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Cumulative effects of chronic deer browsing and clear-cutting on regeneration processes in second-growth white spruce stands

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ABSTRACT

Interactions between multiple disturbances can alter resilience mechanisms, thereby triggering alternative successional pathways. Regeneration processes are important mechanisms of forest resilience because they drive successional pathways. On Anticosti Island, chronic browsing by introduced white-tailed deer (*Odocoileus virginianus*) shifted composition of understory regeneration of overmature balsam fir (*Abies balsamea*) forests toward dominance by white spruce (*Picea glauca*). Historic clear-cutting of these altered forests generated mature second-growth white spruce stands. However, the cumulative effect of chronic deer browsing and recent clear-cutting on regeneration processes of mature second-growth white spruce stands has not yet been evaluated. Our objective is to evaluate if regeneration processes would enable white spruce stands to recover from the cumulative effects of these two disturbances. We studied regeneration in relation to seed availability, substrate suitability for seedling establishment, and substrate availability in mature second-growth white spruce stands and recent clear-cuts of mature second-growth white spruce stands. Our results indicate regeneration failure in both ecosystems, which can be explained by a lack of suitable rotten logs for sufficient establishment of white spruce seedlings. Hence, the cumulative effects of chronic deer browsing and clear-cutting of mature second-growth white spruce stands have altered regeneration processes and triggered an alternative successional pathway toward parklands, i.e., partial deforestation. We propose shelterwood cuttings that create nurse logs should be investigated to maintain white spruce stands without planting.

1. Introduction

Interactions between multiple disturbances can alter resilience mechanisms of forests, thereby triggering alternative successional pathways (Paine et al., 1998; Tremblay et al., 2007; Buma and Wessman, 2011). Resilience is the capacity of a system to absorb disturbance and reorganize so that the same structure and functions are essentially recovered, e.g., forest recovering to forest following perturbation (Holling, 1973; Gunderson, 2000). Regeneration processes are important mechanisms of forest resilience because they drive successional pathways (Buma and Wessman, 2011; Hidding et al., 2013). For example, cervids such as white-tailed deer (*Odocoileus virginianus*) can shift the composition of understory regeneration by selectively browsing seedlings (Tremblay et al., 2007; Nuttle et al., 2014), while forest management practices can change the composition and density of regeneration through diverse silvicultural scenarios (Boucher et al., 2009; Lundmark et al., 2013; Rist and Moen, 2013). Interaction between these two disturbances could potentially alter regeneration processes, triggering alternative successional pathways that move the system toward assemblages of species that have not co-occurred historically. The occurrence of such novel ecosystems can represent a threat to biodiversity and ecosystem services that are provided by preindustrial forests (Hobbs et al., 2006; Bridgewater et al., 2011). In this context, a recent cause for concern is increasing cervid densities in the forests of North America (Côté et al., 2004; McLaren et al., 2004; Chollet and Martin, 2012), which increases the probability for potential interactions between cervid browsing and forest management.

Following the introduction of 200 white-tailed deer into the forests of Anticosti Island (Quebec) at the end of the 19th century,

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their population densities have now reached more than 20 individuals km^{-2} in the absence of predators (Rochette and Gingras, 2007). Since the 1920s, chronic deer browsing has shifted the understory composition of balsam fir forests on the island from regeneration that is dominated by balsam fir (*Abies balsamea* (L.) Miller) towards one that is dominated by white spruce (*Picea glauca* (Moench) Voss), together with a recalcitrant ground layer that includes blue joint grass (*Calamagrostis canadensis* (Michaux) P.Beauv.), bracken fern (*Pteridium aquilinum* (L.) Kuhn), and thistle (*Cirsium* spp.), which are species that are not browsed by deer (Potvin et al., 2003; Tremblay et al., 2007; Hidding et al., 2013). Recalcitrant understory layers are dense and persistent monodominant strata that can impede regeneration, by altering the rate and shifting the direction of forest succession (Royo and Carson, 2006). Such a layer can persist even after reductions in deer densities (Nuttle et al., 2014). Historically, the unaltered forests of Anticosti Island were driven by gap disturbance and gap-filling processes that assured the maintenance of overmature balsam fir stands, mixed with white spruce and paper birch (*Betula papyrifera* Marshall; Barrette et al., 2010). Balsam fir regeneration created dense and persistent understory seedling banks, which were highly tolerant of shade and that were prompt to react and fill canopy gaps (Côté and Bélanger, 1991; McCarthy, 2001; McCarthy and Weetman, 2007a). From the 1920s onwards, white spruce has represented the sole remaining tree species that is available to recreate a forest after disturbances. In such a context, white spruce regeneration formed white spruce stands following historic clear-cutting (1910–1915) of altered balsam fir stands (Fig. 1; Beaupré et al., 2004). These now mature second-growth white spruce stands represent a threat to biodiversity and the services that were provided by the preindustrial forest (Barrette et al., 2010), since they are novel ecosystems which are not commonly found in eastern North America (Stiell, 1976; Bell et al., 1990; Lieffers et al., 2008; Saucier et al., 2009). Many mature second-growth white spruce stands have been recently clear-cut (1999) under a system of timber production that uses even-aged management. However, the cumulative effects of chronic deer browsing and clear-cutting on regeneration processes within white spruce stands has yet to be evaluated. If regeneration processes cannot enable the recovery of white spruce stands from these two disturbances, then alternative successional pathways could develop and lead towards deforestation, since white spruce is the only remaining tree species. The occurrence of a non-forest state would represent an even greater threat to biodiversity and ecosystem services. To avoid deforestation and meet sustainable forest management objectives, forest managers would then have to resort to plantation silviculture.

