UNIVERSITÉ DU QUÉBEC À MONTRÉAL

DYNAMIQUE DE LA FAUNE CAVICOLE LE LONG D'UN GRADIENT D'ÂGE EN FORÊT BORÉALE MIXTE DE L'EST DE L'AMÉRIQUE DU NORD

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AVANT-PROPOS

Ce mémoire comporte deux chapitres rédigés sous forme d'articles. À titre de candidat à la maîtrise, j'ai procédé à la récolte des données, à l'analyse des résultats et à la rédaction des articles à titre de premier auteur. Ces deux articles seront soumis dans des revues scientifiques avec jury de pairs : 1) "Nest tree selection by cavity excavators along an age gradient of naturally disturbed boreal mixedwood forests in eastern North America" et 2) "Nest webs in mature and old boreal mixedwood forests of eastern North America". Antoine Nappi est co-auteur des deux articles, il a participé à l'élaboration du protocole de recherche, à la récolte de données sur le terrain pour les mesures de disponibilité d'habitat ainsi qu'à la rédaction des articles.

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PCN	Primary cavity nester
WPCN	Weak primary cavity nester
SCN	Secondary cavity nester
RBNU	Red-breasted Nuthatch
DOWO	Downy Woodpecker
YBSA	Yellow-bellied Sapsucker
HAWO	Hairy Woodpecker
NOFL	Northern Flicker
PIWO	Pileated Woodpecker
CBM	Complete boreal mixedwood nest web
D&M	Deciduous and mixedwood nest web
COG	Conifer old-growth nest web
FCT	Forest cover type
DBH	Diameter at breast height

RÉSUMÉ

La disponibilité des arbres à cavités joue un rôle important dans le maintien de la biodiversité des écosystèmes forestiers. L'objectif général de ce projet est d'apporter de nouvelles connaissances portant sur la dynamique de la faune cavicole le long d'un gradient d'âge en forêt boréale mixte. Cette dynamique a été caractérisée par une étude de sélection d'arbres de nidification par les oiseaux excavateurs et par une analyse de réseaux d'utilisateurs de cavités. Entre 2003 et 2010, 12 placettes de 24 à 40 hectares, distribuées sur un gradient d'âge de peuplements (61 à 245 ans depuis le dernier feu), ont été inventoriées dans la Forêt d'Enseignement et de Recherche du Lac Duparquet (FERLD) en Abitibi. À l'aide de modèles mixtes généralisés, nous montrons d'abord que, tout au long du gradient d'âge, les espèces excavatrices sélectionnent préférentiellement des peupliers faux-trembles (*Populus tremuloides*) de grand diamètre morts ou sénescents. Globalement, cette essence héberge 95 % des cavités de nidification, malgré une disponibilité qui diminue fortement le long du gradient de couverts forestiers qui s'étend d'une forêt dominée par le peuplier faux-tremble aux forêts mixtes et de conifères. Nous présentons ensuite les réseaux d'utilisateurs de cavités pour différents stades de composition forestières. Ceux-ci sont composés de 5 excavateurs primaires (pics), deux excavateurs faibles (sittelles et mésanges) et 7 utilisateurs secondaires (canards, oiseaux de proie, écureuils). Malgré une baisse d'abondance de cavités de nidification, le réseau des vieilles forêts (> 180 ans) présente un degré de complexité plus élevée que celui des forêts matures à âgées (61 à 180 ans) en raison, entre autres, d'une plus grande diversité d'essences utilisées comme arbres à cavités. Dans les deux réseaux, les utilisateurs secondaires ont des liens forts avec des excavateurs spécifiques. Le Grand Pic (*Dryocopus pileatus*) est désigné espèce « clé de voûte » étant donné l'importance disproportionnée de ses cavités pour les utilisateurs secondaires de forte taille. Le Pic maculé (*Sphyrapicus varius*) représente l'excavateur le plus abondant. Enfin, les peupliers faux-trembles de grand diamètre couvrant une large gamme d'états de dégradation constituent l'essence clé nécessaire au maintien des communautés cavicoles le long du gradient d'âge et de couverts forestier, allant des forêts matures décidues aux forêts conifériennes anciennes.

Mots clés : *Réseaux d'utilisateurs de cavités, forêt boréale mixte, sélection d'arbre de nidification, peuplier faux tremble, pics*

INTRODUCTION GÉNÉRALE

1.1 Problématique

La communauté cavicole de la forêt boréale mixte du Québec est formée d'une multitude de vertébrés tels que des oiseaux et des mammifères ayant comme caractéristique commune la nécessité d'utiliser des cavités dans les arbres pour la complétion de leur cycle vital (Darveau et Desrochers 2001). Les membres de cette communauté interagissent par la création de cavités et par la compétition subséquente pour celles-ci (Martin et Eadie 1999). Cependant, ces relations interspécifiques ne sont pas bien connues.

