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ECOLOGICAL FEEDBACKS OF FOREST COMPOSITION MANIPULATIONS; CONSEQUENCES ON INSECT OUTBREAK REGIMES AND ECOSYSTEM STABILITY

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Abstract

Forest protection against natural disturbance is an important part of forest management. Yet the overall effectiveness of this approach is sometimes questioned in the light of its potentially negative effects on forest ecosystem dynamics. Treatments that change forest composition indirectly or directly (e.g. for simplicity, forest protection, economic or productivity purposes) can affect a whole suite of ecosystem processes like forest succession, productivity and disturbance regimes. They can thus affect the stability of ecosystems, thereby increasing the uncertainty related to forest resource exploitation.

Different cases of unexpected drastic changes in ecosystem dynamics or regime shifts following composition modifications are reviewed in this report. That of Anticosti Island in eastern Canada is particularly relevant for studying insect outbreak regimes and ecosystem stability. The formerly dominant balsam fir-white birch forest – typically host to the spruce budworm (SBW) and hemlock looper (HL) insect defoliators – is now intensively browsed by predator-free white-tailed deer and is giving way to pure white spruce forests which are uncommon to eastern North America. Consequently, the abundance of insect parasitoids has decreased as a result of the low diversity of food and habitat availability. This novel ecosystem already gave rise in the early 2000s to a spruce beetle (SB) outbreak of unprecedented duration. The impact on SBW and HL remain uncertain; although white spruce is a primary host for these insects, stands dominated by white spruce do not usually bring these pests to outbreak levels.

The potential impacts on SBW outbreak regime and the interactions with host plant and natural enemy populations are explored using a tritrophic conceptual model. The model suggests that SBW outbreaks in such conditions could be of shorter duration and amplitude, thereby generating lower damage to a white spruce-dominated ecosystem. Due to the decreasing abundance of natural enemies, the role of SB will potentially increase in the future. In terms of forest dynamics, the composition change that occurred is comparable to what occurs in intensively managed forests where forest composition is modified. Forests may become more resistant to the irruptive insect of focus, but not necessarily to other pests. Thus forest composition modifications could trigger regime shifts on susceptible ecosystems, and in such cases increase the uncertainty linked with natural forest management, as opposed to forest protection initial objectives.

Keywords: regime shift, insect outbreaks, forest protection, composition change, Anticosti Island.

Introduction

Since the beginnings of forest exploitation foresters have tried to stabilize forest yield in compliance with traditional silvicultural and economic objectives. This led to the creation of the "normal" forest concept, where silviculturists adopted the "command & control" approach with the forest resource (Holling and Meffe 1996). Forest development was tightly monitored and stands were maintained under an even-aged structure and homogeneous composition. This was done using silviculture and forest protection treatments against disturbances like wildfires or insect outbreaks. Any disturbance was considered a threat to forest productivity and everything possible was undertaken to eliminate their impacts. As with agriculture, foresters tried to ensure that wood production was as steady and as predictable as possible; the need for regularity was reflected in every aspect of the practice, from logging to forest protection, growth and yield modeling and timber supply allocation (Puettmann et al. 2009). This approach is still observable nowadays probably because foresters were once successful in reducing short term uncertainty and risks related to future forest condition (Puettmann et al. 2009).

Traditional forestry was seeking forest stability; resistance to disturbance (or constancy; staying essentially unchanged (Grimm and Wissel 1997)) was enhanced via fire suppression (Holling and Meffe 1996) or insecticide spraying and constancy of forest productivity was promoted through the sustainable yield paradigm (Holling and Meffe 1996; Puettmann et al. 2009). However, by minimizing the importance of natural disturbance, it ignored an essential aspect of long term stability, which is ecosystem resilience (ecological resilience - the capacity of a system to remain in the same regime or attractive domain - vs. engineering resilience - the speed of return to reference state (or dynamic) (Holling 1996)). Focusing on forest resistance, forest management has left legacies which have modified forest disturbance regimes (Blais 1983; Robert et al. 2012) by reducing ecosystem tolerance (vulnerability) to wildfires or insect outbreaks, leading to higher severity events (Blais 1983; Swetnam and Lynch 1993; Raffa et al. 2008).

Regime shifts were observed in various ecosystems where a given action on the ecosystem remained undetected for a long period of time, until the accumulated effects of the action reaches a point where the system suddenly switches to an alternate, often undesired state (Folke et al. 2004; Peterson 2008) due to compound disturbances (Mallik 1995; Payette et al. 2000), invasive species introduction (Chouinard and Filion 2005), environmental change (Holling 1973; Raffa et al. 2008), or intensive management (Holling and Meffe 1996; Puettmann et al. 2009). Modification brought to forest ecosystems by the command and control approach have in many cases made the system less predictable when faced with disturbance. For instance, years of fire suppression caused important impacts on disturbance dynamics, allowing a majority of stands to reach overmature stage, and consequently increase forest susceptibility to age-specific insect pests, thereby leading to highly severe disturbance like the recent mountain pine beetle (Raffa et al. 2008), western spruce budworm (Swetnam and Lynch 1993) or spruce budworm (Blais 1983) outbreaks. Some also suggests that fire suppression allowed fuel to accumulate and paved the way for catastrophic fire events such as the 1988 Yellowstone fire (Christensen et al. 1989; Holling and Meffe 1996), although this is a matter of debate (Keeley et al. 1999). Subsequently, forest management legacies and their interactions with different forest disturbances have become an important source of uncertainty for forest succession and productivity predictions.

Forest protection strategies that modify forest characteristics is one aspect of forest management that can have substantial impacts on forest dynamics. Common protection strategies attempt to increase forest resistance against disturbance by modifying stand structure (Fettig et al. 2007, but see MacLean & Piene 1995), age (MacLean 1996), fuel accumulation (Schoennagel et al. 2004) or species composition (Needham et al. 1999). In particular, modifications of stand species composition are used as preventive treatments against insect pests by reducing the abundance of hosts or primary hosts (Needham et al. 1999; Fettig et al. 2007). Forest composition manipulations in the boreal forest can either tend to increase the abundance of non-host or secondary host coniferous trees through tree planting, or increase the presence of non-host tree species through brushing treatments when associational resistance is possible (i.e. the reduction in herbivore pressure due to an increase in biotic, structural or microclimatic complexity of natural vegetation (Tahvanainen and Root 1972)). Plantation of minor or non-host conifer trees can result, however, in biodiversity decline (gamma diversity, i.e. species diversity at the landscape level; (Whittaker 1972)) if the most vulnerable stand types and their associated flora and fauna become rare within landscapes (Holling and Meffe 1996). On the other hand, promoting associational resistance may enhance species diversity through an increased presence of non-host species within stands composed primarily of host species (Tahvanainen and Root 1972; Jactel et al. 2005; Sturtevant et al. In prep.). In boreal forests in particular, where tree species diversity is low, inclusion of deciduous trees within softwood stands has been shown to increase the abundance of natural enemies and thereby reduce damage for specific pest species. In both cases, the objective is to modify the insect disturbance regime; yet the long term beneficial (or detrimental) effects of this change on forest productivity and successional dynamics are not known.

The initial questions that motivated this report were the following: (1) can the uncertainty linked to natural resource management be reduced by modifying tree composition at multiple scales? (2) What is the evidence and likelihood that it is a workable approach to reducing future damage by major insect pests in Canada? The objective of this report is to discuss these questions and refine them in the light of the recent and less recent scientific literature. To do so, a focus is made on the impact of compositional change on forest succession and insect disturbance regimes as they are the targeted aspects on forest management uncertainty. Through the angle of ecosystem stability theory, uncertainty is assessed with regards to the various successional paths that forest ecosystems may take under the influence of forest management legacies and natural disturbances, but also to the impacts of recurrent insect outbreaks on forest stability given the change in forest composition. To further explore these long term dynamics, the case of Anticosti Island in the Gulf of St-Lawrence is discussed, as it represents a living laboratory in terms of drastic forest compositional change within a complex forest-pest system. The Island is also home to a complex irruptive insect community composed of three potentially important irruptive insects: the spruce budworm (*Choristoneura fumiferana* (Clem.)) and hemlock looper (*Lambdina fiscellaria* (Guen.)) as well as the spruce beetle (*Dendroctonus rufipennis* (Kirby)), whose outbreaks occur at intervals of 35-60 (Royama 1984), 10-12 (Otvos et al. (1979) cited in Iqbal et al. 2011), and 30-50 years (Werner and Holsten 1983), respectively. Balsam fir (*Abies balsamea* (L.) Mill.) is the preferred host of spruce budworm and hemlock looper, whereas spruce beetle, a bark beetle usually more present in western North America, preferably feeds on white spruce (*Picea glauca* (Moench) Voss) in its eastern range. A trophic model of insect herbivore population dynamics in relation with natural enemies and host quality is applied to the Island ecosystem as a means of estimating the impact of composition change on the resilience of the ecosystem and its resistance to the different insect pests.

Chapter 1: Uncertainty linked to natural resource management and forest composition modifications

1.1 uncertainty in forest ecosystems

All aspects of forest ecosystems are subject to important fluctuations, which can nonetheless can generate stable states over large spatial and temporal scales (Holling 1973). Ecosystem stability and sustainability of resource exploitation has long been of concern to humans (Perry 1998). Anthropogenic footprints are now found in most ecosystems and there is a growing concern for natural resource exploitation sustainability (Perry 1998; Puettmann et al. 2009). A thorough knowledge of ecosystem functioning is needed in order to promote their stability in spite of a plethora of disturbances, of either natural (biotic or abiotic) or anthropogenic (direct or indirect, e.g. exploitation or climate change) origins. These processes generated a considerable literature on ecosystem dynamics, whose complexity engendered equally complex theories and definitions (Grimm and Wissel 1997). To better understand stability and the uncertainty related to forest ecosystems, some of their basic concepts are reviewed here.

