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Reclamation strategies for mined forest soils and overstorey drive understorey vegetation

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Abstract

1. Understorey vegetation accounts for the majority of plant diversity in boreal forest ecosystems and contributes to ecosystem functioning. In restoration of degraded forested ecosystems, however, understorey vegetation is often restored passively, contrasting to clear strategies such as informed species choice and site improvement intervention for overstorey vegetation. The choice of overstorey-centred restoration strategy may have important consequences for understorey vegetation.
2. We examined the effects of substrate material, overstorey type and time since reclamation (age) on understorey vegetation following reclamation of oil sands mining in Alberta, Canada. We sampled cover, richness, evenness and composition of understorey vegetation at 94 sites of conifer, mixedwood and broadleaf overstorey types on three reclamation substrates (overburden, secondary overburden and tailings sand), with age ranging from 4 to 30 years.
3. Total, woody and non-woody understorey cover and species richness were the highest on secondary overburden and the lowest on tailings sand, and total cover also decreased with age. Woody cover and richness were the highest under broadleaf overstorey, while non-woody cover and richness were the lowest under conifer overstorey. Overall species evenness was not significantly affected by substrate type, overstorey type or age, but woody evenness was the highest on secondary overburden and the lowest on tailings sand, and non-woody evenness showed overstorey-dependent responses to age. Species composition varied with substrate type, overstorey type and age. Indicator species analysis revealed that tailings sand with conifer overstorey favoured grasses, while overburden and secondary overburden supported a mix of grasses, forbs and shrubs.
4. *Synthesis and applications*. Our study demonstrates that overstorey-centred reclamation strategies impact the abundance, diversity and composition of understorey plant communities following oil sands mining. Landforms constructed with secondary overburden substrates and revegetated with mixedwood or broadleaf tree species provide the most favourable habitats for understorey vegetation, while tailings sand provide a poor substrate for understorey species diversity and composition. We therefore recommend utilizing secondary overburden and overburden substrate material during landform construction, and employing revegetation

prescriptions that target mixedwood and broadleaf overstorey types to promote productive and diverse understorey plant communities on the reclaimed landscape.

KEYWORDS
oil sands mining, overstorey, plant diversity and composition, restoration and reclamation, stand dynamics, substrate material, time since reclamation

1 | INTRODUCTION

Increasing human population and its demand for natural resources contributes greatly to the global degradation of forested ecosystems, with important consequences for biodiversity and ecosystem functionality (Aerts & Honnay, 2011; Chazdon, 2008). Restoration of forest biodiversity, community structure and associated ecological complexity is thus a key task in contemporary ecology (Hobbs & Harris, 2001; Palmer, Ambrose, & Poff, 1997). Because understorey vegetation accounts for a large part of forest overall biodiversity and contributes greatly to ecosystem functioning (Gilliam, 2007; Hart & Chen, 2006; Nilsson & Wardle, 2005; Vockenhuber et al., 2011; Zhang, Chen, & Taylor, 2017), diverse and productive understorey vegetation is an important determinant of restoration success (Koch, 2007; Macdonald et al., 2015). In many instances, however, understorey vegetation is restored passively (Aerts & Honnay, 2011; Harris, Leishman, Fryirs, & Kyle, 2012). That is, development of understorey vegetation following the restoration of degraded forested ecosystems may depend on strategies aimed at improving abiotic site conditions and overstorey development (Palmer et al., 1997). This approach is common in diversified contexts ranging from severely degraded sites such as Bauxite mines (Koch, 2007), oil sands mines (Macdonald et al., 2015) and granite quarries (Zhang, Zhuang, & Chu, 2013) to mildly degraded riparian vegetation (Harris et al., 2012).

While specific restoration strategies usually depend on the nature of ecosystem degradation or land use history (Hobbs & Harris, 2001), the outcomes of restoration often depend on multiple factors including the abiotic site conditions, biotic factors and time since restoration (Stuble, Fick, & Young, 2017). Abiotic site conditions such as substrate materials often play important roles to shape the diversity and composition of plant assemblages (Mueller-Dombois & Ellenberg, 1974). Soil moisture, nutrients and microbial assemblages are critical determinants of seed germination and plant growth and development; whereas, soil texture is important for the development of plant roots (Jung, Duan, House, & Chang, 2014) and for the retention of water and nutrients in the soil (Hillel, 1998; Leatherdale, Chanasyk, & Quideau, 2012). Furthermore, forest floor material typically contains a large seed bank that can be beneficial for establishing a plant community during restoration/reclamation (Alday, Pallavicini, Marrs, & Martínez-Ruiz, 2011; Jung et al., 2014). Therefore, sites reclaimed with substrate materials that have complex structure and a higher availability of nutrients and water and contain forest floor materials should support more diverse and productive understorey plant communities compared to substrate material with less structural complexity and lower nutrient and water availability (Alday et al., 2011; Kardol & Wardle, 2010; Zhang & Dong, 2010).

