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SIMILARITIES AND DIFFERENCES BETWEEN HARVESTING- AND WILDFIRE-INDUCED DISTURBANCES IN FIRE-MEDIATED CANADIAN LANDSCAPES

TECHNICAL BULLETIN NO. 924

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PRESIDENT'S NOTE

Forests are often disturbed by fire, wind, and other natural forces. Immediate effects may include tree mortality and soil erosion. Over time, however, disturbance can lead to forest renewal with beneficial effects on biodiversity and opportunities for human use.

Emulation of natural disturbance is often recommended as a strategy for conserving biodiversity in managed forests. The underlying concept is that plant and animal species are adapted to natural disturbance regimes and may be able to tolerate some degree of comparable disturbance by timber harvest. Exploring the validity and limitations of this concept in various circumstances and applications has been a major theme in forest ecosystems research in recent decades.

Wildfire and timber harvest are significant causes of disturbance in Canada's forests. Fire affects about 2.1 million hectares per year on average, while harvest affects about 0.9 million hectares per year. Varying perceptions of the relative ecological effects of fire and harvest are often debated by stakeholders in Canada's forestry sector and sometimes have important effects on forest management decisions and wood supplies.

This report is a review of scientific literature on the ecological effects of wildfire and timber harvest with emphasis on forest types found in Canada. The authors demonstrate that ecological differences between burned and harvested stands are greatest immediately after disturbance and are usually difficult to detect within a few decades after disturbance. At the landscape scale, the greatest difference between harvesting and fire regimes is the resulting stand age distributions, with fire regimes generally having a greater proportion of forest area in older age classes. The authors provide management recommendations for minimizing ecological differences between harvest and fire regimes. They also suggest priorities for research to fill key information gaps.

Information in this report suggests a need to define ecological circumstances and outcomes of interest when comparing fire and harvest. Relevant ecological circumstances include soil characteristics, forest type, fire intensity, wildlife community characteristics, and forest management history. Outcomes of interest often vary among stakeholders and depend on their perceptions of the social, economic, and ecological aspects of sustainable forestry. This report will help increase understanding of outcomes related to ecological effects of fire and harvest.

Ronald A. Yeske

October 2006

MOT DU PRÉSIDENT

Les forêts sont souvent perturbées par le feu, le vent ou d'autres forces naturelles. La mortalité des arbres et l'érosion des sols constituent habituellement les effets immédiats associés à ces perturbations. Avec le temps, toutefois, ces perturbations peuvent entraîner le renouvellement de la forêt et, du même coup, créer des effets bénéfiques sur la biodiversité ainsi que des opportunités d'utilisation par l'humain.

On recommande souvent de s'inspirer de la dynamique des perturbations naturelles pour développer une stratégie de conservation de la biodiversité dans les forêts aménagées. En effet, les espèces de plantes et d'animaux sont adaptées aux régimes de perturbations naturelles et peuvent être en mesure de tolérer un certain niveau de perturbation comparable lors des activités forestières. Depuis les dernières décennies, l'exploration de la validité et des limites de ce concept dans diverses circonstances de même que ses applications demeurent un thème majeur de la recherche sur les écosystèmes forestiers.

Les feux de forêts et les coupes forestières constituent des causes importantes de perturbations dans les forêts canadiennes. Le feu affecte environ 2,1 millions d'hectares par année en moyenne, tandis que la récolte affecte environ 0,9 million d'hectares par année. Les parties prenantes du secteur forestier canadien débattent souvent des différentes perceptions liées aux effets écologiques entraînés par le feu et la coupe forestière. Parfois, ces perceptions influencent de façon importante les décisions reliées à l'aménagement de la forêt et l'approvisionnement en bois.

Dans ce rapport, on retrouve une revue de la littérature scientifique portant sur les effets écologiques des feux de forêts et de la coupe forestière, en mettant l'accent sur les types de forêts retrouvées au Canada. Les auteurs démontrent que les différences écologiques entre les peuplements incendiés et récoltés sont plus importantes immédiatement après la perturbation et sont généralement difficiles à détecter quelques décennies après la perturbation. À l'échelle du paysage, la plus grande différence entre les régimes de récolte et d'incendie se situe au niveau de la distribution d'âges des peuplements. En comparaison avec des paysages sous l'influence de la coupe forestière, les paysages sous un régime de feu ont généralement une plus grande proportion de la surface forestière comportant des classes plus âgées. Les auteurs fournissent des recommandations d'aménagement pour minimiser les différences écologiques entre les régimes d'incendie et de récolte. Ils proposent également des priorités de recherche afin de combler le manque d'informations dans ce domaine.

L'information contenue dans ce rapport souligne le besoin de définir les circonstances écologiques et les résultats d'intérêt lors de la comparaison entre l'incendie et la récolte. Parmi les circonstances écologiques pertinentes, mentionnons les caractéristiques des sols, le type de forêt, l'intensité du feu, les caractéristiques de la communauté faunique et l'historique d'aménagement forestier. Les résultats varient souvent selon les parties prenantes et dépendent de leurs perceptions des aspects sociaux, économiques et écologiques de la forêt durable. Ce rapport aidera à améliorer la compréhension des résultats reliés aux effets écologiques des incendies et de la récolte.

Ronald A. Yeske

Octobre 2006

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ABSTRACT

For decades, many have hypothesised that the effects of harvesting and wildfire differed significantly and that this would have significant effects on ecosystem processes and biodiversity. However, it is only recently that an appreciable amount of scientific data has emerged on this topic. In this report, we present our review of the similarities and differences between the ecological effects of fire- and harvesting-induced disturbances that have been noted in the scientific literature. Comparisons of the effects of these disturbances on numerous forest attributes (coarse woody debris, soil nutrients, productivity, plant diversity, wildlife response) are presented at two distinct spatial scales: stand and landscape.

At the stand scale, our review noted significant differences between harvesting and wildfire early after disturbance. Structurally, young post-fire stands are characterized by more snags, less downed woody debris, and significantly thinner forest floors than logged sites. Additionally, while both disturbances generate a pulse of extractable nutrients, the intensity of the pulse is greater after wildfire than clearcut harvesting and an increase in soil pH is observed after fire as opposed to little change or a slight decrease after harvesting.

Early after disturbance, biodiversity elements significantly differ between burned and logged sites. Dissimilar understory vascular and non-vascular communities generally colonize burned and logged sites, although differences are usually a question of abundance rather than species absence/presence. As compared to fire, faunal assemblages, be it mammals, invertebrates or birds, all seem to respond differently to harvesting. Among these faunal groups, species specifically associated with snags were the most likely to show a contrasting response to harvesting- and wildfire-induced disturbances.

Tree species respond differently to fire- and harvesting-induced disturbances, with harvesting favouring the establishment of deciduous species (notably trembling aspen, *Populus tremuloides*) and of coniferous tree species not adapted to fire such as balsam fir (*Abies balsamea*). Furthermore, there are commonly more residual deciduous trees in clearcuts than in fires. Because of this and the differential response of tree species to these two types of disturbances, divergent successional patterns with respect to overstory tree species compositions can be observed in burned and harvested stands. While we noted some variability among studies, stand and tree productivity are generally similar in burned and logged sites.

When the effects of harvesting- and wildfire-induced disturbances are compared at longer temporal scales, our review noted that most forest attributes that were reported as dissimilar early after disturbance converged a few decades post-disturbance. Nonetheless, thicker forest floors observed after logging as compared to fire appear to persist numerous decades after disturbance. Additionally, while faunal communities do become less different as time passes, late in succession, some species present in burned stands are either significantly less abundant or absent in similarly aged logged stands. Finally, several studies warn that while the effects of wildfire- and harvesting-induced disturbances do not significantly differ after a few decades, there is some concern about the ability of harvesting-induced disturbances to recreate the full range of natural variability observed during post-fire stand succession.

Unfortunately, little research has compared the effects of alternative silvicultural interventions (partial retention, partial cutting, etc.) or site preparation techniques (controlled burning, scarification, etc.) to the effects of wildfires. However, the few studies comparing the effects of post-logging control burns and different levels of retention indicate that these practices may attenuate some of the differences observed early after disturbance. Our review indicates that as compared to wildfire alone, salvage logging can have significant effects on ecological processes, biological legacies and the abundance of species commonly encountered only after fire. Removal of fire-killed trees can affect tree regeneration, understory composition, the abundance and distribution of dead wood, wildlife habitat, and soil properties. Nonetheless, many of these effects are site-specific; hence, additional investments in research are needed to support management decisions and policy development.

At the landscape scale, the main difference between fire and harvesting regimes is the distribution of stand age classes. The proportion of stands older than the rotation period (usually 100 yrs) tends toward zero under a fully regulated harvesting regime, while it is around 35% under a fire regime of similar rotation period. This fundamental difference results in a significant loss of advanced seral stage forests in managed landscapes, thereby affecting organisms that are primarily associated with such stands. Interestingly, since harvesting-induced disturbances are unable to recreate the conditions commonly found in young burned stands, landscapes under the influence of harvesting will also be characterized by a reduction of stands capable of replacing the ecological role of young burned stands within landscapes. Unfortunately, only a few studies have empirically compared the effects of wildfire and harvesting at the landscape scale under similar rotation periods. Nonetheless, research demonstrates that fires usually produce more heterogeneous landscapes than clearcuts, with more remnant islands. Fires are also more complex in shape, and have edges that are more gradual than clearcuts.

In conclusion, our review reveals two main challenges faced by forest managers in order to generate similar ecological effects as produced by fire. First, managers need to improve management practices in order to minimize the differences observed between young post-harvest stands and young post-fire stands, particularly with respect to coarse woody debris and soil conditions. Second, managers need to maintain some areas with the tree species composition and structural attributes characteristic of over-mature fire-origin stands. Such stands can occupy a significant portion of fire-mediated landscapes. This may necessitate lengthening the rotation period of a certain proportion of stands within managed landscapes or may require the application of alternative harvesting methods that can recreate the structure and tree composition characteristic of advanced seral stage stands. This review concludes by identifying future research needs that might help meet these challenges.

KEYWORDS

biodiversity, clearcut, coarse woody debris, compound disturbance, disturbance regime, forest productivity, harvesting landscape, landscape composition, landscape configuration, salvage logging, soil nutrients, scientific literature review, soil organic matter, stand, stand age distribution stand structure, wildfire, wildlife habitat use

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Technical Bulletin No. 822 (February 2001). *Accommodating birds in managed forests of North America: A review of bird-forestry relationships*.

Technical Bulletin No. 728 (January 1996). *Influence of landscape pattern, forest type, and forest structure on use of habitat by marten in Maine.*

SIMILARITÉS ET DIFFÉRENCES ENTRE LES PERTURBATIONS CAUSÉES PAR LA COUPE FORESTIERE ET LES FEUX DANS LES PAYSAGES CANADIENS AFFECTÉS PAR LES INCENDIES FORESTIERS

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RÉSUMÉ

Depuis des décennies, plusieurs ont soutenu que les effets de la coupe forestière et des feux de forêts étaient significativement différents et que ceci aurait des effets significatifs sur les processus des écosystèmes et sur la biodiversité. Toutefois, c'est seulement récemment que des quantités appréciables de données scientifiques ont été amassées à ce propos. Dans ce rapport, nous présentons une revue des similarités et des différences entre les effets écologiques des perturbations associées aux incendies et à la coupe forestière qui ont été observées dans la littérature scientifique. Les comparaisons des effets de ces perturbations sur de nombreux attributs forestiers (les débris ligneux grossiers, les éléments nutritifs du sol, la productivité forestière, la diversité des plantes et la réponse de la faune) sont présentées selon deux échelles spatiales distinctes : celle du peuplement et celle du paysage.

À l'échelle du peuplement, notre revue a révélé des différences significatives entre les coupes forestières et les feux de forêts tôt après la perturbation. D'un point de vue de la structure des peuplements, les forêts après incendie sont caractérisées par un plus grand nombre de chicots et moins de débris ligneux au sol, de même qu'un humus forestier significativement plus mince que celui des sites récoltés. De plus, même si les deux perturbations génèrent une augmentation dans la quantité d'éléments nutritifs extractibles dans le sol, l'intensité de cette augmentation est plus grande après feu qu'après coupe. Également, on observe une augmentation du pH du sol après un incendie contrairement à peu de changement ou à une faible baisse après coupe.

Tôt après la perturbation, les éléments de biodiversité diffèrent significativement dans les sites incendiés comparativement aux sites récoltés. Des communautés différentes de plantes vasculaires et non vasculaires du sous-bois colonisent généralement les sites incendiés et récoltés quoique les différences soient habituellement une question d'abondance plutôt que d'absence/présence des espèces. Comparativement au feu, les assemblages fauniques, que ce soit les mammifères, les invertébrés ou les oiseaux, semblent tous répondre différemment à la récolte. Parmi ces groupes fauniques, les espèces spécifiquement associées aux chicots étaient les plus susceptibles de montrer une réponse différente selon la perturbation (coupe ou feu).

Les espèces d'arbres répondent différemment selon la perturbation (feu ou coupe), la récolte favorisant l'établissement d'espèces feuillues (notamment le peuplier faux-tremble, *Populus tremuloides*) et d'espèces de conifères qui ne sont pas adaptées aux incendies telles que le sapin baumier (*Abies balsamea*). Par ailleurs, il y a typiquement plus d'arbres feuillus résiduels suite aux coupes à blanc qu'après incendies. Étant donné ce fait et à cause de la réponse différentielle des espèces d'arbres à ces deux types de perturbations, des dynamiques de succession divergentes, pour ce qui est de la composition des arbres, peuvent être observés entre les peuplements incendiés et récoltés. Même si nous avons observé une certaine variabilité entre les études, la productivité forestière est généralement similaire dans les sites incendiés et récoltés.

Lorsqu’on compare les effets des perturbations associées à la récolte et aux feux de forêts à des échelles temporelles plus longues, notre revue indique que la plupart des attributs forestiers, qui étaient différents tôt après la perturbation, convergeaient quelques décennies après perturbation. Néanmoins, les humus forestiers plus épais observés après la récolte, comparativement à ceux observés après un incendie, semblaient persister plusieurs décennies après la perturbation. De plus, même si les communautés fauniques deviennent plus similaires avec le temps, plus tard dans la succession, certaines espèces présentes dans les peuplements incendiés sont soit significativement moins abondantes ou soit absentes dans les peuplements récoltés d’âge similaire. Enfin, plusieurs études soulignent que même si les effets des perturbations associées aux feux et à la récolte ne diffèrent pas significativement après quelques décennies, il y a certains doutes qui subsistent quant à la capacité des coupes forestières à recréer le large éventail de variabilité naturelle observée à la suite d’un incendie.

Malheureusement, peu de recherches se sont penchées sur la comparaison entre les interventions sylvicoles innovatrices (rétention variable, coupe partielle, etc.) ou des techniques de préparation de terrain (brûlage dirigé, scarifiage, etc.) et ceux des feux de forêts. Toutefois, les quelques études qui comparent les effets des brûlages dirigés et les différents niveaux de rétention indiquent que ces pratiques peuvent atténuer certaines différences observées entre les coupes forestière et le feu tôt après la perturbation. Notre revue indique que comparativement aux feux, la coupe de récupération après feu peut avoir des effets significatifs sur les processus écologiques, les legs biologiques et l’abondance des espèces généralement rencontrées seulement après un incendie. L’enlèvement des arbres morts à la suite d’un incendie peut affecter la régénération des arbres, la composition du sous-bois, l’abondance et la distribution du bois mort, l’habitat faunique et les propriétés du sol. Néanmoins, plusieurs de ces effets sont spécifiques au site. Par conséquent, il est nécessaire de déployer des efforts de recherche additionnels afin de soutenir les décisions d’aménagement et l’élaboration des politiques.

