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Prioritizing boreal forest restoration sites based on disturbance regime

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ABSTRACT

Selection of high priority sites for ecological restoration becomes essential with globally decreasing forest cover following natural and anthropogenic disturbances. A disturbance gradient resulting from native insect (*Choristoneura fumiferana*) outbreaks and non-native moose (*Alces alces*) browsing was studied in balsam fir forest stands in Newfoundland (Canada) to inform land managers where active *vs.* passive restoration would be most appropriate. The disturbance gradient ranged from small gaps (area <5 ha) to medium and large gaps created by insects, in addition to a control (i.e., "no gap") closed canopy mature balsam fir forest. In all areas seedlings and saplings (<2 m) were browsed by moose causing failed forest regeneration. Differences in the vegetation community, environmental conditions and species functional groups were quantified across the disturbance regime using non-metric multidimensional analysis and nested analysis of variance. In this study, the closed canopy stand retained the optimal conditions for balsam fir forest regeneration and does not need active restoration to regenerate if moose densities are low. Insect-disturbed areas <5 ha retained conditions that would allow them to regenerate naturally under conditions of low herbivory (i.e., they would not need active restoration); they were dominated by late succession forbs, retained low densities of balsam fir adults and optimal abiotic conditions for seedlings, with an increase in sunlight and decline in the quality of feathermoss seedbed. In contrast, a complete shift was observed in open areas >5 ha, which were dominated by grasses, early succession forbs and had abiotic conditions closer to early succession boreal forest, indicating an ecological threshold had been crossed, confirming the need for active restoration. To allow regeneration regardless of gap size, reduction of moose numbers must be continued. Threshold identification in the boreal forest should be based on disturbance regime and used to inform critical areas for future forest restoration strategies. Based on our study, insect outbreak areas >5 ha should be prioritized for active restoration, as the crossing of a biotic threshold indicates that such sites cannot naturally return to pre-disturbance balsam fir forests.

1. Introduction

The degradation and loss of forest globally has led to an urgent call for restoration protocols (Hobbs and Harris, 2001; Lamb et al., 2005). Forests are declining due to multiple synergistic causes, resulting in the alteration of important ecosystem function and services (Hansen et al., 2013). For example, on Santa Cruz Island (California, USA) an increase of 97% of the carbon sequestration followed the removal of grazing ungulates and recovery of the native woody vegetation on the island (Beltran et al., 2014). Prioritization of restoration sites has become a pressing issue given limited resources (i.e. financial, technical and social) faced by land managers (Hobbs et al., 2014). Priority sites can be determined by identifying the state at which assisted or active regeneration becomes crucial along the gradient of forest degradation (McIntyre and Hobbs, 1999; Chazdon, 2008; Hobbs et al., 2014). The highest priority will be assigned to the most heavily altered forest stands that have undergone significant community-level change, while allowing natural regeneration (passive recovery) to occur in the least degraded stands. This approach would be especially helpful to support ecological integrity targets within protected areas (Parks Canada, 2008; Keenleyside et al., 2012). Traditional restoration projects are sometimes carried out in areas so degraded that establishing novel ecosystems is seen as the best solution (Hobbs et al., 2009); however since protected areas are usually less degraded (Wiens and Hobbs, 2015) limiting efforts to areas that actively require restoration would be most efficient (Holl and Aide, 2011).

Depending upon the stand regeneration trajectory, spontaneous succession might occur naturally when stressors are removed, reducing the need for active management efforts (Prach and Hobbs, 2008; Holl and Aide, 2011); however, when ecological

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thresholds are crossed, active management becomes necessary (Whisenant, 1999; Hobbs and Harris, 2001). Passive restoration occurs in areas where disturbance is removed (e.g. removal of herbivores to reduce browsing pressure), allowing natural unassisted recovery, compared to active restoration where, in addition to herbivore reduction, land is managed by burning, thinning and/or planting vegetation to achieve a desired state (Benayas et al., 2008). A threshold is defined as a point where a small change in environmental conditions following natural or anthropogenic disturbance leads to a large change in the ecosystem state (Suding and Hobbs, 2009). In Tasmania, a shift from forest to an alternative grassland state was observed, originating from fire and stabilized by eco-hydrological feedbacks during the last 7000 years (Fletcher et al., 2014). Because of the potential hysteretic behavior of ecological thresholds, restoration leading to ecosystem recovery might take a different trajectory than the trajectory that led to the degraded state, and may involve complex and costly intervention (Suding et al., 2004; Suding and Hobbs, 2009). Therefore, identification of such ecological thresholds is important for effective and efficient management and restoration of ecosystems.

Detecting ecological thresholds usually involves large-scale and long-term data collection for modeling purposes (Scheffer and Carpenter, 2003; Scheffer et al., 2012); hence, identifying thresholds is difficult for land managers and often leads to restoration decisions based on qualitative expert knowledge. Suding et al. (2004) suggested more manageable, and scientifically sound, proxy lines of evidence. For instance, determining abiotic and biotic interactions helps to predict ecosystem resilience, as strong ecosystem interactions indicate a self-organized structure more prone to thresholds behavior due to biotic feedbacks (Suding and Hobbs, 2009). Heffernan (2008) found positive feedbacks between soil stability and plant growth on some soil substrates, causing a bimodal response in plant communities to floods in Arizona. Species functional groupings also provide a mechanistic understanding of important ecosystems capacity that might have been lost or gained in a community and gives a more general response than is provided by individual species (McGill et al., 2006; Suding and Hobbs, 2009; Standish et al., 2014).

