Lessons learned from 12 years of ecological research on partial cuts in black spruce forests of northwestern Québec

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ABSTRACT
Multi-cohort management that creates or maintains an uneven structure within forest stands has been widely advocated as a means to attenuate the impact of forest harvesting. An experimental network was put in place in black spruce forests of northwestern Québec to test this assertion. Here we synthesize the biodiversity results in two main lessons: (1) at least 40% to 60% retention of pre-harvest basal area was required to maintain pre-harvest conditions for most species groups; (2) partial harvests showed the potential to be efficient deadwood delivery systems. In addition to these two main general conclusions, we emphasise that future research should examine whether partial harvest may be able to advance forest succession.

Keywords: partial harvest, biodiversity, retention, black spruce, boreal

RÉSUMÉ
L'aménagement multi-cohortes qui crée ou maintient une structure irrégulière dans les peuplements forestiers a été largement préconisé pour atténuer l'impact de l'exploitation forestière. Un réseau expérimental a été mis en place dans les forêts d'épinettes noires du nord-ouest du Québec pour tester cette affirmation. Dans cet article, nous retenons deux enseignements des résultats obtenus sur la biodiversité: (1) il a fallu laisser au moins de 40 % à 60 % de la surface terrière avant coupe pour maintenir des conditions d'avant la récolte pour la plupart des groupes d'espèces, (2) les coupes partielles ont montré qu'elles avaient la capacité de produire et de maintenir de façon efficace le recrutement" du bois mort. En plus de ces deux principales conclusions, nous soulignons que les recherches à venir devraient tenter de déterminer si la récolte partielle a le potentiel de faire progresser la succession forestière.

Mots-clés : récolte partielle, biodiversité, conservation, épinette noire, forêt boréale

Introduction

In boreal regions where tree diversity is limited, post-fire stand development results in multiple cohorts of trees, and the development of compositionally simple, yet structurally complex forests (Fig. 1; Bergeron and Fenton 2012). As a consequence, the use of multi-cohort management and other silvicultural practices that create or maintain an uneven structure within forest stands have been widely advocated in the literature (Bergeron and Harvey 1997, Work *et al.* 2004, Aubry *et al.* 2009) as a means to attenuate the impacts of even-aged management maintained through clearcut harvesting.

The removal of all or nearly all of the forest canopy during clearcut forest harvest has multiple impacts on both the forest environment and the resident biota, which have been enumerated by many authors (e.g., Keenan and Kimmins 1993). Canopy removal results in higher wind speeds due to greater fetch, and a dominantly open canopy. Higher wind speeds lead not only to a greater intensity of disturbance for individual organisms during storms, but also to greater drying and evapotranspiration potential. A predominantly open canopy obviously increases incident light, which in turn leads to increased temperatures and decreased humidity after harvest (Keenan and Kimmins 1993, Nyland 1996).

In addition to the immediate stresses of an altered microclimate, one of the main threats to forest-dwelling organisms posed by an even-aged harvest system is the reduction or elimination of deadwood, upon which many species depend for shelter or food (Hansen *et al.* 1991, Esseen *et al.* 1997). Significant species loss in boreal Fennoscandinavia has been linked conclusively to loss of deadwood following "normalization" of the forest landscape (Siitonen 2001, Gustafsson *et al.* 2010). Therefore, it is essential to evaluate the effects of partial harvesting on the availability and recruitment of this key attribute in forest ecosystems.

Partial cuts can mitigate some of these problems, as they maintain forest structure and biological legacies, such as snags and downed deadwood. Furthermore, residual living trees have the potential to continuously add inputs of new snags and logs, which is generally interrupted for several years after clearcut logging (Vaillancourt *et al.* 2008). Such a discontinuity in deadwood decay stages availability is often responsible for the loss of saproxylic species in managed forests (Similä *et al.* 2003).

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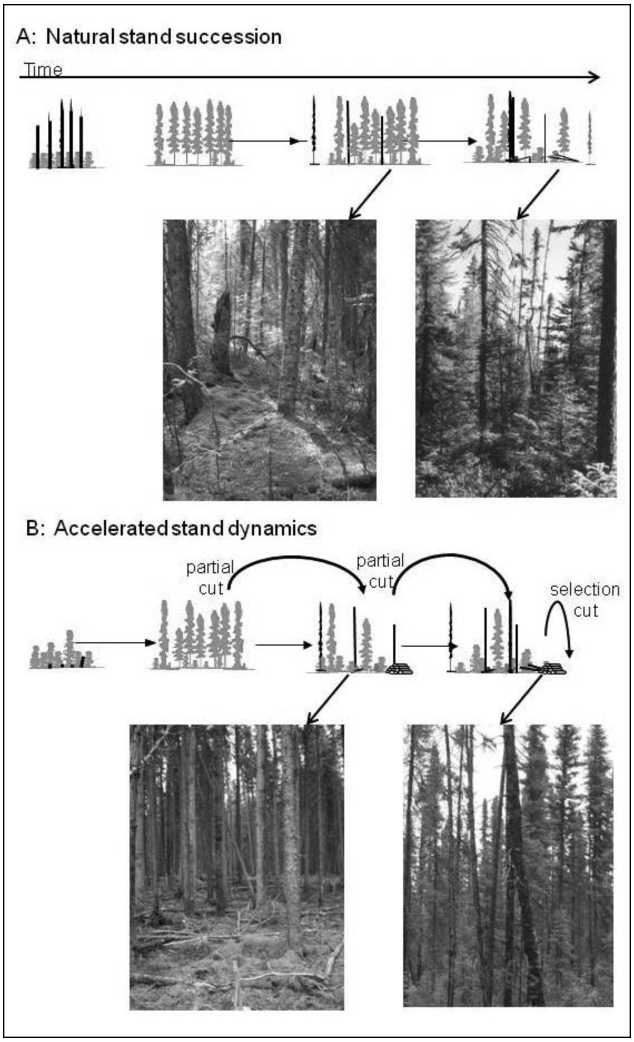