Consequently we investigated if regeneration processes would enable white spruce stands to recover from the cumulative effects of chronic deer browsing and clear-cutting. To meet this objective, we studied regeneration in relation to seed availability, substrate suitability for seedling establishment, and substrate availability in mature second-growth white spruce stands and in recent clear-cuts of mature second-growth white spruce stands. We also studied regeneration processes in the understory and within canopy gaps of overmature balsam fir stands to provide a baseline of regeneration characteristics which have enabled fir stands to recover partially from historic clear-cuts and reproduce white spruce stands. We predicted that regeneration in mature second-growth white spruce stands would not be sufficient for them to recover from clear-cutting because of a lack of suitable substrates for establishment. Effectively, white spruce requires specific substrates for optimum seedling establishment (e.g., large woody debris, exposed mineral soil; Simard et al., 1998) and rarely forms such pure even-aged stands under natural conditions (Stiell, 1976; Bell et al., 1990). We also predicted that regeneration would not be sufficient in recent clear-cuts of mature second-growth white spruce stands for them to return to a forest state because of encroachment by recalcitrant understory layer species, thereby exacerbating the lack of suitable substrates for establishment.

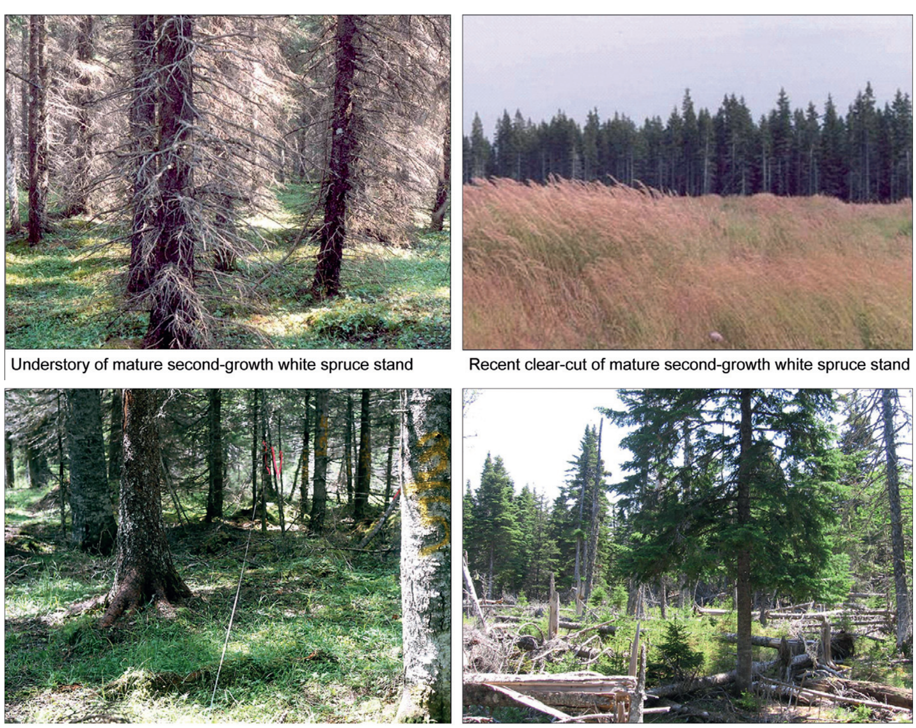

Fig. 1. Photographs showing the four ecosystem types of the study.