The stability concept in forest ecosystems and a large part of the uncertainty related to their future development involves the occurrence of disturbance, forest succession and ecosystem productivity (Lehman and Tilman 2000). These three aspects of natural systems generate important uncertainty in forest biomass production estimation, which are essential for timber resource exploitation, even more so for sustainable forest management. They correspond to the structural and temporal uncertainty classes as defined by Rowe (1994), where uncertainty is related to the complexity and to the future (or past) of a system. Other types of uncertainty, i.e. the absence of information or information that may or not be obtainable, according to Rowe (1994), are metrical (due to measurement) or translation-based (related with the communication of an uncertain result). All types of uncertainty occur in forest exploitation but some may dominate depending on the situation (Rowe 1994; Kangas and Kangas 2004). Time scale is one aspect that influences the relative importance of uncertainty, as sampling errors may have more importance in the short term and structural errors such as ignorance about growth functions or disturbance regimes may dominate over the long term (Kangas and Kangas 2004). Estimates of future growth of growing stock are often based on long term simulations (Buongiorno and Gilless 2003), following claims of sustainability (Ludwig et al. 1993); this stresses our lack of knowledge of long term disturbance dynamics, but also the growing risks of disruptions of key ecosystem processes following species invasion, climate change, or habitat modifications (Holling 1973; Moir and Mowrer 1995; Folke et al. 2004).

Ecological surprises that arise from the lack of knowledge of forest complexity can have considerably larger impacts than other types of uncertainty (Holling 1973; Moir and Mowrer 1995). One characteristic of managed pest systems is the belief that one can have control over disturbance characteristics and reduce natural systems variability at its source, through induced forest resistance (Holling and Meffe 1996; Perry 1998; Puettmann et al. 2009). Modifications of forest composition, whether intentional or not, are such treatments that can potentially generate important impacts on ecosystem dynamics, as has been suggested from past observations (Blais 1983, Swetnam & Lynch 1993, Raffa et al. 2008, but see Miller & Rusnock 1993). The "command and control" approach to resource exploitation is a two-edged sword; the apparent and comforting regularity brought to a given exploited resource often comes at the expense of ecosystem resistance, resilience and persistence (i.e., ecosystem stability, see next section) (Holling and Meffe 1996; Gunderson and Holling 2002; Puettmann et al. 2009). The following section investigates ecosystem stability, its definition and characteristics, and the requirements it needs to become a potential solution for dealing with the uncertainty associated with forest resource exploitation.

1.2 Forest ecosystem stability

Ecosystem stability has been thoroughly investigated during the last 50 years (MacArthur 1955; Elton 1958; Holling 1973; Yodzis 1981; Grimm and Wissel 1997; Ives and Carpenter 2007), with a focus on the relationship between biodiversity and its role in the stability of natural systems (McCann 2000, Ives & Carpenter 2007, Grman et al. 2010 , but see Hillebrand et al. 2008). Stability can be measured on various processes and levels, whether it is based on ecological characteristics (composition, structure, etc.), ecosystem biodiversity, productivity, trophic networks / food webs, and at various scales, from global cycles to local nutrient cycling, from landscapes to individuals and from ecosystems to populations. Nowadays, the various mechanisms involved in forest ecosystem stability are still being assessed in the face of natural or anthropogenic disturbance (Griffin et al. 2009; Grman et al. 2010). Nevertheless, the concept of stability remains vague and might not be a property of ecological systems in itself but more of a collective term encompassing the fundamental properties of constancy, resilience or persistence (Grimm and Wissel 1997). These three properties gather most of the properties assessed in the literature, as noted by Grimm and Wissel (1997), who further simplified their definition: constancy refers to the property of staying essentially unchanged, resilience as a multifaceted property (Ives and Carpenter 2007) is summarized as the capacity of returning to reference state (or dynamic) after temporary disturbance, and persistence referring to the maintenance through time of an ecological system. Constancy and resilience can be seen as multifaceted properties, constancy being closely linked to resistance (term mostly used in the presence of disturbance, according to the authors), whereas resilience, in addition to the capacity of recovering from disturbance, also includes aspects of "elasticity" (speed of return to the reference state (or dynamic) after a temporary disturbance, term also known as engineering resilience (Holling 1996)) and domain of attraction (state space of an ecological system affected by temporary disturbance, term also known as ecological resilience (Holling 1996)) (Grimm & Wissel 1997).

Table 1: Glossary

Alternate regimes: different regimes that exist simultaneously under the same set of conditions (Beisner et al. 2003).

Associational resistance: the reduction in herbivore pressure due to an increase in biotic, structural or microclimatic complexity of natural vegetation (Tahvanainen and Root 1972).

Atypical regime shift: When a system switches to an often less desired regime in an atypical way (Scheffer et al. 2001; Folke et al. 2004).

Command and control: approach to solving problems either through control of the processes that lead to the problem or through amelioration of the problem after it occurs, with the assumption that the problem is well-bounded, clearly defined, relatively simple and generally linear with respect to cause and effect (Holling and Meffe 1996).

Conceptual model: diagram that provides a compact, visual statement of a research problem (Jackson et al. 2000).

Constancy: property of staying essentially unchanged (Grimm and Wissel 1997).

Domain of attraction: The whole of states from which a stable state (or dynamic) can be reached again after a temporary disturbance (Grimm and Wissel 1997). Also known as the ecological resilience.

Ecological resilience: the magnitude of disturbance that can be absorbed before the system changes its structure. Concerns systems with conditions far from equilibrium state (Holling 1996).

Elasticity: speed of return to reference state (or dynamic) after a temporary disturbance (Grimm and Wissel 1997). Also known as the engineering resilience.

Empirical model: quantitative model that represents relationships determined strictly by data (Jackson et al. 2000).

Engineering resilience: speed of return to equilibrium state after disturbance. Concerns systems with conditions near equilibrium state (Holling 1996).

Insect outbreak cycle amplitude: difference between the highest and lowest values of the insect population level cycle, often equated with outbreak intensity (Cooke et al. 1997).

Insect outbreak return interval: time elapsed between two successive outbreaks at the same location (Vaillancourt et al. 2008).

Mechanistic model: quantitative model based on hypothesis about the particular processes that cause an observed pattern (Jackson et al. 2000).

Periodic regime shift: Cyclic or periodic change of a characteristic behaviour of a natural phenomenon, from one behaviour to another (Hare and Mantua 2000), e.g. from latency to epidemic phases (and vice-versa) in pest systems.

Persistence: ecological system property of being persistent through time (Grimm and Wissel 1997).

Regime: 1) a system or ordered way of doing things, 2) the conditions under which a process occurs (Oxford dictionary, 2012).

Resilience: property of returning to reference state (or dynamic) after a temporary disturbance (Grimm and Wissel 1997).

Resistance: Property of staying essentially unchanged when faced with disturbance (Grimm and Wissel 1997).

Stability: collective term that emphasizes the close connection between the three fundamental properties of constancy, resilience and persistence (Grimm and Wissel 1997).

Structural uncertainty: uncertainty due to complexity, including models and their validation (Rowe 1994).

Susceptibility: probability of a forest being damaged by a given disturbance.

Vulnerability: probability of tree mortality or growth loss resulting from a given disturbance.

In disturbance terms, resistance (staying essentially unchanged) and resilience (capacity to recover) can be seen as the susceptibility and vulnerability of ecosystem functioning to a given disturbance (ecosystem functioning: rate, level and temporal dynamics of ecosystem processes (Tilman 2001)). The more resistant a system is, the less susceptible it is to a particular disturbance and the more resilient it is, the less "vulnerable" is its functioning, i.e. less damage to a set of essential functions. Pushing further that analogy, ecosystem functioning might be susceptible to a disturbance (low resistance), but still show low "functional vulnerability" (high resilience;). High vulnerability could be encountered for instance in degraded systems such as those simplified through the removal of undesired species (Folke et al. 2004) or those affected by invasive pests or plant species (Hobbs et al. 2006; but see Timms et al. 2012); in such conditions, regime shifts might occur (Folke et al. 2004). The following section reviews regime shifts as sources of uncertainty associated with the state of ecosystems.

1.3 Regime shifts as sources of uncertainty

Regime shifts are defined as drastic changes of a characteristic behaviour of a natural phenomenon, from one behaviour to another (Hare and Mantua 2000; Scheffer et al. 2001; Folke et al. 2004). Here also various terms are used to define a regime (phase, stable state, stability domain, etc.) and this can bring in uncertainty. This is true of fluctuating systems like those affected by opportunistic insect populations (outbreaking insects (Rhoades 1985)), who experience an alternation of latent (endemic) and epidemic population phases (Wallner 1987); those are drastic ecosystem behaviour shifts while being part of the same outbreak regime. Wallner (1987) called them "density phases", but they are sometimes termed as "equilibrium states" (although Holling (1973) uses that term for domains of attraction) since this alternation of latent and epidemic phases are often associated with stable 2-point cycles (May 1974) despite the chaotic nature of population fluctuations in those systems (Wallner 1987). Therefore, the "state" term is somewhat ambiguous when considering the fluctuating nature of natural systems (Scheffer and Carpenter 2003).

In theory, the switch from latency to epidemic periods corresponds to all criteria of a regime shift except one, that of being atypical, but this is considered as a special, cyclic case of regime shifts, with an interaction of slow and fast processes (Ludwig et al. 1978; Rinaldi and Scheffer 2000; Gunderson and Holling 2002; Peterson 2008). Non-cyclic regime shifts were also observed in forest ecosystems through changes in the magnitude, frequency or duration of disturbance regimes (Folke et al. 2004); those were due to modifications of forest composition and succession (Chouinard and Filion 2005), modifications of insect population dynamics through damage control programs (Holling 1978; Blais 1983), or global climate change (Carroll et al. 2003). Confusingly, regime shifts thus define two different kind of events: periodic, transient shifts are commonplace when forests reach maturity while atypical shifts are uncommon and imply a persistent shift to an alternate regime. This paradox illustrates in a way the uniqueness of pest-host systems relative to ecological theory. For the remainder of this report, regime shifts will therefore be separated into and periodic regime shifts.