Near ground microenvironmental conditions are highly dependent on the characteristics of the established plant communities (Macdonald et al., 2015). The quality of overstorey litter, whose chemical characteristics affect decomposition and soil nutrient availability, varies among broadleaf and coniferous species (Prescott, Zabek, Staley, & Kabzems, 2000). Coniferous litter decomposes at a slower rate than broadleaf litter; consequently, forests with a higher overstorey coniferous component tend to have lower nutrient availability (Prescott et al., 2000). Light transmission through the canopy also varies with overstorey species composition, such that broadleaf overstorey allows more light to reach the understorey than coniferous overstorey, while light environment under mixedwood overstorey (i.e. a mixture of coniferous and broadleaf species) tends to be heterogeneous (Messier, Parent, & Bergeron, 1998). Furthermore, the tree species in the overstorey may also influence water availability (Barbier, Gosselin, & Balandier, 2008). As light, nutrient and water availability vary with overstorey composition, diversity and composition of understorey plant communities are expected to vary with overstorey type (Barbier et al., 2008; Bartels & Chen, 2013; Hart & Chen, 2008; Vockenhuber et al., 2011). In particular, a mixedwood overstorey, which creates a heterogeneous near ground microenvironment, may produce a species rich understorey, as environmental heterogeneity promotes diversity (Bartels & Chen, 2010). Alternatively, in cases where mixedwood overstorey is more productive than conifer or broadleaf overstorey (Zhang, Chen, & Reich, 2012), relatively fewer resources may be available to the understorey. This could lead to a less diverse understorey (Zhang et al., 2017).

Time since restoration or reclamation also affects understorey vegetation (Audet, Pinno, & Thiffault, 2015; Pinno & Hawkes, 2015; Rowland, Prescott, Grayston, Quideau, & Bradfield, 2009). Typically, canopy closure increases over time from stand establishment to maturity (Chen & Popadiouk, 2002; Oliver & Larson, 1996). As such, older sites usually have higher overstorey biomass compared to younger sites, which may result in less resources being available for the understorey (Zhang et al., 2017). Understorey diversity and cover may therefore decrease with time since reclamation due to less available resources in the understorey with stands transiting from stand initiation stage to stem exclusion stage (Bartels & Chen, 2010; Chen & Popadiouk, 2002; Halpern & Lutz, 2013). Alternatively, understorey diversity and cover may increase with time since reclamation due to more time for plant colonization (Bartels & Chen, 2015).

Oil sands mining in the boreal forests of northeastern Alberta, Canada has transformed a large area of natural boreal forests into a heavily disturbed industrial landscape, where mining disturbance includes clearing vegetation and removal and stockpiling of organic and mineral soil materials (Alberta Environment and Water, 2012). Overburden materials are removed to expose the underlying McMurray Formation, which contains the bitumen-laden sands (Fung & Macyk, 2000). Reclamation efforts following oil sands mining thus involve constructing landforms and tree planting (Macdonald et al., 2015). Because site conditions and overstorey structure are among the key determinants of understorey vegetation (Hart & Chen, 2008; Vockenhuber et al., 2011), the choice of reclamation strategy, distinguished by the type of substrate material used for landform construction and type of species used for revegetation, is hypothesized to impact understorey vegetation.

As reviewed by Macdonald et al. (2015), considerable understanding has been developed regarding the effects of reclamation strategy on hydrology, soil physio-chemical properties, and microbial composition or seed banks. However, relative performance of different reclamation strategies in promoting diversity and composition of understorey plant communities has not been evaluated thoroughly (Latifovic & Pouliot, 2014). This understanding is critical because understorey vegetation accounts for the majority of forest plant species diversity and is an important indicator of forest health, ecosystem functionality (Gilliam, 2007; Hart & Chen, 2006; Nilsson & Wardle, 2005) and reclamation success (Society for Ecological Restoration, 2004). Here, we investigated whether understorey abundance, diversity and composition differ among sites reclaimed with different types of substrate materials and overstorey tree species assemblages, and whether these responses vary with time since reclamation.

2 | MATERIALS AND METHODS

2.1 | Study system

The study was conducted in the Regional Municipality of Wood Buffalo at Suncor Energy Inc.'s base mine operations, *c.* 30 km north of Fort McMurray, Alberta, Canada (59°39′N, 111°13′W; 370 m a.s.l.). Based on Environment Canada's record, the study area has mean annual temperature of 1°C and mean annual precipitation of 418.6 mm. The area falls within the central mixedwood sub-region of Alberta. In the study area, upland forests are dominated by trembling aspen (*Populus tremuloides* Michx.), jack pine (*Pinus banksiana* Lamb.), lodgepole pine (*Pinus contorta* Douglas), balsam poplar (*Populus balsamifera* L.), white birch (*Betula papyrifera* Marsh.), black spruce (*Picea mariana* (Mill.), white spruce (*Picea glauca* (Moench) Voss), B.S.P.) and balsam fir (*Abies balsamea* (L.) Mill.), while the forested muskeg is dominated by black spruce and tamarack (*Larix laricina* (Du Roi) Koch) (Beckingham & Archibald, 1996). Common understorey species in the study area as well as in the passively restored understorey are prickly wild rose (*Rosa acicularis*), wild raspberry (*Rubus strigosus*), fireweed (*Chamerion angustifolium*), hawkweed (*Hieracium*) and strawberry (*Fragaria vesca*).

2.2 | Sampling design

Using stratified random sampling, we sampled a total of 94 reclaimed sites with known reclamation history (Table 1). These sites were part

TABLE 1 Characteristics of the study sites (means with 1 *SE*)

					Overstorey species composition (% of stand density)						
Substrate	Overstorey	Age (year)	*n*	Stand density (trees per ha)	Trembling aspen	Balsam poplar	White birch	White spruce	Jack pine	Lodgepole pine	Mountain maple
O	C	13.67 (1.98)	30	2,269.5 (194)	6.5 (2)		1 (1)	86 (5.5)	9 (7)	2 (2)	
O	M	8.20 (4.2)	5	2,373 (589)	30 (7)	12 (8)	2 (2)	55.5 (8)	2 (2)		
O	B	15 (3.48)	8	11,500 (3,082)	25.5 (8.5)	57.5 (9.5)	1 (1)	16.5 (4)			
S	C	4.69 (0.12)	16	2,223.5 (406)	8 (3)	8.5 (2.5)		83.5 (2)			
S	M	5.50 (0.62)	10	3,297.5 (774)	13.5 (7.5)	25 (8.5)	2.5 (1.5)	53 (5.5)			
S	B	8 (1.73)	4	11,801 (1,143)	25.5 (13)	56 (16)	5 (5)	16 (1.5)			
T	C	22.47 (1.04)	15	1,823 (134)	2 (1)	1 (1)		14 (5)	3 (3)	78 (7)	2 (2)
T	M	14 (4.99)	5	3,338 (683)	25 (11)	18 (10)	7 (4)	5 (5)	34 (11)	9 (8)	3 (3)
T	B	20	1	5,779	31	42		1		26	