À l’échelle du paysage, la principale différence entre les régimes d’incendie et de récolte s’avère la distribution des classes d’âges des peuplements. La proportion des peuplements plus âgés que la période de révolution (habituellement 100 ans) tend vers zéro sous un régime de récoltes complètement normalisé, tandis qu’elle se situe autour de 35% sous un régime d’incendies dont la période de révolution est similaire. Cette différence fondamentale donne lieu à une perte significative des forêts comportant des stages avancés de succession dans les paysages aménagés, ce qui affecte les organismes qui sont essentiellement associés à de tels peuplements. Fait intéressant, puisque la coupe forestière n’est pas en mesure de recréer les conditions généralement retrouvées dans les jeunes peuplements incendiés, les paysages sous l’influence de la récolte seront également caractérisés par une réduction des peuplements en mesure de remplacer le rôle écologique des jeunes peuplements incendiés. Malheureusement, seulement quelques études ont effectué la comparaison empirique des effets des feux de forêts et de la récolte à l’échelle du paysage sous des périodes de révolution similaires. Néanmoins, la recherche démontre que les incendies produisent habituellement des paysages plus hétérogènes que des coupes à blanc, incluant plus d’îlots résiduels. Les incendies possèdent également une forme plus complexes et des bordures qui sont plus graduelles que les coupes à blanc.

En conclusion, notre revue a révélé deux principaux défis auxquels font face les gestionnaires forestiers afin de générer des effets écologiques similaires à ceux produits lors d’un incendie. D’abord, les gestionnaires ont besoin d’améliorer les pratiques forestières dans le but de minimiser les différences observées entre les jeunes peuplements coupés et les jeunes peuplements incendiés, particulièrement en ce qui concerne les débris ligneux grossiers et les conditions au sol. Ensuite, les gestionnaires doivent maintenir au sein des paysages aménagés des peuplements forestiers dont la composition et la structure sont similaires à celles retrouvées dans des peuplements matures et sur-matures. De tels peuplements peuvent occuper une portion significative des paysages affectés par le

feu. Ceci peut impliquer le rallongement de la période de révolution d'une certaine portion des peuplements au sein des paysages aménagés ou alors nécessiter l'application de méthodes de récolte innovatrices qui peuvent recréer la structure et la composition des arbres caractéristiques des stages avancés de succession. Cette revue conclue en identifiant les besoins de recherche future qui sont susceptibles d'aider à faire face à ces défis.

MOTS CLÉS

Biodiversité, coupe à blanc, débris ligneux grossiers, perturbations combinées (*compound disturbance*), régime de perturbation, productivité forestière, territoire aménagé, composition du paysage, configuration du paysage, coupe de récupération, éléments nutritifs du sol, revue de littérature scientifique, matière organique du sol, peuplement, distribution des âges des peuplements, structure du peuplement, incendie forestier, utilisation faunique de l'habitat

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SIMILARITIES AND DIFFERENCES BETWEEN HARVESTING- AND WILDFIRE-INDUCED DISTURBANCES IN FIRE-MEDIATED CANADIAN LANDSCAPES

1.0 INTRODUCTION

Forest management in Canada is undergoing a period of redefinition that seeks new models to conciliate cost-effective wood production with biodiversity conservation and long-term forest productivity. One avenue of focus is the establishment of silvicultural practices that mimic as closely as possible natural ecosystem processes (Hunter 1993; Attiwill 1994; Bergeron and Harvey 1997; Bergeron et al. 1999; Franklin et al. 2002; Harvey et al. 2002). The underlying logic is that since organisms are adapted to the environmental forces under which they have evolved over millennia, biodiversity and ecosystem functions should be maintained if forest management interventions resemble these natural forces.

In order to establish a forest management model that is based on natural stand and disturbance dynamics, a three-step process has been suggested (Bergeron and Harvey 1997). The first step deals with the characterization of the natural disturbance regime; the second step is a comparison of the effects of natural disturbances and silvicultural interventions on stand and landscape characteristics and functioning; the third step involves the conception and evaluation of new silvicultural interventions inspired by the effects of natural disturbances. In many regions of Canada, the main stand-replacing disturbance is fire (Heinselman 1981; Johnson 1992; Payette 1992; Bergeron et al. 2004). The objective of this review is to summarize the similarities and differences in the effects of wildfire- and harvesting-induced disturbances based on a pan-Canadian literature review and identify major knowledge gaps.

There is abundant literature looking at specific cases (comparison of two disturbance types in a specific location), but few studies have attempted to summarize this literature. The reviews that do deal with multiple studies rarely incorporate numerous analytical scales or address multiple response variables that include plant species composition and structure, as well as wildlife habitat use and ecosystem functioning. Nonetheless, a few studies incorporating multiple scales and using numerous response variables have recently reviewed the scientific literature with respect to the effects of fire- and harvesting-induced disturbances (e.g., McRae et al. 2001). However, a plethora of research has emerged since then on many forest attributes such as understory vegetation (Haeussler and Bergeron 2004), mammals (Simon et al. 2002), invertebrates (Buddle et al. 2006), and birds (Simon, Schwab, and Otto 2002), just to name a few. We believe this highlights the need for a fresh look at similarities and differences between the ecological processes stemming from fire- and harvesting-induced disturbances. The objective of this literature review is to compare, at the stand and landscape scales, the effects of harvesting and wildfire on many forest attributes in fire-driven Canadian regions. Addressing forest management at different spatial scales is important, for only mimicking natural disturbance processes at the stand scale may not suffice to maintain biodiversity and ecological functions of managed forests. Furthermore, comparing numerous attributes at once is necessary in order to identify which attributes are significantly different after logging as opposed to after wildfire, which should facilitate the identification of the appropriate silvicultural intervention to apply in order to make the ecological processes within harvested stands more similar to those within burned stands. Additionally, this synthesis differs from previous work on this topic by its examination of the effects of compound disturbances occurring in the same stands over a short period of time, notably the effect of salvage logging in burned stands. Finally, our study differentiates itself from previous work by looking at how the effects of the disturbance types vary several decades after disturbance, thus incorporating the temporal aspect of the response of stands and landscapes to disturbances.

2.0 STAND-SCALE SIMILARITIES AND DIFFERENCES

2.1 Introduction

In this section we present the similarities and differences between wildfire- and harvesting-induced disturbances at the stand scale. We first address structural components (coarse woody debris, organic matter and soil nutrients) and then present information that pertains to the effects of these two types of disturbances on numerous biodiversity components (trees, understory vegetation, invertebrates, birds, and mammals). We conclude by addressing how the effects of the special case of harvesting after fire (salvage logging) differ from the effects of wildfire alone.

For each element, variations in different stand-scale variables are considered at three post-disturbance temporal scales when data were available: short (< *ca.* 10 yrs), medium (10-40 yrs), and long (> 40 yrs) term. For each element, unless otherwise stated, comparisons are made regardless of stand type (deciduous, mixedwoods, or coniferous). Despite the warning that "as a rule it is not appropriate to transfer generalizations regarding fire or logging disturbances across forest regions or between ecosystem types within the same forest region" (McRae et al. 2001), our own literature review shows that stand types generally respond in similar directions to disturbance, although not always with the same magnitude. Additionally, while surface fires are relatively common within certain Canadian landscapes (Johnson 1992), few studies have described the effects of this type of disturbance and none, to our knowledge, has compared the effects of surface fires to those induced by harvesting practices. Therefore, in this study we concentrate on comparing the effects of harvesting practices and crown fires. Finally, as clearcutting has been the predominant harvesting technique used in the boreal forest, which comprises the majority of forest lands in Canada (Table 2.1; Messier and Leduc 2004), we compare the effects of this technique to those induced by wildfires. Nonetheless, we conclude this section by reviewing the literature that has addressed how some of the ecological differences identified between conventional harvesting techniques (clearcutting) and wildfires can be mitigated or accentuated with the use of some alternative silvicultural interventions (variable retention, site preparation, etc.).

Table 2.1 Average amount of forest land disturbed by disturbance type in Canada per year (1975-1989) (Canadian Council of Forest Ministers 2005)

Disturbance type	Annual area disturbed (ha)
Fire	2 186 372
Insect	35 138 159
Harvesting (88% clearcut)	865 746

2.2 Coarse Woody Debris

Coarse woody debris (CWD) which include downed woody debris (DWD), snags and underground woody debris, are an important functional and structural component of forested ecosystems. They provide cavities and den sites for mammals and birds, foraging locations for insectivores and birds that rely on this food source, as well as important subnivean structure for nonhibernating mammals during winter (e.g., Harmon et al. 1986). Furthermore, above- and belowground coarse woody debris contribute significantly to nutrient cycling and energy flow in forested ecosystems (Harmon et al. 1986; Brais et al. 2005). Finally, decomposing downed woody debris represent one of the best germination substrates for tree seeds (Simard, Bergeron, and Sirois 1998, 2003). Hence, gaining insight into the similarities and differences in CWD dynamics between harvesting- and fire-induced disturbance is not only important for the conservation of numerous forest-dwelling species, but also for long-term stand productivity.

Since harvesting-induced disturbances remove trees as opposed to fires that simply kill trees, forest harvesting has major effects on the amount and type of CWD present in post-disturbance stands. Perhaps because this is so obvious, this component has rarely been quantified and compared in burns and clearcuts. The few studies that have documented this aspect of forest ecosystems have for the most part only addressed short-term effects, with only a handful of studies looking at longer temporal trends in CWD after wildfire- and harvesting-induced disturbances.

2.2.1 *CWD Dynamics after Fire*

Stand age, pre-disturbance forest characteristics, and the disturbance history of stands prior to stand initiation are all very important in determining the quality and quantity of CWD initially present post-disturbance (Clark et al. 1998). Several studies of CWD within forest chronosequences have described a general "U-shaped" temporal pattern (Harmon et al. 1986; Sturtevant et al. 1997; Brais et al. 2005; Harper et al. 2005; Figure 2.1). In general, debris levels tend to be high following fire. As the residual debris decompose, stand CWD content declines, since the regenerating stand produces little CWD. As the stand matures, tree mortality due to competition and fine-scale disturbances leads to high CWD values numerous decades after fire.

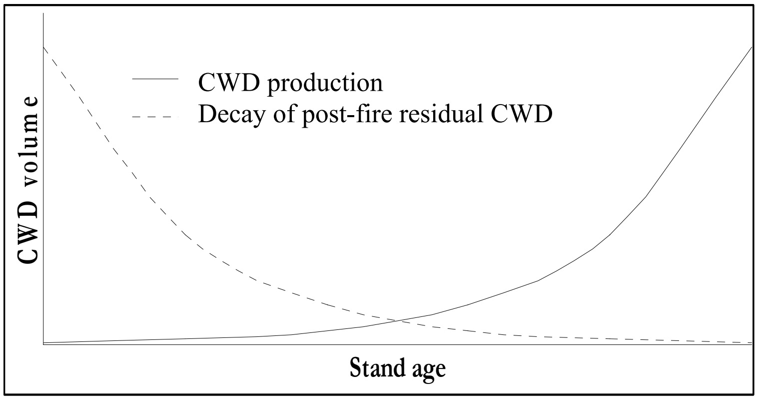


Figure 2.1 Conceptual Relationship between Coarse Woody Debris (CWD) and Stand Age, Showing the Decay of Residual Debris after Fire, Followed by the Accumulation of Debris from the Regenerating Stand (adapted from Sturtevant et al. (1997))

2.2.2 *Short-Term Similarities and Differences in Coarse Woody Debris*

Overall, the total amount of CWD is higher in burned compared to harvested sites early after disturbance (Timoney, Peterson, and Wein 1997; Wei et al. 1997; Tinker and Knight 2000; Kemball 2002; Pedlar et al. 2002; Haeussler and Bergeron 2004). Nonetheless, immediately following stand initiation, little difference is observed between fire- and harvesting-induced disturbances with respect to belowground CWD (Wei et al. 1997). Not surprisingly, the main difference between fire and harvesting is in the quantity and type of aboveground CWD produced (Wei et al. 1997; Hobson and Schieck 1999; Simon, Schwab, and Otto 2002; Simon et al. 2002; Haeussler and Bergeron 2004). While harvesting practices tend to produce significantly more stumps than wildfires, they leave significantly less snags (Wei et al. 1997; Pedlar et al. 2002; Harper et al. 2004). On the other hand, CWD on the ground are usually not significantly different and can even be more abundant after harvesting, especially when stem-only harvesting techniques are used (Noble et al. 1977; Wei et al. 1997; Hobson and Schieck 1999; Pedlar et al. 2002; Simon et al. 2002; Haeussler and Bergeron 2004;

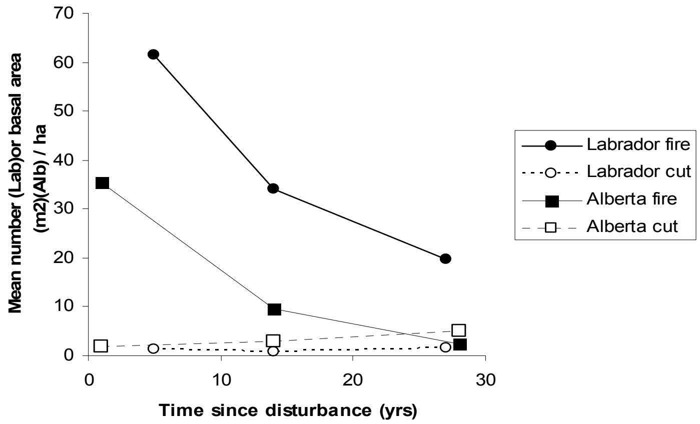
Harper et al. 2004). Interestingly, the initial difference in CWD between disturbance types may be accentuated since decomposition rates early after disturbance can be as much as five times higher in clearcuts than in burned areas (Wei et al. 1997).

2.2.3 *Medium-Term Similarities and Differences in Coarse Woody Debris*

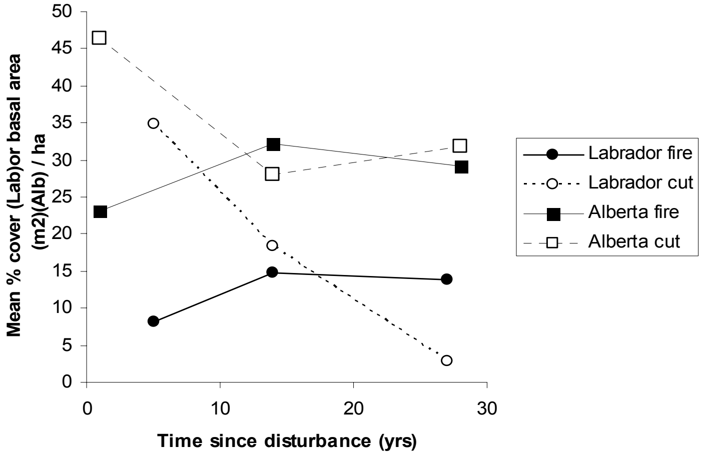
As succession proceeds after fire- and harvesting-induced disturbances, initial differences in CWD quantity and quality become less pronounced (Figure 2.2). One study in Alberta's boreal forest (Hobson and Shieck 1999), and one in central Labrador (Simon, Schwab, and Otto 2002; Simon et al. 2002), found that while young clearcut stands had significantly more CWD than young burns, no significant difference in DWD was observed between clearcut and burned sites 28 years after disturbance (Figure 2.2A). In both studies, a similar converging trend was observed with respect to snags, but with opposite initial proportions (Hobson and Schieck 1999; Simon, Schwab, and Otto 2002; Simon et al. 2002; Figure 2.2B). Moreover, Ferguson and Elkie (2003) even found that the trends reversed later in succession as they observed slightly more CWD in harvested compared to burned sites (Ferguson and Elkie 2003).