Susceptibility to both periodic and atypical regime shifts is increased with reduced ecosystem resilience. Folke et al. (2004) have enumerated three ways through which resilience can be reduced; removal of functional groups of species or whole trophic levels (top-down drivers), emissions of waste and pollutants (bottom-up drivers), and alteration of the magnitude, frequency and/or duration of disturbance regimes to which the system is adapted. This last driver of resilience loss is of particular interest to managed forest ecosystems, where treatments are implemented in order to control disturbance or their impacts (Perry 1998; Haeussler and Kneeshaw 2003). It has been observed in different situations that the effects of local protection treatments against pests or fire suppression on forest characteristics may have accumulated in a sufficiently high level within landscapes in such a way that disturbance regimes could have been modified (Blais 1983; Swetnam and Lynch 1993; Raffa et al. 2008; Robert et al. 2012). Those findings generated the silvicultural hypothesis, which states that anthropogenic modifications of landscape characteristics can influence outbreak regimes. However, those conclusions are contested in light of the uncertainty related to historical outbreak regimes (Miller and Rusnock 1993). In a comparison of different forest management regimes, Robert et al. (2012) have nevertheless shown that forest management legacies can generate different temporal and severity patterns in outbreaks of the eastern spruce budworm (SBW).

Cases of regime shifts were observed in forest ecosystems (figure 1) such as that which is taking place on the Anticosti Island in Quebec, where browsing by introduced white-tailed deer (*Odoicoleus virginianus* (Zimmerman)) is disrupting the balsam fir (*Abies Balsamea* (L.) Mill.)/intolerant hardwoods/SBW system to leave white spruce (Picea glauca (Moench) Voss) dominant (Chouinard and Filion 2005) and pave the way to an ongoing outbreak of the spruce beetle of unprecedentedly high duration (Potvin et al. 2000a; Hébert and Jobin 2001). Anticosti corresponds to a novel ecosystem as defined by Hobbs et al. (2006), but regime shifts have been observed in natural system as well, such as those triggered by compound disturbances (Paine et al. 1998). This occurred within a black spruce (*Picea mariana* (Mill.) B.S.P.)-feathermoss forest of eastern Quebec whose regeneration was jeopardized by the successive occurrence of a SBW outbreak and a severe wildfire, due to seed mining by SBW that had taken out an important proportion of viable black spruce seeds before fire destroyed the canopy (Payette et al. 2000). This resulted in an open black spruce-lichen landscape, with areas of exclusive lichen cover; this happened despite black spruce being both a successful pioneer and shade tolerant species (Frelich and Reich 1995). A similar situation is found in Douglas fir (*Pseudotsuga menziesii* (Mirb.)) stands of western North America, where western spruce budworm (WSBW; *Choristoneura occidentalis* Free.) often feeds on seed cones (Dewey 1970). This is suggested to have generated forested landscapes of lower density in this case as well (Swetnam and Lynch 1993), although in this case, the presence of other fire-adapted species allowed forest cover to grow back (Hadley and Veblen 1993). Unlike the case of this mixed Douglas fir - pine landscape, the situation described by Payette et al. (2000) occurred in monospecific stands in which the absence of non-host tree species momentarily increased vulnerability to regime shifts due to black spruce's high fire susceptibility, which ultimately led to an alternate regime dominated by lichens.

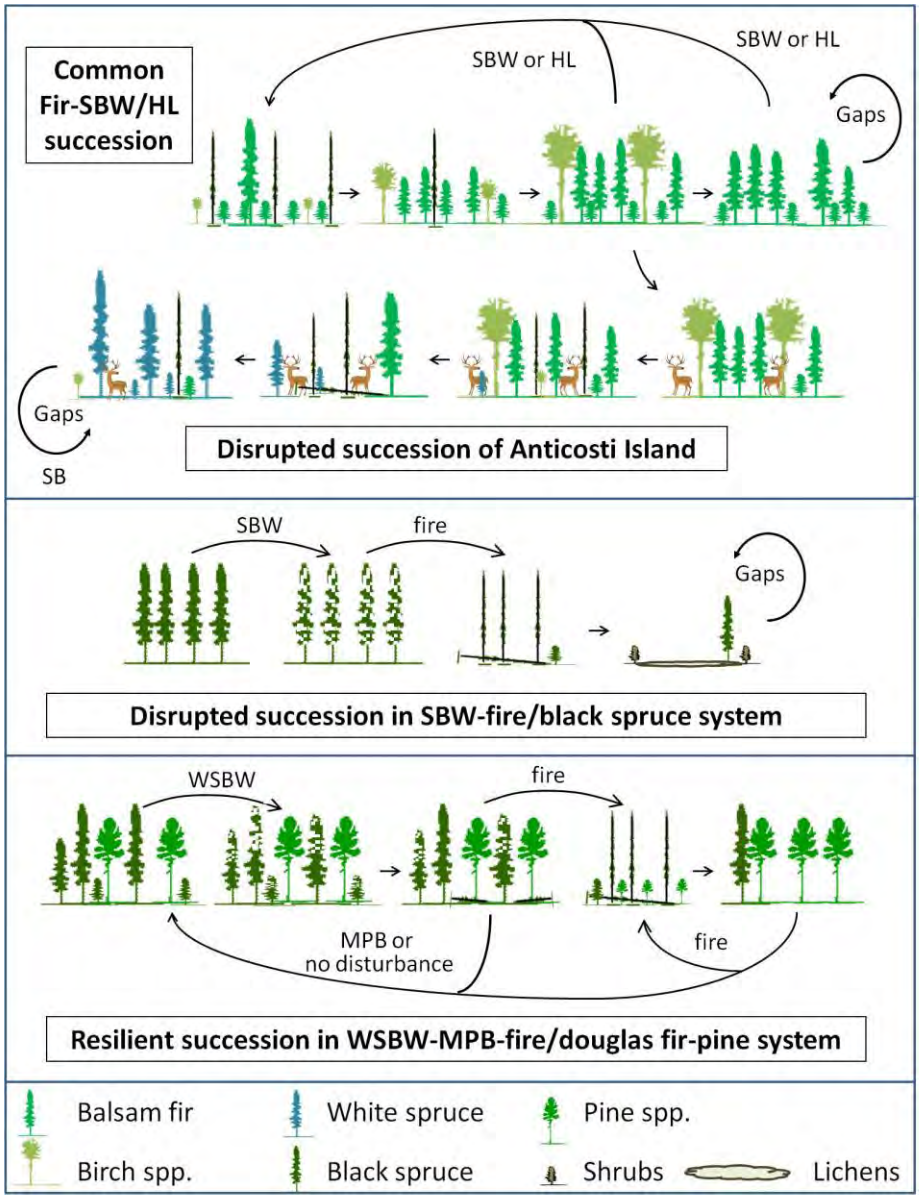

Figure 1: Examples of regime shifts in forest ecosystems due to the occurrence of natural disturbance.

Notes: In the cases of Anticosti Island (Chouinard and Filion 2005)and black spruce system (Payette et al. 2000), forest succession does not return to initial state and deviates to an alternate state dominated by white spruce and lichens, respectively. The case of douglas fir - pine forests (Hadley and Veblen 1993) is an example of a system resilient to compound disturbances.

Regime shifts represent the worse-case scenarios of future ecosystem states (temporal uncertainty) from a resource exploitation perspective. Usually the result of incomplete knowledge of ecosystem dynamics, the alternative, often less desired regimes are no less unexpected. The larger uncertainties often remain hidden (Wynne and Mayer 1993), undetected by empirical and even mechanistic models based on current knowledge. Scenarios of forest succession associated to a given stability domain, although predictable to greater degree, are numerous. As a result, predicting forest successional pathways also brings its load of uncertainty, as discussed in the next section.

1.4 Uncertainty related to successional pathways

The dynamics of pest and wildfire systems are inherently unstable (Holling 1973; Wallner 1987); major disturbance periodically affects the system and destroys important proportions of mature trees. Forest succession following disturbance is also context-dependent and no single path can be generalized to any system (Bergeron et al. 1995; Frelich and Reich 1995; Greene et al. 1999; Chen and Popadiouk 2002). Successional pathways will depend on many factors including pre-disturbance forest characteristics, propagule availability, edaphic conditions, as well as disturbance type, severity, frequency & spatial extent (Greene et al. 1999; Chen and Popadiouk 2002; Taylor and Chen 2011). Although there are various successional paths, natural disturbances often promote ecosystem persistence by generating parallel or cyclic succession (i.e. where pre and post-disturbance compositions are similar (Frelich and Reich 1995)) such as when fire burns black spruce, pine species or intolerant hardwood stands (Heinselman 1973; Heinselman 1981; Peterson 2008), or when insect outbreaks affect conifer (Baskerville 1975) or pure shade-intolerant hardwood stands (Man and Rice 2010). However this model is not generalized and in mid-size gaps, pure stands often converge on mixtures of tolerant and intolerant species (Frelich and Reich), and shrub-dominated regeneration in large slowly forming gaps (Kneeshaw and Bergeron 1998).

The traditional forestry view of ecosystem constancy followed this parallel model and applied it at a large scale (Puettmann et al. 2009); however this model might be far from reality, as observed in an unmanaged boreal forests of Minnesota where tree species self-replacement probabilities were observed to be approx. 30 % (Frelich and Reich 1995). However this proportion might be underestimated considering that fire frequency has decreased as a result of fire suppression, so that fire adapted species that regenerate in monospecific even-aged stands are less frequent (Frelich and Reich 1995; Haeussler and Kneeshaw 2003). Self-replacement is often promoted using silvicultural treatments, such as brushing or tree planting (Haeussler and Kneeshaw 2003; Belle-Isle and Kneeshaw 2007). Nevertheless, this "artificial" parallel succession model remains dependent on natural regeneration, and while harvesting can promote the return of desired species like balsam fir (Haeussler and Kneeshaw 2003; Belle-Isle and Kneeshaw 2007), it often results in an increased presence of undesired shrubs or economically less valuable species like most intolerant hardwoods (Harvey and Bergeron 1989; Haeussler and Kneeshaw 2003; Laquerre et al. 2009). Intensive silviculture is necessary to increase softwood abundance in such cases and it is economically unlikely that it will be applied over all situations where it would be necessary.