La dynamique de relations existant entre la disponibilité des arbres à cavités et les réseaux d'utilisateurs de cavités est un aspect important dans le maintien de la biodiversité des forêts boréales mixtes du Québec. Cela est d'autant plus le cas pour les forêts commerciales les plus convoitées par l'aménagement, soit les forêts matures et celles qui dépassent l'âge d'exploitabilité (> 100 ans) dont la sénescence des arbres dominants accroît la disponibilité d'arbres à cavités. En effet, la plupart des excavateurs de cavités en forêt boréale sont associés aux vieilles forêts (Imbeau et al. 2001, Drapeau et al. 2003, Savignac et Machtans 2006, Schieck et Song 2006, Cooke 2009). Dans un contexte d'aménagement forestier où l'objectif principal consiste à récolter la forêt à rendement soutenu sur de courtes révolutions, les arbres à cavités peuvent devenir une ressource qui limite les utilisateurs de cavités, entre autres les excavateurs primaires comme les pics; ce qui peut entraîner l'extinction locale d'espèces (Angelstam et Mikusinski 1994) et, par conséquent, affecter la structure fonctionnelle des communautés cavicoles (Martin et al. 2004).

Les recherches sur les oiseaux cavicoles sont nécessaires afin de développer des lignes directrices d'aménagement forestier qui permettront d'établir un équilibre entre les besoins de la faune avec la production forestière (Adkins et Cuthbert 2003). Les réponses aux questions fondamentales posées par notre étude seront utiles pour orienter les décisions concernant le maintien de la biodiversité dans le contexte de l'aménagement forestier.

1.2 Étude de la faune cavicole : Les réseaux d'utilisateurs de cavités, la sélection d'arbres de nidification et les espèces clé de voûte

Le concept du « nest web » ou de réseau d'utilisateurs de cavités, proposé par Martin et Eadie (1999) a suscité beaucoup de discussion au sein de la communauté scientifique ces dernières années (Bednarz et al. 2004). Ce nouveau cadre conceptuel a ouvert l'étude de la faune cavicole à de nouvelles perspectives. Le réseau d'utilisateurs de cavités est conceptualisé comme étant analogue à un réseau trophique (Martin et Eadie 1999), où une ressource centrale, c'est-à-dire les cavités, est partagée selon une hiérarchie d'utilisateurs et de liens entre ces derniers (Blanc 2007). Ces réseaux sont composés de nœuds (ressources en cavité), de liens (création et utilisation de cavité) et de niveaux de nidification (guildes) (Blanc et Walters 2007). Les excavateurs primaires sont les pics (PCN - de l'anglais, primary cavity nesters) et ces derniers excavent généralement une cavité annuellement pour y nicher. Les utilisateurs secondaires (SCN - de l'anglais, secondary cavity nesters) sont un groupe diversifié : passereaux, oiseaux de proie, canards et mammifères qui dépendent des cavités, mais ne peuvent les excaver. Les excavateurs faibles (WPCN - de l'anglais, weak primary cavity nesters) peuvent excaver ou réutiliser les cavités (Martin et Eadie 1999).

Les oiseaux excavateurs de cavités, tels que les pics, sont généralement à la base de ces importants réseaux, car ils sont responsables de l'excavation de la majorité des cavités utilisées. En effet, plusieurs études ont montré que les cavités naturelles non excavées ne forment qu'une infime partie des cavités utilisées dans les forêts nord-américaines de conifères ou de peuplements mixtes (< 10%) (Raphael et White 1984, Martin et Eadie 1999, Aitken et Martin 2004, Aitken et Martin 2007, Blanc et Walters 2008, Cooke 2009). La création de cavités est donc considérée comme un processus clé dans les communautés forestières (Bednarz et al. 2004). Par contre, dans d'autres systèmes, il est possible que les cavités non excavées soient la source principale de cavités utilisées, dérobant ainsi le rôle des pics comme fournisseurs clé de cavités. Wesolowski (2007) montre que les SCN de certaines forêts anciennes de la Hollande utilisent majoritairement des cavités non excavées lors de la nidification.

Plusieurs études portent sur la sélection d'arbres de nidification par les oiseaux excavateurs en Amérique du Nord (Raphael et White 1984, Keisker 1986, Swallow et al. 1986, Dobkin et al. 1995, Hartwig et al. 2004, Martin et al. 2004, Savignac et Machtans 2006, Cooke 2009). Cependant, peu de ces études ont été conduites en forêt boréale et la majorité ont été effectuées dans l'ouest de l'Amérique du Nord. Les excavateurs, dont les pics, les sittelles et les mésanges, ont été associés aux arbres de grand diamètre sénescents et morts sur pied. Il existe une partition dans les stades de décomposition des arbres sélectionnés, les excavateurs variant en fonction de leur pouvoir d'excavation (Schepps et al. 1999, Martin et al. 2004). Certains ont la capacité d'excaver dans des arbres vivants, d'autres sont limités à l'excavation dans du bois fortement décomposé. Dans les écosystèmes forestiers où le peuplier faux-tremble (Populus tremuloides) est commun, cette essence est hautement sélectionnée comme arbre de nidification (Dobkin et al. 1995, Aitken et al. 2002, Martin et al. 2004). Certaines études ont associé la préférence de cette essence à la présence d'infection par un champignon : la carie blanche (Phellinus tremulae (Bondartsev) Bondartsev & Borisov) (Kilham 1971, Hart et Hart 2001, Jackson et Jackson 2004, Martin et al. 2004, Savignac et Machtans 2006, Cooke 2009). Cette infection est la forme de dégradation avancée la plus commune et sérieuse que l'on trouve chez le peuplier faux-tremble (Basham 1991). Ce champignon s'attaque seulement aux arbres du genre Populus et pourrit le bois du cœur de l'arbre lorsque celui-ci est encore vivant. Ceci rend l'excavation plus facile et la cavité plus sécuritaire, car l'aubier offre encore une bonne rigidité (Conner et al. 1976, Hart et Hart 2001, Jackson et Jackson 2004).