Fig. 1. Stand dynamics in black spruce forests with illustration and photos of (A) natural conditions and (B) using partial cuts to advance succession.

Therefore, partial cuts may maintain some aspects of forest biodiversity associated with ecosystem functions (Rosenvald and Lõhmus 2008). In this way, residual structures and ecological legacies serve as coarse-filter conservation, which may maintain species on the landscape following harvesting. Potential benefits of the residual structure left following multi-cohort approaches include 1) "retention lifeboats" that maintain species that require mature forest as surrounding harvested stands regenerate, 2) reduced dispersal distances among viable habitat patches that minimize "matrix effects" of the regenerating forest and 3) increased structural diversity of the regenerating forest that resembles the heterogeneity observed following disturbances such as insect outbreaks and windthrow (Bergeron *et al.* 1999, Kneeshaw *et al.* 2011). Furthermore, leaving residual structure may be useful for advancing forest succession to a later stage (Bergeron *et al.* 1999; Seymour and Hunter 1999). As such multi-cohort management is attractive to land managers in that it is purported to "reduce impact" and falls within accepted notions of "ecosystem-based management" (Seymour and Hunter 1999, Gauthier *et al.* 2008). Nonetheless, empirical verification of the success of multi-cohort management and operational implementation has lagged behind much of the enthusiasm and calls to action, particularly in the North American boreal forest where even-aged management remains predominant (CCFM 2011).

Extending from eastern Alberta to Newfoundland, a significant portion of boreal North America (approximately 205 million ha) is covered in black spruce and jack pine forests (Rowe 1972). In some regions, black spruce stands can remain dense and productive for millennia (Pollock and Payette 2010); however, in other areas where decomposition is significantly slower than production, many black spruce forests accumulate very thick organic layers over the mineral soil (Bonan and Shugart 1989). The Clay Belt of Québec and Ontario is a region where such stands are common. This large physiographic region has a variety of particularities associated with its low topographic relief and compact clay soils (Grondin 1996). Considerable portions of the landscape are prone to paludification, (the transformation of a forest on mineral soil to a forested peatland [Payette and Rochefort 2001]) between fires. During paludification a thick organic layer is accumulated over the mineral soil, changing the carbon balance (Bisbee *et al.* 2001, Bond-Lamberty *et al.* 2004, Lecomte *et al.* 2006) and lowering site productivity (Simard *et al.* 2007).

To better understand the efficacy of residual structure in mixed forests and black spruce feathermoss forests, a network was established in 1998 across northwestern Québec (RECPA or RÉseau des Coupes Partielles en Abitibi; Fig. 2). Each of the nine sites in the network includes one block of even-aged management (CPRS or cut with protection of soils and regeneration, which removes all trees with a DBH of 9 cm or greater), one block of partial harvest (primarily variable canopy retention, a non-diameter limit harvest type), and a control block that was not harvested. Each block is at least 20 ha in size in order to evaluate operational harvest conditions. Retention in the partial cut blocks of the RECPA sites varied from 11% to 75% retention (Table 1). Permanent plots were established in each block to monitor stand development as well as changes in communities of organisms that represented a cross-section of the biodiversity within these forests post-harvest. These organisms include birds, small mammals, hares, grouse, lichens, bryophytes, mushrooms and arthropods.

After almost 15 years of operation the effect of these cuts on the diversity and survival of a variety of organisms has been evaluated. In this article we present our general conclusions based on the 18 studies that have been carried out in the nine sites in the black spruce feathermoss zone. Specifically, we address the following questions: how much canopy needs to be retained if pre-harvest conditions are to be maintained? And can partial harvest maintain the function of structural diversity (Rosenvald and Lõhmus 2008) by keeping enough deadwood in the system (i.e., addressing in part the structural diversity function). Here we synthesize overall trends in the biodiversity of a variety of taxa into two general lessons regarding the effectiveness of partial cutting for biodiversity. We also offer some thought on future directions to improve our understanding of partial cutting effects and further support our experience in the Clay Belt region with published findings from other partial cut experiments conducted in similar boreal forests.

