ syl	0.11
Gal bor	0.12
Imm. moss	0.18
Lat och	0.10
Lat ven	0.10
Ros aci	0.11
Bare ground	0.54
Fra vir	-0.32
Pet pal	-0.14
Rub ide	-0.47
Vic ame	-0.11

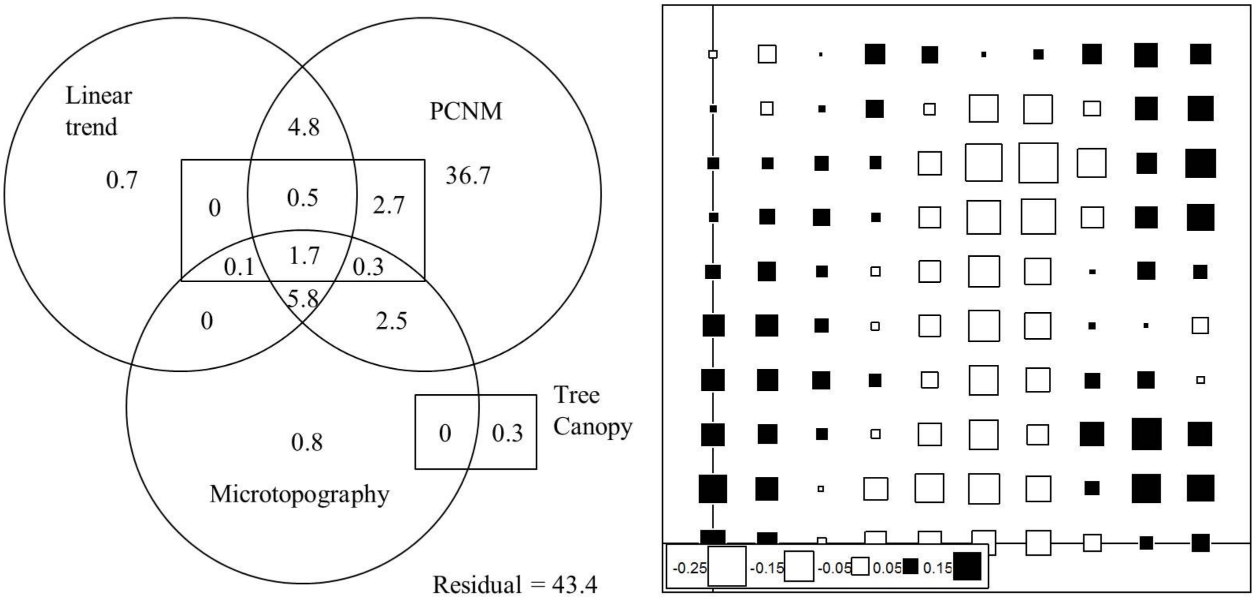
Figure B25: Results of PCNM analysis (right) and variation partitioning (left) for grid 11, which was an older – rich-mesic site type. The variation partitioning included linear trend, PCNM (spatial) and microtopography components; the percent variation for each is given and the value in overlapping sections of the diagram indicates the percent of variation shared by the two. None of the tree canopy variables were chosen in the forward selection process so were not included in the variation partitioning. Residual indicates the unexplained variation. The PCNM diagram shows the results for correlation of species with the first RDA axis; the diagram is representative of the layout of the grid plot. Species driving the spatial pattern are shown below it (Arc uva = *Arctostaphylos uva-ursi*, Equ arv = *Equisetum arvense*, Equ syl = *Equisetum sylvaticum*, Gal bor = *Galium boreale*, Lat och = *Lathyrus ochroleucus*, Lat ven = *Lathyrus venosus*, Ros aci = *Rosa acicularis*, Fra vir = *Fragaria virginiana*, Pet pal = *Petasites palmatus*, Rub ide = *Rubus idaeus*, Vic ame = *Vicia americana*). Species with positive scores were associated with the positive (black) pattern and species with negative scores are associated with the negative (white) pattern. The magnitude of the species score, indicating the strength of the association, is shown by the symbol size.



