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Spatial patterning of underrepresented tree species in canopy gaps 9 years after group selection cutting

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ABSTRACT

Group selection and gap-based silvicultural systems are often proposed to promote compositional and structural heterogeneity across forest landscapes. The gap environment creates gradients of resources, especially light and moisture, that are important for maintaining and enhancing tree species diversity. To advance understanding of spatial variability of tree regeneration in forest gaps, seedlings and saplings of yellow birch (*Betula alleghaniensis* Britton) and eastern hemlock (*Tsuga canadensis* (L.) Carrière) were mapped in 49 group-selection openings with diameters of 1, 1.5, and 2 times canopy tree height (22 m), 9 years after the openings were created. We used Ripley's K, kernel density estimates, and raster-based local statistics to analyze spatial point patterns. Our results indicate that spatial patterns in the openings were mostly aggregated. The southern edges of the largest openings contained the highest magnitude of yellow birch and eastern hemlock per unit area. Moisture availability and opening size appear to be important factors underlying regeneration success in this study. Over time, the spatial patterns of these species may shift as the southern locations become less suitable for the shade mid-tolerant yellow birch. Continued monitoring and additional treatments, such as gap expansion along southern borders, will likely be necessary in order to ensure underrepresented species successfully reach maturity.

1. Introduction

Past forest management practices have altered forest structure and composition (Jacquemyn et al., 2003; Rhemtulla et al., 2009) leading, in some cases, to declines in structural and biological diversity (Hansen et al., 1991; Jenkins and Parker, 1998). Current silvicultural objectives often include promoting and sustaining certain aspects of ecosystem integrity such as health, diversity, and resilience (Lähde et al., 1999; Franklin et al., 2007). Group selection and gap-based silvicultural systems have increasingly been suggested as a means of promoting species diversity by increasing heterogeneity across forest landscapes (Murphy et al., 1993; Coates and Burton, 1997).

Resource heterogeneity within forest stands may facilitate coexistence of species with contrasting life-histories. Gap partitioning, resulting from heterogeneity in resources such as light and moisture across forest openings, is thought to be a factor promoting tree species diversity by allowing species with contrasting life history strategies to coexist (Denslow, 1980; Powers et al., 2008; Kern et al., 2013, 2014). Nevertheless, many factors are involved in structuring vegetation dynamics in canopy gaps and gap partitioning has not been found to occur consistently in all gap environments. For example, if species have similar requirements for establishment, then partitioning during the early establishment phase may not be apparent, but could occur later as a result of differential survival (Coates, 2002; Raymond et al., 2006). Alternatively, partitioning may vary with shade-tolerance. For example, Busing and White (1997) observed that shade-intolerants partitioned gaps, but shade-tolerant species did not in an old-growth temperate forest.

Spatial patterning of regeneration is likely partly influenced by resource partitioning (i.e., heterogeneity in resources) as well as legacy effects such as advance regeneration and chance location of desirable pre-disturbance substrates [e.g., rotten coarse woody debris (CWD)]. The spectrum of spatial patterns range from aggregated to random to dispersed (Dale, 1999, p. 206–207, 231). Aggregated spatial patterns can arise in heterogeneous environments where suitable regeneration microsites or resources are limiting but competition between individuals for these resources is weak (Beatty, 1984; Gray and Spies, 1997). Homogenous environmental conditions or chance events that include the presence of advance regeneration or short-term weather patterns can create random

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spatial patterns (Brokaw and Busing, 2000; Miller et al., 2002). Dispersed patterns have been linked to competition between individuals for a limited set of resources (Dale, 1999, p. 23). However, a myriad of processes control spatial patterns and the factors responsible are not always apparent or easily explained.

To test the applicability of gap partitioning theory in the design of silvicultural treatments for enhancing compositional diversity and restoring underrepresented species, we examined the spatial patterning of two species with contrasting tolerances to shade but similar seedbed requirements in 49 openings 9 years post-treatment. Specifically, we sought to answer the following questions: What are the intra- and inter-specific spatial patterns of regeneration of focal species within openings? Do observed spatial patterns provide evidence for gap-partitioning? Finally, were spatial patterns of abundance concurrent with patterns of plant stature and likely canopy recruitment? We hypothesized that the inter- and intra-specific spatial patterns would be aggregated due to similarities in requirements for successful germination and growth. Since both species require adequate moisture for successful development, we also hypothesized that both species would have higher densities in the southern portion of the openings where shading by border trees might reduce evaporative demand.