Les réseaux d'utilisateurs de cavités que l'on décrit actuellement dans la littérature montrent clairement les liens existants entre les espèces aux trois niveaux hiérarchiques présentés ci-dessus (Martin et Eadie 1999, Martin et al. 2004, Blanc 2007, Cooke 2009), suggérant ainsi une dépendance entre les espèces du niveau hiérarchique supérieur à celles du niveau hiérarchique inférieur. L'abondance de cavités peut être considérée comme un facteur limitant si elle contrôle la densité des couples nicheurs (Newton 1994). Dans l'ensemble des écosystèmes forestiers, la proportion des cavités utilisées par les oiseaux cavicoles varie entre < 10 % là où les cavités abondent et 90 % là où les cavités sont rares (Newton 1994). De plus, la sélection de cavités par les SCN varie selon l'espèce : certaines sont généralistes et utilisent une variété de types de cavités et d'autres sont spécialistes et nécessitent un type précis de cavité (Aitken et Martin 2008). Certains excavateurs ont été identifiés comme étant des espèces clé de voûte en raison de leur faible abondance relative et de l'importance disproportionnée des cavités qu'ils produisent (Paine 1969, Power et al. 1996). Dans la majorité des écosystèmes étudiés, seulement un ou deux excavateurs primaires fournissent la majorité des cavités utilisées (Bednarz et al. 2004). Entre autres, les excavateurs de cavités de grande taille sont pourvoyeurs d'une ressource limitée. En effet, plusieurs études portant sur les réseaux d'utilisateurs de cavités retrouvées dans la littérature ont identifié le Pic flamboyant (Colaptes auratus) comme une espèce clé de voûte (Martin et al. 2004, Blanc et Walters 2008b, Cooke 2009). Aussi, certaines études ont proposé le Grand Pic (Dryocopus pileatus) comme espèce clé de voûte (Bonar 2000, Aubry et Raley 2002, Martin et al. 2004). Les cavités excavées par cet excavateur sont significativement moins nombreuses que les autres types de cavités (Bonar 2000) et ceci limite les utilisateurs de ce type de cavité.

Cet excavateur est le seul à pouvoir créer des cavités assez grandes (soit deux fois le volume des cavités du Pic flamboyant) pour abriter les plus gros des utilisateurs secondaires, tels que le Garrot à œil d'or (Bucephala clangula) ou le Garrot d'Islande (Bucephala islandica) (Bonar 2000, Darveau et Desrochers 2001, Aubry et Raley 2002, Evans et al. 2002, Martin et al. 2004, Cooke 2009).

La recherche sur les réseaux d'utilisateurs de cavités n'en est qu'à ses débuts. Les réseaux d'utilisateurs de cavités retrouvés dans la littérature sont principalement des structures descriptives utilisées pour représenter les interactions entre les espèces et les arbres à cavités des communautés cavicoles (Blanc et Walters 2007). Par contre, la recherche touchant les réseaux dans d'autres domaines en biologie, comme l'étude des réseaux des gènes et des protéines et l'étude des réseaux trophiques, est considérablement développée (Proulx et al. 2005). Les théories et les concepts appliqués à l'étude de ces réseaux sont des voies prometteuses pour l'étude des réseaux d'utilisateurs de cavités (Blanc et Walters 2007). La quantification des caractéristiques telles que la connectance (richesse des interactions - nombre total de liens/nombre possibles de liens), la force des liens, la longueur des liens (combien de niveaux hiérarchiques) et la distribution des degrés (« degree distribution » en anglais) peut permettre la comparaison de la structure des réseaux d'utilisateurs de cavités (Blanc et Walters 2007). Ces dernières années, la connectance s'est retrouvée au cœur d'un débat animant l'étude de l'écologie depuis les années 1950 : le débat stabilité-diversité (McCann 2000, Vaillancourt et al. 2008, Gilbert 2009). Ce débat tourne autour du concept suivant : un système plus diversifié n'est pas nécessairement plus stable. En effet, dans sa revue, McCann (2000) précise que les explications de la relation stabilité-diversité se trouvent davantage liées aux interactions entre les espèces que dans la mesure de la richesse spécifique (McCann 2000, Gilbert 2009).

Une telle quantification des réseaux d'utilisateurs de cavités permet d'analyser l'effet que des conditions forestières sur les liens interspécifiques et sur la structure générale du réseau d'une communauté (Blanc et Walters 2007). Elle permet également de jauger le poids relatif des espèces animales et des essences d'arbres aptes à jouer un rôle clé dans l'écosystème.