Substrate types are: O = overburden, S = secondary overburden, and T = tailings sand.
Overstorey types are: C = conifer, B = broadleaf, M = mixedwood.

of the Cumulative Environment Management Association (CEMA)'s Long Term Plot Network, which was established in 2000 to monitor long-term changes in vegetation and soils following oil sands mining and reclamation (Pinno & Hawkes, 2015). To determine the effects of substrate type, we selected sites that were reclaimed with three different substrate materials: overburden, secondary overburden and tailings sand. At our study sites, overburden substrate was *c.* 80 cm thick, non-saline, and had a texture ranging from sandy loam to sandy clay loam. Secondary overburden substrate had *c.* 30 cm of secondary overburden material over top of *c.* 50 cm of overburden. Secondary overburden contained a large proportion of B and C horizon soil, was also non-saline, and had a texture ranging from sandy clay loam to clay loam, suggesting that clay content was higher in secondary overburden compared with overburden. Tailings sand was the remains of the McMurray Formation following removal of bitumen. Tailings sand is coarse to medium textured, devoid of structure and nutrients, and has small amounts of water, clay, silt, trace metals, salts, bitumen and other hydrocarbons. Tailings sand substrate was *c.* 80 cm thick. Approximately 20 cm of peat-mineral mix, i.e. mixture of A, upper B, and O horizon soil, material was added to the top of all substrate types.

To determine the effects of overstorey type, we selected sites with different proportions of coniferous and broadleaf tree species. A site with a coniferous or broadleaf overstorey had ≥70% coniferous or broadleaf species by stem density, while mixedwood overstorey had a mixture of coniferous and broadleaf species in relatively equal proportions (Hart & Chen, 2008). While we attempted to sample at least three replicate sites for each combination of substrate type and overstorey type, we could locate only one site with a tailings sand substrate and broadleaf overstorey type. Time since reclamation (hereafter referred to as age) of the selected sites, determined as the difference between the sampling year (2013) and the year of planation, ranged from 4 to 30 years (Table 1). Year of planting data was collected from Suncor Energy's official records. Replicate sites for a particular substrate and overstorey type combination were separated from each other by at least 75 m.

TABLE 2 The effects of substrate type (*S*), overstorey type (*O*) and age class (*A*) on vegetative cover, species richness, evenness and species composition, separately for all vegetation, woody vegetation and non-woody vegetation. Deviance explained by each factor (%) is relative to null deviance. Significance at $p < .05$ is in bold

			All		Woody plants		Non-woody plants	
Attribute	Source	*df*	Deviance or variance explained (%)	*p*	Deviance or variance explained (%)	*p*	Deviance or variance explained (%)	*p*
Vegetative cover	*S*	2	17.01	**<.001**	8.44	**.009**	7.36	**.006**
	O	2	3.89	.110	13.08	**.001**	10.36	**.001**
	A	1	4.43	**.026**	0.42	.484	4.56	**.012**
	S × *O*	4	2.87	.507	5.65	.164	12.27	**.003**
	S × *A*	2	0.30	.839	0.61	.696	2.43	.176
	O × *A*	2	2.82	.200	4.33	.083	8.22	**.004**
Species richness	*S*	2	51.20	**<.001**	34.06	**<.001**	40.27	**<.001**
	O	2	2.04	.141	10.47	**<.001**	3.89	**.043**
	A	1	1.93	.054	0.72	.276	1.95	.076
	S × *O*	4	1.08	.720	4.81	.095	1.86	.556
	S × *A*	2	0.23	.799	0.57	.627	0.05	.959
	O × *A*	2	1.95	.153	0.60	.611	2.54	.129
Species evenness	*S*	2	4.93	.096	21.45	**<.001**	2.66	.227
	O	2	3.81	.161	0.82	.677	1.31	.477
	A	1	1.56	.220	2.55	.124	0.38	.513
	S × *O*	4	1.44	.842	3.51	.507	5.73	.175
	S × *A*	2	3.34	.201	1.19	.570	5.36	.053
	O × *A*	2	3.34	.201	3.32	.213	14.14	**.001**
Species composition	*S*	2	11.19	**.001**	5.96	**.001**	12.28	**.001**
	O	2	4.04	**.001**	3.33	**.044**	4.08	**.001**
	A	1	12.75	**.001**	4.63	**.001**	14.11	**.001**
	S × *O*	4	3.82	.106	3.81	.219	3.79	.089
	S × *A*	2	3.14	**.006**	2.68	.183	3.46	**.004**
	O × *A*	2	3.15	**.001**	2.29	.397	3.47	**.003**

2.3 | Field measurements

At each site, a circular plot of 154 m^2 (radius = 7 m) was established in May 2013. Tree layer was measured for the entire plot with each tree being identified to the species level, and measured for height and diameter at breast height (DBH; 1.3 m above the root collar). In July–August 2013, understorey vegetation sampling was conducted following Canada's National Forest Inventory Ground Sampling Guidelines (Canadian Council of Forest Ministers, 2008). In this protocol, woody plants (i.e. shrubs) and non-woody vegetation (i.e. herbaceous plants and bryophytes) are sampled differently, because woody plants require larger spatial sampling efforts (Hart & Chen, 2008). At each of a total of 94 sites, woody plants were sampled within three non-overlapping 25 m^2 circular subplots (located within the main circular plot of 154 m^2), each subplot placed at a random distance from the site centre, and at a random azimuth direction. All woody species within each subplot were identified to the species level, and their percent covers were visually estimated (Mueller-Dombois & Ellenberg, 1974). For non-woody plants, 10 circular subplots of 1 m^2 were randomly allocated within each main plot, and all plants were identified to the species level, and their percent covers were visually estimated. Subplot level percent cover data by species were averaged to represent the sample site.