2.2.4 *Long-Term Similarities and Differences in Coarse Woody Debris*

Few studies have compared long-term dynamics of CWD in harvested and burned sites. One study in Newfoundland demonstrated that harvested and burned stands, in the prolonged absence of disturbance, appear to generate equal amounts of CWD (Sturtevant et al. 1997). Lussier, Morin, and Gagnon (2002), comparing mortality patterns in clearcut- and fire-origin stands, found no significant difference in the production of CWD between these two types of disturbances.



A. Snags



B. Downed woody debris

Figure 2.2 Snag (A) and Downed Woody Debris (B) Dynamics in the Prolonged Absence of Disturbance after Fire and Clearcut Harvesting. Values taken from Hobson and Schieck (1999) (Alberta); Simon, Schwab, and Otto 2002; and Simon et al. 2002 (Labrador). Note: different units used in both studies.

2.2.5 *Summary*

Studies addressing CWD dynamics indicate that differences between fire- and harvesting-induced disturbances are significant in the short term with logged sites having less snags and more downed woody debris than burned sites. However, these initially diverging CWD dynamics eventually converge a few decades post-disturbance.

2.3 Forest Floor Thickness

Many stands accumulate thick forest floors as succession proceeds in the absence of fire, although the rate of accumulation varies with numerous factors including forest composition (e.g., Yu, Apps, and

Bhatti 2002) and stand disturbance history (Lecomte et al. 2006a). In general, as coniferous litter is more acidic and recalcitrant to decomposition than deciduous litter, coniferous stands accumulate more organic matter above the mineral soil than do deciduous stands (Yu, Apps, and Bhatti 2002). The formation of a thick forest floor can have many effects on forest ecosystems. Thick forest floors insulate the mineral soil, which lowers soil temperature and can induce a rise in the water table which creates water-logged conditions detrimental to forest productivity and favours the establishment of bog-associated species (Van Cleve et al. 1983a, 1983b; Viereck et al. 1983; Van Cleve et al. 1991; Lecomte et al. 2006b). Furthermore, reduced nutrient availability by the progressive sequestration of soil nutrients in the forest floor could further decrease forest productivity.

2.3.1 *Forest Floor Dynamics after Fire*

At the stand level, the primary regulating force that controls forest floor thickness is wildfires. Fires generally consume significant amounts of organic matter; however, the quantity consumed varies significantly within and between burns (Miyanishi and Johnson 2002) and the least amount of residual organic matter is usually concentrated around the boles of the fire-killed trees (Charron and Greene 2002; Miyanishi and Johnson 2002). The consumption of the forest floor can have important effects on surface soil attributes, including a significant increase in mineral soil temperature, which increases decomposition and hence the availability of nutrients for plant growth. Numerous studies have demonstrated the effect of variations of organic matter thickness on germination and growth of tree species (Chrosciewicz 1976; Dyrness and Norum 1983; Zasada et al. 1983; Charron and Greene 2002). The consumption of the forest floor by fire greatly influences post-fire tree composition and structure of stands. Furthermore, since many organs (rhizomes, roots, seeds, etc.) of understory vascular and non-vascular species are not evenly distributed within the forest floor, the burning of the forest floor significantly impacts the diversity and composition of the regenerating understory community.

2.3.2 *Post-Harvest Forest Floor Dynamics*

As conventional harvesting techniques do not remove the forest floor, it is generally thicker in harvested sites compared to burned sites immediately after disturbance (Ehnes 1998; Simard et al. 2001; Rees and Juday 2002; Haeussler and Bergeron 2004). Moreover, this trend appears to persist numerous decades after fire in some stands (Timoney, Peterson, and Wein 1997; Simard et al. 2001; Figure 2.3). Interestingly, since the presence of trembling aspen (*Populus tremuloides*) enhances decomposition rates and hinders organic matter accumulation (Yu, Apps, and Bhatti 2002), in regions where a significant post-harvest shift in tree species composition from coniferous to deciduous is observed, harvested sites tend to have significantly thinner forest floors than similarly aged burned sites a few decades after disturbance (Carleton and MacLellan 1994).

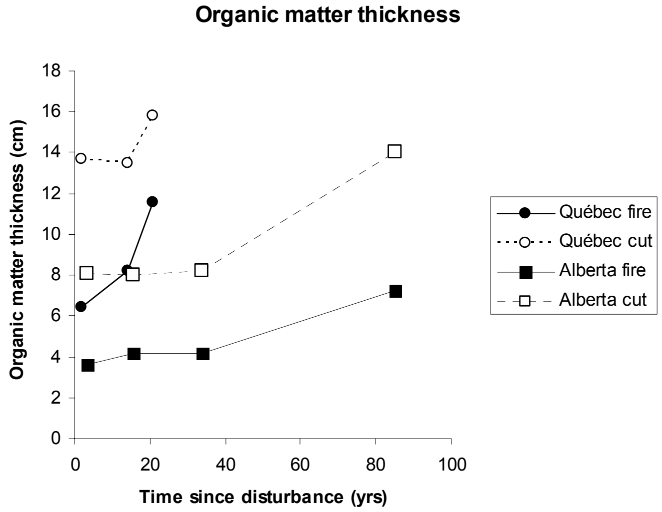


Figure 2.3 Organic Matter Thickness as a Function of Time since Disturbance. Data taken from Timoney, Peterson, and Wein 1997 (Alberta) and Simard et al. (2001) (Québec).

2.4 Soil and Forest Floor Nutrients

Despite the fact that changes in forest productivity and biodiversity may occur in the future if processes that control soil fertility and structure differ significantly between clearcut and burned stands, few studies have compared this aspect of both disturbances (Simard et al. 2001; Reich et al. 2001). Nonetheless, research studying the effects of disturbances on soil fertility and structure independently suggests similarities and differences between wildfire and clearcut harvesting.

2.4.1 *Effects of Fire on Nutrients*

Wildfires commonly generate a pulse of plant-available nutrients in the soil that can be taken up by regenerating vegetation. On the other hand, wildfires can cause substantial losses of nitrogen (N), carbon (C) and sulphur (S) through volatilization (Dyrness and Norum 1983; O'Neill, Kasischke, and Richter 2002). Wildfires also increase the amount of exchangeable base cations, notably calcium (Ca), which significantly increases soil and forest floor pH immediately after fire (Simard et al. 2001). Wildfire-produced ash has also been shown to be rich in phosphorous (P), causing a substantial increase of P after fire (Simard et al. 2001). Furthermore, the direct effects of wildfire on the soil microbial community can de detrimental and it can take the microbial community up to 12 years to recover (Pietikainen and Fritze 1995), which significantly affects soil biological processes. Since the actual intensity of the response of soil and forest floor nutrients to fire varies with respect to numerous variables, Grenon et al. (2004) warn that generalizations should not be made about the nutritional effects of disturbances.

2.4.2 *Short-Term Similarities and Differences for Nutrients*

It has been reported that both wildfire and clearcut harvesting are capable of producing a pulse of extractable and plant-available nutrients. However, the intensity of the pulse is greater after wildfire than clearcut harvesting (Simard et al. 2001). Fire also increases the amount of exchangeable base cations (notably calcium (Ca)) which increases soil pH. In contrast, logging induces a slight decrease in forest floor and mineral soil pH (Keenan and Kimmins 1993; Simard et al. 2001).

Significant differences have also been observed in the concentrations and mass of mineralizable N in the forest floor and mineral soil, which were greater in cuts than in burned stands (Simard et al. 2001). Increased nitrogen availability and mineralization rates following clearcutting have been attributed to fresh inputs of organic matter, mixing of the mineral soil and forest floor, and increased soil temperature and moisture availability (Keenan and Kimmins 1993). Alternatively, these differences in N mineralization may be caused by direct detrimental effects of fire on the microbial community, hence hampering N mineralization rates after fire (Pietikainen and Fritze 1995).

2.4.3 *Medium- and Long-Term Similarities and Differences for Nutrients*

Simard et al. (2001) observed that the pulse in extractable nutrients is short lived and differences between wildfire and clearcut harvesting diminish with time since disturbance. Notably, while the total concentration of N, P, and Ca in the forest floor differed significantly between burns and cuts early after disturbance, no significant difference was observed 22 years after disturbance (Simard et al. 2001). Nonetheless, the concentrations of net N mineralized in the forest floor and mineral horizon were still higher after harvesting than fire 22 years post-disturbance. This indicates that some differences between wildfire- and harvesting-induced disturbances may persist for numerous decades (Simard et al. 2001).

In a study addressing long-term impacts of logging and fire on forest dynamics, Reich et al. (2001), found that soil and litter attributes differed very slightly between post-fire and post-logged deciduous (trembling aspen) and coniferous (jack pine, *Pinus banksiana*) stands. However, these authors did find that these two types of stands showed opposite trends for nutrients late in succession. Percent C and cationic exchange capacity (CEC) were higher in burned vs. harvested sites for aspen but lower for jack pine. Base saturation, Ca, and magnesium (Mg) were lower in burned vs. harvested sites for aspen but higher for jack pine.

Wei et al. (1997) and Wei, Kimmins, and Zhou (2003) conducted simulation experiments to explore whether the cumulative effect of several intensive management rotations could induce a decline in timber yields in Canada, as observed in other countries. The results showed that the nutritional impacts of timber harvesting were within the range of variability of burned sites.

2.4.4 *Summary*

Studies indicate that initial effects on forest floor and soil nutrients are significantly different for some soil attributes, notably nitrogen, phosphorous, and calcium, which are more abundant after fire than after harvesting. Some of these differences disappear a few decades after fire while others, such as N mineralization rates, may persist for at least a couple of decades. The only study conducted at a longer temporal scale suggested that most differences between burned and harvested sites were imperceptible numerous decades after disturbance (> 40 yrs; Reich et al. 2001). Interestingly, while the nutrient pulse caused by wildfire is a result of the combustion of the forest floor into ash, the less intense pulse in nutrients observed after logging is due to increased biological mineralization of nutrients (Simard et al. 2001). Since logging, as opposed to wildfire, does not consume the organic layer, the regenerating vegetation in harvested sites is usually exposed to a greater mass of soil and forest floor nutrients which may be able to sustain tree productivity over the long term and compensate for the loss of nutrients as a result of the removal of trees (Simard et al. 2001).

2.5 Tree Composition, Structure, and Productivity

2.5.1 *Effects of Fire on Trees*

Considering the major role played by fire in the dynamics of boreal forests (Payette 1992), it comes as no surprise that some tree species developed adaptations to fire (Greene et al. 1999). Moreover, fire, rather than climate, is the primary explanation of the present distribution limit for some boreal species (Suffling 1995; Lozon and MacIsaac 1997; Flannigan and Bergeron 1998; Asselin, Fortin, and Bergeron 2003).

Serotinous cones are an example of adaptation to fire in boreal tree species (e.g., jack pine, lodgepole pine (*Pinus contorta* var. *latifolia*), black spruce (*Picea mariana*)). Such an aerial seed bank allows rapid colonization of burned sites. Another important adaptation to fire is root suckering or stump sprouting (e.g., trembling aspen, balsam poplar (*Populus balsamifera*), paper birch (*Betula papyrifera*)). Such vegetative means of reproduction can be very effective when fire consumption of organic matter is incomplete (Wang 2003). Finally, some species produce very small, plumed seeds that can travel long distances to colonize burned sites (e.g., trembling aspen).

Other species, known as late-successional species, are ill-adapted to fire and become dominant only late after fire (although they might be present from the start, but out-competed by colonizing species). Balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and eastern white cedar (*Thuja occidentalis*) are shade-tolerant species that rely on nearby residual trees to act as seed sources in order to reinvade burned sites (Asselin, Fortin, and Bergeron 2001). They grow slowly and become dominant > 150 years following fire (Bergeron and Dubuc 1989).

Consumption of most of the soil organic matter during fire exposes mineral soil—an excellent seedbed (Simard, Bergeron, and Sirois 1998)—and thus creates many favourable sites for re-colonization. Regeneration is usually massive after fire, and seedling densities are high.

2.5.2 *Short-Term Similarities and Differences in Tree Composition and Structure*

Clearcutting and wildfire being stand-replacing disturbances, the basal area of live trees is low early after disturbance and values are similar for burned and harvested sites (Nguyen-Xuan et al. 2000; Haeussler and Bergeron 2004). However, density is generally higher in harvested sites as compared to burned sites (Nguyen-Xuan et al. 2000; Harper et al. 2004). With respect to tree composition, clearcuts tend to be colonized by more deciduous trees and less coniferous trees than burns (Carleton and MacLellan 1994; Timoney, Peterson, and Wein 1997; Peltzer et al. 2000; Reich et al. 2001; Kemball 2002). However, in areas were balsam fir is present in the pre-disturbance stand, this species tends to invade logged stands, whereas being a non-fire adapted species it is scarcely distributed in recent burns (Simon and Schwab 2005). Furthermore, clearcuts tend to leave more deciduous trees than would have been left naturally after severe fires, which can lead to divergence in composition between burned and harvested sites (Dyrness 1973; Carleton and MacLellan 1994, Timoney, Peterson, and Wein 1997; Kemball 2002; Rees and Juday 2002; Simon and Schwab 2005). Timoney, Peterson, and Wein (1997) even suggested that succession following harvesting in mixedwood forests could fail to reach a pre-disturbance state and lead to the long-term establishment of a deciduous disclimax.

Regeneration from seeds is more abundant in burned compared to harvested sites (Peltzer at al. 2000; Asselin, Fortin, and Bergeron 2001; Kemball 2002; Harper et al. 2004; Weyenberg, Frelich, and Reich 2004). This could be explained by the deeper and more heterogeneous edges found in burned sites compared to harvested sites (Harper et al. 2004), favouring greater seed production and dispersal (Greene et al. 2002). Furthermore, fire creates better conditions (mineral seedbeds, light, and resources) for seed germination and survival than harvesting (Whittle, Duchesne, and Needham 1997;

Greene et al. 1999). Notably, black spruce regeneration from layers is more abundant in harvested than in burned sites (Kemball 2002; Harper et al. 2004).

2.5.3 *Medium- and Long-Term Similarities and Differences in Tree Composition and Structure*

The basal area and density of live trees tends to be higher in burned sites late after disturbance (Ehnes 1998; Kemball 2002; Ruel et al. 2004), although burned and harvested sites sometimes yield similar values (Nguyen-Xuan et al. 2000; Reich et al. 2001).

Although Groot and Horton (1994) and Lussier, Morin, and Gagnon (2002) showed convergence of stand structures originating from fires and clearcuts in the prolonged absence of disturbance, Ehnes (1998) found that overstories were more resilient to fire than to logging. Indeed, burned sites are less different from, and take less time to return to, the pre-disturbance state than harvested sites in terms of overstory species composition.