1.3 Dynamique de la faune cavicole en fonction d'un gradient d'âge en forêt boréale mixte

Dans une revue de littérature sur le sujet de la succession aviaire, May (1982) identifie une tendance générale : il y a une augmentation de la diversité et de la richesse des espèces avec l'avancement de la succession forestière. Newton (1994), émet l'hypothèse selon laquelle l'abondance de cavités créées par les pics, les insectes et la sénescence augmenterait en fonction de l'âge de la forêt. Il propose qu'un pic d'abondance de cavités serait atteint après une centaine d'années et qu'il serait soutenu par la suite. Il est fort probable que ce ne soit pas le cas en ce qui concerne la forêt boréale mixte, compte tenu des changements importants qui ont lieu à mesure que la forêt vieillie. Cependant, peu d'études portent sur ces questions de recherche. Cela dit, on sait qu'il y a généralement une corrélation entre la diversité et la densité d'oiseaux cavicoles et la densité de bois mort sur pied, celui-ci étant utilisé par la plupart des PCN et des WPCN pour l'excavation de leur cavité (Mannan et al. 1980, Raphael et White 1984, Zarnowitz et Manuwal 1985, Newton 1994, Drapeau et al. 2002). Aussi, il y a généralement une augmentation de la densité de reproduction dans les années qui suivent l'ajout de nichoirs (Brawn et Russell 1988, Newton 1994, Aitken 2007). La réduction de l'abondance d'arbres à cavités ou de substrats à cavités peut donc avoir un impact important sur la distribution de la faune cavicole. Selon les études réalisées en forêt mixte nord-américaine, les oiseaux cavicoles utilisent de façon préférentielle le peuplier faux-tremble (Martin et al. 2004). Un plus grand nombre de cavités sont localisées dans cette essence que leur disponibilité dans les peuplements. Or, le long d'un gradient d'âge en forêt boréale mixte, la présence du peuplier faux-tremble varie grandement.

En effet, des changements considérables dans la structure et le couvert forestier se produisent tout au long du vieillissement des forêts boréales mixtes débutant par le peuplier faux tremble. Cette succession peut être résumée en trois cohortes grossièrement définies (Bergeron et Harvey 1997). La première cohorte qui a une durée d'approximativement 100 ans est caractérisée par une structure homogène et par une dominance d'arbres décidus : le peuplier faux tremble et le bouleau blanc (Betula papyrifera). La seconde cohorte est mixte, les arbres tolérants à l'ombre comme le sapin baumier (Abies balsamea) et l'épinette blanche (Picea glauca) partagent la canopée avec les essences intolérantes à l'ombre. La troisième cohorte est dominée par les conifères, mais on y retrouve aussi des arbres intolérants à l'ombre dans les nombreuses ouvertures de la canopée crées par des perturbations naturelles telles que les épidémies d'insectes.

Nous prévoyons que l'abondance et la diversité d'espèces cavicoles n'augmentent pas proportionnellement avec l'âge de la forêt, mais que celles-ci auront plutôt une distribution modale associée à l'abondance et à la disponibilité du substrat d'excavation préféré dans les peuplements : le peuplier faux-tremble de grand diamètre sénescent et mort. En effet, bien que le potentiel du peuplier faux-tremble pour l'excavation augmente avec l'âge de la forêt, la transition d'un couvert dominant de mixte à un couvert résineux s'accompagne par une diminution importante de l'abondance de cette essence. Si cette essence est bel et bien préférée aux autres, il est logique de penser que l'abondance des cavités de nidification suivra une tendance modale le long du gradient d'âge. Ces résultats pourraient s'apparenter à ceux de Drapeau et al. (2002), qui ont observé que, pour la forêt boréale résineuse d'épinettes noires, les très vieilles forêts (> 200 ans) ne jouent pas un rôle important dans l'apport d'un substrat adéquat à l'excavation de cavités par les oiseaux cavicoles.

1.4 Objectifs de l'étude

L'objectif de cette étude consiste à décrire la dynamique de l'utilisation des cavités par la faune cavicole le long d'un gradient d'âge en forêt boréale mixte de l'est de l'Amérique du Nord. Afin de bien caractériser cette dynamique, nous effectuerons une étude de sélection d'arbres de nidification par les oiseaux excavateurs et une analyse de réseaux d'utilisateurs de cavités pour différents stades de couverts forestiers.

De façon plus détaillée, le chapitre 2 a pour objectif de 1) déterminer les caractéristiques des arbres de nidification utilisés et sélectionnés par les excavateurs de cavités et de 2) déterminer la plasticité dans l'utilisation et la sélection des arbres de nidification par les oiseaux excavateurs le long d'un gradient d'âge qui couvre des peuplements dominés par des feuillus intolérants comme le peuplier faux-tremble, des peuplements mixtes (feuillus et résineux) plus âgés et des vieux peuplements dominés par un couvert résineux.

Dans le chapitre 3, les objectifs spécifiques sont de 1) décrire la structure fonctionnelle des réseaux d'utilisateurs de cavités et d'identifier les espèces « clé de voûte » du système, et 2) de comparer la structure fonctionnelle des réseaux d'utilisateurs de cavités des forêts matures et âgées à celle des vieilles forêts au moyen d'une analyse de réseaux.