2.4 | Statisical analysis

We computed total vegetative cover at each site as the sum of percent covers of all understorey species present, total species richness as the number of species sampled at each site and overall evenness as how evenly species were distributed within a site. Overall evenness was computed following Pielou (1980) as, $\text{Evenness} = \frac{-\Sigma p_i \log p_i}{\ln(\text{Richness})}$, where p_i is the proportion of species i percent cover to total vegetation cover. These calculations were also performed separately for woody and non-woody species.

To examine the dependence of understorey species diversity on substrate type, overstorey type and age, we used generalized linear model analyses, separately for all species (i.e. total or overall), woody species only, and non-woody species only. Following our hypothesis, we fitted the model as,

$$Y_{ijkl} = \mu + S_i + O_j + A_k + S \times O_{ij} + S \times A_{ik} + O \times A_{jk} + \varepsilon_{l(ijk)} \quad (1)$$

where the response Y_{ijkl} is vegetative cover, species richness or evenness, μ is the overall mean, S_i (i = 1, 2, 3) is substrate type, O_j (j = 1, 2, 3) is overstorey type, A_k is age as a continuous variable and $\varepsilon_{l(ijk)}$ is the error term. Species richness was fitted using a Poisson error distribution and log link function, while vegetative cover and evenness were examined using Gaussian distribution and identity link function. For each fitted model, linearity and homogeneity assumptions were tested and met. Tukey's post hoc analyses were performed as required. Our model simultaneously accounted for the effects of substrate, overstorey and age as we have no logical or theoretical basis for considering any variable to be prior in terms of a hypothetical causal structure of the data (Cohen, Cohen, West, & Aiken, 2013). We graphically presented partial dependence of vegetative cover, species richness and species evenness on substrate, overstorey, and age, following the method described by Chen, Luo, Reich, Searle, and Biswas (2016). Since woody and non-woody plants may respond differently

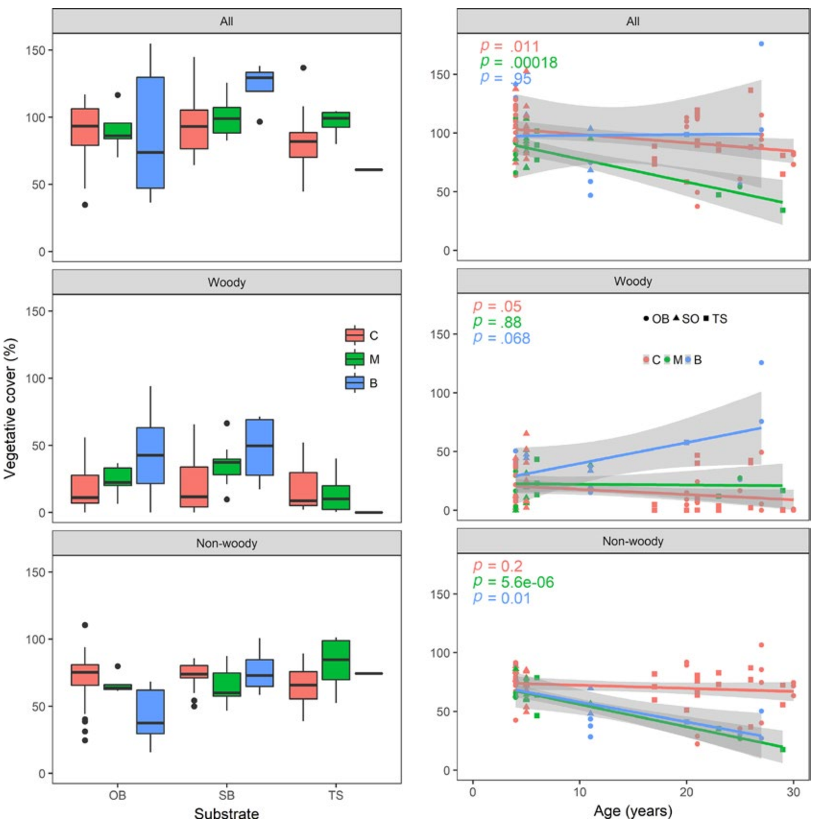

FIGURE 1 Partial dependence of understorey vegetative cover on substrate type, overstorey type and age. Values for boxplots are medians, 75% observations in boxes, and whiskers above and below the box indicate 95th and 5th percentiles. P values in the right column correspond to individual overstorey type [Colour figure can be viewed at wileyonlinelibrary.com]

to substrate, overstorey and time since disturbance (Bartels & Chen, 2013; Hart & Chen, 2008), we examined the patterns of all understorey species as well as by woody and non-woody plants. Moreover, since our sampling efforts for woody and non-woody vegetation differed, i.e. larger versus smaller sampling areas within a site, we quantified rarefied species richness (Gotelli & Colwell, 2010) as the expected species richness in random subsamples from the community (function "rarefy" in the R library "*vegan*") and repeated our analysis on rarefied data. The overall results regarding species richness did not differ qualitatively (see Figure S1), and we reported the results without rarefication.