2.5.4 *Similarities and Differences in Tree Productivity*

Many studies have compared forest productivity after logging and wildfire (Lussier et al. 1992; Morin and Gagnon 1992; Paquin et al. 1999; Paré, Bergeron, and Longpré 2001; Lussier, Morin, and Gagnon 2002; Huang et al. 2004; Ruel et al. 2004). Most of these studies have been conducted in mesic black spruce forests, where most of the post-logged regeneration is composed of suppressed layers that show a growth release after harvesting of the dominant trees (Paquin and Doucet 1992a, 1992b). In these forests, tree-ring reconstructions have shown that post-fire trees initially had greater diameter at breast height (DBH), specific volume, and height increment (and consequently site index) compared to post-logged trees (Lussier, Morin, and Gagnon 1992; Morin and Gagnon 1992; Paquin et al. 1999; Lussier, Morin, and Gagnon 2002; Ruel et al. 2004). After some time, no differences were detectable (at 15 yrs in Paquin et al. (1999); at 50-60 yrs in Lussier, Morin, and Gagnon (1992) and Ruel et al. (2004)), or otherwise post-logged trees showed higher increments (after ~30 yrs in Morin and Gagnon (1992)). However, because of the initial size of the layers at the time of logging, post-logged trees always showed greater total height, diameter, and volume than post-fire trees (Morin and Gagnon 1992; Paquin et al. 1999; Lussier, Morin, and Gagnon 2002). Overall, productivity of post-fire and post-logged mesic black spruce stands is comparable. In northwestern Québec, height growth of aspen was not affected by disturbance type (Paré, Bergeron, and Longpré 2001), whereas the site index of scarified, post-logged lodgepole pine in Alberta was higher than in post-fire stands (Huang et al. 2004). Finally, stem wood and total above ground production (mg ha^{-1} yr^{-1}) were similar in post-logged and post-fire boreal stands in northern Minnesota (Reich et al. 2001).

Although most studies indicate that short-term productivity is comparable in burned and harvested stands, many natural or anthropogenic processes, such as invasion by ericaceous shrubs, paludification on hydric soils, and compound disturbances, can interact with—or be caused by—harvesting practices and result in reduced forest productivity in the short or long term. In many of these cases, the ecological effects of harvesting are not similar to those of fire, and site preparation techniques (prescribed burning, scarification, etc.) may be needed to maintain long-term productivity of harvested forests.

Invasion by Ericaceous Shrubs and Tree Productivity

Forest harvesting is known to increase the cover of ericaceous shrubs, such as *Kalmia angustifolia* and *Ledum groenlandicum*, that grow in association with black spruce in the boreal forests of eastern Canada (Titus, Sidhu, and Mallik 1995; Ruel et al. 2004). These shrubs, particularly *Kalmia angustifolia*, are known to produce organic molecules (Mallik and Inderjit 2001; Inderjit and Mallik 2002) that affect tree establishment and growth (Mallik 1987; Wallstedt et al. 2002; Yamasaki, Fyles, and Titus 2002; Ruel et al. 2004), sometimes producing open, unproductive heathlands (Damman

1971; Mallik 2003). In contrast, high severity fires kill the subterranean organs of these shrubs, delaying their return in the burned stand by about a century (Lecomte et al. 2005). Additionally, it has been shown that activated charcoal produced by fire adsorbs allelochemicals that have been accumulating in the forest humus (Zackrisson, Nilsson, and Wardle 1996; Wardle, Zackrisson, and Nilsson 1998; DeLuca, Nilsson, and Zackrisson 2002). Harvesting in black spruce stands that already show high *Kalmia* cover has the potential to seriously reduce short- and long-term forest productivity. In these stands, the use of prescribed fire, scarification, fertilization or herbicides might prevent the conversion of the stand to a low productivity forest (Mallik and Inderjit 2001; Thiffault et al. 2004).

Paludification on Hydric Soils and Tree Productivity

In most boreal regions, the accumulation of soil organic matter is favoured by low temperatures and high humidity (Swanson, Lacelle, and Tarnocai 2000). In some regions where surface deposits are relatively fine and compact, such as the Clay Belt of Ontario and Québec, soil organic matter can accumulate in large quantity in a process known as paludification (Fenton et al. 2005). The gradual build-up of thick peat deposits on top of the mineral soil eventually raises the water table, decreases soil temperatures, slows nutrient cycling, and reduces forest productivity (Van Cleve et al. 1983a, 1983b; Viereck et al. 1983; Van Cleve et al. 1991; Lecomte et al. 2006a). In these ecosystems, wildfires are drivers of forest productivity because smouldering fires consume the organic matter (Miyanishi and Johnson 2002), release nutrients that were locked up in the humus (Prescott, Maynard, and Laiho 2000), and stimulate nutrient cycling (Smithwick et al. 2005). Harvesting in these stands will accelerate paludification by raising the water table (Roy, Jeglum, and Plamondon 1997), mimicking the effects of low severity fires that do not burn much of the forest floor (Lecomte et al. 2006a). In stands prone to paludification, harvesting should be accompanied by severe disturbance of the forest floor to expose mineral soil, increase nutrient cycling, increase soil temperatures, and lower the water table, with the combined effect of augmenting stand productivity.

Compound Disturbances and Tree Productivity

The addition of an anthropogenic disturbance regime like forest harvesting in systems already driven by natural disturbance regimes (fire, insect outbreaks, wind, etc.) has the potential to result in unexpected successional pathways (Paine, Tegner, and Johnson 1998). The interaction of disturbances is a topic currently at the forefront of ecological research (Turner 2005), and much has to be learned. In particular, recent work has addressed the ecological effects of salvage logging of burned stands (Karr et al. 2004; Lindenmayer et al. 2004; Nappi, Drapeau, and Savard 2004; Donato et al. 2006; Greene et al. 2006), which is one of the most obvious interactions between natural and human disturbances. Salvage logging will not be included in this section however, but will be addressed in a separate section.

Because fire is a random process in most boreal forests, recently logged stands have the same chance of burning as undisturbed stands (Johnson 1992). Many tree species adapted to fire rely on their aerial seed bank, contained in serotinous cones, for post-fire regeneration (Rudolph and Laidly 1990; Viereck and Johnston 1990). Recently logged stands show reduced seed banks because cone production is proportional to basal area (Sirois 2000; Greene et al. 2004). The passage of fire in recent cuts therefore has the potential to transform previously closed-canopy forests into open woodlands because there are not enough seeds for adequate sexual regeneration (Payette and Delwaide 2003). The same outcome has been shown to happen when fire is preceded by an outbreak of insect defoliators that feed on cones and seeds of black spruce (Payette et al. 2000; Jasinski and Payette 2005; Simard and Payette 2005). The compound effect of insect defoliators followed by harvesting has been shown to result in reduced density, volume, and productivity of black spruce stands and in their conversion to shrub-moss woodlands (Dussart and Payette 2002). On boreal rock outcrops, successive fire disturbance events that resulted in the complete removal of the organic matter layer resulted in a primary succession instead of a secondary succession, and a drastic opening of the forest cover (Asselin, Belleau, and Bergeron 2006). Successive fire disturbances have also been hypothesized to result in an opening of the forest if the return interval is shorter than the time needed to reach sexual maturity (Zedler, Gautier, and McMaster 1983; Bussière, Payette, and Filion 1996).

The interaction between harvesting, fire, and insect outbreaks resulting in regeneration failure or reduced forest productivity seems to be marginal in the boreal forest. However, the response of vegetation and disturbance regimes to climate change might yield complex disturbance regimes that could increase the probability of such interactions (Overpeck, Rind, and Goldberg 1990; Dale et al. 2000). It has been hypothesized that outbreak-forming insect species living at their thermal range limit could respond rapidly and drastically to global warming (Fleming and Volney 1995; Fleming 1996; Fleming and Candau 1998; Logan, Régnière, and Powell 2003). Fire regimes will also probably be affected by global warming (Flannigan et al. 1998). The interaction of disturbances under future climate forcing will likely stay a major research topic for the years to come.

2.5.5 *Summary*

Our review concludes that tree establishment by seed is more abundant in burned stands than in logged stands. Early after disturbance, basal areas of clearcut and burned stands are similar, while stem density is greater in logged stands. Later on, basal area and stem density in post-fire stands are either greater than or similar to post-harvest stands. Tree composition is greatly affected by disturbance type, with recent clearcuts showing a higher proportion of balsam fir and deciduous species as compared to recent burns. Tree productivity, measured in annual increments of DBH, height, and specific volume, is significantly higher in burned stands than in second-growth stands. In absolute values however (height, diameter, and volume), most studies show no detectable differences between disturbance type, mostly because post-logged stands show advanced regeneration that compensates for the slow growth rate. Harvesting has the potential to result in significant indirect productivity reductions through its interaction with natural processes such as invasion by ericaceous shrubs, paludification, and compound disturbances.

2.6 Understory Plants

2.6.1 *Effects of Fire on Understory Communities*

Understory plant species can be classified into three main reproductive strategies with respect to their adaptations to fires (Rowe 1983). Some species with deeply buried reproductive organs are capable of surviving most fires and are known as endurers (notably *Vaccinium*, *Ledum*, and *Kalmia* spp. with their extensive root systems). Others have high dispersal capacities and are quickly able to colonize recent burned areas and are known as invaders (notably fireweed (*Epilobium angustifolium)* and many pioneering non-vascular species). Finally, some neither survive nor have the capacity to invade burns and are known as avoiders (for example, the understory shrub *Gaultheria hispidula* with its shallow root system or the common forest-dwelling moss *Pleurozium shreberi*). Immediately after fire, stands are rapidly colonized by invaders as endurers begin to re-sprout. Eventually, as succession proceeds, invaders are rapidly replaced by endurers and later on by avoiders. The precise response of the understory community to wildfire is highly dependent on soil-borne fire severity, hence the consumption of the forest floor and the exposure of the mineral soil (Dyrness and Norum 1983; Nguyen-Xuan et al. 2000).

2.6.2 *Short-Term Differences and Similarities in Understory Vascular Species*

Immediately after disturbance, vegetation cover of understory vascular species is usually significantly greater after harvesting than after fire. However, comparable values are observed between clearcut and burned sites after one year (Abrams and Dickman 1982). Some have shown that the understory communities in recently harvested and burned sites do not differ with respect to species richness, evenness or diversity (Peltzer at al. 2000), others have observed higher diversity and richness in harvested sites (Johnston and Elliot 1996; Carlsson 2000; Harper et al. 2004), while even others have found higher values after fire (Abrams and Dickman 1982; Rees and Juday 2002). The disparate results from this group of studies suggest that species diversity and richness depend on ecosystem- and disturbance-specific circumstances rather than being inherent to wildfire or clearcutting (Haeussler and Bergeron 2004).

All studies comparing the short-term effects of wildfire- and harvesting-induced disturbances on understory vascular plant communities have clearly shown that certain understory vascular species respond significantly differently to these two types of disturbances (e.g., Noble et al. 1977; Johnston and Elliot 1996; Timoney, Peterson, and Wein 1997). Logged sites appear to begin and continue succession with a greater share of the original mature forest understory plants, while burned sites initiate succession with more distinctive and specialized plant species (Nguyen-Xuan et al. 2000; Rees and Juday 2002). Abrams and Dickman (1982), studying the early vegetation of clearcut and burned jack pine sites, found a total of 40 species exclusive to burned sites while only two species were exclusively found on clearcut sites. For example, bush honeysuckle (*Diervilla lonicera*), pin cherry (*Prunus pensylvanica*), and Houghton's sedge (*Carex houghtonii*) were consistently more abundant in burned than logged stands, while clearcuts had more understory re-sprouting tall shrubs (namely mountain maple (*Acer spicatum*), beaked hazel (*Corylus cornuta*), and green alder (*Alnus crispa*)) and low lying vegetation such as large-leaved aster (*Aster macrophyllus*), fireweed (*Epilobium angustifolium*), and prickly rose (*Rosa acicularis*) (Noble et al. 1977; Johnston and Elliot 1996; Peltzer et al. 2000; Haeussler and Bergeron 2004; Simon and Schwab 2005). However, conflicting results were obtained for some species. For example, some authors report that raspberry (*Rubus idaeus)* is more abundant after fires than clearcuts (Peltzer et al. 2000; Simon and Schwab 2005), while others observed the opposite trend (Timoney, Peterson, and Wein 1997) or no difference at all (Haeussler and Bergeron 2004).

Another difference between wildfire- and harvesting-induced disturbances is the higher presence of invasive species in clearcuts as opposed to burned sites (Noble et al. 1977; Abrams and Dickman 1982), although this is not always observed (Haeussler and Bergeron 2004) and these species can be very abundant in some burned sites (Abrams and Dickman 1982; Johnston and Elliot 1996). Finally, some claim that competing vegetation such as the ericaceous shrubs *Kalmia angustifolia* and *Ledum groenlandicum* are more abundant after clearcuts than after fire (Mallik 2003) and that this could be detrimental to tree growth (see above). While studies have shown that these species can directly and indirectly negatively affect tree growth, our literature review is inconclusive with respect to the differential effects of fire and logging on these two endurer species. Numerous studies report little difference between wildfire and harvesting (Reich et al. 2001; Harper et al. 2004; Simon and Schwab 2005), while others report these species to be more abundant in clearcuts as opposed to burns (Nguyen-Xuan et al. 2000). These results indicate that generalizations across forest regions with respect to the response of understory vascular species should be made with caution.

In a landmark study addressing early post-disturbance differences between fire and harvesting at numerous spatial scales, Haeussler and Bergeron (2004) found that at larger spatial scales, clearcut – wildfire differences were more evident and wildfire variability greater. This suggests that harvesting-induced disturbances were not capable of reproducing the large variability in understory communities commonly found after fire. Conversely, in a study of 131 post-logged and 250 natural post-fire stands, Carleton and MacLellan (1994) concluded that there was no convincing evidence in their data that "the post-logged plant communities are unnatural or abnormal in any sense" with respect to post-fire natural stands. Nonetheless, as understory plant composition is highly influenced by overstory composition (Légaré et al. 2001), they found that by favouring *Populus tremuloides* over *Picea mariana,* harvesting-induced disturbances only recreated part of the overall range of variability in understory vascular plant composition that was observed after fire (Carleton and MacLellan 1994).

2.6.3 *Medium- and Long-Term Differences and Similarities in Understory Vascular Species*

While the diversity and the richness of the understory vascular plant community sometimes differ early after disturbance between fire and logging, differences between these two types of sites tend to disappear later on (Reich et al. 2001). Timoney, Peterson, and Wein (1997) and Rees and Juday (2002) found that after logging, temporal changes in composition and dominance occurred more rapidly than during post-fire succession. In the later years following fires, species that perpetuated themselves mainly by vegetative means and that were probably members of the pre-existing vegetation dominated. A study in Labrador found that initial significant differences in the abundance of *Alnus crispa* between burned and logged stands disappeared after 27 years (Simon and Schwab 2004). Others have found that differences in the herb layer are also much reduced during the second decade after disturbance as compared to the differences observed during the first decade (Noble et al. 1977; Timoney, Peterson, and Wein 1997).

Carlsson (2000) noted that the decrease in diversity observed with time in harvested sites was due to the loss of rare species, with only common species being retained. Decreased diversity can lead to lesser resilience in harvested compared to burned sites. Indeed, early after disturbance, understories are more resilient to harvesting than to burning. However, the trend reverses rapidly and post-fire stands show greater similarity to undisturbed sites than post-harvest stands *ca*. 40 years after disturbance (Ehnes 1998).

Finally, in a study of 80 post-logged and post-fire stands that spanned numerous decades after disturbance, Reich et al. (2001) could find very little evidence that the composition, diversity, or richness of the understory vascular plant communities in jack pine, trembling aspen, or black spruce stands differed between burned and logged stands. Longer-term studies suggest that regardless of disturbance type (fire or harvesting), diverging understory vascular plant community characteristics (richness, diversity, and composition) converge in the prolonged absence of disturbance (Reich et al. 2001).

