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Broadleaf competition interferes with balsam fir regeneration following experimental removal of moose

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A B S T R A C T

Changes to ecosystems caused by introduced herbivores can be predictable, stepwise transitions or unpredictable and even irreversible state changes. This study's objectives were to explore effects on forest succession and soil development 5 years after moose (*Alces alces* L.) were fenced out of areas within and adjacent to a national park in Newfoundland, Canada. Study plots spanned a range of understorey broadleaf plant associations with regenerating balsam fir (*Abies balsamea* (L.) Mill.), an important winter forage plant for moose and a dominant canopy tree throughout Newfoundland. After 5 years, height–diameter ratios were significantly larger for larger basal diameters of understorey balsam fir in unfenced, but not in fenced subplots, suggesting that growth of the conifer is compromised within the exclosure. In contrast, for most broadleaf trees and shrubs, moose removal by fencing results in greater heights and basal diameters than in control subplots. The competitive advantage of broadleaf trees and shrubs over balsam fir in the short-term may be a result of past sustained heavy moose browsing benefiting plants that are better at investing resources into below-ground growth or benefiting plants that have broader leaf canopies. It is not clear how long the broadleaf transition state we document will continue. Restorative actions intended to mimic usual patterns of forest regeneration in this region of Newfoundland might best consider moose removal with site preparation and/or planting to historic densities.

1. Introduction

The alteration of biotic communities as a result of introductions of wild ungulates ultimately constitutes an indirect effect of humans on landscapes that dates back thousands of years (Gill, 2006; Van der Wal, 2006). In the past few decades, however, densities of wild ungulates have shifted ever more rapidly as a result of predator control, habitat alteration, further introductions, and targeted management programs (Weisberg and Bugmann, 2003). Resulting shifts in plant community composition and regeneration failure in the ecosystems that sustain wild ungulates are a mounting concern for biodiversity management (Vavra et al., 2007). Many of the changes directly caused by herbivores are predictable, stepwise transitions from one ecosystem state to another (Van der Wal, 2006), while other changes appear to be unpredictable (Gill, 2006) and even irreversible (Côté et al., 2004). In situations of herbivore hyperabundance, unpredictable, unique transitions and new stable states for forest and grasslands have been widely documented (e.g., Olofsson, 2006; Abraham et al., 2005; Tripler et al., 2005; Coomes et al., 2003; also see reviews by Côté et al., 2004; Hobbs, 1996). Westoby et al. (1989) developed a system for cataloguing the suite of states and transitions (state-and-transition models) to formulate existing knowledge toward better management and restoration of herbivore-dominated ecosystems when they are not at equilibrium. To date there is no better system to guide biodiversity management from the perspective of herbivore management.

Davidson (1993) suggested that, to allow predictions of the long-term effects of human intervention on forests and to provide information for ecosystem restoration, generalizations of the effects of herbivores on plant succession are needed. In her review, she concluded that succession is typically hastened by herbivores in boreal forests, where plants of early seres are often consumed and that succession is reversed or halted in temperate forests, savannahs, and grasslands, where plants of later seres are typically consumed. In subsequent reviews and experiments, effects of ungulates on forest succession and related processes are rarely considered predictable across landscapes, even for the same species of herbivore (Côté et al., 2004; Gill, 2006). A well-studied example is moose (*Alces alces* L.), which have increased in number

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in roughly half of North American hunting jurisdictions and have been reported as overabundant (beyond ecological or social carrying capacities) in 14% of these areas (Crête and Daigle, 1999). Therefore, moose, like other members of the deer family, will be increasingly significant forces in structuring future forests on this continent (McShea et al., 1997; Côté et al., 2004). However, moose effects on forests have been described both as hastening and as reversing normal succession, with little guidance as to when or where each effect arises (Davidson, 1993; Persson et al., 2000, 2005a). This confusion occurs in part due to the relative absence of research that takes a systems approach rather than a species approach (Rooney and Waller, 2003); in part, it is due to the failure to consider herbivores in the context of other interacting ecological factors (Weisberg et al., 2002; Weisberg and Bugmann, 2003), including the interactions created by episodic disturbances that initiate forest succession (Wisdom et al., 2006).

In Newfoundland, Canada (112,000 km^2), the potential for interactions involving non-native, periodically overabundant herbivore populations started with 19th-century introductions of snowshoe hare (*Lepus americanus* L.) and moose to this island province (Pimlott, 1953; Bergerud and Manuel, 1968; Dodds, 1960). Both herbivores are affected by changes to forest structure created by fire, logging and insect outbreaks. Moose occupy all parts of Newfoundland, with higher densities in forested areas (ca. 2 per km^2) than in non-forested areas (ca. 0.5 per km^2), and an overall average density ca. 10 times that in other parts of their range in North America (Crête and Daigle, 1999). Their high densities occur as a result of extirpation of their only wild predator, the wolf (*Canis lupus* L.), in 1932 (Pimlott, 1959). Locally extreme densities (6–9 per km^2) have occasionally approached ecological carrying capacity, estimated from population recruitment and density relationships (Mercer and McLaren, 2002).