Ely inn 0.17
Equ arv 0.10
Rub ide 0.39
Bare ground 0.43

Ag tra -0.11
Fra vir -0.70
Lat och -0.12
Pet pal -0.10
Tar off -0.11

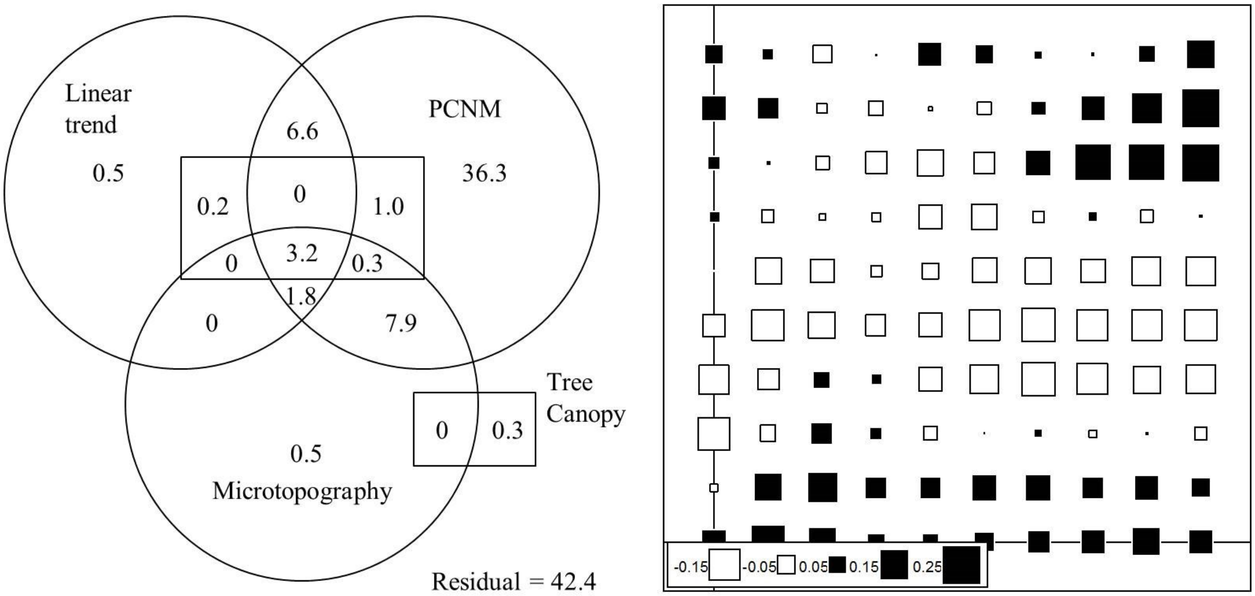
Figure B26: Results of PCNM analysis (right) and variation partitioning (left) for grid 12, which was an older – rich-mesic site type. The variation partitioning included linear trend, PCNM (spatial), microtopography and tree canopy components; the percent variation for each is given and the value in overlapping sections of the diagram indicates the percent of variation shared by the two. Residual indicates the unexplained variation. The PCNM diagram shows the results for correlation of species with the first RDA axis; the diagram is representative of the layout of the grid plot. Species driving the spatial pattern are shown below it (Ely inn = *Elymus innovatus*, Equ arv = *Equisetum arvense*, Rub ide = *Rubus idaeus*, Ag tra = *Agropyron trachycaulum* var. *trachycaulum*, Fra vir = *Fragaria virginiana*, Lat och = *Lathyrus ochroleucus*, Pet pal = *Petasites palmatus*, Tar off = *Taraxacum officinale*). Species with positive scores were associated with the positive (black) pattern and species with negative scores are associated with the negative (white) pattern. The magnitude of the species score, indicating the strength of the association, is shown by the symbol size.