Table 1. Description of the intensity of harvest for the sites in the RECPA (RÉseau des Coupes Partielles en Abitibi) network. Three replicate blocks were within the Muskuchii site, and two replicate blocks at the Cramolet site.

	Living trees			
Site	Basal area before harvest (m2/ha)c	Basal area after harvest (m2/ha)c	Percent of basal area harvested	Percent of stems >9cm harvested
Muskuchii 1a	23.80	6.79	71.47	55.54
Muskuchii 2[a]	24.57	9.50	61.33	43.52
Muskuchii 3[a]	12.54	4.12	67.15	50.90
Dufaya	17.67	5.74	67.52	69.62
Maïcasagib	–	7.51	45.00	–
Gaudetb	12.55	2.13	83.03	76.13
Fénelonb	22.66	3.47	84.69	76.97
Puiseauxb	19.68	4.87	75.25	63.17
Surimaub	10.62	1.11	89.55	85.00
Villarsb	17.33	9.71	43.97	42.78
Cramolet 1b	30.37	23.22	23.53	32.66
Cramolet 2b	27.66	11.03	60.11	63.99

[a] Sites harvested by CPPTM (harvest with protection of small merchantable stems)
[b] Sites harvested by CAMC (harvest variable canopy retention)
[c] Basal area includes all of the stems

Lesson 1: At least 40% to 60% retention of pre-harvest basal area is required to maintain pre-harvest levels of biodiversity for a variety of taxa

Partial cuts should be able to attenuate some of the impacts of clearcut harvesting by retaining part of the forest stand. Can we observe a biological effect of the reduced physical changes associated with partial harvest compared to clearcut harvest?

Based on ten species groups that include hundreds of species with diverse life histories, we observed three broad and generalized patterns of species response to partial cutting. These groups include: 1) species that show no response to either clearcutting or partial cutting and for whom harvesting less than 40% retention is acceptable, 2) species that are sensitive to clearcutting but where 40% to 60% retention is acceptable and 3) species for whom even 40% to 60% retention is insufficient to maintain populations (see Table 2).

A species groups for which 40% to 60% retention maintains similar community composition to unharvested forest, is cryptogams. Two years post-harvest, Fenton and Bergeron (2007) observed shifts in *Sphagnum* species composition in patches where retention was less than 20%, as at these low levels of retention sun-loving species established and thrived, to the detriment of shade-tolerant species. Arseneault *et al*. (2012) found that epixylic bryophyte (moss and liverwort) richness decreased with decreasing retention, with on average only one epixylic species per log with less than 40% retention. Similar results were found by Paltto *et al*. (2008) in oak forests in Sweden. However, in Alberta epiphyte bryophyte communities were severely affected at retention levels below 75% (Caners *et al*. 2010). Similarly, two