To examine if composition of understorey species varies with substrate type, overstorey type and age, we conducted permutational multivariate analysis of variance (PerMANOVA) tests (Anderson, 2001), separately for woody and non-woody species and all species combined (overall). In PerMANOVA, we used Bray–Curtis dissimilarity matrix to summarize species composition, and used 999 permutations to determine statistical significance. We then visualized the compositional data using nonmetric multidimensional scaling with Bray–Curtis dissimilarity measure. Moreover, we performed indicator species analyses to identify the list of species that are associated with particular substrate type and overstorey type combinations (De Cáceres & Legendre, 2009), and computed specificity (i.e. positive predictive value of the species as an indicator of a site group) and sensitivity (i.e. the probability of finding the species in sites belonging to the site group) associated with each indicator value (De Cáceres & Jansen, 2016). All analyses were conducted in the statistical program R 3.3.2.

3 | RESULTS

We recorded a total of 88 understorey species (Table S1), 62 of which were non-woody species and 26 were woody species.

3.1 | Vegetative cover

Total vegetative cover was mostly affected by substrate type and followed by age, as indicated by percentage of variance explained (Table 2). Total vegetative cover was on average higher on sites with secondary overburden and overburden substrates than those with tailing sand (Table 2, Figure 1). The effect of overstorey type on total vegetative cover was insignificant (Table 2). Total vegetation cover on average declined with age with the most pronounced decline under mixedwood overstorey (Figure 1).

Woody vegetative cover varied with both substrate type and overstorey type independently (Table 2, Figure 1). Across all ages, sites with a broadleaf overstorey had an average woody vegetative cover of 41.9 ± 8.7% (*M* ± 1 *SEM*), which is about 24% and 14% higher than those with conifer and mixedwood overstorey types, respectively (Figure 1). Sites reclaimed with secondary overburden had higher

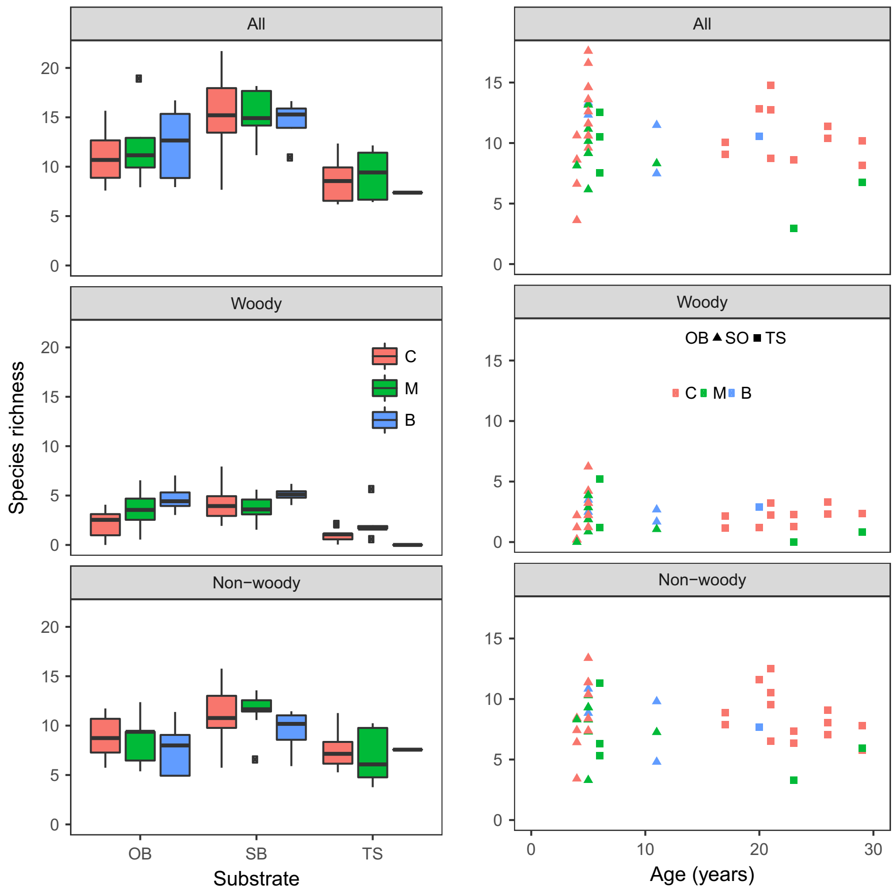

FIGURE 2 Partial dependence of understorey species richness on substrate type, overstorey type and age. Values for boxplots are medians, 75% observations in boxes, and whiskers above and below the box indicate 95th and 5th percentiles [Colour figure can be viewed at wileyonlinelibrary.com]

woody cover than those reclaimed with overburden or tailings sand. The relationship between age and woody vegetative cover, was insignificant (Table 2; Figure 1).

The effect of overstorey on non-woody cover was dependent on substrate type (Table 2; Figure 1). Non-woody cover decreased from conifer and mixedwood to broadleaf overstorey on overburden substrate, but it was similar among overstorey types on the other two substrate types (Figure 1). The effect of age on non-woody cover also changed with overstorey type (Table 2). Non-woody cover decreased with age under broadleaf and mixedwood overstorey types, but not under conifer overstorey (Figure 1).