CHAPITRE 2

NEST TREE SELECTION BY CAVITY EXCAVATORS ALONG AN AGE GRADIENT OF NATURALLY DISTURBED BOREAL MIXEDWOOD FORESTS IN EASTERN NORTH AMERICA

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The availability of cavity-trees plays an important functional role in maintaining the biodiversity of forest ecosystems. Cavity excavators have been found to be architects of cavity nesting assemblages, providing the vast majority of cavities used by cavity nesting species. However, they depend on quality excavation substrates, which can vary considerably between forest cover types. The overall objective of this study is to better understand nest tree use and selection by cavity excavators along an age and compositional gradient of naturally disturbed boreal mixedwood forest stands. Between 2003 and 2010, twelve 24 to 40 ha plots ranging from 61 to 245 years since the last fire were surveyed in the Lake Duparquet Research and Teaching Forest in Abitibi, Quebec, to detect cavities with active nests. Cavity excavators selected large diameter trembling aspen (*Populus tremuloides*) in varying stages of decay. Almost all live aspen nest trees and half of dead aspen nest trees bore fungal conks (*Phellinus tremulae*), while their availability in aspen stems of >20 cm in DBH was much lower (7%). The nest tree use and selection was similar across forest cover types and forest age. Nest abundances followed the availability of quality excavation substrate, as there seemed to be a modal distribution of nests along the succession, the highest abundance being in old deciduous and mixedwood forests. The presence of large diameter trembling aspen that cover a wide range of decay stages from senescent to highly degraded trees is necessary for maintaining cavity excavators in mixedwood boreal forests under natural disturbance regimes.

Key words: Trembling aspen, Phellinus tremulae, nest site plasticity, large dead trees, Abitibi

2.1 Introduction

The availability of quality cavity substrates for cavity excavation plays a critical role in the conservation of cavity nesters in forest ecosystems. In North American forests, excavators have been found to exert a disproportional influence on the function and structure of the community of cavity nesters by providing the vast majority of the cavities occupied by secondary cavity users (Martin et al. 2004, Aitken and Martin 2007, Blanc and Walters 2008, Cooke 2009). Accordingly, the excavation process has been proposed as a keystone ecological process in such ecosystems (Bednarz et al. 2004).

In the boreal forest, most cavity excavators have been associated with old forests (Hobson and Bayne 2000, Imbeau et al. 2001, Drapeau et al. 2003, Savignac and Machtans 2006, Schieck and Song 2006, Cooke 2009) since they are dependent on large senescent or dead trees for their excavations. In mixedwood ecosystems, it has been well documented that cavity excavators have a strong tendency to choose the trembling aspen (*Populus tremuloides*) as their keystone nest tree species, especially in western North America (Dobkin et al. 1995, Aitken and Martin 2004, Martin et al. 2004, Savignac and Machtans 2006, Cooke 2009). Aspen availability may vary considerably as forests age in boreal mixedwood forests; from shade-intolerant tree dominated stands, where aspen is abundant, to conifer dominated stands where aspen is much less abundant (Bergeron and Dubuc 1989, Bergeron 2000). Such changes in the composition and structure of the forest cover in mixedwoods are known to affect forest songbird communities directly at both the stand (Hobson and Bayne 2000) and landscape scales (Drapeau et al. 2000). For cavity nesting birds, shifts in the availability of aspen in mixedwood landscapes could affect the dynamics and plasticity of nest tree selection by cavity excavators. Although a high number of studies have documented the importance of trembling aspen as a cavity tree, little information exists about the dynamics and plasticity of nest tree selection by cavity excavators along an age gradient in mixedwood landscapes.

Understanding such dynamics becomes critical in the context of the extensive application of short rotation even-aged forest harvesting in boreal mixedwoods. Such practices are altering the composition of forest landscapes from mixedwood and conifer dominance to deciduous dominance (Bergeron and Harvey 1997, Bergeron et al. 2001, Laquerre et al. 2009). These potential changes in forest composition have been proposed to be the most important threat to the integrity of bird communities in these ecosystems (Drapeau et al. 2000). Such practices also have the potential of eliminating or considerably reducing forest cover types that are older than the rotation age, thus severely truncating the composition of boreal mixedwood forest landscapes, (Bergeron et al. 2001, Harvey et al. 2002) what Hobson and Bayne (2000) qualify as "unmixing" the mixedwoods. In such managed systems, cavity trees could become a limiting factor for cavity excavators, bringing about local extinctions of excavating species (Angelstam and Mikusinski 1994, Imbeau et al. 2001) and thus affecting the structure of cavity user assemblages (Martin et al. 2004).

In this paper we document the use and selection of nest trees by cavity excavators along a natural (post-fire and post-spruce budworm outbreak) compositional and time since fire gradient in the eastern boreal mixedwood forest of North America. Even though considerable changes occur in the composition and structure of the forest along this age gradient, we hypothesize that cavity excavators have limited nest site plasticity and consequently we predict that their selection for large trembling aspen will remain constant.

2.2 Methods

2.2.1 Study area

The study took place in the boreal mixedwood forest of northern Quebec in the balsam fir-white birch bioclimatic domain, which is located on the northern Clay Belt of Quebec and Ontario. This region is characterized by clay soils and low rocky hills (Robitaille and Saucier 1998). The average annual temperature is 0.6 °C and the average total annual precipitation is 822.7 mm (Environment Canada 2008). The study site is located within the conservation area of the Lake Duparquet Research and Teaching Forest (LDRTF) at the southern fringe of the boreal forest in Québec (48°30' N, 79°22' W). This area, of ~2000 ha, contains a complex natural forest mosaic formed by different forest cover types and by a variety of natural disturbances (Harvey 1999). Fire history in the LDRTF is well documented (Bergeron 1991, Dansereau and Bergeron 1993) and includes eight major fires that have occurred over the last three centuries. Stand composition varies according to the time that has elapsed since the last fire in the study area (Bergeron and Harvey 1997). Young and mature forests are dominated by early succession tree species: paper birch (*Betula papyrifera*), trembling aspen and jack pine (*Pinus banksiana*). In our study area, trembling aspen and white birch mostly dominated these stands. They were thus named "decidous forests". Old forests ("mixedwood forests") are characterized by mixed stands where balsam fir (*Abies balsamea*), black spruce (*Picea mariana*) and white spruce (*Picea glauca*) share the forest canopy with the deciduous species. Old-growth stands ("conifer old-growth forests") are dominated by coniferous species where the white cedar (*Thuja occidentalis*) becomes more abundant (Bergeron and Harvey 1997, Harvey et al. 2002). Over the last century, the balsam fir-dominated stands were severely affected by three spruce budworm outbreaks, the most recent occurring between 1970 and 1987 (Morin et al. 1993). These outbreaks reduced the abundance of large balsam firs, killing as many as 75% of mature firs (>15 cm in diameter) in the study area (Bergeron et al. 1995).