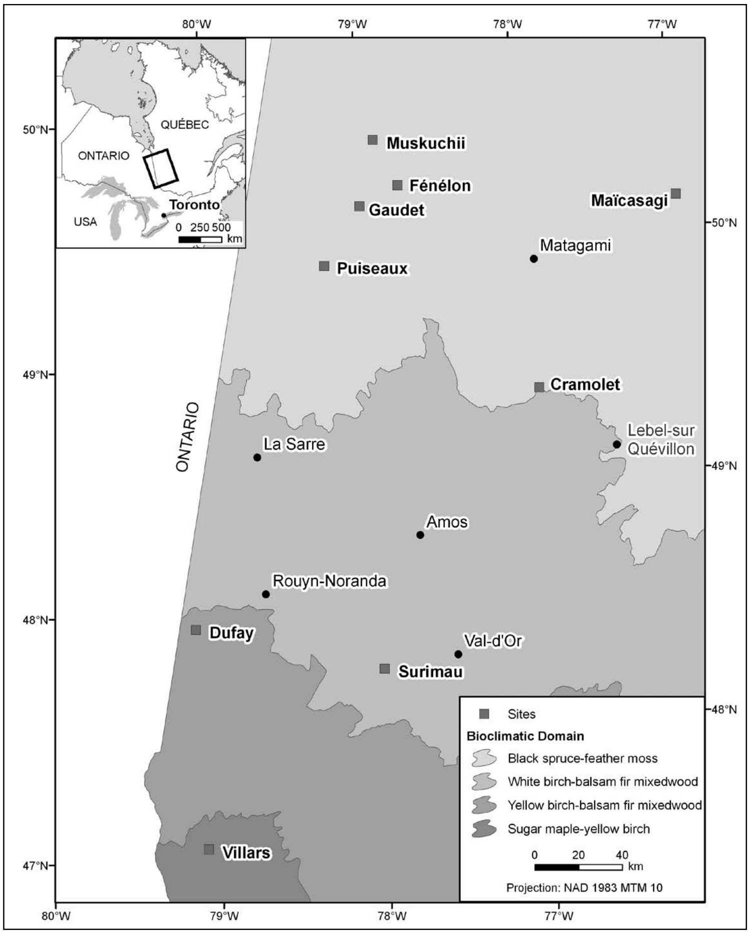

Fig. 2. Map of the RECPA Network (RÉseau des coupes partielles d'Abitibi). Squares indicate the sites (including one block each of clearcut, partial cut and control), circles indicate cities in the regions of Abitibi-Témiscamingue and Nord-du-Québec. Two sites indicated on the map represent several sites: Muskuchii (three sites) and Cramolet (two sites). The location of the region represented in the map is indicated by the square in the inset map.

Table 2. Summary of response of different groups to different levels of retention (Lesson 1)

Response groups	Response sub-group	Species groups	Source
Conservation of community at retention below 40%		Vascular plants	Bescond *et al*. 2011
		Small mammals	Cheveau 2003
Conservation of community at 40% to 60% retention		Forest floor *Sphagnum*	Fenton and Bergeron 2006
		Epixylic bryophytes	Arseneault *et al*. 2012
		Epiphytic lichens	Boudreault 2011
		Forest birds	Poulin 2005
No conservation of community at 40% to 60%	Potential conservation of community at retention levels of 60% or higher	Soil arthropods	Paradis and Work 2011
		Beetles (fungi and wood feeding and predators)	Jacobs and Work 2012
	No conservation even at high levels of retention	Snowshoe hare	Bois *et al*. 2012
		Spruce grouse	Lycke *et al*. 2011

species of epiphytic lichen, *Evernia mesomorpha* Nyl. and *Bryoria nadvornikiana* (Gyeln.) Brodo & D. Hawksw., had significantly lower growth rates when retention was less than 30% and 60%, respectively (Boudreault 2011).

Invertebrate assemblages were profoundly affected by harvest-induced changes in stand structure. For litter-dwelling spiders and ground beetles, partial cutting treatments with low retention (<40%) provided little conservation value and assemblages in these partial cuts did not differ from those found in clearcuts (Paradis and Work 2011, Jacobs and Work 2012). There is some evidence suggesting that high levels of retention (greater than 60%) may be sufficient to maintain arthropod assemblages consistent with older, uncut forests. This evidence is based on data collected at Cramolet within the RECPA network. Studies that have added additional stands with higher levels of standing retention continue to examine this question. Interestingly, the results of Légaré *et al*. (2011) also suggest that higher levels of retention maintain communities similar to older, uncut forests.

For beetles, harvesting provoked a fundamental shift in trophic webs (Jacobs and Work 2012), as changes in stand structure cascaded to directly influence the composition of wood-feeding fungi and beetles, which then had indirect effects on fungus-feeding and predatory beetles. However, the degree of change was proportional to basal area removed, suggesting that while the low retention levels in the RECPA sites resulted in dramatic change, higher levels of retention (thus lower extraction rates) would potentially result in communities more similar to the pre-harvest stand.

Taken together, partial cutting with the low levels of retention created invertebrate assemblages that are similar to those found in clearcut stands. This pattern is repeated among wood-feeder beetles, fungivore beetles, predatory beetles, soil microarthropods and mites, and reflects the responses of 531 species. This includes 12 species that are currently not described to science. The most intriguing response was an undescribed Latridiidae species in the genus *Corticaria* that was found in 10 of the 13 uncut forests sampled but none were found in the six harvested stands examined. Consequently, the results from the RECPA sites strongly support the assertion that higher levels of retention are necessary to conserve arthropod communities similar to unharvested forest.

Our findings support the general trend that relatively high levels of retention are necessary to maintain invertebrate assemblages that has been reported in Canada and elsewhere. For example in boreal mixedwood forests, Work *et al*. (2010) reported that retention levels of greater than 50% were required to maintain ground beetles and that higher levels of retention were required in later successional stages. Thus, the effectiveness of partial cutting as a conservation tool will necessarily depend on the stand type and higher levels of retention are required in later successional stages. For spiders dwelling in mixedwood forests, Buddle and Shorthouse (2008) observed that retention levels ranging from 66% to 75% were required to maintain spider assemblages in early successional aspen stands in both Quebec and Alberta, at least initially following harvest. The response of spiders in Alberta in early successional stands was later reinterpreted by Pinzon *et al*. (2012) based on longer-term monitoring seven years post-harvest. As was true of ground beetles, Pinzon *et al*. (2012) also found that 10% retention was sufficient to mitigate impacts on spider assemblages in early successional stands but that higher retention levels, >75% retention, were required in later successional stages. In a related article, Pinzon *et al*. (2011) also reported significant effects of increased variable retention on spiders living on ground vegetation. Outside of Canada, the response of litter-dwelling arthropods to increased levels of post-harvest retention has been less definitive. For example Martikainen *et al*. (2006) observed that retention levels up to 50 m^3/ha (approximately 17% retention) had some influence on the abundance and total species richness of ground beetles, but the effect was limited when compared to those of prescribed burning in boreal pine forests in Scandinavia. In the Douglas-fir forests of the Pacific Northwest, Halaj *et al*. (2008) reported that retention levels of up to 40% provided no significant conservation value for ground beetles and spiders. These studies corroborate findings from the RECPA and elsewhere that indicate that lower levels of retention (below 40%) will likely provide little benefit for biodiversity of litter-dwelling arthropods.

