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Repeated insect outbreaks promote multi-cohort aspen mixedwood forests in northern Minnesota, USA

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Characterizing the timing, severity, and agents of historic forest disturbances is critical to developing management and conservation strategies based on natural processes. Typically such information is derived from retrospective studies of remnant old-growth forests; however, this approach has limited application in regions dominated by secondary forests heavily influenced by past land-use. One striking example is the secondary aspen mixedwood forests of northern Minnesota, which have risen in both abundance and aerial extent, the result of post-settlement harvesting and subsequent land-use changes. Given their recent rise in abundance, as well as their dominance by relatively short-lived aspen, they have not been the focus of retrospective studies examining pre-settlement conditions.

Using methods of dendrochronology, we reconstructed nearly a 90-year history of canopy disturbances and stand development for nine secondary mesic aspen mixedwood forests of northern Minnesota. Results show all stands initiating after near stand-replacing disturbance, presumably harvests, marked by initial recruitment dominated by *Populus tremuloides*. Ensuing development included an extended recruitment period by shade-tolerant species such as *Abies balsamea*, *Acer rubrum*, and *Picea glauca*. However, some stands experienced defoliation by forest tent caterpillar (*Malacosoma disstria*) quite early during the stem exclusion stage (major events occurring as early as 23 years after stand initiation), causing tree mortality and giving rise to a new cohort. Subsequent repeated outbreaks of tent caterpillar and spruce budworm (*Choristoneura fumiferana*) further opened the canopy, resulting in complex mixed-species, multi-cohort stands.

This study is one of the first to link chronic defoliation events with long-term community dynamics for this forest type. Our findings highlight the critical roles these events play in structuring aspen mixedwood forests, particularly within the early stages of stand development, resulting in multi-cohort stands. Moreover, our findings support the growing body of literature suggesting that the range of variability in aspen age structures extends beyond the single-cohort model that has guided forest management in this region. Collectively, these findings have important implications for the design of forest management practices that approximate this range of variability and emulate defoliation disturbances, with early harvest entries aimed at increasing stand structural and compositional complexity.

1. Introduction

Natural canopy disturbances and tree species' autoecologies, in conjunction with site conditions, largely govern the development of forest composition and structure (age, size and distribution of live and dead trees; Oliver and Larson, 1996; Bergeron, 2000). Correspondingly, knowledge of disturbance and species traits are imperative for predicting and understanding how forest conditions develop over time and in response to disturbance. Understanding these relationships is of particular interest when managing forests for objectives that include the restoration of historically important and currently underrepresented forest conditions (Engstrom et al., 1999). Typically, information on disturbance regimes is derived from retrospective studies of remnant old-growth forests; this approach has been less often applied in regions dominated by secondary forests heavily influenced by past land-use (Oliver and Stephens, 1977). As a result, such long-term data are rare for many secondary forest types, and when such information exists, it may depict historical reference conditions that no longer apply (White and Walker, 1997). Thus, considerable knowledge gaps impede the development and application of forest management and conservation strategies based on historic patterns of disturbance.

The historic range of variability in successional pathways for a given forest type is often quite large, reflecting differences in

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disturbance regimes and site conditions. For example, a wide range of disturbance and successional patterns has been documented for the mixed aspen (*Populus tremuloides*)-conifer forests (hereafter referred to as 'aspen mixedwoods') of the sub-boreal and boreal regions of North America (cf. McCarthy, 2001; Chen and Popadiouk, 2002), despite general compositional similarities of this community across the continent. Studies of aspen mixedwood forests within northeastern Minnesota, USA have documented relatively frequent stand-replacing fires (70–110 years; Heinselman, 1996) that result in stands and landscapes largely dominated by pioneer species, including *P. tremuloides* and *Betula papyrifera* (paper birch). In contrast, studies of aspen mixedwoods within Quebec, Canada suggest a disturbance regime of less frequent high severity disturbances with conifers dominating the later stages of succession due to species' shade tolerances and gap dynamics driven by insects, fungi, and wind (Bergeron, 2000). Similarly, studies of disturbance in aspen mixedwoods in western Canada also reveal regimes dominated by fine-scale, gap dynamics; however, gaps served to recruit additional cohorts of pioneering hardwoods as opposed to shade tolerant species (Cumming et al., 2000). These findings are part of a growing body of literature that recognizes the role of small-scale disturbances in producing the highly varied patterns of stand structure and composition observed within boreal and sub-boreal landscapes (McCarthy, 2001).

In addition, *P. tremuloides* populations may exhibit a considerable range in age structures within this broad forest type. Nonetheless, single-cohort populations of *P. tremuloides* have served as the model for current forest management; however, recent work has highlighted that multi-cohort aspen populations may develop within these systems (Bergeron, 2000; Cumming et al., 2000; Man and Rice, 2010). The age-cohort structure of this forest type has important implications for understanding the demographics of this species and thus for developing appropriate forest management prescriptions. However, detailed age-structure analyses for this forest type in the US Lake States region have not been undertaken.