2.6.4 *Short-Term Differences and Similarities in Understory Non-Vascular Species*

Early after disturbance, late-successional non-vascular dominants are more common in logged stands while non-vascular early-successional dominants are sometimes as much as an order of magnitude more numerous in burned stands than logged stands (Rees and Juday 2002). Species that are typically more abundant after fire than clearcutting are *Polytrichum* spp., *Dicranum* spp., *Marchantia polymorpha*, and *Ceratodon purpureus* (Noble et al. 1977; Johnston and Elliot 1996; Timoney, Peterson, and Wein 1997; Nguyen-Xuan et al. 2000; Rees and Juday 2002; Haeussler and Bergeron 2004). Forest dwelling species typically more common after logging than fire include *Pleurozium schreberi* and *Hylocomium splendens* (Johnston and Elliot 1996; Nguyen-Xuan et al. 2000; Rees and Juday 2002). Nguyen-Xuan et al. (2000) also noted that crustose lichens (notably *Trapeliopsis granulosa*), cup lichens (*Cladonia* spp.) and reindeer lichens (*Cladina* spp.) were more abundant in burns than in clearcuts. All studies demonstrate that the composition of the understory vegetation after fire is significantly different than after harvesting. Nonetheless, most studies noted that even the most fire-dependant species are patchily distributed within clearcuts, indicating that the differences are usually a question of abundance rather than presence or absence of species (e.g., Rees and Juday 2002; Haeussler and Bergeron 2004).

2.6.5 *Medium- and Long-Term Differences and Similarities in Understory Non-Vascular Species*

Rees and Juday (2002) found that while dominant species are usually different between logged and burned plots early after disturbance, late in succession (a few decades after disturbance) the dominant non-vascular species and total species richness are similar. Nonetheless, some initial differences were still apparent 22 years after disturbance (Nguyen-Xuan et al. 2000). After numerous decades, Reich et al. (2001) observed no significant difference between the diversity or richness of the understory non-vascular species community between logged and burned stands. Furthermore, with respect to composition, virtually no significant difference was observed between the two disturbances for almost all species with only *Polytrichum commune* being more abundant in burns than in clearcuts while the opposite trend was observed for two other non-vascular species (Reich et al. 2001).

2.6.6 *Summary*

While our review identified many conflicting results with respect to understory species response to wildfire and harvesting, most studies report important differences early after disturbance between logged and burned stands with respect to understory vascular and non-vascular species composition (e.g., Rees and Juday 2002; Nguyen-Xuan et al. 2000). Nonetheless, as succession proceeds and overstory canopies gradually close, the diverging understory plant communities established after these two types of disturbances eventually converge in the prolonged absence of disturbance (Timoney, Peterson, and Wein 1997; Reich et al. 2001; Rees and Juday 2002).

2.7 Wildlife Habitat Use

From a wildlife perspective, stand-replacing fires and timber harvesting both represent major disturbances which significantly alter habitats by replacing mid- to late-successional forests by early-successional ones. In the short term, this shift from closed to more open stands greatly influences habitat conditions such as food resources, cover and shelter but also several aspects of population and community dynamics such as dispersion, predation or competition (Smith 2000; Fisher and Wilkinson 2005). Wildlife responses to these disturbances generally reflect changes in habitat conditions and are often most important soon after disturbance (Hobson and Schieck 1999; Smith 2000; Fisher and Wilkinson 2005; Buddle et al. 2006; Schieck and Song 2006). Over time, natural succession will gradually lead to habitat conditions and wildlife assemblages that are more similar to those present before disturbance, although successional trajectories may differ between fire and harvesting (Niemelä, Langor, and Spence 1993; Fisher and Wilkinson 2005; Buddle et al. 2006). In general, the more severe the disturbance, the more drastic wildlife response will be and the longer it will take to return to pre-disturbance state (Smith 2000).

Despite their similarities, fire and logging differ in several of the habitat conditions they procure for wildlife. Wildfires, especially when severe, generate large amounts of standing (eventually downed) dead trees including large ones which represent an important habitat and food source for many wildlife species (Drapeau et al. 2002; Pedlar et al. 2002). While both wildfires and harvesting may be detrimental to bird or mammal nestlings during the nesting period, wildfires may be more severe and may induce additional mortality to less mobile organisms such as soil invertebrates (Smith 2000; Wikars and Schimmel 2001). However, in a review of the effects of fire on wildlife populations, Smith (2000) concluded that this direct impact was relatively less important than habitat changes. In comparison to harvesting, the spatial variability of fire severity creates various amounts of green or mixed-severity stands over the burned landscape (e.g., Kafka, Gauthier, and Bergeron 2001; Smyth et al. 2005), which represent important refuge sites for some wildlife species (Norton and Hannon 1997; Tittler and Hannon 2000; Lance and Phinney 2001; Tittler, Hannon, and Norton 2001). Contrarily, clearcut harvesting removes most of the large live trees, leaves few standing deadwood, and retains variable amounts of non-commercial trees and understory vegetation. In this subsection, we address how these differences between wildfire- and harvesting-induced disturbances affect the response of wildlife, specifically, invertebrates, birds and mammals.

2.7.1 *Invertebrates*

While fire may negatively affect many species of invertebrates, many others are clearly favoured by some post-fire conditions such as high abundance of dead wood, reduction of forest cover, increase in dry and sun-exposed areas, and decrease in competition (Ahnlund and Lindhe 1992; Wikars 1992, 1997; McCullough, Werner, and Neumann 1998). In fire-prone ecosystems, some pyrophilous species have even developed behavioural mechanisms or sensory organs such as infra-red or smoke detectors that allow them to take immediate advantage of the newly created post-fire environment (Evans 1966; Schütz et al. 1999; Schmitz, Schmitz, and Bleckmann 2000; Suckling et al. 2001). In Canadian and Fennoscandian boreal forests, several studies have documented distinct invertebrate assemblages between burned and other forest types (McCullough, Werner, and Neumann 1998; Saint-Germain, Drapeau, and Hébert 2004a; Larrivée, Fahrig, and Drapeau 2005; Buddle et al. 2006; Saint-Germain et al. 2005; Buddle, Spence, and Langor 2000). In eastern Canadian boreal forests for example, Saint-Germain, Drapeau, and Hébert (2004a) found that Coleoptera richness and abundance were greater in recently-burned (1-2 years post-fire) than in unburned stands and more than 40 species were found exclusively in burned stands. Saproxylic species—species that depend on dead wood or wood-inhabiting fungi during part of their life cycle (Kaila, Martikainen, and Punttila 1997)—which include bark and wood-borer species (Cerambycidae, Buprestidae, Scolytidae), are an important component of post-fire assemblages, which also include forest or open-stand generalists and predators (Ahnlund and Lindhe 1992; Wikars 1992, 1997; Werner 2002; Saint-Germain, Drapeau, and Hébert 2004a, 2004b).

Like wildfire, harvesting also has major impacts on invertebrate species composition and may reduce or eliminate habitat for species associated with older forest structures such as large trees and coarse woody debris (Niemelä 1997; Buddle et al. 2006). In boreal forests of Alberta, Niemelä, Langor, and Spence (1993) found three types of responses of carabids to logging: a) an increase of open-habitat species, b) an initial decrease of forest generalists followed by an increase with forest regeneration, and c) a decrease in mature forest specialists. Interestingly, the less sensitive forest species may persist during the first years following disturbance but seem to disappear as succession proceeds (Niemelä, Langor, and Spence 1993). Therefore, the highest richness found in some post-harvest forests may be a result of these habitats being occupied by both new colonizers and declining forest populations.

Despite similarities between burned and harvested sites, initial post-disturbance differences in invertebrate assemblages are consistently reported in boreal forest studies. Whereas clearcuts may often support similar or higher species richness and diversity than burned sites (e.g., Larrivée, Fahrig, and Drapeau 2005; Saint-Germain et al. 2005), changes in species assemblages are clearly not reflected by these measurements. For example, Buddle et al. (2006) reported a higher number of spider species in the most recent harvested sites (1-2 yrs after disturbance) compared to burned sites of similar age, but reported distinct species assemblages with several species being more abundant in one of either stand types.

The majority of the comparative studies undertaken in fire-mediated Canadian forests have been conducted on ground invertebrates (Buddle, Spence, and Langor 2000; Larrivée, Fahrig, and Drapeau 2005; Saint-Germain et al. 2005; Buddle et al. 2006). For soil- and litter-dwelling arthropods such as ground beetles and spiders, fire has been shown to cause instant mortality, to create more xeric habitat conditions unsuitable for many species and to promote colonization of several species more favoured by the specific habitat characteristics created by fire (McCullough, Werner, and Neumann 1998;

Wikars and Schimmel 2001; Larrivée, Fahrig, and Drapeau 2005; Saint-Germain et al. 2005; Buddle et al. 2006).

In contrast to fire, harvesting is less severe and may maintain undisturbed patches of forest floor resulting from silvicultural operations (Nguyen-Xuan et al. 2000). These may help to maintain, at least for a short period, many of the species usually associated with mature forests (Niemelä, Langor, and Spence 1993; Saint-Germain et al. 2005). On a longer term, it has been suggested that the higher severity of fire as compared to logging may cause a successional delay in wildlife response (Niemelä 1999; Buddle et al. 2006). Larrivée, Fahrig, and Drapeau (2005) and Buddle et al. (2006) also reported that post-fire sites are much more variable in terms of species composition, suggesting that logging produces a more homogeneous landscape. Despite these initial differences and the potential delay in post-fire succession, invertebrate assemblages generally converge over time. For example, arthropod assemblages in boreal forests of Alberta were shown to converge, although not completely, over a 30-year period and showed partial recovery of the pre-disturbance stage (Buddle, Spence, and Langor 2000; Buddle et al. 2006).

Because they offer similar sun-exposed conditions and a considerable but variable amount of CWD, harvested stands may support some saproxylic species as it has been suggested in some European boreal studies (Kaila, Martikainen, and Punttila 1997; Gibb et al. 2006). However, it has also been argued that harvested sites may not fully substitute burned forests in order to maintain the more specialized fire-associated species (Wikars and Schimmel 2001; Wikars 2002; Gibb et al. 2006). Few quantitative studies have directly compared saproxylic assemblages between burned and clearcut sites. In a study in white spruce forests of Alaska, Werner (2002) reported a higher abundance of wood borers (Cerambycidae, Buprestidae) in fringe areas of burned stands than in clearcuts, especially the first year following disturbance (as compared to 5 and 10 years post-disturbance). Different habitat-species associations were also found for bark and wood-boring beetles among burned, fringe of burned, clearcut and shelterwood logged stands. In a study in Sweden, Wikars (2002) examined the affinity of wood-living insects to disturbance (burned, clearcut and unburned forests) and log treatments (burned and unburned logs in burned forest only). Interestingly, he found that species assemblages were much more similar between logs in burned forest (burned and unburned logs) than between disturbance types (unburned logs between burned, harvested and unburned forests). Pyrophilous insect species were also mostly found in burned sites (on both burned and unburned logs). This study stresses the importance of stand disturbance effects on wood-living insect assemblages (fire-created conditions for pyrophilous species) and strongly suggests that dead wood in clearcut sites alone may not be sufficient to maintain saproxylic insect diversity. While species-specificity to wood condition may decrease over time (Wikars 2002), we found no studies that directly addressed the issue of convergence over successional time for this insect guild.

2.7.2 *Birds*

Effects of fire and harvesting on bird assemblages have been well documented by several studies in the boreal and other coniferous forests (Raphael, Morrison, and Yoder-Williams 1989; Hutto 1995; Hobson and Schieck 1999; Imbeau, Savard, and Gagnon 1999; Morissette et al. 2002; Simon, Schwab, and Otto 2002; Simon et al. 2002; Table 2.2). In general, both disturbances cause a shift from a bird assemblage dominated by forest species to one mainly dominated by open-habitat and ground nesting species (Westworth and Telfer 1993; Crête et al. 1995; Imbeau, Savard, and Gagnon 1999; Schieck and Hobson 2000). However, bird response may vary according to study area, vegetation type, severity, and time since disturbance. For example, it has been shown that the magnitude of species-specific responses to fire was greatly influenced by fire severity (Kotliar et al. 2002; Smucker, Hutto, and Steele 2005). Similarly, bird assemblages vary according to the level of retention that is left after harvesting, with partial retention being generally more beneficial to forest species than clearcuts (Norton and Hannon 1997; Tittler and Hannon 2000; Lance and Phinney 2001; Tittler, Hannon, and Norton 2001).

All studies directly comparing bird assemblages in burned and harvested stands reported an important divergence in bird assemblages, especially for the first years following disturbance (Hutto 1995; Schulte and Niemi 1998; Hobson and Schieck 1999; Imbeau, Savard, and Gagnon 1999; Schieck and Hobson 2000; Morissette et al. 2002; Simon, Schwab, and Otto 2002). One of the most striking differences lies in the abundance of the snag-associated guild in post-fire stands. In recently burned forests, several woodpecker species (e.g., Black-backed (*Picoides arcticus*), American Three-toed (*Picoides dorsalis*) and Hairy (*Picoides villosus*) Woodpeckers, Northern Flicker (*Colaptes auratus*)) are responding to the increased density of standing fire-killed trees which provide foraging and nesting structures (Murphy and Lehnhausen 1998; Hoyt and Hannon 2002; Nappi et al. 2003). Cavities excavated by woodpeckers may also be used by several secondary cavity nesters such as Tree Swallow (*Tachycineta bicolor*), House Wren (*Troglodytes aedon*) and Bluebird (*Sialia* sp.) (Saab, Dudley, and Thompson 2004). Other species such as aerial insectivores (e.g., Olive-sided Flycatcher, *Contopus cooperi*) and birds of prey such as the Northern Hawk Owl (*Surnia ulula*) take advantage of the more open habitat, the abundance of prey (small mammals for owls) and availability of snags used as perches (Hutto 1995; Kotliar et al. 2002; Hannah and Hoyt 2004). However, these high snag densities are clearly missing in harvested stands (Schulte and Niemi 1998; Pedlar et al. 2002; Simon, Schwab, and Otto 2002). Concordantly, Imbeau, Savard, and Gagnon (1999) found no resident and cavity-nesting species in recent clearcuts, where little retention (green or dead trees) has been left on site. Similarly, Hobson and Schieck (1999) found very distinct assemblages between burned and harvested forests, a difference that was partly explained by the dominance of several snag-associated species. These major differences in the abundance of snag-associated species are of particular importance considering that several of these have been identified as the most sensitive to the long-term effects of forestry (Imbeau, Mönkkönen, and Desrochers 2001). In addition, several species associated with open and shrubby habitats such as Le Conte's Sparrow (*Ammodramus Leconteii*), Alder Flycatcher (*Empidonax alnorum*), Common Yellowthroat (*Geothlypis trichas*) are often more abundant in post-harvested stands because much more vegetation is retained after harvesting (live canopy trees, grass and shrubs) compared to fire (Hobson and Schieck 1999; Imbeau, Savard, and Gagnon 1999).

Because fire-created snags eventually fall and decay (Raphael, Morrison, and Yoder-Williams 1989), these differences in bird assemblages usually converge over time (Hobson and Schieck 1999; Imbeau, Savard, and Gagnon 1999). Hobson and Schieck (1999) found that initial differences between burned and harvested stands decreased by 14 years after disturbance. The convergence was attributed to decreased densities of open-habitat species in post-harvested stands, decrease of snag-associated species in post-fire stands and increase of shrub nesters and foragers in both 14-year post-disturbance types. In their study, convergence continued up to 28-year stands although it was not totally complete probably due to differences that still persisted in vegetation composition and structure.

The magnitude of the initial divergence and eventual convergence in bird communities between fire and harvesting may greatly depend on the level of residual vegetation (Schieck and Hobson 2000). Schieck and Hobson (2000) found that bird assemblages from larger patches within disturbed stands supported more species from older forests than smaller ones. In contrast, bird communities from smaller patches (within cut blocks vs. burned stands) mainly reflected the surrounding post-disturbance communities, therefore showing the same initial divergence in bird assemblages between post-fire and post-harvest stands reported by Hobson and Schieck (1999). Nonetheless, over time these small patch communities also became more similar to those inhabiting mature fire origin forests and hence converged as succession proceeded (although some differences still persisted up to 60 years after disturbance).