2.2.2. Field methods

Between 2003 and 2010, we collected data on cavity nesters in 12 sampling plots ranging from 24 to 40 ha in size (and totalizing 448 ha). Three plots originating from

1944 and 1916 fires represented deciduous forests. Three plots located where one large fire occurred in 1870 represented mixedwood forests. Conifer old-growth forests were represented by six plots located where fires occurred in 1823, 1816, 1797 and 1760 (Dansereau and Bergeron 1993). The time since the last fire was calculated using 2005 as a point of reference, and ranged from 61 to 245 years. Rectangular shaped vegetation-sampling stations measuring 600 m^2 (10 m X 60 m) were distributed 200 m apart in each plot (112 in total). Six of them were located on rocky cliffs and were not used in the analysis in order to limit the variation in the vegetation data.

Three variables were used to characterize available trees and nest trees: tree species, decay stage and diameter at breast height (DBH). The vegetation-sampling plots were sampled in 2005 and all trees having a DBH greater than 10 cm were characterized. Tree decay was classified based on visual appearance in 5 categories according to a modified version of Maser et al. (1979) (Nappi and Drapeau 2009): Decay 1 (alive, >20% foliage); Decay 2 (declining, <20% foliage); Decay 3 (recently dead, hard wood, firm bark cover); Decay 4 (moderate decay, soft wood, no dead foliage present, no small twigs, some branches remaining, usually intact top); Decay 5 (high decay, soft decomposed wood, very few branches, often broken top).

Six cavity excavator species were common in our study site: the Red-breasted Nuthatch (*Sitta canadensis*), the Downy Woodpecker (*Picoides pubescens*), the Yellow-bellied Sapsucker (*Sphyrapicus varius*), the Hairy Woodpecker (*Picoides villosus*), the Northern Flicker (*Colaptes auratus*) and the Pileated Woodpecker (*Dryocopus pileatus*). Nest search efforts and data collection protocols in the study site varied between years but were relatively constant between sampled plots. From mid-May to early July from 2003 to 2004, data on cavity nesters were collected as part of a study on the foraging ecology of woodpeckers (Nappi 2009) which consisted of surveying transects with 100 m buffers on each side, covering 104 ha in the deciduous forest, 120 ha in the mixedwood forest and 220 ha in the conifer old-growth forest. In 2005, data on cavity nesters was collected as part of a preliminary study on cavity nesters in which the same area was sampled. From 2008, data was collected on transects with a buffer zone of 50 m on each side to increase detection power. In 2008 and 2010, data was collected on 24 ha of the deciduous forest and 120 ha of the mixedwood forest. In 2009, data was collected on 90 ha of the deciduous forest, 90 ha of the mixedwood forest and 180 ha of the conifer old-growth forest. Nest searches were conducted between the beginning of May and mid-July, from sunrise to 14h00 under adequate conditions (without significant rain or wind > 20 km/h). Observers walked along line transect and used visual and auditory cues that would indicate the presence of an occupied cavity: breeding-bird behavior, begging nestlings or wood chips on the ground. All trees in which an occupied cavity was found were marked with an aluminum tag and geo-referenced. These cavities were then inspected with a camera mounted on a telescopic pole (TreeTop Peeper$^{(tm)}$, Sandpiper Technologies, Manteca, California) to determine the state of the cavity: non-completed excavation, suitable cavity or occupied cavity. A cavity was considered "occupied" if it contained at least one egg or nestling (Martin et al. 2004). For nests that were not accessible with the telescopic pole and camera (higher than 15.24 m), and for nests that were in cavities with an opening too small for the camera (ex: some of the Red-breasted Nuthatch nests), we used nesting clues (behavior of adult cavity nesters) to confirm the state of the cavity. In addition, nests discovered by chance within or near the LDRTF, but outside the study site, were also characterized and geo-referenced.

We further investigated the relationship between excavator species and the status of trembling aspens by sub-sampling the presence of fungal conks on nest trees. In 2008, all nest trees were verified to detect the presence of fungal conks. Pursuing this further in 2009 and 2010, all nest trees and nest sites trees (400 m^2 surrounding the nest trees) were inspected for fungal conks and fungi were identified to the species. Seven common species were identified: *Phellinus tremulae*, *Phellinus igniarius*, *Fomes fomentarius*, *Fomitopsis pinicola*, *Ganoderma applanatum*, *Tremetes versicolor and Trichaptum pargamenum*. Heartrot by *Phellinus tremulae* is the most common and serious form of advanced decay in aspen (Basham 1991). This fungus rots the heartwood of living aspens, leaving a strong protective living outer shell (Kilham 1971, Conner et al. 1976, Hart and Hart 2001, Jackson and Jackson 2004). Savignac and Machtans (2006) found that all cavity trees used by the Yellow-bellied Sapsucker in mixedwood forests of the western boreal plain were infected by this fungus.