2. Methods

2.1. Study system

Yellow birch (*Betula alleghaniensis* Britton) and eastern hemlock (*Tsuga canadensis* (L.) Carrière) are two tree species native to the temperate mixed deciduous and coniferous forests of northeastern North America (Erdmann, 1990; Godman and Lancaster, 1990; Barbour and Billings, 2000, p. 357–395). Both species have declined greatly in abundance as a result of historic exploitive logging practices and associated slash fires, herbivory, lack of suitable substrates for establishment, and contemporary silviculture treatments that favor intolerant species or shade-tolerant maples (*Acer* spp.; Godman and Krefting, 1960; Rooney et al., 2000; Schulte et al., 2007; Lorenzetti et al., 2008; Salk et al., 2011). Wind is the primary disturbance type in theses temperate forests creating openings through blow-down of one to many trees (Runkle, 1982; Frelich and Lorimer, 1991). Canopy gaps add heterogeneity to forest communities both across the landscape and within individual gaps allowing species with a broad range of tolerances to coexist (Pickett and White, 1985). While eastern hemlock is extremely shade tolerant, yellow birch is shade mid-tolerant (Baker, 1949). Both species are small seeded and depend on wind for dispersal (McGee and Birmingham, 1997). Eastern hemlock dispersal distances are usually no more than the height of individual trees, whereas yellow birch seeds can be blown some distance along snow covered surfaces (Ribbens et al., 1994). Eastern hemlock and yellow birch prefer cool, moist conditions for growth (Davis et al., 1998; Goerlich and Nyland, 1999; Jackson and Booth, 2002). Temperature requirements for germination are very similar and both species are particularly susceptible to moisture stress during the seedling stage (Olson et al., 1959; Godman and Krefting, 1960; Winget and Kozlowski, 1965).

2.2. Study area

The study site is a northern hardwood forest located south of Alberta, MI, in the western Upper Peninsula of Michigan at the Ford Center Research Forest (section 30, T49 N, R33 W, 46°37′N, 88°29′W). Geology in the study area is classified as glacial drift over Precambrian bedrock (Albert, 1995). Soils are well-drained to somewhat poorly-drained silt loams (Berndt, 1988, p. 15–83). Mean elevation is 430 m (Gesch et al., 2002; Gesch, 2007). Average temperatures range from −9 °C in January to 17 °C in July (NOAA, 2012a). Mean yearly precipitation has been 84 cm and mean snowfall has been 371 cm per year (MRCC, 2012; NOAA, 2012a). *Acer saccharum–Tsuga canadensis/Dryopteris spinulosa* (ATD) is the primary habitat type at the study site (Burger and Kotar, 2003). The dominant tree species are sugar maple (*Acer saccharum* Marsh.) and red maple (*Acer rubrum* L.). Yellow birch and eastern hemlock are co-dominants, but their abundances are much lower than the maples. Minor species include: American basswood (*Tilia americana* L.), American elm (*Ulmus americana* L.), balsam fir (*Abies balsamea* (L.) Mill.), black ash (*Fraxinus nigra* Marshall), black cherry (*Prunus serotina* Ehrh), eastern white pine (*Pinus strobus* L.), ironwood (*Ostrya virginiana* (P. Mill.) K. Kock), northern white cedar (*Thuja occidentalis* L.), serviceberry (*Amelanchier* spp. Medik), trembling aspen (*Populus tremuloides* Michx.), and white spruce (*Picea glauca* (Moench) Voss). Prior to the 1890’s, the land surrounding the Ford Center was classified as a pine-hardwood forest (Erickson et al., 1990). In the 1930’s, most of the merchantable timber was harvested from the area (Erickson et al., 1990). Since the 1960’s, the northern hardwoods at the Ford Center Research Forest have been managed using single-tree selection (Schwartz et al., 2005).

2.3. Experimental design

In the winter of 2003, 49 group-selection openings were created in three size classes. Mean ± 1 SE opening area (m^2) were 267 ± 62 ($n = 16$) for the small, 642 ± 85 ($n = 17$) for the medium, and 1192 ± 155 ($n = 16$) for the large, with areas corresponding to opening diameters of 1, 1.5, and 2 times average tree height (22 m). All stems >10 cm dbh were removed from the openings except a single yellow birch legacy tree that was retained in the center of each opening. For a more detailed description of the initial study design and results refer to Shields et al. (2007b).

2.4. Data collection

Initial studies pertaining to the group-selection openings occurred in 2004–2005 (Shields and Webster, 2007; Shields et al., 2007a,b, 2008). Group-selection opening and legacy-tree canopy area values were re-measured in 2011 (Klingsporn et al., 2012). Tree regeneration data was collected in twelve regeneration plots in each opening in 2005 and 2012 (Shields et al., 2007b; Poznanovic et al., 2013). However, the subplot network did not fully capture the spatial variability of our targeted species. Therefore, we chose to expand sampling by mapping all existing yellow birch and eastern hemlock regeneration within the openings.

During the spring of 2012, each of the 49 group-selection openings were surveyed for all yellow birch and eastern hemlock regeneration ⩾0.1 m tall. In order to map the locations of regeneration, the yellow birch legacy tree located at the center of each opening served as a permanent anchor point. The distance and bearing from the legacy tree to each sample point was recorded using a compass and Haglöf DME™ sonic rangefinder. Height and seedbed substrate were noted. Seedbed classes were characterized as: forest floor, moss, CWD, pit, mound, or skid road. Heights were calculated using a meter stick or rangefinder and Suunto™ clinometer, depending on tree size. Other tree species were also present and ubiquitous in the understory layer (Poznanovic et al., 2013). Only eastern hemlock and yellow birch were mapped because both species have become less common across their native ranges and the effort required to map all of the understory regeneration was beyond the scope of this project. Gap border tree data (>8 cm diameter at breast height) was collected in 2004 as part of an initial study; the three border trees closest to the gap edge in the cardinal and