Forest Ecology and Management 401 (2017) 117–124

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Demographic disequilibrium caused by canopy gap expansion and recruitment failure triggers forest cover loss

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A R T I C L E   I N F O

Article history:
Received 9 June 2017
Received in revised form 7 July 2017
Accepted 8 July 2017

Keywords:
Alternative successional pathways
Balsam fir
Canopy openness
Climate change
Novel ecosystems
Regeneration process
White spruce

A B S T R A C T

In the absence of large-scale stand replacing disturbances, boreal forests can remain in the old-growth stage over time because of a dynamic equilibrium between small-scale mortality and regeneration processes. Although this gap paradigm has been a cornerstone of forest dynamics theory and practice for decades, evidence suggests that it could be disrupted, threatening the integrity and sustainability of continuous forest cover. The objective of this study was to evaluate the gap dynamics in old-growth boreal forests across a large landscape where deer populations currently exist at high abundance. We hypothesized that chronic deer browsing is limiting recruitment, particularly of palatable species, creating a demographic disequilibrium between canopy mortality and recruitment. We analysed understory regeneration density and distribution in relation to canopy gap size and condition on multiple sample areas within a 360 km^2 area of old-growth balsam fir (*Abies balsamea* [L.] Miller) forest on Anticosti Island, Canada. The combined effect of accelerating canopy gap expansion and recruitment failure created a demographic disequilibrium important enough to cause a loss of forest cover. The forest is now at risk of shifting to alternative successional pathways that seem to be dependent upon gaps size. Rather than sustaining historic balsam fir composition, sucession in 57% of gap area was more susceptible to following a pathway leading toward white spruce parklands, while sucession in the other 43% was more susceptible to following a pathway toward white spruce forests. The occurrence of these novel ecosystems represents a threat to biodiversity and ecosystem services that are provided by preindustrial forests. Climate change could exacerbate these threats by allowing deer to go into as yet unoccupied boreal forests that are driven by gap dynamics. Novel management issues will arise in these boreal ecosystems and challenge forest managers. When the traditional approaches of identifying gaps will not work because the forest itself is losing cover, the method we have developed will help forest managers recognize demographic disequilibrium threatening maintenance of forests.

1. Introduction

In the absence of large-scale stand replacing disturbances, boreal forests can remain in the old-growth stage over time because of a dynamic equilibrium between small-scale mortality and regeneration processes (Kuuluvainen, 1994; Kneeshaw and Bergeron, 1998; McCarthy, 2001; Caron et al., 2009). The mortality process is driven by the death of a single or of a small group of trees from insect, disease, or meteorological vectors creating a canopy gap (Kuuluvainen, 1994; McCarthy, 2001). The regeneration process in the gap is driven by the release of advance regeneration of shade tolerant species and to a lesser extent by the establishment of new regeneration of light demanding species from buried or dispersed seeds (Kneeshaw and Bergeron, 1998; McCarthy, 2001; Vepakomma et al., 2010). However, if canopy mortality is not offset by seedling establishment and growth, the disequilibrium between the two processes could increase gap turnover time, cause gap expansion, and even lead to multiple gaps coalescing as trees along the gap periphery experience elevated mortality rates (Worrall et al., 2005; Taylor and MacLean, 2007; Vepakomma et al., 2012). The increased light availability within these more persistent and

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http://dx.doi.org/10.1016/j.foreco.2017.07.012
0378-1127/

much larger gaps enhances establishment opportunities for light demanding species which could ultimately result in shifts in species dominance (Ban et al., 1998; Kneeshaw and Bergeron, 1998; Vepakomma et al., 2010).

Although the gap paradigm has been a cornerstone of forest dynamics theory and practice for decades (Pickett and White, 1985; McCarthy, 2001), evidence suggests that a variety of biotic and abiotic forces could disrupt the dynamic equilibrium between small-scale mortality and regeneration processes in gap-driven forests by altering key germination, growth, and survival dynamics that underpin sucession. For example, it is now well-established that filtering of seedling recruitment by dense recalcitrant understory vegetation can alter, stall, or even arrest gap-phase succession (Zackrisson et al., 1997; Aubin et al., 2000; Royo and Carson, 2006). Similarly, trophic interactions can strongly suppress seedling regeneration and thereby contribute to the loss of forest cover and a concomitant shift towards more open woodlands containing large expanses of herbs, shrubs, or lichens (e.g., Dublin et al., 1990; Husheer et al., 2003; Ibáñez et al., 2015; Vézeau and Payette, 2016). Likewise, browsing by both native and introduced deer (Cervidae) can alter and inhibit tree seedling recruitment dynamic leading to regeneration failures, declines in forest cover, and shifts towards communities dominated by unpalatable non-tree species (e.g., ferns, graminoids) following canopy disturbance (Marquis, 1974; Husheer et al. 2003; Pedersen and Wallis, 2004; White, 2012; Nagel et al., 2015). Hence, where gap expansion and coalescence continue unabated and canopy mortality is not offset by seedling establishment and growth, the integrity and sustainability of continuous forest cover itself is at risk.