Ely inn 0.23
Fra vir 0.24
Lat och 0.27
Pet pal 0.19
Bare ground 0.37

Mer pan -0.17
Ros aci -0.72
Rub pub -0.14
Vio adu -0.10

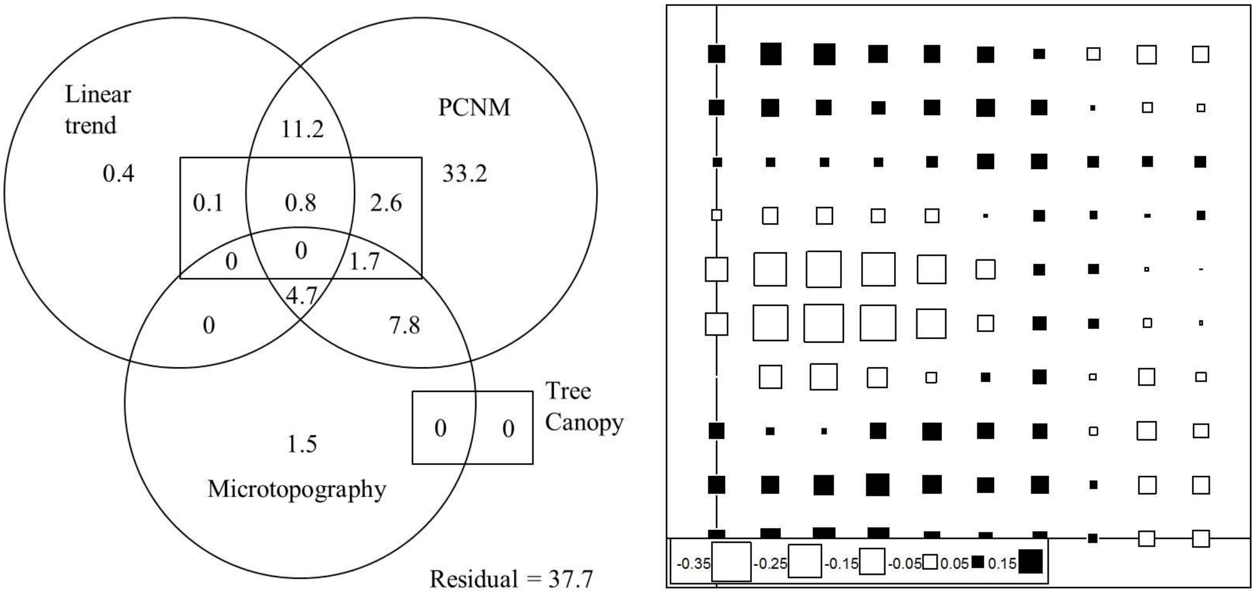
Figure B27: Results of PCNM analysis (right) and variation partitioning (left) for grid 13, which was an older – rich-mesic site type. The variation partitioning included linear trend, PCNM (spatial), microtopography and tree canopy components; the percent variation for each is given and the value in overlapping sections of the diagram indicates the percent of variation shared by the two. Residual indicates the unexplained variation. The PCNM diagram shows the results for correlation of species with the first RDA axis; the diagram is representative of the layout of the grid plot. Species driving the spatial pattern are shown below it (Ely inn = *Elymus innovatus*, Fra vir = *Fragaria virginiana*, Lat och = *Lathyrus ochroleucus*, Pet pal = *Petasites palmatus*, Mer pan = *Mertensia paniculata*, Ros aci = *Rosa acicularis*, Rub pub = *Rubus pubescens*, Vio adu = *Viola adunca*). Species with positive scores were associated with the positive (black) pattern and species with negative scores are associated with the negative (white) pattern. The magnitude of the species score, indicating the strength of the association, is shown by the symbol size.



Cal can 0.19
Fra vir 0.25
Ros aci 0.26
Rub pub 0.37

Mature moss -0.67
Bare ground -0.48

Figure B28: Results of PCNM analysis (right) and variation partitioning (left) for grid 14, which was an older – rich-mesic site type. The variation partitioning included linear trend, PCNM (spatial), microtopography and tree canopy components; the percent variation for each is given and the value in overlapping sections of the diagram indicates the percent of variation shared by the two. Residual indicates the unexplained variation. The PCNM diagram shows the results for correlation of species with the first RDA axis; the diagram is representative of the layout of the grid plot. Species driving the spatial pattern are shown below it (Cal can = *Calamagrostis canadensis*, Fra vir = *Fragaria virginiana*, Ros aci = *Rosa acicularis*, Rub pub = *Rubus pubescens*). Species with positive scores were associated with the positive (black) pattern and species with negative scores are associated with the negative (white) pattern. The magnitude of the species score, indicating the strength of the association, is shown by the symbol size.



Arc uva 0.12
Ast cil 0.10
Equ arv 0.26
Fra vir 0.20
Mature moss 0.19
Rub ide 0.12
Tar off 0.14
Vic ame 0.12
Bare ground 0.34

Cal can -0.65
Ely inn -0.44

Figure B29: Results of PCNM analysis (right) and variation partitioning (left) for grid 15, which was an older – rich-mesic site type. The variation partitioning included linear trend, PCNM (spatial), microtopography and tree canopy components; the percent variation for each is given and the value in overlapping sections of the diagram indicates the percent of variation shared by the two. Residual indicates the unexplained variation. The PCNM diagram shows the results for correlation of species with the first RDA axis; the diagram is representative of the layout of the grid plot. Species driving the spatial pattern are shown below it (Arc uva = *Arctostaphylos uva-ursi*, Ast cil = *Aster ciliolatus*, Equ arv = *Equisetum arvense*, Fra vir = *Fragaria virginiana*, Rub ide = *Rubus idaeus*, Tar off = *Taraxacum officinale*, Vic ame = *Vicia americana*, Cal can = *Calamagrostis canadensis*, Ely inn = *Elymus innovatus*). Species with positive scores were associated with the positive (black) pattern and species with negative scores are associated with the negative (white) pattern. The magnitude of the species score, indicating the strength of the association, is shown by the symbol size.