While a clearer portrait of litter arthropod responses to partial harvesting is emerging, the response of other taxa, such as saproxylic species, is only beginning to emerge, despite a more fundamental ecological link between saproxylic organisms and the abundance of host material (standing and downed deadwood). Jacobs *et al.* (2007) reported little positive effect of variable retention on saproxylic beetles in late successional forests in Western Alberta. Halaj *et al.* (2009) measured activity of arthropods on retention trees and found higher numbers on retention trees in partially cut areas than trees in uncut stands. While providing an interesting comment on the relative importance of individual retention trees within the context of managed stands, the reduction of tree density in partially cut sites offset the relative increase in the observed "concentration" of arthropods suggesting partial cut stands have lower overall densities of bark-dwelling organisms. However, Stenbacka *et al.* (2010) reported that residual structure left following forest thinning maintained saproxylic and particularly red-listed species more efficiently than more intensive clearcutting. Identifying retention targets for partial cutting from Stenbacka *et al.* (2010) is difficult as the study was not designed specifically for this purpose; however, it does draw the critical link between variable retention and the importance of downed deadwood. These authors, like many others (Siitonen 2001, Stokland 2001, Jonsell and Weslien 2003) have stressed the point that tree retention is an important future source of deadwood for saproxylic species.

A study of songbirds' responses to partial cutting in one site of the RECPA network showed that most species associated with late-seral forests (>100 years) tolerated a canopy opening of 31% at the stand level (Poulin 2005). The Golden-crowned Kinglet (*Regulus satrapa* Lichtenstein 1823) was the only late-seral forest species that experienced a significant population decline one year after partial harvesting. This species is already known to be one of the most sensitive boreal songbirds to partial harvesting throughout its range (Vanderwel *et al.* 2007, 2009; Leblanc *et al.* 2010). Overall, these results suggest that partial cutting at retention levels above 66% of the canopy cover may affect bird populations for some forest specialists, but does not drastically change the composition of late-seral bird communities. These results are in agreement with a recent North American meta-analysis showing that uniform harvests that leave at least 70% tree retention could cause a decline in population of up to 25% for a few species, but that this level of retention would not be expected to induce 50% reductions in bird species abundance (Vanderwel *et al.* 2007). Hence, at this level of retention, partial cuts could be a promising silvicultural practice for maintenance of forest songbirds characteristic of older forests.

Other organisms appeared to be tolerant of lower retention levels. Both understory plants (Bescond *et al.* 2011) and small mammal populations (Cheveau 2003) showed patterns where community composition in partial cuts with less than 40% retention maintained most of the characteristics of the pre-harvest community, but with the limited incursion of early successional species. In both cases the generally open nature of black spruce forests may be playing a role of pre-filtering the community for species capable of tolerating high light conditions. Similar results where stands with low levels of retention are very similar to unharvested stands have also been reported for vascular plant communities (Deal 2001, Craig and MacDonald 2009) and for small mammal communities (Vanderwel *et al.* 2009).

Finally, for two boreal game species levels of retention over 55% in the RECPA network (Snowshoe Hare [*Lepus americanus* Erxleben]; Valois 2005) or even 60% in nearby commercially thinned stands (Snowshoe Hare, Bois *et al.* 2012 and Spruce Grouse [*Falcipennis canadensis* (Linnaeus, 1758], Lycke *et al.* 2011) were not sufficient to maintain populations. Within the RECPA, short-term negative effects of partial harvesting (one year post treatment) on hare were initially described (Valois 2005). Although most of the RECPA network was established too recently to provide long-term responses, it was found that 11 to 18 years are needed before commercially thinned stands return to the same level of hare signs (pellets and tracks) as control stands (Bois *et al.* 2012). In both the RECPA and thinning studies, lateral cover was the dominant parameter influencing hare habitat use (Valois 2005, Bois *et al.* 2012). Similar negative effects of commercial thinning were also found for spruce grouse (Lycke *et al.* 2011). Regardless of the presence of mature trees in commercially thinned stands, this treatment was comparable, in terms of grouse selection in spring (site occupancy) or in summer (telemetry), to areas without mature trees such as clearcuts. Similar results were obtained in a winter habitat use study with 66% retention in British Columbia (Huggard 2003). Because these two game species are known to be associated with dense vegetation cover, the presence of skid trails increasing the effect of the removal of stems on residual protective cover may explain these results in RECPA as well as in commercially thinned sites.