Table 2.2 Summary of Studies That Compared Bird Assemblages between Wildfire and Harvest Sites in Fire-Mediated Canadian Forest Landscapes

Study	Study area	Stand type	Comparison	Level Of Retention[b]		Period (years)[c]		
				Wildfire (% unburned canopy trees)	Harvest (% residual canopy trees)	0-10	10-40	40+
Hobson and Schieck (1999)	Alberta	Boreal mixedwood (*Picea glauca*, *Populus tremuloides*)	Harvest vs wildfire	< 5%	≈ 6%	1	13-15	22-28
Imbeau et al. (1999)	Quebec	Black spruce (*Picea mariana*)	Harvest vs wildfire	0	0	Development stages based on regeneration height: recent (< 2m), young (5-11m)		
Morissette et al. (2002)	Alberta	Boreal mixedwood (*Pinus banksiana*, *Populus tremuloides*)	Unburned vs wildfire vs post-fire salvaged	Not measured	Not measured	2-3		
Schieck and Hobson (2000)[a]	Alberta	Boreal mixedwood (*Picea glauca*, *Populus tremuloides*)	Live residual tree patches within disturbed stands (harvest vs wildfire)	Patches of 1 to > 3000 live residual trees	Patches of 1 to > 3000 live residual trees	2	15, 30	60
Simon et al. (2002)	Newfoundland and Labrador	Black spruce (*Picea mariana*)	Harvest vs wildfire	< 5%	< 5%	5	14, 27	

[a] Results for small patches (≤ 10 trees) have been considered because bird communities were largely influenced by the disturbed matrix (wildfire and harvest).

[b] Percentage of pre-disturbance canopy trees that were unburned (wildfire) or retained (harvest). Information is based on study site description or interpreted from results.

[c] Only the periods for which both burned and harvested sites were sampled are indicated.

2.7.3 *Mammals*

Response of mammals to fire or logging is mainly linked to composition and structure of vegetation which provides food, shelter, and visual cover for mammal species (Smith 2000; Fisher and Wilkinson 2005). The impact of fire on small mammal composition and abundance has been well documented in several forest regions in Canada. Two general trends are generally reported in these studies: a) a higher abundance of Deer Mice (*Peromyscus maniculatus*) following wildfire and prescribed burning (a response that is mainly linked to the availability of seeds) and b) an initial lower abundance of Red-backed Voles (*Clethrionomys gapperi*) followed by an increase over successional time (a response mainly linked to vegetation cover). Other small mammals such as Chipmunks (*Tamias* sp.) and Red Squirrels (*Tamiasciurus hudsonicus*) may benefit from the increased availability of seeds while others such as Meadow Voles (*Microtus pennsylvanicus*) will colonize burns as herbaceous and shrub vegetation become more important (Krefting and Ahlgren 1974; Martell 1984; Simon et al. 1998; Fisher and Wilkinson 2005). It has also been shown that mammalian predators such as Marten (*Martes americana*) and other weasels may also take advantage of the increased availability of small mammals soon after fire (Koehler and Hornocker 1977; Paragi et al. 1996; Sullivan, Lautenschlager, and Wagner 1999). Several large mammals such as Moose (*Alces alces*) and Black Bear (*Ursus americanus*) also use burned sites to forage upon the high abundance of berries, herbaceous vegetation, and shrubs (Crête and Jordan 1981; Boileau, Crête, and Huot 1994; Crête et al. 1995; Smith 2000).

In a recent review on the effect of forest fire and harvesting on mammals in the North American boreal forest, Fisher and Wilkinson (2005) found similar temporal trends between fire and harvesting in mammal abundance over successional time. Small mammals and ungulates are generally abundant in the early stages of post-disturbance succession (1-10 years); hares and lynxes tend to peak in mid-successional stands where understory vegetation is abundant (11-75 years); arboreal sciurid, bat, and mustelid abundances increase with stand age until mature and over-mature conditions are reached (> 75 years). Unfortunately, in Canadian fire-mediated forests, very few studies have been undertaken that directly compare the response of mammals to fire and harvesting for the same study area. In a study in central Labrador, Simon et al. (2002) reported similar responses of small mammals to disturbance types over a 30-year period. Whereas Red-backed voles were significantly more abundant in clearcuts than in burned stands, a difference attributed to higher abundance of CWD and residual vegetation, the difference in the abundance of this and other small mammals tended to converge as vegetation and stand structure became more similar with time.

2.7.4 *Summary*

Responses of invertebrates, birds, and mammals to fire and harvesting are clearly linked to changes in habitat conditions created by these disturbances. While considerable literature has been published on the effects of fire and harvesting on wildlife (Niemelä 1997; McCullough, Werner, and Neumann 1998; Smith 2000; Fisher and Wilkinson 2005), few studies have directly addressed the comparative effects of fire and harvesting on wildlife, especially for mammals. Moreover, few studies have yet addressed wildlife responses over long successional periods (> 10 years), especially for invertebrates and mammals. Finally, as pointed out by Fisher and Wilkinson (2005), comparison of fire and logging is hampered by the fact that few studies specifically address post-disturbance heterogeneity (amount, spatial pattern, and temporal dynamics) of structural legacies such as unburned residual vegetation (islands, clumps, and individual trees), post-harvest residual vegetation, snags, and CWD.

However, it is clear from the available literature that the main divergence in wildlife response between fire and harvesting occurs soon after the disturbance event (<10 years). This difference is linked to two major differences between these disturbance types: a) specific structural legacies left by fire (e.g., dead wood) and harvesting (e.g., residual vegetation), and b) differences in the severity of soil disturbance (invertebrate mortality during fire). It has also been shown that convergence in wildlife assemblages occurs over a 30-year period for insects (Buddle, Spence, and Langor 2000), birds (Hobson and Schieck 1999; Imbeau, Savard, and Gagnon 1999; Schieck and Hobson 2000), and mammals (Simon et al. 2002) although this convergence might not be totally complete.

2.8 The Special Case of Post-Fire Salvage Logging

Post-fire salvage logging has become an important issue in many parts of the world (McIver and Starr 2000; Purdon et al. 2002; Sessions et al. 2003; Lindenmayer et al. 2004; Beschta et al. 2004). Proponents of salvage logging emphasize opportunities to minimize economic losses, promote timely regeneration of desirable species, reduce fuel loads and fire hazard, and mitigate a variety of fire-related ecological risks including soil erosion and pest infestations. Opponents cite literature which shows that salvage logging can have significant effects on key ecological processes, biological legacies and fire-favoured species of burned forests (McIver and Starr 2000; Karr et al. 2004; Nappi, Drapeau, and Savard 2004; Greene et al. 2006). In practice, benefits and costs of salvage logging depend on a variety of site-specific factors such as fire severity, topography, soil type, quantity and quality of dead wood remaining after fire and salvage, management objectives, methods of harvest (e.g. ground-based or aerial-based harvest systems), and post-disturbance silvicultural programs.

2.8.1 *Increase or Decrease of Fire Risk*

Salvage harvest is often conducted with the expectation that it will decrease fire risk and promote successful tree regeneration. Interestingly, there is little evidence in the scientific literature to support or refute the hypothesis that salvage harvest reduces the risk of another wildfire on the same site. For example, McIver and Starr (2000), in a literature review of the environmental effects of salvage harvest, found no studies examining the effects of salvage harvest on fuel loads and fire intensity on salvaged sites. More recently, Donato et al. (2006) reported that salvage logging on a site in Oregon damaged a cohort of tree seedlings and increased fine and coarse fuel loads. They concluded that salvage logging can be “counterproductive to goals of forest regeneration and fuel reduction.” However, Donato et al. have been criticized for drawing inappropriate conclusions from a single short-term case study and for failing to mention information about their study site that would support alternative conclusions (Newton et al. 2006; Baird 2006).

2.8.2 *Vegetation and Soil Response*

Salvage harvest may alter post-fire communities and ecological processes in two distinct ways: directly by the impact of harvesting operations and indirectly by the removal of fire-killed trees (McIver and Starr 2000; Purdon, Brais, and Bergeron 2004; Donato et al. 2006; Greene et al. 2006). First, logging operations may mechanically kill natural regeneration established after fire (Fraser, Landhäusser, and Lieffers 2004; Kurulok and Macdonald 2004; Greene et al. 2006). Additionally, a recent study has shown that removal of coniferous seed trees soon after fire may also eliminate seed sources which can significantly decrease the regenerative capacity of some tree species, notably black spruce (Greene et al. 2006). In some areas, to reestablish productive stands of desired species and to minimize the colonization of persistent hardwood or shrub cover, it can be desirable to replant stands manually after salvage harvest operations (Sessions et al. 2003).

Soil disturbance and removal of snags may also lead to changes in species composition as the drying potential of sites increases with the higher sun and wind exposure experienced following snag removal (Purdon, Brais, and Bergeron 2004; Greene et al. 2006). For example, a study on understory vegetation showed that salvaged sites supported species that are typically associated with severe forest floor disturbance and more xeric conditions (Purdon, Brais, and Bergeron 2004). Species composition after salvage harvest was still within the natural range of variability observed after fire only. However, the vegetation of salvaged sites was much more homogeneous than in post-fire sites and, with respect to the natural range of variability, salvaged communities only resembled post-fire communities having experienced severe fires while differing substantially from communities having experienced lower severity fires. Alternatively, salvage logging can have beneficial effects by disrupting the water repellent layer that may build up after fire (Poff 1989) and by placing slash on the ground to shelter bare watersheds after fire, thus reducing erosion by impeding overland flow (Ice, Neary, and Adams 2004; Shakesby et al. 1996).

In the longer term, it has been shown that salvage harvest, because of the combined effects of fire and the removal of burned trees, may cause depletion of nutrients such as Ca, Mg, and K over a 110-year forest rotation, especially after severe fires (Brais, Paré, and Ouimet 2000). In steep terrain, such effects on soil fertility and plant nutrition may be small relative to those of severe erosion events that sometimes occur in the aftermath of severe but infrequent fires (Kirchner et al. 2001). Neary and Hornbeck (1994) concluded that there is little evidence that salvage harvest cannot be carefully planned and conducted so as to avoid significant off-site impacts (Neary and Hornbeck 1994).

2.8.3 *Wildlife Response*

Removal of fire-killed trees alters major wildlife habitat structures of post-fire forests, which enhances habitat for some species and diminishes it for others. Many of the species that are typically associated with burned forests are affected by salvage harvest (Kotliar et al. 2002). Morissette et al. (2002) showed that the difference in species composition between salvaged and unburned sites was greater than between burned and unburned sites, thus suggesting that salvaging represents a greater disturbance than fire alone. They found that resident species, canopy and cavity nesters, and insectivores were the least likely to occur in salvaged sites whereas generalists, omnivores, and ground- and shrub-nesters were more likely to occur on salvaged sites. Cavity nesting birds are especially affected by salvage harvest, although each species may respond differently to harvest intensity (Saab and Dudley 1998; Lecoure et al. 2000; Haggard and Gaines 2001). Stands with low snag densities may support higher abundance of species that nest in snags but forage in open areas (e.g., Northern Flicker, Bluebird), whereas high snag densities may better support species that rely on snags for both foraging and nesting such as certain *Picoides* species (Black-backed, Three-toed, and Hairy Woodpeckers) (Saab and Dudley 1998; Haggard and Gaines 2001), where higher snag densities may be required to support sufficient prey species. However, it has also been suggested that extremely high snag densities may support large increases in prey species such as bark beetles, which may overwhelm the defences of neighbouring unburned areas (McIver and Starr 2001). Although we found no studies that specifically compared post-fire salvaged sites to unburned harvested sites, it is expected that bird assemblages will be generally similar mainly with regard to open-habitat generalists. However, differences might be expected and will likely depend on the level of retention left on site (fire-killed and unburned trees on burned sites; uncut trees on harvested sites). Measures such as minimum snag-retention guidelines would be expected to reduce salvage impacts.

2.8.4 *Summary*

Because salvage harvest has not been extensively utilised or studied, many of the impacts of this practice and the effectiveness of alternative harvesting and retention strategies have yet to be assessed. Research is complicated by a general lack of pre-treatment data from sites affected by wildfire and by high variability of fire impacts. Nevertheless, post-fire salvage harvest represents an additional disturbance that can have significant ecological effects compared to fire alone. Removal of fire-killed trees can affect tree regeneration, understory composition, the abundance and distribution of dead wood, wildlife habitat, and soil properties. Whether salvage logging is beneficial or detrimental depends on management objectives and many site-specific factors. Additional investments in research are needed to support management decisions and policy development.

2.9 Effects of Alternative Silvicultural Treatments

While up to now we have compared mainly one type of harvesting technique, i.e., clearcutting either of healthy or fire-killed forests, many alternative harvesting approaches (partial cutting or retention) and site preparation techniques (prescribed burning, scarification, etc.) are increasingly applied. While many studies compare these alternative techniques to conventional clearcutting, relatively little research has compared the effects of these nonconventional silvicultural approaches to the ones induced by wildfire (e.g., Johnston and Elliot 1996; Whittle, Duchesne, and Needham 1997; Wikars and Schimmel 2001). Nonetheless, some studies report that prescribed burning does improve the regeneration of many pioneer species commonly observed after fire but scarcely distributed after clearcut harvesting only (Morgan and Neuenschwander 1987; Johnston and Elliot 1996; Whittle, Duchesne, and Needham 1997). In general, the understory species composition on sites that have experienced controlled burning is more similar to wildfire than clearcutting immediately after disturbance (Johnston and Elliot 1996).

Although not identical to wildfires in their severity and the habitat conditions they create, prescribed burns after harvesting also affect ground invertebrates with some species favoured by either post-fire or post-harvest conditions (Beaudry, Duchesne, and Côté 1997; Wikars and Schimmel 2001). Interestingly, Wikars and Schimmel (2001) showed that differences in tree densities in burned stands (cut-burned vs. uncut-burned) did not affect survival of invertebrates immediately after fire. However, the number of invertebrates 60 days after fire was higher in uncut-burned stands than in cut-burned stands. Uncut-burned stands also supported a higher number of cucujoid beetles, one of the most common taxa in burned plots. These differences have been attributed to the less adverse conditions procured by standing snags (shelter from wind and sun) and highlight differences that might be found between habitat conditions created by wildfires and traditional clearcut prescribed burns.

Differences in initial post-disturbance responses may be attenuated, at least for some species, through different silvicultural approaches that maintain or create key structural elements of post-fire habitats such as soil disturbance, residual vegetation, dead wood, and CWD. For example, variable retention (seed-tree retention, partial logging) may reproduce green residuals that are common within burns and may provide valuable habitat for some mature or late successional forest species (Norton and Hannon 1997; Tittler and Hannon 2000; Lance and Phinney 2001; Tittler, Hannon, and Norton 2001; Gandhi et al. 2004). Moreover, prescribed burning, especially when applied to variable amounts of retention may represent the best strategy for mimicking natural wildfire effects (Wikars and Schimmel 2001). However, considering that key structural elements important to ecological processes of post-fire habitats (abundant standing snags, high degree of forest floor consumption and production of insect-attracting fire signals) may not be entirely maintained with prescribed burning, the maintenance of post-fire habitats within fire-mediated Canadian forests may be a necessary strategy for the maintenance of biodiversity.