3.2 | Species richness and evenness

Total species richness varied strongly with substrate type, but was not affected by overstorey type nor age (Table 2, Figure 2). Sites reclaimed with secondary overburden had the highest total species richness (16.03 ± 0.57 species per plot) and sites reclaimed with tailings sand had the lowest (8.1 ± 0.5 species per plot). Substrate type and overstorey type affected both woody and non-woody species richness (Figure 2, Table 2). Woody species richness was the highest on secondary overburden substrate and the lowest on tailing sand substrate among overstorey types, and was the highest under broadleaf overstorey and the lowest under conifer overstorey. Non-woody species richness was also the highest on secondary overburden substrate and the lowest on tailing sand substrate, but it was the highest under conifer overstorey and the lowest under broadleaf overstorey (Table 2, Figure 2).

Overall species evenness was not significantly affected by substrate type, overstorey type or age (Table 2; Figure 3). Woody evenness, by contrast, varied significantly with substrate type (Table 2). Sites reclaimed with secondary overburden had the highest woody species evenness, while those reclaimed with tailings sand had the lowest (Figure 3). Non-woody evenness showed overstorey-dependent responses to age (Table 2), with an increase in broadleaf and a decrease in mixedwood with age (Figure 3).

3.3 | Species composition

Overall species composition, woody and non-woody species composition varied strongly with substrate type, overstorey type and age (Table 2). When considering all species together, younger sites were grouped on the left and older sites on the right of axis 1 in ordination space (Figure 4), indicating that younger sites had different overall species composition from older sites. Moreover, two distinct substrate type groupings were prominent: sites with overburden and secondary overburden substrates formed one group and those with tailing sand formed the other. Non-woody species composition showed age- and substrate-based patterns identical to those of overall species composition (Figure 4). For woody species composition,

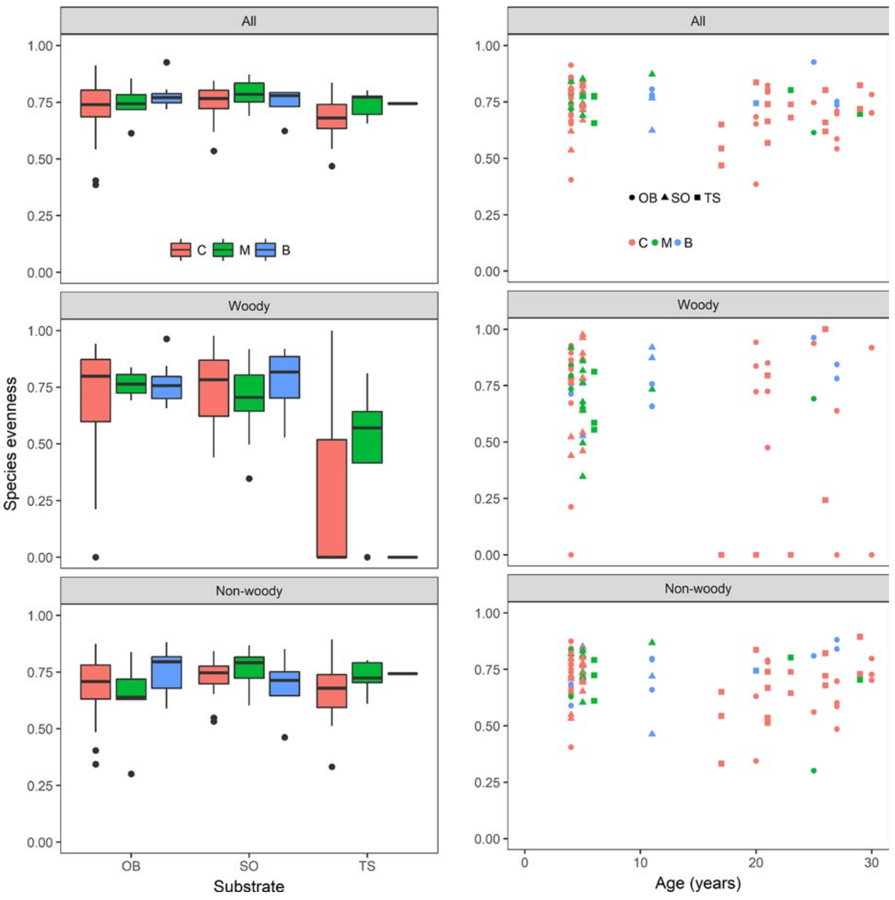

FIGURE 3 Partial dependence of understorey evenness on substrate type, overstorey type and age. Values for boxplots are medians, 75% observations in boxes, and whiskers above and below the box indicate 95th and 5th percentiles [Colour figure can be viewed at wileyonlinelibrary.com]