In order to limit the impact of partial cuts on game species linked to a dense vegetation cover, we suggest that it should be applied in stands where there is already significant regeneration or where the lateral cover is over 60% (Potvin *et al.* 2005). Even if high levels of retention are used, these studies highlight the importance of maintaining protective cover for game species, as they probably respond more strongly to lateral cover reduction rather than tree removal per se. Indeed, in selection cuts where there is a negligible effect on the reduction of lateral cover (with approximately 50% retention), a recent study conducted in eastern feathermoss forests has shown that this treatment appears to be a promising avenue for maintaining snowshoe hare, even over the short term (Hodson *et al.* 2012).

Lesson 2:Partial harvests offer the potential to be a sufficient deadwood delivery system and maintain deadwood-associated species

The amount of deadwood present in a stand and the processes of deadwood deposition and decomposition is dynamic (Jonsson *et al.* 2005). Deadwood is created by tree death, which can be simultaneous, as is created by fire, or gradual (Angers *et al.* 2010, 2011). In both post-fire and older forest stages, tree senescence and death provide host sources for saproxylic insects that may colonize standing deadwood (Saint-Germain *et al.* 2004, 2007; Boulanger and Sirois 2007) and downed deadwood (Vanderwell *et al.* 2006) of different decay stages. Standing deadwood represents the first deadwood pool, followed by lying deadwood, which is slowly depleted. Clearcut harvesting decreases or significantly alters deadwood pools, which become concentrated in unharvested remnant habitats including riparian buffers, linear habitats or small patches (Vaillancourt *et al.* 2008, Webb *et al.* 2008, Saint-Germain and Drapeau 2011). By harvesting all of the mature trees no new deadwood can enter the system. During harvesting much of the existing deadwood on the forest floor is crushed by harvesters and the uncrushed deadwood that pre-dated the harvest is no longer suitable as habitat as it is dry (Haeussler *et al.* 2007, Arseneault *et al.* 2012). Also, the exit of deadwood from the system is modified in a clearcut, where higher temperatures lead to changes in fungi and wood-eating beetle species compositions and growth rates accelerate downed deadwood decomposition (Jacobs and Work 2012). Ultimately, this would lead to a longer period of extremely low stand-level deadwood volumes until the regenerating forest starts creating new deadwood (Jacobs and Work 2012). Natural disturbances such as fire and insect outbreaks typically create large volumes of deadwood, and typically generate trees that will die and enter the deadwood pool as the forest regenerates (Kafka *et al.* 2001, Bergeron *et al.* 2002, Perera *et al.* 2009, Angers *et al.* 2011). Saproxylic insect populations can be maintained through time by variations in fire severity or insect outbreak severity, which in turn causes delayed tree mortality and a continuous input of deadwood (Nappi *et al.* 2010). Unlike natural disturbances, extensive clearcuts are likely to generate important dispersal constraints for saproxylic insects and local population breakdowns given 1) the decrease in the density of suitable host trees and 2) the increase in their dispersion within a matrix mainly composed of regenerating areas (Saint-Germain and Drapeau 2011).

Studies in RECPA have illustrated that snag abundance decreases after partial cuts with low retention, and remains constant at higher retention levels (Table 3). Additionally, a number of deadwood-dependent species in both standing and downed deadwood pools were maintained in the partial cuts at levels similar to or even above the control.

For example, the Black-backed Woodpecker (*Picoides arcticus* [Swainson, 1832]), the American Three-toed Woodpecker (*Picoides dorsalis* S.F. Baird, 1858) and Hairy Woodpeckers (*Picoides villosus* [Linnaeus, 1766]) were more abundant in mature partial cuts than in mature uncut control stands in one of the RECPA sites (Muskuchii) where woodpecker surveys were conducted (Nappi 2009). Black-backed and American Three-toed Woodpeckers also foraged more often in partial cuts than in controls. Moreover, active nesting cavities of these two species were also found in partial cuts (Nappi 2009). The combination of open habitat and high recruitment of recently dead trees in these partial cuts generated suitable forest conditions for standing deadwood associates such as woodpeckers. Maintaining these cavity excavators is also important for many other cavity users that do not excavate cavities, but rely upon those created by woodpeckers for nesting or roosting purposes (Drapeau *et al.* 2009). Persistence of suitable foraging and nesting habitat conditions for woodpeckers is thus critical for cavity-using communities often referred to as nest webs (*sensu* Leupin *et al.* 2004), an important component of the functional diversity associated to deadwood in the boreal ecosystem. Breeding activity of keystone species such as woodpeckers is also an indication that partial cuts harbour appropriate deadwood pools for saproxylic insects, a main prey for woodpeckers (Nappi 2009).