3.0 LANDSCAPE-SCALE SIMILARITIES AND DIFFERENCES

3.1 Introduction

Until now, we only have considered differences between fire and harvesting disturbances at the *stand* scale, i.e., within the boundaries of a single disturbance event. At a broader scale, the *landscape* is composed of a mosaic of forest stands of different post-disturbance age. In landscapes driven by stand-replacing disturbances, the proportions and configuration of stands of different age-classes across the landscape is determined by the disturbance regime, i.e., the spatial and temporal dynamics of the individual disturbance events over a long period of time (Turner, Gardner, and O'Neill 2001). Disturbance regime parameters describe recurrence (frequency, rotation period, return interval, cycle), spatial characteristics (size, configuration) or magnitude (intensity, severity), although they are sometimes intercorrelated. The rotation period (also called fire cycle for fire regimes) is the mean time required to disturb an area equal in size to the study area, and will be used to compare the ecological effects of fire and harvesting regimes on a similar basis. In this section, we will first stress the importance of the non-spatial component of the disturbance regimes, i.e., the distribution of stand age-classes over the landscape. We will then explore the spatially explicit differences between fire and harvesting disturbance regimes by looking at spatial configuration of forest stands. These first two sections address the two main concerns usually associated with forest management practices: the loss of over-mature forests and habitat fragmentation. Finally, we will specifically address the response of wildlife to fire and harvesting regimes at the landscape scale.

3.2 Distribution of Stand Ages, Structures, and Forest Types

3.2.1 *Theoretical Distributions*

The most important effect of disturbance regimes is their impact on the relative proportions of stand ages across the landscape. Because fire and harvesting events reset the age of forest stands to zero, the rotation period of these disturbances directly affects the age structure of stands across the landscape. In general, short rotations result in a higher proportion of young stands, while longer rotations increase the area occupied by advanced seral stage forests. However, theoretical work has shown that even for a similar rotation period, fire and harvesting regimes yield considerably different distributions of stand ages at equilibrium (Van Wagner 1978). In a landscape managed under a harvesting rotation of 100 years for example, 1% of the forest is logged each year and the regulated landscape shows a rectangular stand age distribution at equilibrium, with no stand older than the rotation period (Figure 3.1). On the other hand, landscapes under a fire cycle of 100 years show a negative exponential or Weibull stand age distribution at equilibrium, because fire is a random process (Van Wagner 1978; Johnson and Van Wagner 1985; Johnson 1992; Johnson and Gutsell 1994; Johnson, Miyanishi and Weir 1998). If probability of burning is independent of forest age, stand age distribution follows a negative exponential, with 37% of the landscape occupied by stands older than the fire cycle (Johnson 1992). This is because some stands burn more often than predicted by the fire cycle while some do not burn at all by chance alone. If the probability of burning increases with stand age, more young stands will escape fire and the burning will mostly occur in older stands, resulting in a Weibull distribution of stand ages (Figure 3.1). In this case, the proportion of forests older than the fire cycle will be lower than 37%, but the exact proportion will depend on the relationship between the hazard of burning and stand age (see Johnson (1992) and Johnson and Gutsell (1994) for further explanations). These theoretical distributions, however, do not consider the important year-to-year variability in area burned that exists under natural conditions (Van Wagner 1988). Nevertheless, modeling studies using real landscapes have shown that adding temporal stochasticity to the annual area burned still resulted in a negative exponential distribution of stand ages, but with the addition of some noise (Boychuk et al. 1997; Kuuluvainen 2002).

3.2.2 *Empirical Distributions*

The negative exponential distribution of stand ages has been found empirically in many boreal forests (Heinselman 1973; Yarie 1981; Weir, Johnson, and Miyanishi 2000; Bergeron et al. 2001, 2004), where the fire regime is thought to be largely controlled by climate and little affected by stand age (Johnson 1992). In most cases, however, mixed distributions are found (Heinselman 1973; Johnson and Larsen 1991; Lesieur, Gauthier, and Miyanishi 2002) because long-term changes in the fire cycle occur more rapidly than the time needed for the system to reach equilibrium (Johnson 1992). The rectangular distribution of stand ages associated with a regulated forest has not been observed empirically because industrial logging is fairly recent in North America and no managed landscape has yet undergone a complete rotation nor reached equilibrium. However, landscape modeling has shown that a clearcutting regime aiming at a fully regulated forest landscape leads to a nearly rectangular stand age distribution after 150 years of simulation (Gustafson and Crow 1998). This model assumed that the entirety of the forested landscape was composed of stands remaining unharvested, which would change the distribution. Empirical support for the rectangular distribution of stand ages comes from Fennoscandia, where forest management has a longer history than in North America, and managed areas comprise almost the entirety of small landbases. Forest inventories in Finland showed that at the beginning of the century (1921-1926), 26% of forest stands were older than 110 years, while this proportion had dropped to 13% in 1986-1994 (Finnish Forest Research Institute 2003). Similarly, forest inventories showed that in the 1910s more than 80% of the northern Swedish forests were older than 150 years while in the 1980s this proportion fell to 3% (Östlund, Zackrisson, and Axelsson 1997). This lends support to the hypothesized rectangular distribution of stand ages in managed forests, where stands older than the rotation age disappear from the landscape after several rotations.

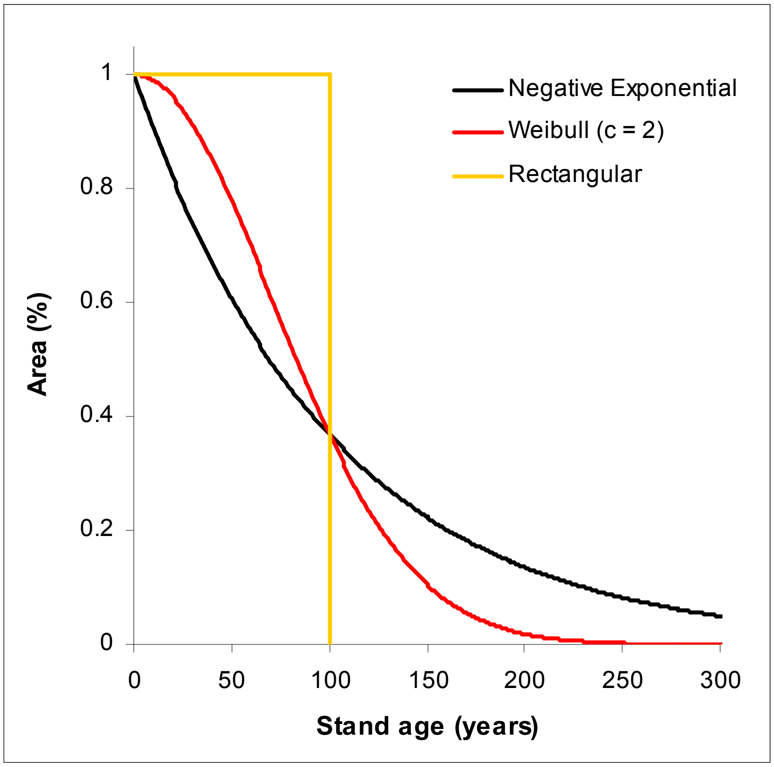


Figure 3.1 Theoretical Rectangular, Negative Exponential, and Weibull (shape parameter, c = 2) Age Distributions of Stands across the Landscape for a Disturbance Rotation of 100 Years [The corresponding proportions of stands older than the rotation period (100 years) are 0%, 37%, and 25%, respectively. Note that the negative exponential is a special case of the Weibull, where c = 1 (modified from Van Wagner (1978) and Johnson (1992)).]

3.2.3 *Ecological Implications*

The lower proportions or complete absence of over-mature stands under a harvesting regime with a fixed rotation period, compared with a fire regime of the same rotation period, reduces the diversity of stand types and changes the proportions of these types across the landscape. The structure and composition of older forests have been shown to differ from that of young stands on many aspects. Over-mature boreal forests are characterized by uneven age, height, and diameter structures, and show a higher biomass of snags and coarse woody debris than mature post-fire or post-logging stands (Harmon et al. 1986; De Grandpré, Archambault, and Morissette 2000; Harper et al. 2002; Rouvinen, Kuuluvainen, and Karjalainen 2002; Kneeshaw and Gauthier 2003; Lecomte et al. 2006a, 2006b). Many structural characteristics of these older forests are in fact caused by secondary disturbances such as insect outbreaks (Holling 1992; Bergeron and Leduc 1998), wind (Kramer et al. 2001; Ruel and Pineau 2002), and canopy gap dynamics (Kneeshaw and Bergeron 1998; McCarthy 2001). In addition, in forest ecosystems that show a succession of tree species over time, forest composition itself is altered: forests under harvesting management typically show a reduction of stands dominated by late-successional species and an increase in early-successional stands (Mladenoff et al. 1993; Gauthier, Leduc, and Bergeron 1996; Bergeron and Harvey 1997; Bergeron 2000). This alteration of forest structures and composition might reduce the abundance of organisms that are often associated with older forests, including understory plants (Scheller and Mladenoff 2002), epiphytic lichens and bryophytes (Lesica et al. 1991; Esseen, Renhorn, and Pettersson 1996; Boudreault et al. 2002), invertebrates (Niemelä 1997; Jonsell, Weslien, and Ehnström 1998), birds (McGarigal and McComb 1995; Edenius and Elmberg 1996; Drapeau et al. 2000; Imbeau et al. 2001), and mammals (Fisher and Wilkinson 2005).

The landscape-scale change in age-class distributions and forest types (early-successional mostly deciduous vs. late-successional coniferous) anticipated as landscapes become progressively more under the influence of harvesting will change timber productivity at the landscape scale; first because stand productivity is maximal in young through to mature forests, declining with stand age, and second because deciduous stands are more productive than coniferous stands (Gower, McMurtrie, and Murty 1996; Murty, McMurtrie, and Ryan 1996; Ryan, Binkley, and Fownes 1997). Hence, the larger proportion of the landscape occupied by young deciduous forests in managed as opposed to fire-mediated landscapes should result in higher tree productivity at the landscape scale in managed fire-mediated landscapes.

3.2.4 *Disturbance Variability*

One last major difference between fire and harvest disturbances within landscapes is variability in time and space. Under a given fire regime, the annual area burned will show large year-to-year variation. In Canada, the coefficient of variation of the annual area burned between 1959 and 1999 ranges from 100% to 250%, depending on the province (Canadian Forest Service 2002). On the other hand, the interannual variability of harvesting is close to zero because roughly the same area is harvested every year. The ecological implications of this temporal variability still have to be investigated. Similarly, the distribution of fire size shows a much greater range (Bergeron et al. 2002, 2004; Gauthier et al. 2004) than that of cut blocks (DeLong and Tanner 1996), which are regulated by strict guidelines. The large extent of contiguous burned areas could, however, eventually be matched by harvesting if cut blocks were aggregated in space. Spatial configuration of disturbances will be the topic of the next section.

3.3 Configuration

The spatial configuration of disturbed patches is another level of organization that can be used to compare fire and harvesting disturbance regimes. Theoretical work has shown that for fixed proportions of cover types, increasing fragmentation by disturbance (fire or harvesting) reduced mean and maximum patch size, and the amount of interior habitat (i.e., not affected by edge effects), while it increased the amount of edge habitat and the perimeter to area ratio of the patches (Franklin and Forman 1987; Hunter 1993; Li et al. 1993; Wallin, Swanson, and Marks 1994; Hargis, Bissonnette, and David 1998; Turner, Gardner, and O'Neill 2001). Landscape simulation models have also shown that for the same area cut, highly dispersed cutting patterns resulted in high fragmentation, whereas concentrating the harvesting in some parts of the landscape could increase the area of older forest (Li et al. 1993; Gustafson 1996; Gustafson and Crow 1996, 1998; Klenner, Kurz, and Beukema 2000; Mehta et al. 2004). The spatial configuration of disturbed patches thus greatly influences the amount of forest/non forest interface. But how do landscapes fragmented by fire compare to landscapes fragmented by harvesting? Although many studies have compared the spatial configuration of disturbed vs. undisturbed forests (e.g., Mladenoff et al. 1993; Spies, Ripple, and Bradshaw 1994; Mehta et al. 2004), few have been able to directly compare landscapes disturbed by fire and harvesting regimes. There are many ways of empirically studying the effects of landscape fragmentation on ecosystem pattern and processes: by comparing whole landscapes composed of many discrete disturbed patches (Gluck and Rempel 1996; D'eon and Glenn 2005); by comparing within-disturbance spatial patterns of residual vegetation and post-disturbance succession (Schroeder and Perera 2002); and by studying ecotones between residual forest and disturbed patches, thereby directly studying local edge effects of fire and harvesting disturbances (Harper et al. 2004).

3.3.1 *Whole Landscapes*

Several problems arise when attempting to study multiple landscapes, however. First, the quantification of configuration relies heavily on the way patches are defined, which in turn depends on the scale (grain and extent) of the map used, and on the neighbourhood rule used to aggregate individual elements of a map (usually pixels) (Turner et al. 1989; Wickham and Riitters 1995; Turner, Gardner, and O'Neill 2001; Turner 2005). Trying to compare landscapes of different scales might be misleading, and a difference attributed to disturbance type might in fact be caused by the chosen analytical scale (e.g., Gluck and Rempel 1996). Second, many of the landscape metrics used to describe configuration are highly sensitive to the proportion of the landscape occupied by a particular forest or disturbance type (O'Neill et al. 1988; Gustafson and Parker 1992; Tischendorf 2001; Turner, Gardner, and O'Neill 2001; Fortin et al. 2003; Remmel and Csillag 2003; Wu 2004); therefore, trying to compare disturbance types that occupy different proportions of the landscape might yield conclusions that have nothing to do with patch configuration but more with their spatial extent (e.g., D'eon and Glenn 2005). Third, most studies do not explicitly state the rotation period of the studied fire-driven and managed landscapes (e.g., Gluck and Rempel 1996), or compare landscapes with different rotation periods, which may confound the effects of configuration with those of annual area disturbed, i.e., of the age-class distribution of stands (e.g., D'eon and Glenn 2005). To our knowledge, no empirical study has compared the spatial configuration of fire and harvesting using a rigorous experimental and statistical design, which may be nearly impossible given the impossibility of designing classical experimental setups at broad scales. Future studies should a) concentrate on replicated stochastic modeling using real landscapes and real disturbance patch configurations, but allowing to control for scale, disturbance extent, and rotation period; b) take multiple samples from real or simulated landscapes to be able to make statistical inferences (Cardille et al. 2005); and c) generate probability distribution and confidence intervals for landscape indices to be able to statistically detect differences between landscapes (Fortin et al. 2003).

3.3.2 *Within-Disturbance Heterogeneity and Edge Effect*

Using a sampling design that circumvented most of the above limitations, Schroeder and Perera (2002) compared post-disturbance revegetation patterns within clearcut and burned areas between 1951 and 1990 in the boreal forest of Ontario. Their maps were based on a 10 ha grain, disregarding heterogeneity at finer scales that might be important in explaining post-disturbance successional patterns (Turner et al. 1994, 1997). Nonetheless, they found that the vegetation patterns within clearcuts were more heterogeneous than within burned areas, with fires having a larger mean patch size than clearcuts (Schroeder and Perera 2002). This is in sharp contrast to other findings (DeLong and Tanner 1996; Gluck and Rempel 1996) that fires created more complex landscape spatial patterns, had more residual island remnants, and had smaller vegetation patches than clearcuts. The finer grain of these studies (0.2 ha in DeLong and Tanner (1996) and ~1 ha in Gluck and Rempel (1996)) probably captured heterogeneity at a finer scale within the disturbed patches. This stresses the importance of scale when trying to quantify landscape heterogeneity (Turner et al. 1989; Turner 2005). The boundaries of burned patches have also been found to be more irregular than those of clearcuts, resulting in more complex shapes (Eberhart and Woodward 1987; DeLong and Tanner 1996; but see Gluck and Rempel (1996)) which may affect animal movement patterns. This conforms to earlier work on patch complexity, which suggested that patches with simpler shapes reflected anthropogenic influence (Krummel et al. 1987).