Composition manipulations and the command and control approach in general often interferes with forest succession processes (Holling and Meffe 1996; Puettmann et al. 2009). However compositional change can also be attempted on deteriorated or monospecific stands in order to restore stand diversity (MacLean 1996; Needham et al. 1999; Battisti et al. 2000). Stand composition and species dominance turnover have an important role on biotic disturbances like recurring insect outbreaks (Holling et al. 1996). Irruptive insects can sometimes generate their own favorable conditions, as tree mortality perpetrated during an outbreak might promote host species regeneration for future generations of insect herbivores like the spruce budworm (Baskerville 1975; Morin 1994). Abiotic disturbance like wildfires promote self-replacement of fire-prone species like pines (*Pinus* spp.) and consequently, favorable conditions for future wildfire events (Heinselman 1981). Forest succession is closely linked with natural disturbance and this dynamic, combined with species functional traits and site productivity, shape the forest landscape and promotes the maintenance of ecosystem functioning and stability (Balvanera et al. 2006). This fragile cycle has often been viewed as critical to ecosystem stability (Holling et al. 1996) and biodiversity is seen as a key factor of ecosystem resilience (McCann 2000) as discussed next.

1.5 effect of tree composition on ecosystem stability

Ecosystem stability has frequently been associated with ecosystem biodiversity, which is often seen as an insurance policy against regime shifts and catastrophic disturbance (Yachi and Loreau 1999; McCann 2000; Elmqvist et al. 2003; Folke et al. 2004). Biodiversity increases functional redundancy so that stabilizing mechanisms are maintained even if a disturbance eliminates a portion of species having stabilizing roles (McCann 2000). However, the effect of biodiversity on stability is context-dependent (Johnson et al. 1996); the specific identity of tree species within a mixture is critical within forest-pest systems (Grimm and Wissel 1997; Jactel et al. 2005). A mixture of hosts and non-host species will generally reduce outbreak regime amplitude by diminishing pest species food resources, providing barriers to host location as well as alternative natural enemy habitat (Jactel et al. 2005; Sturtevant et al. In prep.).

The role of species composition on ecosystem stability has also been studied with respect to natural disturbance (Holling et al. 1996) and its effect on forest succession (Johnson et al. 1996; Sankaran and McNaughton 1999). Disturbance plays a key role in ecosystem stability (Holling and Meffe 1996). By resetting some stands to seral stages of development, it maintains species diversity through the establishment of species that do not persist under climax conditions (Johnson et al. 1996). In the case of insect outbreaks, the addition of specific tree species have been shown to reduce damage (Jactel and Brockerhoff 2007) through an increase in natural enemy community diversity (Simmons et al. 1975; Cappuccino et al. 1999; Quayle et al. 2003; Eveleigh et al. 2007) and a reduction in stand susceptibility or vulnerability (Blum and MacLean 1984; Su et al. 1996; Liebhold et al. 1998; Jactel et al. 2002; Campbell et al. 2008). In this particular case, biodiversity *per se* is not a causal factor (Vehviläinen et al. 2007;

Sturtevant et al. In prep.); reduced pest damage is due to species composition that respects three factors: herbivore food resources, barriers to herbivore host location, and alternative natural enemy habitat (Sturtevant et al. In prep.). As discussed next, in the case of pest systems also, tree composition may improve ecosystem stability through an increase in parasitoid diversity and a reduction in outbreak severity.

1.6 Stability of forest pest systems

The concept of stability is context-dependent and can have different definitions depending on the ecosystem, trophic level or spatial scale of focus (Grimm and Wissel 1997). For instance, the stability of predator-prey interactions can be viewed as the coexistence of the two species involved, the system being characterized as unstable when one species goes extinct (Lehman and Tilman 2000). In fluctuating systems where species have coexisted for thousands of years such as forests affected by major insect outbreaks, the amplitude of fluctuations has been proposed as an indicator of long term stability (Ives and Carpenter 2007). Outbreak cycle amplitude (outbreak severity) could play an important role in ecosystem stability, but the specific aspect of stability being affected (namely resilience, persistence and constancy) remains obscure. Stability as measured by forest productivity has also been used in pest systems, where it was observed that phytophagous insects may regulate primary production, acting inversely relative to tree vigor or productivity (Mattson and Addy 1975).

In the balsam fir / white birch (*Betula papyrifera* Marsh.) - yellow birch (*Betula alleghaniensis* Britt.) bioclimatic domain, outbreaks of the eastern spruce budworm are a fundamental part of the ecosystem (Holling 1973; Baskerville 1975; MacLean 1988). We can generally consider this system to be resilient essentially because the SBW outbreak cycle is long enough (Royama 1984; Jardon et al. 2003) for mature balsam fir to produce a dense seedling bank in the understory that will later fill the gaps created in the canopy by spruce budworm-induced mortality (MacLean 1988; Morin 1994; Osawa 1994). White birch and trembling aspen (*Populus tremuloides* Michx.), being spared from defoliation by spruce budworm, can temporarily dominate the canopy in the years following severe outbreaks, until they are eventually replaced by fir when the seedling bank reaches the canopy level, thus perpetrating this cyclic balsam fir dominance. Balsam fir-dominated forests therefore have a high capacity to recover from age-specific disturbances like SBW outbreaks (Holling 1973), as long as fir regeneration is not destroyed by the disturbance (Ruel 1992). Such disturbance can be either natural (e.g. severe wildfires) or anthropogenic (e.g. clearcutting with no protection of regeneration (Doucet 1988), precommercial thinning (Blum and MacLean 1984; Needham et al. 1999), but a large scale eradication of the fir seedling bank seems unlikely, although in some situations fire risks can be increased after an outbreak and generate high severity fires (Stocks 1987; MacLean 2004)}. However, this is less likely to happen in regions with low fire risks, light or moderate tree mortality or once "green up" occurred in the understory after tree mortality (Péch 1993; Fleming et al. 2002). Whether resilience is referring to the speed of return to reference state or dynamic after disturbance (elasticity) or to the state-space of an ecological system (domain of attraction) (Grimm and Wissel 1997), outbreaks of higher severity are not likely to disrupt the balsam fir regeneration cycle. Hence, a spruce budworm outbreak regime of higher amplitude should not negatively affect fir regeneration, as seen following an intense and uncontrolled SBW outbreak on Cape Breton Island (MacLean 1988); intense outbreaks may even improve fir regeneration through the creation of more abundant canopy openings.

The spruce budworm-fir forest ecosystem is not the only case where the association of an irruptive herbivore insect and forest ecosystem produces a resilient system. The western spruce budworm - douglas fir forest ecosystem is considered even more ecologically resilient (or less likely to switch to an alternate regime) than that of eastern spruce budworm, essentially due to the fact that *C. occidentalis* does not kill its host as much as SBW (Ryerson et al. 2003), thereby disturbing the forest to a lesser degree (Cooke et al. 2007). Yet, *C. occidentalis* often feeds on douglas fir seed cones (Dewey 1970), which might affect its regeneration on some occasions (Swetnam and Lynch 1993).

The persistence of the SBW-balsam fir regime (maintenance through time of the regime) is closely linked with the capacity to recover from disturbance; it is also a matter of getting the balsam fir seedling bank to maturity repeatedly through time. The last main property of stability, constancy (staying essentially unchanged), may depend on the spatial or temporal scale of focus. For instance, forest composition, structure, age, biomass, etc. are characteristics that fluctuate over time within forest ecosystems, but often in repeatable patterns (Frelich and Reich 1995; Chen and Popadiouk 2002) or within a given state-space so that it can also be considered constant over a longer time frame. Constancy is also a matter of spatial scale; forest characteristics may be modified by wildfires or insect epidemics at local scales, but remain constant through time at a larger scale. Therefore, in the presence of disturbance, resistance is a preferred term, defining the susceptibility of an ecosystem to disturbance. The property of resistance is disturbance-specific, as an ecosystem may be resistant to a particular disturbance but not to others. This is the case for jack pine (*Pinus banksiana* Lamb.) stands which are resistant to spruce budworm for instance, but highly susceptible to wildfires, whereas stands that are more resistant to wildfires such as hardwood stands in the boreal forest (Bergeron et al. 2004) are much more susceptible to defoliation by forest tent caterpillar (*Malacomosa disstria* Hubner) (Cooke and Lorenzetti 2006). Some stands like balsam fir – birch stands are vulnerable to both spruce budworm outbreaks and wildfires, although they are typically more resistant to wildfires compared to pure spruce stands for instance (Foster 1983). Finally, despite the fact that the mountain pine beetle (*Dendroctonus ponderosae* Hopkins)-lodgepole pine (*Pinus contorta* Dougl. ex. Loud.) system is highly vulnerable to both fires and mountain pine beetle (MPB), it still shows great resilience over the long term (Romme et al. 1986). It is interesting to note that in this case, wildfires and not MPB itself favour the establishment of MPB's main hosts (lodgepole and ponderosa pine - *Pinus ponderosa* Dougl. ex Laws.); in the absence of fire, MPB outbreaks usually promote favorable conditions for shade tolerant species like douglas fir, subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) or spruce species like Englemann spruce (*Picea engelmannii* Parry ex Engelm.) (Amman 1977). While there still exists a risk of regeneration failure in this system following a severe MPB outbreak, the critical conditions are less likely to occur compared to the case described by Payette et al.. Saplings must be absent from the understory, most of the pine seed trees must have been killed by MPB, and fire must occur long enough after the outbreak for the seeds contained in the closed serotinous cones of dead pines to lose their viability, which is a matter of years (Lotan and Critchfield 1990). Mountain pine beetle is therefore dependent upon the occurrence of wildfires and the entire ecosystem is shaped by (and ecologically resilient to) these co-occurring disturbances.