Balsam fir (*Abies balsamea* (L.) Mill.) is a species that typically gains forest dominance throughout mesic areas of Newfoundland and is an important winter forage plant for moose when it occurs in the understorey. With the exception of one forest type, occurring on sites of very rich soils and where succession may be to red maple (*Acer rubrum* L.), balsam fir forest in the North Shore and Central ecoregions is considered stable or self-perpetuating following logging and insect disturbances, because 'advanced regeneration' normally occurs at densities of 5000–50,000 stems per ha in the understorey (Damman, 1983, 1964). White spruce (*Picea glauca* (Moench) Voss), black spruce (*P. mariana* (Mill.) BSP) and white pine (*Pinus strobus* L.) is typical of balsam fir forest transitions following disturbance, and it is not atypical after an acute disturbance (complete and sudden canopy removal) like fire or clear-cut logging that birch (*Betula cordifolia* Regel. and *B. papyrifera* Marsh.) will form a transition forest.

Balsam fir has experienced regeneration failure in several areas of central and eastern Newfoundland, primarily as a result of moose browsing (Bergerud et al., 1968; McLaren et al., 2004). The extent of economically important reductions of balsam fir caused by moose browsing was first described in the scientific literature by Pimlott (1955, 1963). This early work and most subsequent studies in Newfoundland have focused on changes to commercial forest values. During the 1950s, moose browsing resulted in regeneration failure in only one of six sites that Pimlott (1955) surveyed. In other sites, browsing on birch reproduction was much heavier than on balsam fir. Pimlott (1963) suggested that "overcrowding of [balsam fir] reproduction can be severe, and browsing ... could be a boon" (p. 109). This point was later substantiated for dense balsam fir forest in central Newfoundland (Thompson and Curran, 1993). However, Thompson (1988) and McLaren et al. (2000) showed that dense balsam fir forest, in fact, receives less use by moose than pre-commercially thinned (PCT) forest, as less dense PCT forest produces larger and heavier twigs with higher levels of protein and some nutrients (Thompson et al., 1989). Bergerud and Manuel (1968) classified areas as experiencing commercially significant reductions in balsam fir density and suggested that these areas correspond to winter densities of >6 moose per square mile (>16 per km^2). In these areas, moose left up to 8% of regenerating forest not stocked by suppressing terminal growth and uprooting small stems of balsam fir. Sites of highest fertility experienced the most severe effects of moose, while white spruce dominated sites were more affected than black spruce dominated sites; again, birch was much heavier suppressed than balsam fir. Winter forage for moose in central Newfoundland has been estimated to be highest in mixed regenerating balsam fir forest of 8–10 years old (Parker and Morton, 1978), where the amount of browsing by moose increases with the fraction of balsam fir among trees <3 m in height (Thompson, 1988). In such stands, moose still consume much more birch, pin cherry (*Prunus pensylvanica* L. f.), mountain ash (*Sorbus americana* Marsh. and *S. decora* [Sarg.] Schneid) and willow (*Salix* spp.) than balsam fir (Parker and Morton, 1978; McLaren et al., 2000).

Moose browsing has several documented effects on less dominant, non-commercial components of balsam fir forest. For example, Dodds (1960), Pimlott (1963), Albright and Keith (1987), Thompson et al. (1992) and Connor et al. (2000) all document the loss of Canada yew (*Taxus canadensis* L.) from much of the forest in Newfoundland as a result of heavy browsing by moose. Like similar results from other regions where introduced cervids have changed forest understorey composition considerably (Risenhoover and Maass, 1987; Pastor et al., 1993; Tremblay et al., 2007a), it has now become evident that colonization of intact boreal forest by non-native, invasive plants has been facilitated by moose in Newfoundland (Rose and Hermanutz, 2004). In addition, rare components of the forest are being lost as a result of foraging by introduced moose (Yetman, 1999; Connor et al., 2000; McLaren et al., 2004).

Moose or deer 'exclosure' (fencing) has often resulted in balsam fir forest returning to pre-disturbance conditions (Risenhoover and Maass, 1987; Pastor et al., 1993; Tremblay et al., 2007a). However, Bédard et al. (1978) documented changes to balsam fir forest succession for the Gaspé Peninsula, Québec (just west of Newfoundland), which they artificially created by fencing. In the Gaspé study, mountain maple (*Acer spicatum* Lam.) was able to compete effectively with the less palatable beaked hazelnut (*Corylus cornuta* Marsh.) in fenced areas, but not in unfenced areas, exposed to heavy moose browsing. Mountain maple masked any effect of moose exclusion on balsam fir recovery over 4 years of study. Thompson et al. (1992) concluded that moose significantly alter forest regeneration on black spruce sites in central Newfoundland, such that a typical intermediate succession to balsam fir does not occur; the transition to balsam fir was experimentally produced in 225-m^2 exclosures. Thompson and Mallik (1989) hypothesized that unpalatable sheep laurel (*Kalmia angustifolia* L.) increases in density as an indirect effect of browsing on balsam fir; sheep laurel then suppresses black spruce due to allelopathic effects, proposed to occur over 10–30 years.

In conjunction with Parks Canada and the Newfoundland and Labrador Forest Service, which jointly supported a new 'exclosure' study, we set out to evaluate whether eliminating the effects of high moose density by fencing can return forests in eastern and central Newfoundland to an expected early succession, based on similar forests with lower moose densities elsewhere. We planned on-going comparison of forest regeneration inside and outside exclosures constructed in 1998, ca. 10 years after the last peak moose density. We also planned to compare the results our surveys to predictions for forest succession based on site quality described by Damman (1964), at a time when moose effects were only first being documented in eastern Newfoundland. Exclosure locations in both