The objective of this study was to evaluate the gap dynamics in old-growth boreal forests across a large landscape where deer populations currently exist at high abundance. We hypothesized that chronic deer browsing is limiting recruitment, particularly of palatable species, creating a demographic disequilibrium between canopy mortality and recruitment. Thus, we predict seedling and sapling densities, particularly of palatable species, will be low. Moreover, we predict large proportion of the forest area will be in gaps and these individual gap size will be large as they expand and coalesce as recruitment fails to offset mortality. To test these predictions we analysed understory regeneration density and distribution in relation to canopy gap size and condition on multiple sample areas within a 360 km^2 area of old-growth balsam fir (*Abies balsamea* [L.] Miller) forest on Anticosti Island, Canada.

2. Materials and methods

2.1. Study area

Anticosti Island (7943 km^2) is located in the Gulf of St. Lawrence (49°28′N, 63°00′W; Fig. 1). The island forms part of the eastern balsam fir-paper birch (*Betula papyrifera* Marshall) bioclimatic subdomain of the Province of Quebec, Canada (Saucier et al., 2009). Forests on the island are managed using ecosystem management principles that seek to reduce differences between natural and managed forests (Provincial legislation: RLRQ, c. A-18.1, article 1). Mean annual temperature is 2 °C and mean annual precipitation is 907 mm (Environment Canada, 1982). Large-scale disturbances of the forest cover are rare events and partial canopy disturbances

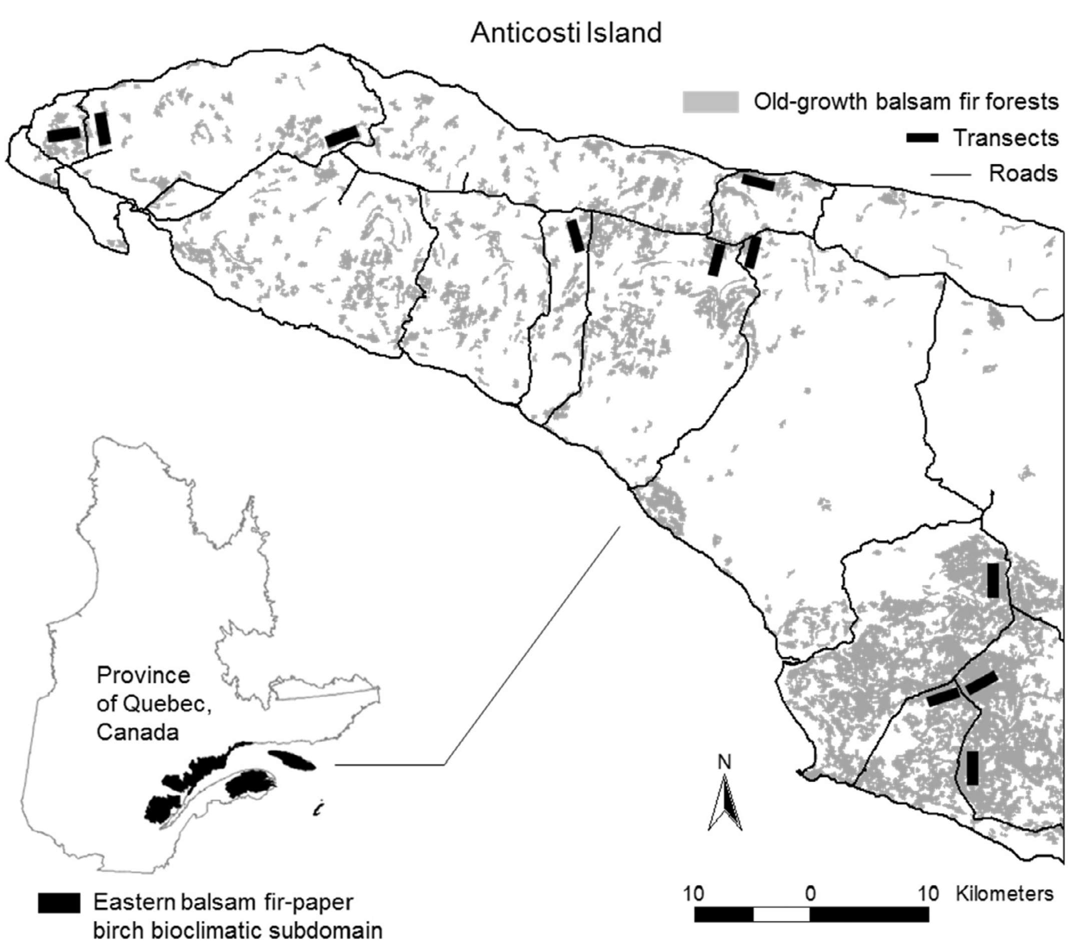

Fig. 1. Location of the 11 transects in the old-growth balsam fir forest.