The overarching objective of this study was to characterize the link between natural disturbance and patterns of stand development in mature, secondary, aspen mixedwood forests of northern Minnesota, USA. Our specific objectives were to (1) quantify rates of canopy disturbance through the analysis of tree-growth patterns, (2) describe compositional and structural development utilizing tree-age demographics, (3) and to examine the relationships between disturbance history and successional and stand developmental pathways. Our findings identify critical mechanistic relationships between disturbance patterns and community development that can guide management prescriptions meant to emulate the historic successional and forest developmental pathways for this system.

2. Methods

2.1. Study area

Study sites were located in the Laurentian Mixed Forest Province ecoregion of northern Minnesota, USA (Fig. 1), an area typified by a continental climate of short warm summers and long cold winters, with mean annual temperatures of 1.1–4.4 °C and annual precipitation ranging from 53 to 71 cm (Albert, 1995). Sites were underlain by glaciolacustrine deposits, till plains, and stagnation moraines, and they span elevations of 335–488 m. Extensive post-settlement land use in this region has produced an aspen mixedwoods land-base of secondary forests quite different from those of the pre-settlement era (Friedman and Reich, 2005; Schulte et al., 2007).

When compared to pre-settlement forests, contemporary forests of the region are younger on average (Frelich, 1995), and overstory composition is dominated by the pioneer species *P. tremuloides* and *B. papyrifera* (Frelich, 2002; Friedman and Reich, 2005; Schulte et al., 2007). Companion species typical of regional aspen mixedwoods include *Abies balsamea* (balsam fir), *Acer rubrum* (red maple), *Fraxinus nigra* (black ash) and *Picea glauca* (white spruce). Advance regeneration is composed of shade tolerant conifers such as *A. balsamea* and *P. glauca* and the shade tolerant hardwood *A. rubrum*. Typical shrub species include *Acer spicatum* (mountain maple), *Amelanchier* species (Juneberries), and *Corylus cornuta* (beaked hazel).

Study sites were selected from a Geographic Information System (GIS) of mapped and inventoried stands provided by the Minnesota Department of Natural Resources (MNDNR). Sites were selected that were sufficiently large to encompass a minimum of three 0.04 ha plots, contained a *P. tremuloides* cohort older than the regional rotation age of 40–60 years, contained no evidence of recent harvest, and were field-classified as northern wet-mesic boreal hardwood-conifer forest communities based on the state community classification system (MNDNR, 2003). Sites were not randomly selected; instead, we sampled a set of stands that met the aforementioned criteria – a rather small set due to the extensive regional harvest of 40–60 years old aspen mixedwoods. Site indices, tree densities, and basal areas were representative of fully stocked and productive *P. tremuloides* stands (Perala, 1977; Edgar and Burk, 2001). Stands had moderately well to poorly drained aqualf soils originating from clayey glaciolacustrine deposits or fine-textured glacial till.

2.2. Composition, demographics, and structure

Three to six 0.04 ha circular plots (depending on site size) were established at each of the nine sites (site codes A-I), totaling 49 plots. Plots were systematically established every 30–50 m on one or two parallel transects. Transect origins maximized sampling of stand interior conditions and ensured that plot perimeters began at least 30 m from stand boundaries to reduce edge effects (Fraver, 1994). On each plot, all living trees >10.0 cm diameter at breast height (DBH = 1.37 m) were cored at approximately 30 cm above the forest floor. Cores were extracted and processed using standard dendrochronological methods (Stokes and Smiley, 1968). Species, DBH, and crown class (dominant, codominant, intermediate, and suppressed) were determined for all cored trees, and height was measured for one tree in each crown class per plot. Seedlings and saplings were defined as woody stems $\leqslant$0.5 m tall or >0.5 m tall and $\leqslant$1.0 cm DBH, respectively. Both were tallied by species on eight 1.0 m^2 subplots within the main plot. Stems >1.0 cm and $\leqslant$5.0 cm DBH and those >5.0 and $\leqslant$10.0 cm DBH were tallied by species in eight 5.0 m^2 subplots within the main plot. All field work was conducted during the growing season 2009.

2.3. Tree ring analysis and disturbance chronology development

Increment cores were secured in wooden mounts, sanded to a flat, polished surface, and cross-dated using both skeleton plots (Stokes and Smiley, 1968) and marker years (Yamaguchi, 1991). Rings were measured (0.005 mm resolution) using a Velmex micrometer, and dating accuracy of all tentatively cross-dated series were statistically verified using COFECHA (Appendix A; Holmes, 1983). The pith date was taken as the year of recruitment, that is, the year a tree achieved coring height (30 cm). For cores that did not pass directly through the pith, Applequist's (1958) pith locator was used to estimate the number of years required to reach pith. Trees that missed the pith by greater than ten years