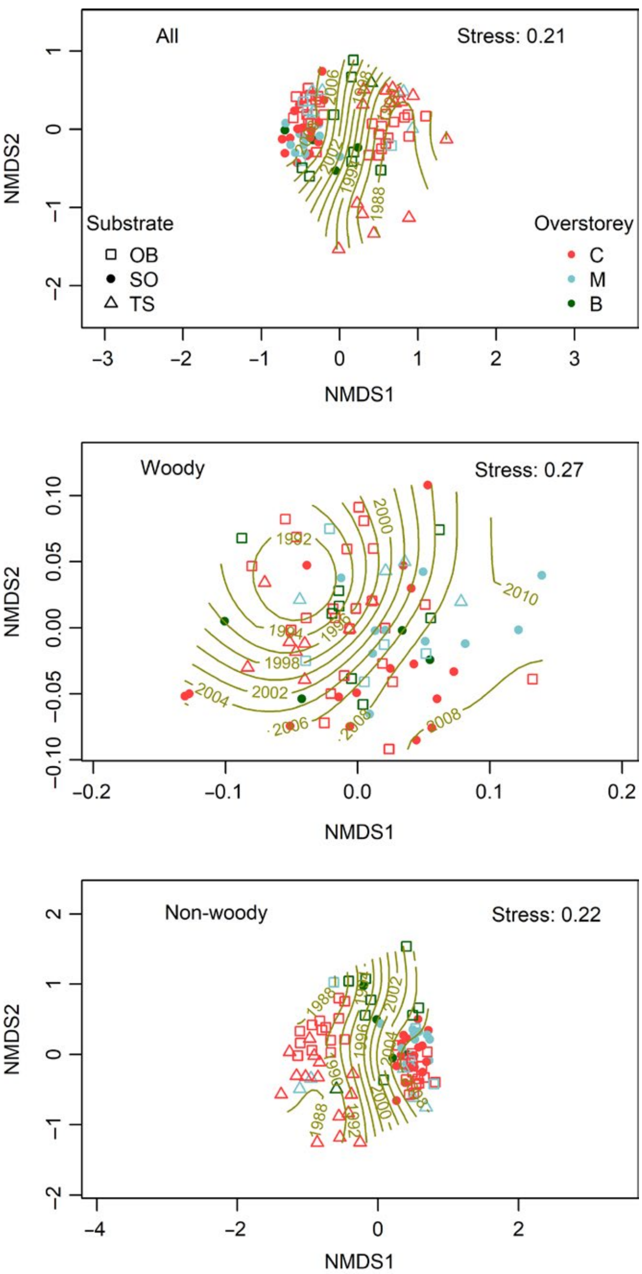

FIGURE 4 Nonmetric multidimensional scaling ordination of all species, woody and non-woody species composition for different substrate and overstorey type combinations. Substrate types included overburden (OB), secondary overburden (SO) and tilling sand (TS). Overstorey types included conifer (C), mixedwood (M) and broadleaf (B). Sites nearest each other in ordination space have similar floristic assemblages, whereas those farther apart are less similar. Contours indicate time since reclamation [Colour figure can be viewed at wileyonlinelibrary.com]

sites reclaimed with tailings sand were also separated in ordination space from those reclaimed with overburden and secondary overburden (Figure 4).

Indicator species analysis revealed that tailings sand substrates more commonly supported grasses (e.g. *Bromus inermis*, *Festuc rubra*, *Carex argyrantha*) and a single forb (*Medicago sativa*), while overburden substrates more commonly supported herbs (e.g. *C. angustifolium*, *Pyrola asarifolia*), shrubs (e.g. *Salix lucida*) and a moss (*Pleurozium schreberi*) (see Table 3 for the list of species). By contrast, secondary overburden substrates more commonly supported a mix of grasses, forbs and shrubs. Among overstorey types, broadleaf overstorey more commonly supported both forbs and shrubs, while grasses and shrubs were more commonly found under mixedwood overstorey. Plants of all life-form types (e.g. forbs, grasses and shrubs) were associated with the list of indicator species for conifer understories (Table 3).

4 | DISCUSSION

Our results support our central hypothesis that reclamation strategy, distinguished by the type of substrate material used during landform construction and type of overstorey species, are major drivers of understorey abundance, diversity and composition following oil sands mining. Note that, here understorey is restored passively (i.e. operators usually do not plant or seed understorey species) and the possible sources of plant species are the viable seed banks in the forest floor and peat-mineral mix (Alday et al., 2011; Jung et al., 2014) and the incoming propagules from adjacent areas through wind or animal dispersal. Nevertheless, we found that understorey species richness and vegetative cover were higher on sites reclaimed with secondary overburden and overburden than those with tailings sand. Overburden and secondary overburden substrate is composed of largely mineral subsoil, which should be conducive to native understorey plant establishment, growth and persistence. By contrast, tailings sand has little to no water holding capacity due to its coarse texture and lack of structure (Jung et al., 2014; Mendez & Maier, 2008), no mycorrhizal associations, few nutrients, and high salinity, suggesting that species with moderate to high water and nutrient requirements and a lack of salt tolerance would not do well on this substrate type (Greenway & Munns, 1980; Kessler, Barbour, van Rees, & Dobchuk, 2010; Purdy, MacDonald, & Lieffers, 2005). The highest understorey species richness on secondary overburden substrate is perhaps related to its highest clay content that promotes soil resource availability for understorey vegetation, which is key to understorey plant diversity (Bartels & Chen, 2010). Indeed, our indicator species analyses confirm that sites on secondary overburden substrate support a more diverse mix of shrub, forb and grass species than the other two substrate types (see Table 3).

We found that overstorey type is a key driver of understorey vegetative cover and understorey species richness (Gilliam, 2007; Vockenhuber et al., 2011). Different types of overstorey structures and compositions create different degrees of light and soil resources available in the understorey (Barbier et al., 2008; Chávez & Macdonald, 2012; Hart & Chen, 2008), and in turn affect understorey vegetation abundance and species diversity (Bartels & Chen, 2010, 2013). Under the broadleaf overstorey, high understorey cover and species richness are attributable to high understorey light availability and high quantity of nutrient-rich foliage litter (Chen, Brant, Seedre, Brassard, & Taylor, 2017; Gilliam, 2007; Hart & Chen, 2006) since understorey resource availability acts positively on understorey vegetation abundance and

