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Spatial patterns and competition in trees in early successional reclaimed and natural boreal forests

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ABSTRACT

Spatial distribution of plants in early successional stands provides an indication of future plant community structure and population dynamics. Determining the factors driving plant interactions and their demographic relationships at stand initiation is critical to gain a better understanding of plants' responses to competition and limited resource conditions. Reclaimed ecosystems are ideal for studying such community mechanisms because they are completely reconstructed ecosystems with known community filters such as soil type, propagule composition, and the presence of both planted and naturally establishing trees. The current study explored the spatial patterns and competition-facilitation mechanisms in deciduous and evergreen trees in two oil sands reclaimed sites with different reclamation age (2-year old and 5-year old) and cover soils (wetland peat origin – PMM; and forest floor origin – FFMM) in Alberta, Canada, and compared this with a naturally-disturbed site at 5 years since fire. Spatial point pattern analysis was performed using pair correlation function $g(r)$, mark correlation function $k_{mm}(r)$, and bivariate g -function. Intraspecific competition in deciduous seedlings was stronger in the 5-year old reclaimed site than in the 2-year old site. Spatial patterns in deciduous seedlings on PMM were aggregated at 1–3 m scale similar to the natural site, whereas seedlings on FFMM sites had aggregated patterns at greater than 5 m scale. Planted conifers had regular pattern at 1–2 m scale in the 2-year old sites which reflects the plantation spacing, but showed a random pattern in the 5-year old sites indicating the effect of random mortality. Bivariate spatial analysis indicated a significant repulsion between deciduous and coniferous seedling at 1 m in the 2-year old PMM site and a significant attraction in the 5-year old FFMM site suggesting that the mechanism of competition-facilitation between trees is different in different cover soils. Density dependent thinning was only observed in the 2-year old PMM and natural sites; however, a gradual increase in nearest neighbour distances with increasing seedling size in all the reclaimed sites suggests that density dependent thinning has started.

1. Introduction

Competition is thought to be one of the key ecological mechanisms defining neighbourhood species distribution, survival and mortality, productivity, stand structure, population dynamics, and overall ecosystem function (Felinks and Wiegand, 2008; Getzin et al., 2006; Tilman, 1994). In boreal ecosystems, large scale disturbances (natural or anthropogenic) work in parallel with competition to shape the spatial pattern of vegetation (Felinks and Wiegand, 2008; Gray and He, 2009). As competition is a process mainly affecting neighbouring individuals, spatial locations of plants might reveal important information on community mechanisms directly related to competition such as dispersal, isolation, and density dependence (Gray and He, 2009; McIntire and Fajardo, 2009). Spatial patterns can also be used as an

indicator of vegetation succession since the distribution of one species may have influence on the surrounding species and the interplay among different species changes with time (Bertness and Callaway, 1994; Dale, 2000; Felinks and Wiegand, 2008). In natural ecosystems, most species show a systematic change in spatial patterns over time starting from random or aggregated and progressing to regular pattern due to competition driven either by density dependent mortality (He and Duncan, 2000; Newton and Jolliffe, 1998) or by the cumulative effects of competition and gap dynamics (Moeur, 1997). Disturbance generated heterogeneity in resource availability may also contribute to creating an aggregated pattern which can in turn be amplified or suppressed by biotic processes such as competition or facilitation (Miller et al., 2010).

Spatial patterns in naturally established plant communities are often a result of multiple complex processes working simultaneously, and

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disentangling the interplay between processes and emerging patterns may not always be possible due to our limited understanding of the intricate relationships among the contributing factors (Felinks and Wiegand, 2008; McIntire and Fajardo, 2009; Miller et al., 2010). Using fully stem mapped data, any small scale spatial correlation structure in the pattern of tree distribution can be quantified and the nature of their association (positive or negative) can be detected through spatial statistics such as Ripley's K-function and pair-correlation function (Ripley, 1976; Stoyan and Stoyan, 1994). For example, a positive association between two species at a certain scale may indicate a possible facilitation or mutual stimulation, whereas a negative association suggests repulsion and therefore interspecific competition (Callaway and Walker, 1997; Wiegand et al., 2007).

Studying spatial patterns of plant communities in reclaimed ecosystems has potential to answer some of these questions due to the controlled and known community filters such as soil type, propagule composition, and trackable early successional vegetation dynamics. Moreover, analysis of community structure and spatial distribution in the reclaimed areas may provide empirical evidence for improving reclamation techniques to achieve a target population structure. Although the aim of land reclamation and ecological restoration is to create conditions for natural ecosystem processes to operate, spatial patterns have rarely been considered as a key success attribute (SERI (Society for Ecological Restoration International Science & Policy Working Group), 2004).