The link between outbreak cycle amplitude and resistance is a direct one; less resistance means higher severity outbreaks. However, resistance (staying essentially unchanged), resilience (returning to reference state) and persistence (maintenance over the long term) are not necessarily interdependent properties and none determine by itself the stability of an ecosystem. In certain cases, favouring resistance to disturbance has detrimental effects on resilience and consequently on ecosystem persistence (Holling and Meffe 1996; Puettmann et al. 2009). The definition of stability has often been limited to that of resistance to disturbance, following resource management objectives. Forest ecosystems were managed as to reduce disturbance impacts and regularize timber yield (Puettmann et al. 2009); forest were thus given higher constancy and resistance. Paradoxically this resulted, in many cases, in decreased forest resistance with higher severity disturbance, like wildfires (Christensen et al. 1989) and insect outbreaks (Blais 1983; Swetnam and Lynch 1993). Forest protection strategies like fire suppression or the reduction of forest susceptibility to insect pests through silviculture are used to reduce damage from disturbance (i.e. increase forest resistance to those disturbances). In these systems, regime shifts have occurred but the new state of the system remains unknown.

One way of preventing such regime shifts in forest ecosystems would be to use resilience indicators (Carpenter et al. 2001; Contamin and Ellison 2009; Scheffer et al. 2009; Thrush et al. 2009). A common characteristic of many of the reported regime shifts in forest ecosystems is the temporary alteration of the regeneration capacity of disturbed systems. Whether it is due to the occurrence of compound disturbances (Paine et al. 1998), invasive species (Chouinard and Filion 2001), or disturbance regime alteration (Christensen et al. 1989), the state of the seed or seedling banks may be critical for forest renewal (Simard and Payette 2005). A study like that of Simard and Payette (2005) is an example of an indicator of ecological resilience based on reproductive potential; in this case, they identified a period of high vulnerability to regime shift as long as 20 years following SBW outbreaks.

The cases of regime shifts in forest-pest systems reported here occurred at the landscape scale, but they usually do not affect the whole geographical range of the insect, which often spread on multiple ecological regions. This highlights the scaling issue related to regime shifts and ecosystem resilience in general. Resilience itself is dependent on environmental properties and disturbance characteristics which may fall within smaller spatial scales than that of ecological regions or tree and insect species geographical range. Forest disturbance can be of lower severity and affect isolated forest patches or stands, which implies that the effects of compound disturbances, for instance, could probably be observed over relatively small scales. However, in cases where resilience is reduced due to an altered forest regeneration capacity, tree seed dispersal might be an important factor determining the minimum observable size of regime shifts; unforested land may appear if seed trees are not found within maximum effective seed dispersal distance, i.e. less than 100 m for common boreal forest tree species like balsam fir, black spruce, lodgepole pine, douglas fir or white birch (Burns and Honkala 1990). In terms of uncertainty related to forest management and timber supply predictions, the spatial extent of management units (i.e. usually landscape scale (*sensu* Holling 1992)) would be the reference scale for the consideration of regime shifts.

Chapter 2: Case study: the dramatic forest composition change on Anticosti Island and its impact on insect outbreak dynamics

2.1 Ecosystem description

Anticosti Island in the Gulf of St-Lawrence (figure 2) is a living laboratory in terms of large scale forest composition change and its effects on insect outbreaks. The island is covered with boreal forest and is now subject to intense herbivory pressure due to the introduction of white- tailed deer in the late 1890s which has overpopulated the island since the 1930s (Potvin et al. 2000b); The case soon became interesting for ecologists who foresaw important impacts on the whole ecosystem (Newsom 1937; Leopold et al. 1947; Pimlott 1965; Marie-Victorin and Rolland-Germain 1969; Potvin et al. 2000b). Balsam fir is normally used as starvation food by white-tailed deer, but intolerant hardwood seedlings and shrubs have become rare on the island (Potvin et al. 2000b) and fir becomes the most available palatable winter food for deer (Potvin et al. 2003). By 1999, balsam fir stands went from 40 to 20 % of the area since deer were introduced (Centre d'études), and it has now become scarce in the regeneration since the 1930s (Potvin et al. 2000b). White spruce has taken over regenerating areas comprising over 90 % of total seedlings (Potvin et al. 2003).

This situation is slowly reducing the resilience of this system in which balsam fir dominance is renewed mainly by an age/host-specific outbreaking insect, the hemlock looper (HL), and to a lesser extent, spruce budworm (Martel 1999; Potvin et al. 2000b). The hemlock looper is a highly polyphagous defoliator that preferably feeds on mature or overmature balsam fir and eastern hemlock (*Tsuga canadensis* ((L.) Carrière) (Carroll 1956), although it also feeds on other conifers like white and black spruce as well as eastern white cedar (*Thuja occidentalis* L.), and also on deciduous species like paper birch, sugar maple (*Acer saccharum* Marsh.) and trembling aspen (*Populus tremuloides* Michx.) (Hébert et al. 2006). Localized outbreaks occur each 10-12 years and usually last less than three years, killing most of the hosts in the infested area (Carroll 1956; Otvos et al. (1979) cited in Iqbal et al. 2011). Possibly ten outbreaks of the hemlock looper occurred on the island since 1845 (Barrette et al. 2010) and the only spruce budworm outbreak to have occurred in the 20th century is that of the 1970s (Blais 1983; Martel 1999; Barrette et al. 2010).

Stand initiating disturbances are rare on the island (Lavoie et al. 2009; Barrette et al. 2010) perhaps due to the cold and wet climate that prevails, which also reduces the severity and extent of SBW outbreaks (Blais 1968; Barrette et al. 2010). A similar disturbance regime has been observed in Maine, where differences in tree composition and species longevity (more abundant long-lived species like red spruce (*Picea rubens* Sarg.) and non-host deciduous species (e.g. *Acer saccharum* Marsh., *Fagus grandifolia* Ehrh., and *Betula alleghaniensis* Britton (Fraver et al. 2009)) relative to eastern Canada's ecosystem is believed to reduce the role of SBW forest dynamics (Fraver et al. 2007). However, wildfires in Northern Maine were not observed since at least 1870 (Fraver et al. 2009), which possibly reduced the presence of early successionnal tree species relative to Anticosti Island's forest. Nevertheless, wildfires have affected the island, but not extensively (Lavoie et al. 2009); the last important fire dates back to 1955 and affected approximately 10 % of the island (Chouinard and Filion 2005) (see figure 3).

Despite these issues, Anticosti Island is mostly famous for its deer-hunting potential. With their primary food resource disappearing, deer populations are facing an upcoming collapse and various measures are being tried, such as exclosure fencing to allow fir and hardwood regeneration to grow free of herbivory and eventually act as seed trees (Casabon and Pothier 2008) (figure 4). Lately, most research has been conducted on sustainable development on the Island with measures such as natural regeneration fencing ((Casabon and Pothier 2008). Since forest management activities have been ongoing for a while, post-harvesting regeneration dynamics outside fenced areas is also of concern. Although the forest industry might feel spared (or even advantaged) from Anticosti biodiversity issues due to the continued inflow of softwood timber with white spruce instead of balsam fir, it nevertheless faces an irruptive insect in the spruce beetle *D. rufipennis* (Potvin et al. 2000b; Hébert and Jobin 2001). Its preferred hosts in its eastern habitat range such as Anticosti are white and red spruces (Balch 1942; Werner et al. 2006; L. Morneau, personal communication). It shares common characteristics with other bark beetles, like that of restricting feeding to dead and mature, slow growing trees in latent periods and to more vigorous trees during outbreaks (Balch 1942).

D. rufipennis is the most damaging insect affecting spruces (*P. engelmannii* Parry ex Engelm., *P. X lutzii* Little, *P. glauca* [Moench] Voss, *P. sitchensis* [Bong.] Carr.) in western North America (Holsten et al. 1999). It is less present in eastern North America essentially due to the lower abundance of hosts, white spruce being present but to a lower degree, essentially due to its association with balsam fir which has better regeneration success (Greene et al. 1999; Ruel and Pineau 2002). Spruce beetle generated important outbreaks in eastern Canada in the past (1887-1901, 1915-1921, and 1928-1934), but the most important occurred in 1928-1934 and seriously affected Anticosti (L. Morneau, personal communication). This went unnoticed in a recent dendrochronological analysis, and this particular event was attributed to hemlock looper, although only white spruce was affected (approx. 50% of surviving white spruce stems affected; Barrette et al. 2010), which is unlikely considering HL's preference for balsam fir, which was still abundant at the time. Therefore, spruce beetle is not new to this ecosystem, but the current outbreak persistence is (10-15 years; Potvin et al. 2000, Hébert & Jobin 2001).