Although many studies have addressed edge effects of clearcuts (e.g., Rheault et al. 2003), to our knowledge only one has directly compared the structure and vegetation at fire and clearcut edges (Harper et al. 2004). In this study conducted in the black spruce forest of northwestern Québec, fire edges were found to be more diffuse (influence up to 40 m into interior forest) than clearcut edges (influence up to 5 m), which was explained by partial burning of the forest by low intensity fire (Harper et al. 2004). Fire edges also showed more structural variation, significantly more snags, and a different composition of shrubs, herbs, mosses, and lichens compared with clearcut edges.

Spatial configuration of undisturbed patches and edges has a significant influence on post-disturbance recovery. Forest edges or island remnants are an important source of propagules for recolonization of the disturbed patch (Turner et al. 1994; Kafka, Gauthier, and Bergeron 2001). The distance from forest edge will largely determine the capacity of tree species to disperse seeds into the burn (Greene and Johnson 1989, 2000) or clearcut patch (Greene and Johnson 1996; Hughes and Bechtel 1997). This is especially true for tree species that are not adapted to fire, like balsam fir, which rely on survivors to persist in the landscape (Hughes and Bechtel 1997; Gauthier, De Grandpré, and Bergeron 2000; Asselin, Fortin, and Bergeron 2001).

3.4 Wildlife Response

As reviewed above, wildlife responses to disturbance at the stand scale generally reflect changes in habitat conditions. However, wildlife responses may also be influenced at broader scales by the proportions of forest types and their configuration in the landscape. Several aspects of landscape pattern effects have been addressed in the literature, but the focus has mainly been on edge effects, connectivity, and landscape-scale responses (see NCASI (2004) for a review on birds). Birds have been widely used to study spatial effects as their ecology is well known, most species show strong affinities to specific habitat conditions, and because they use habitats of intermediate scale (which closely match harvesting block sizes) while still being influenced by broader scale effects (e.g., Drapeau et al. 2000; Lahti 2001; NCASI 2004). Although the spatial effects of harvesting on birds have been widely compared between natural and harvested forests, the real question is: “Do birds respond differently to harvest- and fire-fragmented landscapes?”

Because fragmentation increases the forest/non forest interface, questions regarding the integrity of forest edges for forest-dwelling species (flora and fauna) and their use by wildlife have been the focus of numerous studies (e.g., Imbeau and Desrochers 2002; Rheault et al. 2003; Wolf and Batzli 2004). A major issue has been edge effect on bird nest predation and parasitism. Although results on this topic are equivocal, higher predation and parasitism at forest edges have been reported for agricultural landscapes and have been generally attributed to higher nest densities, higher use of these ecotones by predators, and higher densities of generalist predators in the surrounding agricultural matrix as compared to the forest interior (Andrén and Angelstam 1988; Andrén 1995; Lahti 2001; Batary and Baldi 2004). Evidence of edge-related effects is even less clear in managed forest landscapes: most studies did not find an increase of nest predation at clearcut-forest edges while others have found evidence of such effects (Hartley and Hunter 1998; Manolis, Andersen, and Cuthbert 2000; Tittler and Hannon 2000; Ibarzabal and Desrochers 2001; Lahti 2001; Manolis, Andersen, and Cuthbert 2002; Brongo 2002). Lack of edge-related effects in managed forest landscapes (as compared to permanent agricultural landscapes) has been attributed to the ephemeral state of harvested stands, the less hospitable conditions of abrupt ecotones for nesting and the lower densities of generalist predators (Boulet and Darveau 2000).

Interestingly, it has been suggested that in fire-driven forest ecosystems, edge effects may be less likely to occur because edges already exist in the patchy environment created by fire and that species have evolved within this context (Andrén 1995; Cotterill and Hannon 1999). A direct comparison of nest predation between fire-induced and harvest-induced edges may therefore provide valuable information on the relative impact of harvesting as compared to natural processes. We are aware of only one study that reports this kind of comparison. In boreal mixedwood forests of western Québec, Brongo (2002) compared edge effect on nest predation (using artificial nests) between an agricultural landscape (> 60 years), a recently managed forest landscape (< 5 years), and a recently burned forest landscape (3 years). Interestingly, predation rate was highest in the managed landscape, lowest in the burned landscape, and intermediate in the agricultural landscape.

Also important to the fragmentation issue is the connectivity of forest patches within managed forest landscapes. There is evidence that forest birds are constrained in their movements by distance between forest stands (Desrochers and Hannon 1997; St. Clair et al. 1998). A correlate to this is that different forms of retention such as riparian buffer strips or upland buffers may serve as corridors for bird movement (although results on that topic are equivocal), and that the role of corridors may decrease with vegetation regrowth (Hannon and Schmiegelow 2002; Robichaud, Villard, and Machtans 2002). Again, how managed landscapes differ from burned landscapes has not been directly assessed. It might be expected that connectivity is much higher in burned landscapes because of the variable amount of unburned and mixed severity stands (Turner et al. 1994; Kafka, Gauthier, and Bergeron 2001) but also because of the presence of snags which provide vertical structure during the initial critical period where regeneration is not high enough to provide cover and facilitate movement between patches. In this sense, various forms or levels of partial retention may greatly improve movement and dispersion in harvested blocks as it might be suggested by the use of these residuals by forest birds (Norton and Hannon 1997; Lance and Phinney 2001; Tittler, Hannon, and Norton 2001).

Although studies on edge effect and connectivity may provide crucial insights on how communities may respond to landscape changes, some broader scale studies are needed to measure these effects. In Ontario, Sleep (2005) examined the responses of boreal forest owls to landscape patterns originating from fire and harvesting at the provincial scale. Interestingly, he found no evidence of different responses to disturbance type for three of the four forest-dwelling owl species, thus suggesting that although habitat patterns diverge between fire and harvesting, owl responses do not necessarily differ. The only species that responded to disturbance type was the Great Gray Owl (*Strix nebulosa*), which was negatively associated with the amount of recent harvest and positively associated with time since fire disturbance. At the landscape scale, Sleep (2005) also found Boreal Owls (*Aegolius funereus*) to differ in their habitat use between burned and harvest landscapes.

Drapeau et al. (2002) compared bird communities between a natural landscape (naturally disturbed by fire and insect outbreaks), an industrial landscape (< 20-year managed forests) and a pre-industrial landscape (human settlement, agriculture, and harvesting dating back to the early 1930s). The transition from the natural to industrial and pre-industrial landscapes implied a conversion from mixedwood to deciduous forest dominance and a decrease in mature forests. Concordantly, bird communities clearly differed among these landscapes, with mature forest- and coniferous-associated species being more abundant in the natural landscape. A key finding was the significant effect of landscape context variables in addition to the local context variables. This suggested that the influence of landscape changes may be more than the sum of stand-level changes. However, patterns of bird community composition were related to composition but not to configuration variables. As shown in this and other studies (McGarigal and McComb 1995; Schmiegelow, Machtans, and Hannon 1997; Trzcinski, Fahrig, and Merriam 1999), configuration effects *per se* (not of habitat loss) in fire-mediated Canadian forests have been found to be relatively minor compared to the effect of net habitat loss (Turner, Gardner, and O'Neill 2001; Fahrig 2003). Here again, one might speculate that wildlife communities in fire-mediated landscapes may be less affected by fragmentation because they have adapted to natural disturbance regimes (Cotterill and Hannon 1999). However, further research is needed to better understand community responses to high levels of fragmentation in these forest landscapes.

3.4.1 *Summary*

The greatest difference between harvesting and fire regimes at the landscape scale is the resulting stand age distributions. Fire-driven landscapes show a negative exponential distribution of stand ages, with 37% of the stands older than the fire cycle, while landscapes under a regulated harvesting regime show a rectangular (or uniform) stand age distribution, with no or few stands older than the commercial rotation period. This results in a significant (37%) loss of old forests (stands older than the mean rotation period) in managed landscapes. There is also an important difference in the spatial and temporal variability of both disturbance regimes, with harvesting showing a constant area disturbed annually and fire regimes showing a very high variability for the same rotation period. Research done on landscape configuration shows that fire-driven landscapes tend to have more complex patterns, more residual island remnants, and smaller vegetation patches than managed landscapes. Fire edges are more diffuse, show more structural variation, have more snags, and show significantly different vegetation than clearcut edges. In boreal ecosystems, wildlife is more affected by landscape composition than configuration. Therefore, the effects on stand age distribution, primarily the loss of old forests, should be regarded as a priority in the preservation of biodiversity in managed landscapes.

4.0 RESEARCH NEEDS

While our review of the scientific literature has revealed numerous similarities and differences between wildfire and clearcut harvesting, it also has highlighted that very little data are available and much research needs to be done regarding many ecosystem attributes. Here we list a few main areas needing further investigation.

- A collaborative effort between industries, governments and the multi-disciplinary scientific community should be put forth in order to **identify comparable sites having experienced harvesting- or wildfire-induced disturbances over the past 40-50 years**. This would enable the comparison of the effects of harvesting and wildfire for numerous decades after disturbance, data which are scarce for all stand attributes presented in this review.

- Within and around large burns, **permanent plots should be systematically established in burned, clearcut, and salvaged logged sites** to be able to obtain quantitative, long-term data in many regions across Canada.

- With respect to salvage logging, **alternative levels of retention need to be studied** for all stand attributes presented in this review.

- For all stand attributes, **long-term studies comparing the effects of salvage logging and wildfire** need to be undertaken.

- Given the paucity of scientific data comparing nutrient cycling aspects in harvesting- and fire-origin stands, post-disturbance **stand nutrient dynamics is an area of research needing particular attention** given its role in determining long-term stand productivity.

- **More studies should be done systematically at multiple scales** (site/stand/landscape) in order to quantify and compare the heterogeneity of the effects of harvesting- and wildfire-induced disturbances.

- Studies should be undertaken that **compare the effects of alternative silvicultural interventions** (e.g., partial retention, scarification, controlled burning) to not only pre-harvesting state and to the effects of clearcutting, but also to those induced by wildfire.

- **Comparisons are needed of clearcut and burned landscapes of similar grain, extent, and rotation period at multiple scales using sound statistical analyses**. This should be done both empirically and with simulation modelling.

- To **address wildlife issues** at the landscape scale, species dynamics should be compared **in multiple landscapes having experienced different levels of harvesting and wildfire.**

- Studies are needed on the **effects of variability of disturbance regimes** (in time and space) on landscape patterns and processes.

- Studies should be conducted in order to **compare the effects of different levels of partial cutting to the effects of secondary disturbances** (insect-damaged, windthrow) that are the forces influencing the structure and composition found in over-mature stands.

- **Attention should be given to certain processes that may interact with harvesting to produce unexpected reductions in productivity**, including invasion by ericaceous shrubs, paludification, and compound disturbances.

5.0 CONCLUSION

Early after disturbance, most stand-level attributes differ between harvesting and wildfire. Structurally, young post-fire stands are characterized by more snags and less downed woody debris than young post-harvest stands. These stand types are, however, similar with respect to the quantity of underground woody debris. With respect to forest floor depth, early post-harvest sites have significantly thicker forest floors than burned sites. Additionally, while it is reported that both wildfire and clearcut harvesting are capable of producing a pulse of extractable nutrients, the intensity of the pulse is greater after wildfire than clearcut harvesting. Finally, soon after fire there is a pulse in base cations which increases soil pH, while a decrease of soil and forest floor pH is observed after harvesting.

The basal area of live trees is low early after disturbance by fire or harvesting but density is generally higher in harvested sites. Furthermore, there are more residual deciduous trees in clearcuts than after fires and this can lead to divergent successional patterns in burned and harvested stands. Regeneration from seeds is more abundant in burned compared to harvested sites, and black spruce layers are more abundant in harvested than in burned sites.

Shortly after disturbance, the productivity (growth increment per year) of black spruce stands is higher in burned sites than in logged sites. However, because harvesting leaves the advance regeneration, absolute height and volume are larger immediately after logging than after fire. Eventually, both productivity and biomass converge later in succession. Post-logging productivity in other vegetation types has been shown to be either similar (aspen and mixedwood) or superior (scarified lodgepole pine) to post-fire productivity.

Biodiversity elements significantly differ between burned and logged sites. Early after disturbance, significant differences in understory vascular and non-vascular community composition are commonly reported. Faunal assemblages, be they mammals, invertebrates, or birds, all seem to respond differently initially to harvesting- and wildfire-induced disturbances.

At the stand scale, while most forest attributes are different early after disturbance between burned and logged stands, the majority of these converge a few decades after fire. A few exceptions are to be noted, though. First, the thicker forest floors observed after logging as compared to fire appear to persist numerous decades after disturbance. Secondly, while faunal communities do become less different as time passes, late in succession some species present in burned stands are either significantly less abundant or absent in similarly aged logged stands. Finally, numerous studies suggest that while the effects of wildfire- and harvesting-induced disturbances do not significantly differ after a few decades, there is some concern about the ability of harvesting-induced disturbances to recreate the full range of natural variability observed during post-fire succession.

Post-fire salvage logging affects ecological processes, biological legacies, and the abundance of species commonly encountered only after fire. Removal of fire-killed trees can affect tree regeneration, understory composition, the abundance and distribution of dead wood, wildlife habitat, and soil properties. Nonetheless, many of the effects are site-specific and therefore additional investments in research are needed to support management decisions and policy development.

The few studies that have actually compared the effects of alternative silvicultural approaches to the ones induced by wildfire have demonstrated that prescribed burning and the variable retention of trees during harvesting can significantly attenuate the structural differences observed between fire and clearcutting, along with the ecological processes that they may support. Nonetheless, our review suggests that the conservation of some biodiversity elements will necessitate that some post-fire stands within fire-mediated Canadian landscapes be left untouched.

At the landscape scale, the most important difference between fire and harvesting regimes is the distribution of stand age classes. The proportion of stands older than the rotation period (usually 100 yrs) tends toward zero under a fully regulated harvesting regime, while it is around 37% under a fire regime of similar rotation period. This results in a significant loss of over-mature forests in managed landscapes, potentially affecting organisms that are often associated with such stands. Fennoscandian boreal forests, which have been managed for a longer period of time, typically show a lack of stands older than 100-150 yrs. Fire regimes, as opposed to harvesting regimes, also show a greater variability in year-to-year area burned and a greater range of sizes. The difference in the spatial configuration of fire and logging disturbances has been little studied. Few studies have compared landscapes under a similar rotation period, at similar scales, and showing similar proportions of disturbed areas. These factors greatly influence the outputs of spatial analyses, which also have to rely on sound statistical analyses. Nonetheless, we can conclude that fires usually show more heterogeneity than clearcuts, more undisturbed island remnants, more complex shapes, and have edges that are more gradual than clearcuts. Island remnants can play an important role in recolonization by species that are not adapted to fire. The effects of configuration have not been frequently addressed in wildlife studies independently from the effect of habitat loss at the landscape scale, but literature suggests that loss of habitat or change in forest composition have a greater effect on bird communities than landscape configuration in managed forest landscapes.

In conclusion, our review reveals two main challenges faced by forest managers in order to render harvesting-mediated landscapes more similar to fire-mediated ones. First, significant structural differences and species' responses immediately after disturbance suggest that harvesting techniques need to be improved to render young post-harvest stands more functionally and ecologically similar to young post-fire stands. Second, stands with the structural characteristics and species compositions characteristic of over-mature fire-origin stands, which can represent a significant portion of fire-mediated landscapes, must be maintained within the landscape. This may necessitate the lengthening of rotation periods for a certain proportion of stands within landscapes or may require the application of alternative harvesting methods that can recreate the structure and composition characteristics of over-mature stands.

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