2.3 Statistical analyses

Statistical analyses are separated in three parts: 1) description and comparison of forest cover types and nest tree use, 2) selection of nest tree characteristics and 3) differences in abundance of excavator nests along the time since fire gradient. "Use" of nest tree characteristics by excavators refers to the characteristics of nest trees used without any regard to what other tree resources were in the environment and "selection" refers to the use of nest tree characteristics compared to their availability in the environment.

2.3.1 Habitat and nest tree characteristics

We conducted descriptive and comparative tests in order to characterize the different forest cover types and nest tree use by cavity excavators. All normally distributed habitat and nest tree variables were tested using one-way ANOVA's with mixed models and a Tukey HSD test for multiple comparisons. Binomially distributed variables were tested with generalized mixed models. Non-normally distributed variables were $\log_{10}$ transformed to fit the requirements or were analyzed with a Kruskal-Wallis test. A significance level of $\alpha = 0.05$ was used in all tests. The variable *plot* or *nest site* was added in the mixed models to account for the hierarchical structure of the sampling design.

The basal area values were first averaged for each vegetation-sampling plot. The mean proportion of available nest site aspens with fungal conks was calculated at the nest site level (400 m^2 around the nest tree). The relationship between the DBH and the presence of fungal conks on nest site and available aspens was tested using generalized mixed models.

Nest trees were included only once per species regardless of the number of times they were used. For comparison of use in every forest cover type, we included nests that were from the surrounding areas for species that had low sample sizes (Hairy Woodpecker, Northern Flicker and Pileated Woodpecker). We used a contingency table to verify if there were differences between excavator species for decay stage used. For this analysis, the original five decay stages were reduced to three decay stages: 1) live to declining (decay class 1-2), 2) recently dead to moderate decay (class 3-4) and 3) dead with high decay (class 5).

In addition, we present nest tree characteristics along the age gradient: the proportion of nest trees in aspens, the decay stage used and the DBH of nest trees. For the comparison along the age gradient, unoccupied cavities of Pileated Woodpeckers and Northern Flickers were pooled with occupied cavities because of low samples in the study area. We found 56 large unused suitable cavities in the study site, of which 28 were Pileated Woodpecker cavities and 28 were Northern Flicker cavities.

2.3.2 Nest tree selection

We used generalized mixed models with a binomial distribution of the response variable and a logit link (R package lme4 version 0.999375-34, written by Douglas Bates and Martin Maechler) to identify nest tree characteristics that distinguished nest trees from available trees for excavator species. For this analysis, only trees with occupied cavities that were excavated by the nesting species were included. All nest trees within the sampling plots, including a 50 m buffer zone surrounding the plots, were included in the analysis. Generalized mixed models were preferred to classical statistical procedures because they take into account the hierarchical structure of the sampling design. The variable *plot* was used as the random effect to ensure that differences between plots were taken into account. Nest tree data from all years (2003-2010) were pooled together to ensure a large enough sample size. We used a theoretical-information approach using Akaike information criterion adjusted for small samples (AIC_c) to compare candidate models and to select the most parsimonious (Burnham and Anderson 2002). Models having a Δ $AIC_c < 2.0$ were considered as having strong support for the data (Burnham and Anderson 2002). We performed multi-model inference for variables that were in closely competing candidate models (Δ $AIC_c < 4$) by averaging estimates across models weighted by Akaike weights (W_i). The latter quantifies support for individual models in relation to other models in the set (Burnham and Anderson 2002). This method is recommended for making robust parameter estimations (Katsanevakis 2006, Mazerolle 2006). Model averaging was performed using the AICcmodavg R package version 1.09 (written by Marc Mazerolle). The weighted SE was calculated using the Anderson (2008) formula. Odds ratio were calculated for increases of one unit for *Aspen* and *Decay* and for increases of 10 cm for *DBH.*

In order to get a general picture of the selection of nest trees by the excavators, a list of 7 candidate models was constructed using combinations of the variables *Aspen* (binary - yes or no), *DBH* (numeric continuous) and *Decay* (5 categories, ordinal, but treated as a numeric continuous variable). These variables were chosen based on their importance for excavators in other forest ecosystems (Li and Martin 1991, Martin et al. 2004, Savignac and Machtans 2006, Cooke 2009). For the Pileated Woodpecker and the Northern Flicker, unoccupied cavities were pooled with occupied cavities. Therefore, a second list of three models that did not contain *Decay* was used for the Pileated Woodpecker and the Northern Flicker since the unoccupied cavities were not characterized in the same year as the occupation or excavation and this would introduce a bias towards higher decay stage (Table 2.1).

To verify if nest tree selection by excavators changed along the time since fire gradient and forest cover types, we conducted the analyses on two groups of excavators that shared nest tree characteristics: the live tree excavators composed of the Yellow-bellied Sapsucker (n = 133) and the Hairy Woodpecker (n = 14) and the dead tree excavators composed of the Downy Woodpecker (n = 40) and the Red-breasted Nuthatch (n = 24). Excavators in both groups shared similar nest tree species, decay and DBH use (Martin et al. 2004). To further understand the role of large aspen as the nest tree along the time since fire gradient, we only included > 20 cm DBH aspen in this analysis. We created a list of 4 models containing the interactions between the variables *Decay* and *DBH* and the three different forest cover types (Table 2.2).