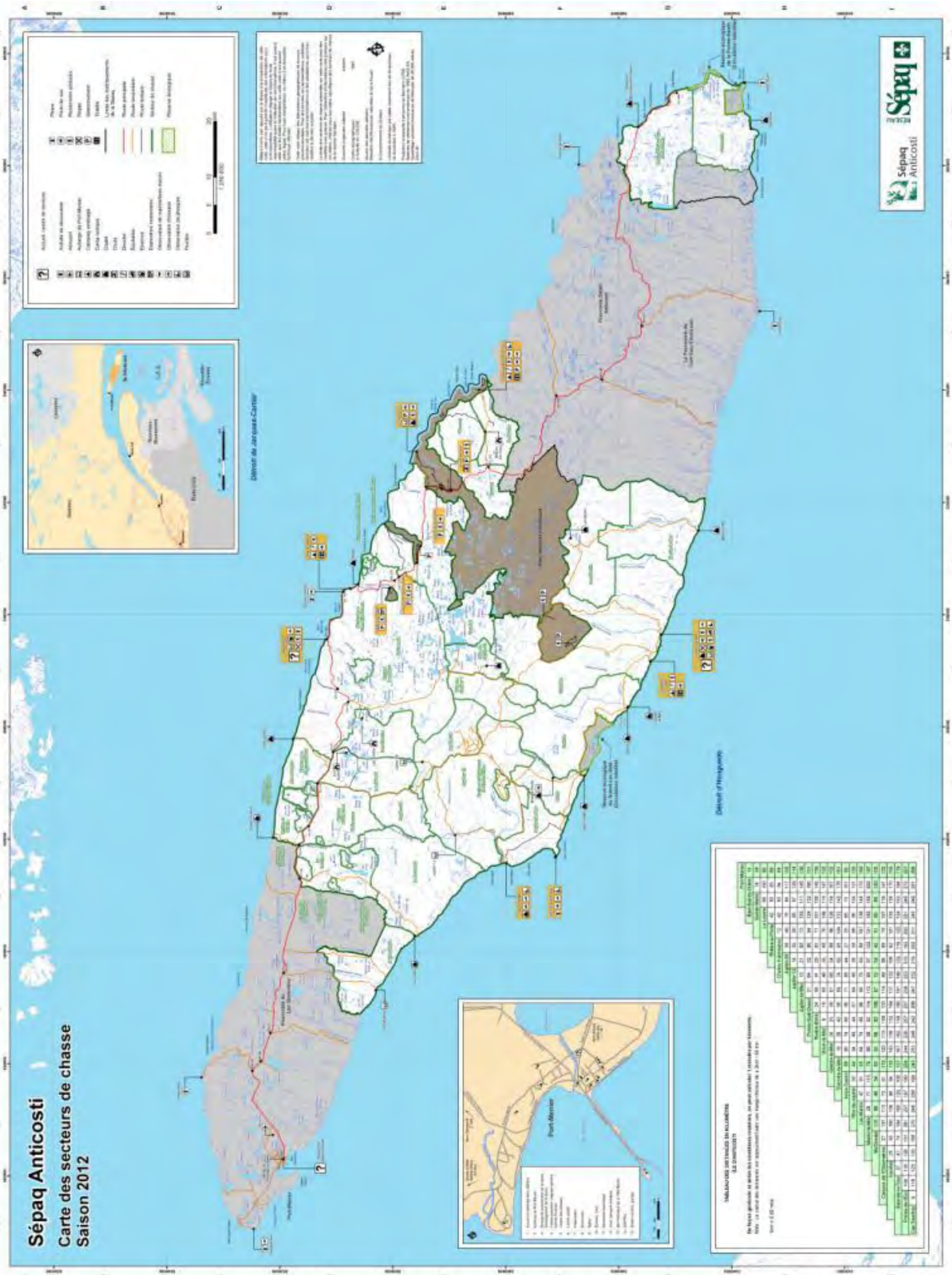

Figure 2: Map of Anticosti Island land use.

Hunting and forest management areas are shown in grey and white zones and conservation area in brown zones. The island is publicly owned, but the area in white is managed by a government agency (SÉPAQ) for tourism and wood/fauna exploitation and area in grey is managed by the city of Port-Menier (west-end of the island). Exclosure fencing areas are indicated as small green contoured area within the white zone.

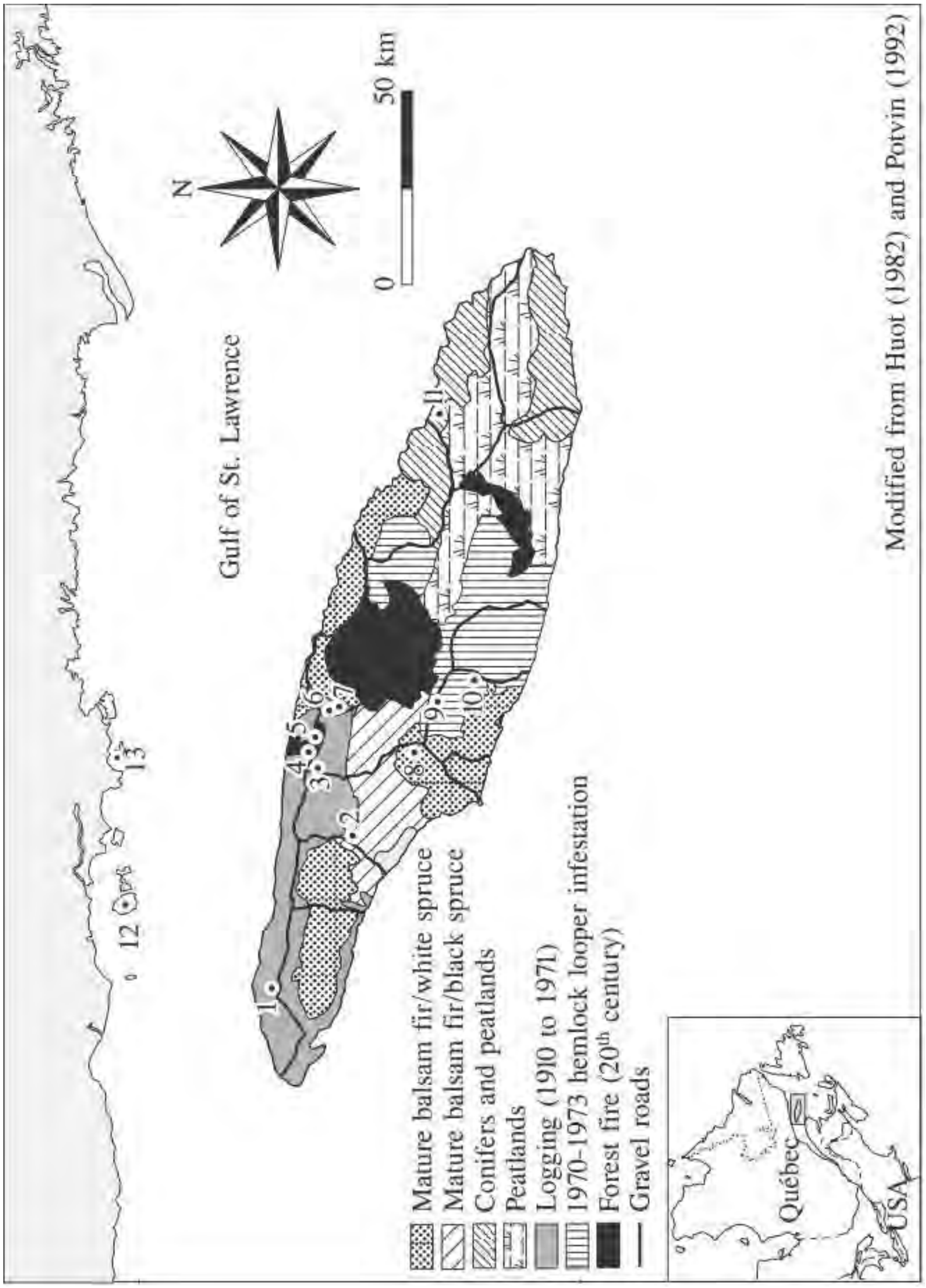

Figure 3:Map of Anticosti Island vegetation types and disturbances. Modified from Chouinard et al. (2005).

Figure 4: Exclosure fencing on Anticosti Island with regenerating white spruce outside fence and a mixture of intolerant hardwood and balsam fir inside fence. (Anonymous)

2.2 Impacts of compositional change

The case of Anticosti island is interesting in the sense that it is subject to most of the issues discussed in this report and on stability-diversity relationships within forest ecosystems. It is a living experiment questioning many of the ecological theories and assumptions built during the last century. The question of long term forest dynamics modeling is important to forest management planning as it is one of the basis of timber supply simulations (Buongiorno and Gilless 2003). For balsam fir-birch forest ecosystems, the cyclical pattern of fir replacing fir is generally accepted and used (Baskerville 1975; MacLean 1988; Morin 1994). However, it has been observed that environmental factors detrimental to balsam fir dominance may operate in certain areas and conditions. The absence of stand-replacing disturbance is one factor that favors shade-tolerant tree species over the long term (Fraver and White 2005). The creation of large gaps helps maintain intolerant hardwood and shrub species and increases the abundance of white cedar in the absence of fire (Kneeshaw and Bergeron 1998). The cyclical fir renewal pattern is furthermore prevented by severe browsing from white-tailed deer, which not only disrupts the balsam fir seedling bank establishment but also eliminates intolerant hardwood regeneration, leaving white spruce as the main regenerating species (Potvin et al. 2000b). This composition change is drastic, but is somewhat similar to the objectives of preventive forest protection treatments aiming at increasing forest resistance to boreal forest defoliators like hemlock looper and the spruce budworm.

An atypical regime shift is under way in this ecosystem, and consequences may be beginning to appear in various ways: (1) heavy browsing by the deer population is depleting balsam fir regeneration to the extent that young stands are now composed of over 90 % white spruce (Potvin et al. 2003), in an ecosystem where the balsam fir-white birch-insect defoliator system has been present for more than 3 000 years, i.e. since a closed forest canopy formed on the island (Lavoie et al. 2009). It is difficult to predict the changes that the outbreak regimes of hemlock looper and spruce budworm will undergo over the next decades with the loss of their preferred host in balsam-fir; a tritrophic model was used to explore that issue (see next section). (2) The loss of intolerant hardwoods, shrub and herbaceous layers, which constitute important habitat and food resources for generalists and specialized insect parasitoids (Simmons et al. 1975; Cappuccino et al. 1998; Cappuccino et al. 1999), caused an important loss of Carabidae and Staphilidae, two families known for their predatory activity on insect pests (Hébert and Jobin 2001). (3) With white spruce increasing in abundance and the loss of parasitoid diversity in these stands (Hébert and Jobin 2001), an unprecedented outbreak of the spruce beetle (*Dendroctonus rufipennis* (Kby.)) has been ongoing for the last 15 years at least (Potvin et al. 2000). Natural enemies having an important role on bark beetles population level (Raffa and Dahlsten 1995), the decrease in parasitoids abundance will likely increase the role of SB on Anticosti Island. The presence of this insect has been reported only on some occasions and over a small extent elsewhere in Quebec (Québec (1986) in Hébert & Jobin 2001; L. Morneau, personal communication). This system is most likely on the edge of another attraction domain, affecting the stability, but more precisely the ecological resilience of the ecosystem (Grimm & Wissel 1997).