TABLE 3 Indicator species for various substrate types and overstorey types

Substrate type[a]	Overstorey type	Indicator species	Life-form	Indicator value	Specificity	Sensitivity	*p*
Overburden	Conifer	*Chamerion angustifolium*	Forb	0.6	0.47	0.77	.04
Overburden	Conifer	*Pleurozium schreberi*	Moss	0.59	0.68	0.5	<.01
Overburden	Conifer	*Taraxacum officinale*	Forb	0.51	0.61	0.43	.02
Overburden	Broadleaf	*Salix lucida*	Shrub	0.5	1	0.25	.05
Overburden	Broadleaf	*Pyrola asarifolia*	Forb	0.49	0.64	0.38	.04
Overburden	Broadleaf	*Cornus sericea*	Shrub	0.46	0.34	0.63	.01
Secondary overburden	Conifer	*Vicia Americana*	Forb	0.58	0.45	0.75	<.01
Secondary overburden	Conifer	*Dasiphora fruticosa*	Shrub	0.53	0.63	0.44	<.01
Secondary overburden	Conifer	*Crepis tectorum*	Forb	0.49	0.38	0.63	.04
Secondary overburden	Conifer	*Bromus tectorum*	Grass	0.48	0.61	0.38	.02
Secondary overburden	Conifer	*Sonchus arvensis*	Forb	0.46	0.49	0.44	.03
Secondary overburden	Conifer	*Ribes oxyacanthoides*	Shrub	0.42	0.46	0.38	.05
Secondary overburden	Broadleaf	*Ceanothus cuneatus*	Shrub	0.5	1	0.25	.05
Secondary overburden	Mixedwood	*Salix lutea*	Shrub	0.56	0.64	0.5	<.01
Secondary overburden	Mixedwood	*Calamagrostis Canadensis*	Grass	0.52	0.88	0.3	.04
Tailings sand	Conifer	*Bromus inermis*	Grass	0.74	0.58	0.93	<.01
Tailings sand	Conifer	*Festuc rubra*	Grass	0.54	0.87	0.33	.03
Tailings sand	Conifer	*Festuca saximontana*	Grass	0.52	1	0.27	.03
Tailings sand	Conifer	*Carex argyrantha*	Grass	0.50	0.74	0.33	.01
Tailings sand	Conifer	*Medicago sativa*	Forb	0.46	0.4	0.53	.04

[a]No indicator species were found for missing combinations.

species diversity (Barbier et al., 2008; Bartels & Chen, 2010; Halpern & Lutz, 2013). Whereas under the coniferous overstorey, low light availability as well as poor soil conditions (e.g. lower pH, colder temperature, lower nutrient availability), which limit shade-intolerant, fast-growing species (Bartels & Chen, 2013; Chávez & Macdonald, 2012), has resulted in low vegetation cover and species richness. Under the mixedwood overstorey, both understorey resource availability and heterogeneity have contributed to the understorey cover and species richness (Bartels & Chen, 2010). Because of the contrasting responses between woody and non-woody plants to light availability and soil substrate conditions (Barbier et al., 2008; Bartels & Chen, 2013; Hart & Chen, 2008), it is not unexpected that woody cover and species richness were maximum in broadleaf stands, intermediate in mixedwood stands and minimum in conifer stands, while non-woody vegetative cover and species richness were higher in conifer stands than in the other stand types.

As hypothesized, time since reclamation impacted vegetative cover, but it has little effect on species richness and evenness of the understorey plant community, except divergent age-dependent responses of evenness among overstorey types. Our results of declining vegetative cover with age are consistent with Rowland et al. (2009) and Pinno and Hawkes (2015). This probably resulted from reduced resource availability in the understorey with increasing overstorey canopy closure and standing biomass as stands age from stand initiation stage to stem exclusion stage (Audet et al., 2015; Bartels & Chen, 2010; Chen & Popadiouk, 2002; Halpern & Lutz, 2013; Pinno & Hawkes, 2015; Zhang et al., 2017).

Understorey species composition varied strongly with substrate type and overstorey type. Shrub and herbaceous species establishment and growth can be more limited in conifer-dominated stands, compared to broadleaf-dominated stands, due to their lower near ground light availability and soil characteristics that include a lower pH, colder temperature and lower nutrient availability. Instead, conifer stands tend to favour the establishment and growth of more non-vascular species (Bartels & Chen, 2013; Hart & Chen, 2006, 2008; Messier et al., 1998). Mixedwood stands have heterogeneous soil and near ground light conditions that result in understorey conditions typical of both broadleaf and conifer stands, leading to mixedwood stands supporting understorey species common to both conifer and broadleaf stands, in support of our analysis. Understorey species composition on tailings sand differed compared to the other two substrate types, irrespective of overstorey type. Differences in observed substrate type-based understorey species compositions may also be attributed to high salinity and low soil nutrient availability limiting the extent to which shrub and forb species, which generally do not tolerate highly saline environments with limited nutrients well, could establish, grow and persist on tailings sand substrates, in contrast to many species of grasses (Jung et al., 2014; Purdy et al., 2005).

In conclusion, our results demonstrate the importance of reclamation substrate and overstorey tree species composition for driving patterns of passively restored understorey vegetation abundance, species diversity and composition following oil stands mining reclamation. Notably, we found tailings sand to be a poor substrate for understorey vegetation abundance and species diversity, and should not be used as a reclamation substrate when possible. Our results suggest that light and soil resources available for understorey vegetation, resulting from different substrate types and overstorey types, have profound effects on the abundance, diversity and species composition of understorey vegetation during the recovery following the reclamation of severely degraded sites from resource extraction.

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AUTHORS' CONTRIBUTIONS

H.Y.H.C. and T.M.S. designed the study; T.M.S. collected data, H.Y.H.C., S.R.B., T.M.S. and S.R.B. analysed the data; H.Y.H.C., S.R.B., T.M.S., B.W.B. and S.F.B. wrote the paper.

DATA ACCESSIBILITY

Data from this paper can be accessed through the Dryad Digital Repository https://doi.org/10.5061/dryad.c49m0 (Chen, Biswas, Sobey, Brassard, & Bartels, 2017).

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