Plant communities in reclaimed ecosystems may not display similar spatial patterns as in natural systems due to altered biotic (propagule availability, density dependence, soil microbial community, and herbivory) and abiotic (soil physical structure and chemical properties, microtopography, and environmental factors) conditions (Miller et al., 2010). Spatial patterns in reclaimed ecosystems may arise from several means such as distribution of cover soils, seed propagules transferred from the donor sites, naturally established seedlings from off-site sources, and planted species (Bakker, 2000; Rokich et al., 2000). Uniform sub-surface soil physical and chemical properties in reclaimed sites may also contribute to generate a uniform (at initial phase) to random (at maturity) vegetation pattern compared to the aggregated to random or regular pattern in natural systems (Milder et al., 2013; Miller et al., 2010; Silk et al., 2006). Spatial structures in plants during stand initiation greatly influences the density dependent interactions and structural complexity at later stages along the successional trajectory of stands (Donato et al., 2012; Swanson et al., 2011; Wild et al., 2014). These effects might be different in reclaimed and natural systems due to the differences in vegetation composition, mode of regeneration (seed origin vs sucker origin), and initial recruitment density, but are expected to change over time as the inter and intraspecific competition change as a result of density dependence (Johnson et al., 2012; Stachowicz, 2001). However, homogenization of substrates during the reconstruction of reclaimed sites may hinder the spatial structuring process for a long time (e.g. 100 years in an abandoned agricultural field (Flinn and Marks, 2007)). According to the resource heterogeneity hypothesis (RHH), the areas with homogeneous limited resource conditions may result in a patch-scale pattern that is less variable than the areas with spatially heterogeneous resource conditions (Tilman and Pacala, 1993). Although reclaimed ecosystems render an ideal opportunity to test such ecological hypothesis, there are actually very few studies that attempted to do so (Blignaut and Milton, 2005; Maestre et al., 2003; Miller et al., 2010; Valladares and Gianoli, 2007) and we are aware of only two studies conducted in oil sands reclaimed ecosystems but with heavy belowground components (Das Gupta et al., 2015; Sorenson et al., 2017).

In this study we explored spatial patterns in tree seedlings at an early stage of secondary succession on young oil sands reclaimed and post-fire sites in northern Alberta, Canada. We quantified spatial structures in both planted and naturally regenerating tree seedlings on sites reclaimed at two different ages with two different cover soils and

compared this with a natural fire disturbed benchmark site. We asked the following questions: (1) What spatial patterns do seedlings show in different reclaimed and naturally-disturbed sites? Spatial patterns in seedlings should be different in reclaimed and naturally-disturbed sites due to the differences in population dynamics (e.g. recruitment density and regeneration mode) and abiotic conditions. (2) Are the competitive forces (intra- and interspecific) different in the reclaimed and naturally-disturbed sites? Importance of interspecific competition should be stronger (high r^2 between seedling size and neighbourhood distance) in the reclaimed sites than the naturally-disturbed site due to the competition for limited resources in the reclaimed sites. (3) Is there any evidence of density dependent competition between seedlings of different size classes in the reclaimed and naturally-disturbed sites? We expected to see a clear evidence of density dependent thinning in sites with high seedling density. A gradual decline in clustering and increase in neighbourhood distances with increasing seedling size may indicate density dependent thinning (Getzin et al., 2008b).

2. Methods

2.1. Site description

This study was conducted in 2015 at an oil sands mine 75 km north of Fort McMurray, Alberta, Canada (57° 20' N, 111° 49' W). The natural forest ecosystem in the region is boreal mixedwood forest with the mesic upland sites consisting of varying mixtures of deciduous (mainly trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*)) and coniferous (mainly white spruce (*Picea glauca*)) trees. The dominant soil type is well drained Orthic Gray Luvisol (Beckingham and Archibald, 1996). The continental climate has a mean July temperature of 16.8 °C and January temperature of – 18.8 °C with mean annual precipitation of 455 mm (Environment Canada, 2016).

Two young reclaimed sites, a 2-year old and a 5-year old site, were used in the current study. The reclaimed sites were overburden dumps constructed of saline – sodic overburden material produced during oil sands mining and subsequent reclamation in 2013 and 2011, respectively. The overburden material was covered with 1 m of suitable (i.e. non-saline) sub-soil and then 0.2–0.5 m of reclamation cover soil was directly placed. Two types of reclamation cover soils were used in the study: (i) peat – mineral mix (PMM) derived from wetland peat deposits and underlying mineral soils, and (ii) forest floor – mineral mix (FFMM) derived from upland forest soil created by salvaging the forest floor layer and underlying mineral soils together. A 5-year old post-fire stand was used as natural benchmark since fire is the main natural disturbance and one of the main drivers of the spatial community processes in the studied boreal region (Nilsson and Wardle, 2005; Payette et al., 2008). Sampling was done in 2015. All the sites were located within a 10 km radius of each other and experienced similar weather conditions and propagule pressure. The deciduous trees in the studied plots were of natural origin and comprised of trembling aspen (70–90% of the total stems) and balsam poplar (15–23% of total stems), whereas white spruce (3–30% of total stems) was the only conifer that was planted on the reclaimed sites at a density of approximately 1900 stems per hectare (Table 1). Plantation is a part of the standard reclamation practice in the oil sands mining areas. Conifer seedlings were nursery grown and 1-year old when they were planted in the reclaimed sites (5-year old in 2015). The deciduous trees on the reclaimed sites are of seedling origin while on the natural site they are of sucker origin (only trembling aspen). The term seedling will be used to refer to all trees regardless of origin: seedling, sucker, planted. The general soil and site characteristics of the studied area can be found in (Pinno and Errington, 2015). In general, PMM soils were more acidic and had lower bulk density and greater N and S than the FFMM and benchmark soils (SI: Table S1).

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