Compositional change found on Anticosti island is perhaps not that unique, as loss of hardwood species and increase in white spruce abundance has also been observed on Prince Edward Island old-fields (Loo and Ives 2003). In that case though, the disturbance resulted in a rapid loss of forest cover: an important land clearing (70 % clearing at its peak in the early 20th century) resulted from human colonization in the 18th century (Loo and Ives 2003). Clearing removed mostly hardwood stands (Anderson 1980) and abandonment of this land in the early 20th century led to regeneration dominated by white spruce (Loo and Ives 2003; Mosseler et al. 2003). Although fir is maintained in relatively low proportions within the remaining forested land (Anderson 1980; Mosseler et al. 2003), spruce budworm outbreaks still occurred on Prince Edward Island in the last century (Kettela 1983; Hardy et al. 1986). However, in the case of Prince Edward Island, the presence of herbivores is not as important as that of Anticosti Island, due in part to the presence of white-tailed deer predators such as the coyote (Gompper 2002). Thus with the balsam fir seedling bank in good condition and the fact that deciduous cover is more important on P.E.I., the maintenance of habitat and food for parasitoids of irruptive insect herbivores like the hemlock looper or spruce budworm becomes more probable (Simmons et al. 1975; Cappuccino et al. 1998; Cappuccino et al. 1999). As PEI, Anticosti usually experiences lower severity range of defoliator outbreaks compared to continental fir-birch forests possibly due to the maritime climate (Blais 1968; Barrette et al. 2010). Nonetheless, as difficult as it may seem to predict the evolution of outbreak regimes considering the interplay of the loss of natural enemies and of HL and SBW prefered host in balsam fir, a tritrophic population model was used and its applicability on Anticosti Island is described in the following.

2.3 Projecting outbreak regime evolution using tritrophic modeling

The future of spruce budworm outbreak dynamics on the white spruce-dominated Anticosti can be overviewed using the tritrophic conceptual model proposed by Cooke et al. (2007) shown in figure 5. The three trophic levels described are host plants, herbivorous insects and their natural enemies. Curves in light gray and black represent herbivore population and their natural enemy population fluctuations through time, respectively. The jagged lines illustrate stochastic fluctuations of population level, due to weather conditions or other density-independent factors. Shaded areas around the curves represent range of population trajectories given varying ecological conditions. Figure 5 illustrates the model for spruce budworm, one of the insect species affecting Anticosti island's forests. The shaded area around the herbivore curve describes population trajectories between extreme cases of weakened populations (bottom end of shaded area) due to poor tree host resource like disconnected landscape or low forest susceptibility (e.g. due to age structure or the low abundance of host trees) and highly adapted populations (top end of shaded area) due to abundant host trees and a connected landscape, for instance. Resource depletion by itself can lead to outbreak collapse, as the theoretical herbivore population decline illustrates (black line on top of light gray shaded area), but natural enemy populations rise before that point to combine with resource depletion and cause outbreak collapse earlier in time. The dark gray shaded area describes cases between a high enemy density (top end of shaded area; due to situations like that where generalist parasitoids have abundant alternate hosts during latency periods and can readily respond to a SBW population rise) and a little abundance and diversity of parasitoids (bottom end of shaded area; due to little habitat or alternate prey for generalist parasitoids to feed on before outbreak start). This is known as the bird feeder effect (Eveleigh et al. 2007), where resource quality (homogeneity) determines the switching behavior of generalist parasitoids.

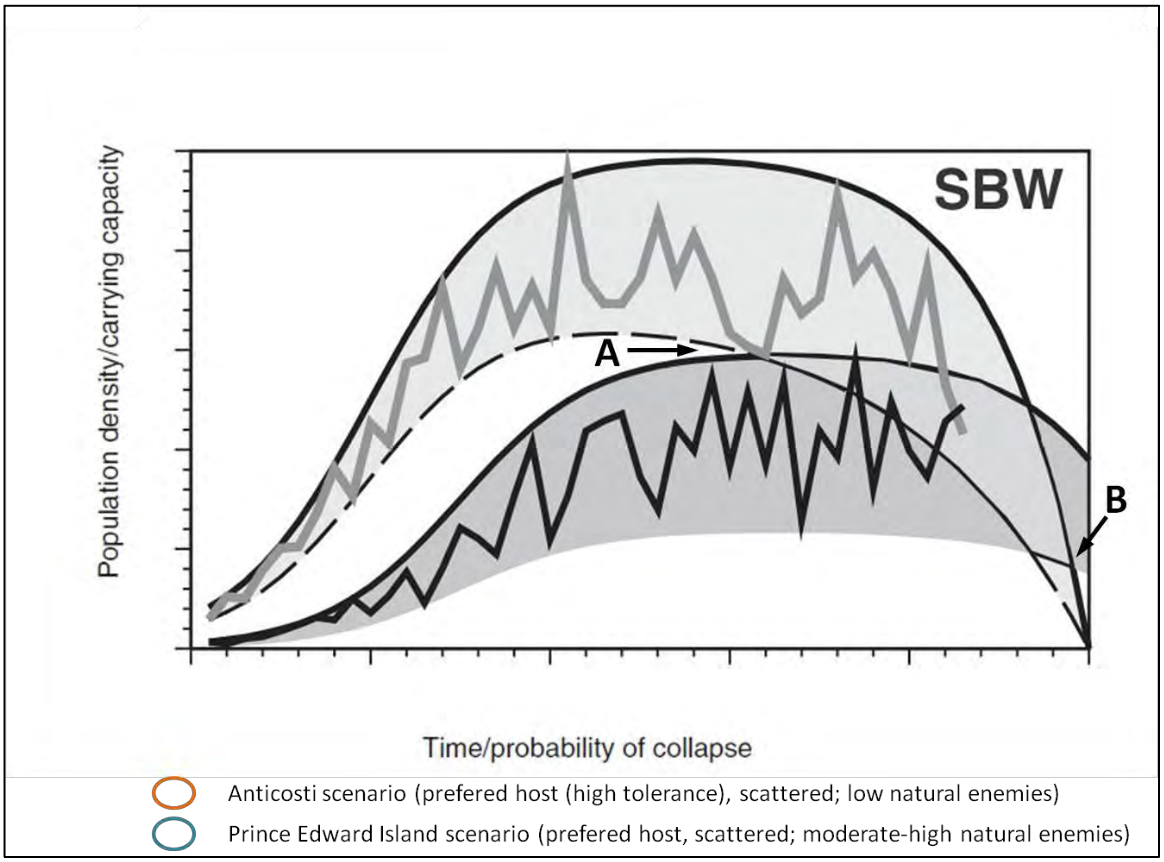

Figure 5: Tritrophic model of SBW dynamics modified from Cooke et al. (2007).

It shows a time sequence of four insect herbivore population density levels (dark gray line) in association with their natural enemy population fluctuations (black line). Shaded regions around the curves are the range of possible population trajectories for both herbivore and natural enemies given varying ecological circumstances. Point A represents a situation where herbivore populations collapse early due to unfavorable herbivore conditions and favorable natural enemy conditions and point B a case where herbivore populations collapse later due to favorable herbivore conditions and low natural enemy population. A and B are thus extreme scenarios of unfavorable and favorable conditions for outbreak development, respectively. Circled areas represent plausible scenarios of outbreak duration in the cases of Anticosti Island with scattered white spruce stands and low natural enemies and Prince Edward Island where balsam fir is present but dispersed and natural enemy populations are more important due to more abundant hardwoods and herbaceous cover. FTC: forest tent caterpillar (Malacomosa disstria Hübner), JPBW: jack pine budworm (Choristoneura pinus Freeman), SBW: spruce budworm (Choristoneura fumiferana Clem.), WSBW: western spruce budworm (Choristoneura occidentalis Freeman).

Figure 5 illustrates outbreak scenarios that could correspond to Anticosti and P.E.I. contexts with SBW, the former having moderate-high susceptibility hosts (white spruce) that are well connected spatially but low natural enemy populations (Hébert & Jobin 2001), and the latter containing a reasonable proportion of the preferred host, although dispersed spatially (Anderson 1980, Loo & Ives 2003) and that possibly faces an important community of natural enemies essentially due to a high hardwood abundance. It is reasonable to expect lower SBW outbreak intensity and damage in white spruce stands compared to balsam fir stands so the Anticosti case would possibly be located somewhere in the bottom half of the shaded area for the herbivore population. Considering the scarcity of natural enemies on Anticosti (Hébert and Jobin 2001), it would possibly be located near the bottom of the shaded area of natural enemy populations. The intersection of both curves, which reflects the combined effects of host resource depletion, natural enemy predation and stochastic elements (e.g. weather) represents the breaking point at which the herbivore population collapses (Cooke et al. 2007) and that point is close to the maximum outbreak duration for Anticosti island, with good or poor tree resource and weather conditions.

On P.E.I., the herbivore population zone could be expected to be somewhere in a middle position within the shaded area, but the natural enemy population could be expected to be in the upper part of the shaded area, as forest composition is more diverse relative to Anticosti island. The intersection between the curves therefore arrives much earlier for P.E.I. than that of Anticosti island and corresponds in the present case to a rough approximation of 80 % of maximum duration (4/5th of total). What is interesting to see in the model is that the role of host condition on outbreak duration increases with the condition of natural enemy populations. Moreover, the role of host condition appears relatively small for moderate condition of natural enemies (middle of dark grey shaded area). Hence, from this model we can presume that an outbreak would last longer and generate more damage in a natural enemy-poor landscape like that of Anticosti, with little importance to host susceptibility, compared to an ecosystem with a diverse natural enemy community such as that of P.E.I. However, the model from Cooke et al. was built from knowledge of stands often composed of a mixture of fir and spruce. It is therefore difficult to verify whether pure spruce stands lie within the predictions of this model.

Nonetheless this conceptual model highlights the chances of greater damage in stands with low natural enemy populations such as that found in pure spruce landscapes. It also illustrates the absence of a correlation between natural enemies and outbreak amplitude, and highlights the link between outbreak duration and natural enemies population levels; the specific role of parasitoids on outbreak duration has also been noted in forest tent caterpillar systems (Roland 1993). Parasitoids responds slowly in SBW systems compared to that of forest tent caterpillar, explaining in part the relatively long SBW outbreak cycle (Cooke et al. 2007). Promoting natural enemies should then have little influence on the extent of a SBW outbreak, which would thus be determined by forest condition and susceptible host connectivity.