Similarly, both the general bryophyte and the epixylic bryophyte communities were found to be richer in partial cuts than in clearcuts or even control plots (Arseneault *et al.* 2012). Furthermore, the percent cover of epixylic species was higher on logs in partial cuts than on logs in either the controls or the clearcuts. This surprising result appears to be due to the larger size of logs and their slightly more decomposed state in the partial cuts. The higher richness of epixylics also suggests that these partial cuts provide a suitable habitat for these sensitive old-growth-associated species.

Partial cuts also provided a deadwood environment sufficient to maintain boreal small mammals. Abundance of five species (i.e., Red-backed Voles [*Myodes gapperi* (Vigors, 1830)], Meadow Voles [*Microtus pennsylvanicus* (Ord, 1815)], Southern Bog Lemmings [*Synaptomys cooperi* Baird, 1858], Deer Mice [*Peromyscus maniculatus* (Wagner, 1845)], and Masked Shrews [*Sorex cinereus* Kerr, 1792]; Fauteux *et al.* 2012) responded positively to volumes of well-decayed coarse woody debris (CWD) in all treatments. Red-backed voles were often less abundant in harvested stands (partial cut or clearcut), but patches of partial cuts with high volumes of well decayed CWD (11.4 m^3 per 0.03 ha) have the potential to maintain numbers similar to those in unharvested controls (Fauteux *et al.* 2012). Furthermore, we found that late-decay CWD promoted the co-occurrence of competing small mammal species (D. Fauteux *et al.* unpublished data). This clearly indicates that the abundance of CWD in late-decay classes can mitigate the impacts of tree removal. Thus, similar abundances of red-backed voles in harvested and uncut stands may occur due to the presence of abundant forest floor resources such as CWD, as reported in other studies (e.g., Potvin *et al.* 1999, Etcheverry *et al.* 2005, Klenner and Sullivan 2009).

The stage of decay is also important for assessing the responses of boreal small mammals to CWD. Benefits provided by decaying logs and stumps for small mammals include abundant food such as fungi and insects, high-humidity microhabitats, and better cover against predators (Maser *et al.* 1979). Partial cuts, by retaining large trees throughout forest cutting rotations, have the potential to ensure continual input of this critical resource. In order for this potential to be reached, however, a concerted effort to maintain snags through the multiple entries inherent to a partial cut treatment needs to be made. The health and safety issues associated with harvesting in stands with snags also need to be addressed.

Table 3. Basal area (m^2/ha) of snags in three sites before, immediately after and five years after harvest, by treatment

Site	Treatment	Before harvest	Immediately after harvest	Five years after harvest
Cramolet	Control	4.25±3.18	4.68±3.10	3.75±2.65
	66% retention	4.90±2.15	4.98±1.75	3.85±2.33
	33% retention	2.73±1.80	0.98±0.75	2.80±1.80
	Clearcut	4.13±1.93	0.35±0.45	0.50±0.80
Fénelon	Control	2.35±1.33	2.35±1.33	2.30±1.05
	15% retention	3.70±2.38	2.00±2.40	2.43±0.30
	Clearcut	4.93±2.70	0.43±0.88	0.63±1.20
Puiseaux	Control	3.43±1.75	3.43±1.75	3.25±2.40
	25% retention	3.55±1.88	1.03±1.03	1.73±1.33
	Clearcut	3.48±1.53	0.63±0.90	0.65+/- 1.00

Future Directions: Partial harvests may be able to advance forest succession

They have been proposed as a tool in ecosystem-based management where the idea would be to "create" older stands through silvicultural techniques, as most stands open up with age, as trees senesce and die (Seymour and Hunter 1999, Gauthier *et al.* 2008). This would allow forest managers to harvest some volume while maintaining or increasing the cover of multi-cohort stands on the forest landscape (Bergeron *et al.* 1999). Results of initial studies on the bryophyte layer and invertebrate communities in the RECPA network begin to suggest results for two transitions (Fig. 1), from young to relatively old forest (i.e., Cohort 1 to Cohort 2) and relatively old forest to very old forest (i.e., Cohort 2 to Cohort 3).

Advancing stand succession from Cohort 1 to Cohort 2 has a higher potential of being operationally feasible. Successional models demonstrate that stands naturally lose almost 50% of their standing biomass (c 10Kg/m^2) in the transition for Cohort 1 to Cohort 2 (Lecomte *et al.* 2006). Alternatively, removing this much biomass from Cohort 2 stands results in stands with levels of biomass much lower than what is observed in the first 2000 years of forest succession (Lecomte *et al.* 2006).

Currently for invertebrates, it is difficult to make strong conclusions on the efficacy of partial cutting for advancing species composition consistent with succession. We have some preliminary evidence suggesting that in young stands (Cohort 1), high levels of retention (66%) may create communities similar to those found in old-growth stands (Cohort 2; Paradis and Work 2011). However, the results for game species (Lycke *et al.* 2011, Bois *et al.* 2012) suggest that special care needs to be taken in maintaining lateral cover when these partial cuts are carried out. For species associated with standing deadwood such as cavity users (birds and mammals) there is a research need to more thoroughly document the dynamics of deadwood recruitment and its use by these organisms in partially cut stands. Given their keystone function as cavity excavators in the boreal forest (Drapeau *et al.* 2009), woodpeckers should be the focal indicators of the efficacy of partial cutting for maintaining nest webs (*sensu* Martin *et al.* 2004) of old forests.