Globally negative impacts of herbivores on ecological thresholds of forest ecosystems have been widely documented (Dublin et al., 1990; Augustine et al., 1998; Tremblay et al., 2007; Hidding et al., 2013). In Kenya, Dublin et al. (1990) report a shift from woodlands to grasslands caused and perpetuated by a combination of fire and elephant browsing. Browsing pressure by overabundant herbivores has created a new disturbance regime in many forested ecosystems (Persson et al., 2000; Wardle et al., 2001; Côté et al., 2004; Hobbs, 2006), that is especially severe on islands where ungulates were introduced (e.g. Anticosti Island, Côté et al. (2014); Haida Gwaii, Vourc'h et al. (2001); Isle Royale, McInnes et al. (1992); Newfoundland, McLaren et al. (2004); New Zealand archipelago, Wardle et al. (2001)). On the island of Newfoundland, the introduction of moose (*Alces alces*) in the early 1900's (Pimlott, 1953) and the absence of natural predators led to an overabundant population (McLaren et al., 2004). Selective browsing on foundation species, such as balsam fir (*Abies balsamea*) and white birch (*Betula papyrifera*) affects advanced regeneration, weakening ecosystem resilience after natural disturbance (Pimlott, 1953; McLaren et al., 2004). The negative effects of moose are widespread on large forest tracts in Newfoundland, making restoration planning difficult (Gosse et al., 2011). Moreover, to date, there has been no protocol to inform if active restoration is needed, and if so which sites should be prioritized.

In the eastern Canadian boreal forest dominated by balsam fir, the primary natural disturbance is insect outbreak (spruce budworm [*Choristoneura fumiferana*] and hemlock looper [*Lambdina fiscellaria*]), which target adult trees opening the mature canopy cover and releasing the young latent regeneration to reach the canopy (Morin and Laprise, 1997). As pointed out by Pureswaran et al. (2015) insect disturbance regimes are currently undergoing rapid changes toward more frequent, extensive and severe outbreaks, caused by climate change and human practices. Other disturbances originate from wind events and forestry activities (Engelmark, 1999). The synergistic effect of natural disturbance and browsing by overabundant moose has shifted the balsam fir forest ecosystem toward the creation of "moose meadows" in highly browsed areas (McLaren et al., 2004; Gosse et al., 2011). While insect outbreaks trigger early succession by removing the canopy trees, moose herbivory modifies vegetation assemblages by selective browsing, decreasing the resilience of the ecosystem. Indirectly, the impact of canopy opening has led to shifts in environmental conditions and degradation of optimal seedbed for foundation species (McLaren and Janke, 1996; Rooney and Waller, 2003). Previous studies noted that seedling survivorship was reduced on broadleaf litter seedbed when compared to needle litter or moss seedbed, explained by a decrease in moisture retention capacity and extreme temperature (Plamondon and Grandtner, 1975; Côté and Bélanger, 1991). Negative impacts are also amplified by balsam fir's short seed dispersal (<75 m) and seed bank viability of <9 months (Greene et al., 1999).

Lack of regeneration of balsam fir forest communities, even when moose pressure is eliminated, suggests that ecological thresholds have been crossed in Newfoundland (McLaren et al., 2009; Gosse et al., 2011) and active management through restoration is necessary to reclaim ecological integrity of the forest. However, research to disentangle the effects of insect outbreak extent and severity, and moose browsing is lacking, and hence selection of high priority restoration site is hampered. Our objectives were (1) to use scientific lines of evidence to: (i) evaluate abiotic factors associated with ecological thresholds in balsam fir forests; (ii) assess vegetation community shifts in balsam fir stands; and (iii) determine if there has been a shift in functional groups by comparing forests across a natural disturbance gradient; (2) to identify ecological thresholds across the insect disturbance gradient (from closed canopy with no gaps to large gaps) for the purpose of restoration site selection and prioritization. We hypothesized that (1) the cumulative moose-insect effects have created negative ecosystem changes that block natural forest regeneration; and (2) thresholds have only been crossed for a small proportion of forest stands across the disturbance spectrum, underscoring that active restoration is needed only in most degraded areas. This study will outline possible thresholds and inform guiding principles for scientifically and cost-effective decision-making toward restoration sites selection.

2. Methods

2.1. Study site

Terra Nova National Park (TNNP; 48°30′N, 54°00′W) is a protected area of ~400 km^2, located in eastern Newfoundland, Canada. The climate is maritime with a mean temperature of −6.8 °C and 16.1 °C in January and July, respectively, and mean annual precipitation of 311.0 cm and 872.7 mm of snow and rain respectively (Environment Canada, 1971–2000). TNNP boreal forest is dominated by black spruce (*Picea mariana*) inland and balsam fir along the coast. Balsam fir forest covers 15% of the park and is restricted to richer soil, predominantly humo-ferric podzols (Deichmann and Bradshaw, 1984). Historically, natural disturbances such as insect outbreaks and severe wind events, triggered balsam fir stand regeneration. Depending on the severity of the insect outbreak, and subsequent wind events, stand openings of