Host tree abundance, susceptibility and connectivity are important factors determining outbreak amplitude (Blais 1958; MacLean 1980; Wesołowski and Rowiński 2006; Cooke et al. 2007). However, at a landscape scale, synchronizing mechanisms can play a significant role on herbivore population amplitude (Royama 1997). A comprehensive description and structuring of the various mechanisms involved was suggested by Cooke et al. (2007) and synthesized below:

1. *composition change; selective removal of white spruce in fir-spruce stands;*
2. *reduced fire frequency increase the abundance of mature and over-mature fir stands;*
3. *increased extent and connectivity of susceptible hosts leads to higher defoliation early in the cycle;*
4. *increased damage leads to increased insect dispersal;*
5. *increased host connectivity improve moth survival and fecundity rates;*
6. *increased migration leads to better synchronization between populations;*
7. *stronger density-dependence of dispersal leads to higher amplitude oscillations;*
8. *delayed response of mortality factors act with increasing strength, further amplifying population oscillations.*

The sequence of events generated by compositional change in a SBW system is well illustrated at the basis of that hierarchical description; the opposite can thus be expected of reductions in the abundance of balsam fir, SBW's primary host, with exception of the decrease in fire frequency. Although this is somewhat controllable with respect to fire suppression, its implementation is unlikely. Insect herbivore population cycle amplitude could nonetheless be reduced through reduction in resource quality, as illustrated with a decrease of the higher herbivore curve in the tritrophic model (higher portion of the light gray zone, fig. 5).

As illustrated in Anticosti Island, the consequences of an increase in forest resistance to defoliators like SBW or HL are three dimensional; the counteracting effects of a reduction in the quality of both herbivore and natural enemy habitat do not appear as equal. No matter the quality of herbivore habitat, the low level of natural enemy abundance appears more important on this outbreak pattern, predicted duration being close to the model's maximum outbreak duration. However, outbreak amplitude could be substantially reduced, thereby generating a regime of low severity outbreaks that last for longer than usual, like what is seen during latent periods. Previous studies have observed white spruce stands acting as outbreak epicentres and sources of moth dispersal, but with low outbreak duration (Hardy et al. 1983). This contrasts with the tritrophic model predictions of longer duration outbreaks, but two factors may be important in this case: considering that the worst habitats considered for the model development still comprised a portion of balsam fir, the model might be overestimating outbreak duration in low density white spruce stands, but as discussed earlier Anticosti has a much lower presence of deciduous species than normal and a low abundance of natural enemies was also found. This further highlights the uniqueness of the Anticosti Island ecosystem.

2.4 Increasing resilience on Anticosti Island

It was suggested earlier in this report that the ecological resilience of many forest ecosystems is dependent on regeneration success and the pre-invasion forest composition is essential to the preservation of the major insect pests that are SBW and HL as well as the parasitoid community. Resilience of the island's ecosystem is dependent on the presence of these insect pests, but also on that of their parasitoids. Therefore balsam fir is important for the two pests themselves, as white birch is for their parasitoids. Considering that deer hunting alone cannot reduce or maintain deer populations at the scale of the island (Lesage et al. 2000; Côté et al. 2008), other strategies that directly targets forest composition are possible. These strategies, consists in (1) the installation of an exclosure fencing network and (2) implementation of an adapted forest management.

(1) This temporary solution has been implemented since 2000 and consists fencing all new cutblocks to prevent browsing of natural regeneration (Côté et al. 2008). Results show that this method is effective in maintaining a vegetative cover representative of the pre-deer period (Potvin et al.), but it remains a costly solution that is not feasible over the long term (Côté et al. 2008).

(2) Efforts were also deployed in forest management since 1995, in order to develop logging practices promoting balsam fir regeneration (Côté et al. 2008). Two approaches were experimented which consisted in reducing habitat suitability to deer and increasing balsam fir seedling survival through the establishment of large number of seedlings (Côté et al. 2008). First, increasing cut block size was the approach used to reduce accessibility to vegetative cover and thereby reduce habitat suitability. However, results indicate that this approach failed to protect the initial plant communities in the center of the cut blocks (Casabon and Pothier 2008). The other approach used seed tree retention and strip cutting with soil scarification to promote high densities of balsam fir seedlings, but also of white birch seedlings, whose presence could spare a portion of fir seedlings from browsing (Beguin et al. 2009). Still this approach failed to maintain balsam fir seedlings in cut blocks (Beguin et al. 2009).

Overall, the high deer density found on Anticosti Island appears beyond control. Without human intervention, the uncertainty linked with timber supply may increase considering the new disturbance regime brought by white spruce stands. Nevertheless, the exclosure fencing experiments showed that the initial regeneration mechanisms are still present and that the initial vegetation is not as extinguished as it appeared (Côté et al. 2008). The question would no longer be if, but when the deer population collapse will occur and whether seed trees will be present and abundant enough for these regeneration mechanisms to renew the initial balsam fir-white birch forest once grazing pressure is reduced. In this scenario, the maintenance and development of an extended exclosure fencing network can certainly help keeping the resilience of this system by promoting the preservation of the fir-birch forest regeneration capacity and consequently the habitat of native irruptive pests and their parasitoids.

While Anticosti Island may be a novel ecosystem, it is nonetheless an example of the impact of radical composition change on ecosystem dynamics. It may easily be seen as a plausible scenario of the future consequences of intensively managed boreal forest, which can be considered as novel ecosystem as well (Holling & Meffe 1996). Pest systems that are subject to silvicultural treatments whose objectives are to increase forest resistance through composition change are part of this category. This island has been studied extensively and for a long time, it is striking to see that areas of research like that of insect outbreak regimes still remain poorly investigated in this ecosystem.

Implications for pest management

Confronted with complex forest ecosystems subject to fluctuating biotic and abiotic drivers, foresters have tried to reduce their inherent variability by regulating forest productivity. Through this paradigm, outbreaking insects are essentially seen as a nuisance and various treatments are implemented to reduce insect population fluctuations or increase forest resistance. While there remains an important uncertainty related to outbreak dynamics and the resulting wood losses, the long term uncertainty brought by modifications of forest characteristics is no less important. This report reviewed some cases where forest ecosystems were abruptly altered towards less desired states (or dynamic).

Among common silvicultural treatments meant to increase forest resistance to insect outbreaks, modifications of forest composition can bring significant change on ecosystem functioning. Although this composition change can sometimes be more related to ecological restoration when tree diversity is increased within monocultures, most species manipulation treatments consist in mono-specific plantation of pest-resistant and economically valued conifer species in monocultures, and in the elimination of the most vulnerable species through precommercial thinning (Belle-Isle and Kneeshaw 2007). In eastern Canada managed boreal forest, pest-resistant plantations of white and black spruce are commonplace due in part to their higher resistance to spruce budworm outbreaks. In certain areas tree plantations cover an important part of the landscape (around 50 % in certain regions (M.Huot, personal communication)) at the expense of balsam fir-dominated stands and its co-occurring deciduous species. While the effect of this composition change remains uncertain, Anticosti Island represents a good example of drastic composition change towards forests less vulnerable to SBW.

Although forest resistance to SBW and HL may have increased with white spruce dominance, various cases illustrate that resistance does not necessarily correlate with resilience (capacity to recover from disturbance) (Larsen 1995). Balsam fir for instance is intolerant of and reproductively adapted to spruce budworm (Morin 1994), the same way as jack pine is towards fire. But in a system historically affected by spruce budworm and modified with a white spruce-dominated composition, different outbreak dynamics are to be expected (Cooke et al. 2007). White-spruce is considered as an important host of SBW and HL, but do not usually sustain high intensity or long outbreaks (Hardy et al. 1983). It is also of concern to forest protection in general as it relates to forest resistance to insect outbreaks and a common preventive strategy which consists in planting less vulnerable species and. It has been observed that old white spruce stands were often used as spruce budworm "epicenters" (Hardy et al. 1983) and although those epicenters are not the areas where outbreaks last the longest (Gray et al. 2000), they nevertheless act as sources of moth emigration to areas suitable for more severe outbreaks (Nealis and Régnière 2004; Cooke et al. 2007).

White spruce might be more tolerant to spruce budworm, but in terms of reproduction, it is clearly not as well adapted as fir to this disturbance (Greene et al. 1999). Thus white spruce may be more resistant than balsam fir to SBW, but its capacity to regenerate after an outbreak is questionable as well as the resilience of pure white spruce stands in this region. White spruce has had regeneration problems both in managed and unmanaged forests due a combination of factors like seed production and scarcity of seed trees (Greene et al. 1999). On Anticosti Island, the exclosure fencing strategy revealed that the regeneration processes typical of the pre-deer invasion period are still present in browsing-free areas, suggesting that the system might not yet have flipped to another regime as the pre-invasion regeneration mechanisms are still effective. This experiment further suggests that fencing could be used to monitor ecological resilience in terms of regeneration potential, but that biodiversity, or species abundance does not necessarily correlate with resilience. In this case, the less desired regime that the island faces does not involve a decrease in species richness as grass species are numerous in this novel ecosystem.

With an increase in white spruce abundance came the reappearance of spruce beetle, which have now lingered on the island for an unusually long period. While SBW an HL future impacts are uncertain, a decrease in outbreak severity is expected due to the disappearance of balsam fir, their primary host. Foresters might now have to cope with spruce beetle that is potentially filling the gaps left by SBW an HL. This new threat to wood supply cumulated with white spruce uncertain regeneration success may therefore have important effects on future wood supply of Anticosti Island.

Despite the fact the Anticosti Island represents an extreme case of composition change, it still constitutes a plausible scenario for intensively managed continental forest-pest systems. As it has been highlighted in this report, the largest sources of uncertainty often remain unknown; the higher productivity and resistance expected of tree plantations and brushed stands might not be possible following a change in insect outbreak regime. Future research on Anticosti Island's irruptive insect community is definitely needed to assess the effect of deer grazing as a surrogate for intensive forest management legacies.

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