In addition to this transition from Cohort 1 (even-aged) to Cohort 2 (uneven-aged), stands that were already old and uneven were included in the network. The partial harvest of these stands would then theoretically push the forest environment towards more open, paludified environments, such as are found in very old stands on the Clay Belt (Lecomte *et al.* 2006, Simard *et al.* 2007). Results from *Sphagnum* species suggest that this transition was successful as the *Sphagnum* species community was shifting towards what is typically found in these very old stands (Fenton and Bergeron 2007).

However, it is not clear that the transition from Cohort 2 to Cohort 3 was entirely successful. The assemblages of arthropods fell outside the range of natural variability observed in 300+ year chronosequence of stands, suggesting that in this case that partial-cut harvesting created assemblages that resembled very old Cohort 3 stands (over 700 years) or assemblages that have no natural analogues (Paradis and Work 2011, Jacobs and Work 2012). However, more work that compares communities after partial harvest to changes along a chronosequence needs to be done.

Finally, it is not clear that it is desirable to create more Cohort 3 stands as their productivity is low, and an abundance of them, in some cases, is maintained on the landscape (Chaieb *et al.* 2010). Low levels of retention (<40%) can result in an increased rate of paludification (Fenton and Bergeron 2007), as the increased light availability stimulates the establishment and growth of light-demanding *Sphagnum* species. These species can grow up to 4 cm per year (Heijmans *et al.* 2002, Fenton and Bergeron 2007) and the humus layer will quickly accumulate beneath them, as their high growth rate is paired with a low decomposition rate (Turetsky *et al.* 2008, Fenton *et al.* 2010). As a consequence of this thick humus layer, soil temperature decreases, nutrient cycling is slowed and productivity is lowered (Simard *et al.* 2007). High levels of retention that do not significantly open the canopy should limit the expansion of light-demanding *Sphagnum* species, as they are rarely found in microhabitats with less than 40% open canopy (Fenton and Bergeron 2006).

General Conclusion

The RECPA network has allowed us to illustrate that partial cutting can limit some of the negative environmental impacts of clearcut harvesting, and can also attenuate the impact of harvest on deadwood flux. The successful use of partial cuts to accelerate succession seems to be more difficult to achieve, and the results from RECPA on this specific topic are for the moment preliminary.

The low level of retention in many of the RECPA sites, and the resultant significant changes in many of the observed taxa, illustrate that partial cuts must be less drastic if the objective is to maintain the same or very similar community of associated forest species. The limit of 40% to 60% retention suggested here is based on the negative effect of lower retention levels on many groups. However, different silvicultural trials across Canada have come to much the same conclusion for a variety of species groups. For example in SAFE (Silviculture et aménagement forestier écosystémiques) in the mixedwood of northwestern Québec retention of 66% of the pre-harvest stand resulted in plant communities much more similar to the control than 33% retention of the pre-harvest stand (Brais *et al.* 2004, Haeussler *et al.* 2007). Similarly, in a meta-analysis Vanderwell *et al.* (2009) found that retention levels down to 50% appeared to have negligible effects on vertebrates in the boreal forest of Ontario. In the mixedwood forests of northern Alberta EMEND (Ecosystem Management Emulating Natural Disturbance), 50% retention was found to be a cutoff point for a variety of species groups, including carabids and bryophytes (Caners *et al.* 2010, Work *et al.* 2010).

In Fennoscandinavia, work has focused on green tree retention (<15% retention) and while these studies have shown that some retention is better than none, the low level of retention could not maintain old forest conditions or communities associated with old forests (Rosenvald and Lõhmus 2008, Gustafsson *et al.* 2010). Results for individual groups reported here are also supported, with similar results for bryophytes (Paltto *et al.* 2008) and soil fauna (Siira-Pietikäinen and Haimi 2009) as was found in the RECPA network.

The very significant amount of work invested in understanding the biological utility of partial cuts in the Canadian forest in Québec (Brais *et al.* 2004, Fenton *et al.* 2009), but also across Canada (Deans *et al.* 2003, Thorpe *et al.* 2007, Craig and Macdonald 2009, Vanderwell *et al.* 2009, Solarik *et al.* 2010), illustrates the enthusiasm of scientists for the use of this technique as a compromise between conservation and harvest. However, as of 2009, the last year for which data are available, partial cuts still comprised a very small proportion of the area harvested in Canada (CCFM 2011). Perhaps the focus should now be on developing economic and operational feasibility (including the development of landscape level planning of partial cuts) for these harvest types so that they may be adopted into an integrated silvicultural system.

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