2.3.3 Relative abundance of nests along the time since fire gradient

The abundance of excavators' nest was calculated using all nests found in 2009. The search effort was relatively constant between the sampling plots. All nests within the sampling plots, including a 50 m buffer zone surrounding the plots, were included in the analysis. Each nest was associated to the closest vegetation sampling station (*n* = 89). We used Kruskal-Wallis test with a Tukey HSD test for multiple comparisons to verify if nest density differed significantly between forest cover types. Polynomial regressions were performed to verify the trend of nests abundance along the time since fire gradient.

2.4 Results

2.4.1 Characterization of forest cover types

Aspen, white birch, balsam fir and white cedar dominated the forest matrix in which our study sites were embedded (Figure 2.1). The study sites bore marks of the last spruce budworm outbreak (Morin et al. 1993, Bergeron et al. 1995). A high proportion of the balsam fir's basal area was found in dead fallen trees (Table 2.3).

Although there was a low availability of large balsam firs (> 20 cm DBH) in the landscape, vegetation in our study sites was found to follow a deciduous to conifer transition along the time since fire gradient. Conifer basal area, dead fallen balsam fir basal area and tree DBH increased with the age of the forest, whereas deciduous, aspen and dead aspen basal area decreased (Table 2.3). No significant differences were found for total basal area, total dead basal area and balsam fir basal area along the time since fire gradient (Table 2.3). Aspen > 20 cm in DBH had a significantly greater probability of being infected by *Phellinus tremulae* as their DBH increased (generalized mixed models, $\beta = 1.34$, $SE = 0.20$, $P < 0.001$). However, the proportion of these aspen trees bearing fungal conks only increased slightly from the deciduous forest to the mixedwood forest and the differences were not found to be significant. In general, the infection rate was very low and aggregated; only 3.6 to 7.8% of available large aspens had fungal conks and many nest sites did not have any infected aspens apart from the nest trees themselves.

2.4.2 Nest tree use and selection across habitats

Although only 29% of available trees were aspen (> 20 cm in DBH), 96% of all nests were found in this tree species, 3% were in paper birch and < 1% occurred in the remaining tree species: balsam poplar, balsam fir and jack pine (Figure 2.1). Some excavator species seemed more inclined to use a greater diversity of tree species. The excavator that used trembling aspen the least was the Red-breasted Nuthatch, with 19% of its nests in other tree species. Cavity excavators used the whole range of decay stages from 1, alive, to 5, highly decayed trees (Figure 2.2). Decay stages differed significantly between excavator species ($\chi^2 = 225.4$, $r^2 = 0.40$, $P < 0.001$). The Yellow-bellied Sapsucker, the Hairy Woodpecker and the Pileated Woodpecker used live trees (Figure 2.2). The Northern Flicker excavated in either live or highly degraded trees (Figure 2.2). With a mean DBH ranging from 28.8 cm to 45.5 cm excavators used larger aspen trees than its availability (mean DBH: 22.9 cm) in the study plots (Figure 2.3). However, results varied significantly between bird species ($F_{20,269} = 17.8$, $P < 0.001$; Figure 2.3). The Pileated Woodpecker used the largest trees and the Red-breasted Nuthatch and the Downy Woodpecker used the smallest nest trees (Figure 2.3).

The majority of aspen nest trees showed signs of fungal decay (88%, $n = 203$; Figure 2.4). Excavators used trembling aspen with heartrot (*Phellinus tremulae*) and no association with other fungi was found. *Phellinus tremulae* was found on 84% of aspen nest trees ($n = 101$), and more precisely, on 99% of live Aspen nest trees and on 58% of dead aspen trees (Figure 2.4). In comparison, only 7% of nest site (400 m^2 around the nest tree) available aspen >20 cm DBH were infected ($n = 1446$) (Figure 2.4). The number of fungal conks of *Phellinus tremulae* per nest tree seemed to vary by aspen decay stage. Live trees excavated by the Yellow-bellied Sapsucker and the Hairy Woodpecker had a mean number of ~10 conks, while dead trees excavated by the Red-breasted Nuthatch and the Downy Woodpecker had a mean number of ~4 conks.

2.4.3 Model selection across forest cover types

The Red-breasted Nuthatch and the Downy Woodpecker selected dead and degraded large aspens. The model, which included *Aspen*, *DBH* and *Decay* had strong support ($W_i > 0.99$) and no models were closely competitive (Table 2.2). The Yellow-bellied Sapsucker selected large aspen. The model including *Aspen*, *Decay* and *DBH* was in close competition with the model excluding *Decay* (Δ $AIC_c < 2$; Table 2.1). Following model averaging, *Decay* was not found to have an important influence (Table 2.4). This is most likely due to 74% of available trees being alive (Figure 2.2). The Pileated Woodpecker and Northern Flicker selected large aspens. The model, which included *Aspen* and *DBH*, had strong support ($W_i > 0.99$) and no models were closely competitive (Table 2.2). The Hairy Woodpecker's nest tree sample size was too low to perform the analysis.

All excavators selected trembling aspen and were 19 to 113 times more likely to select trembling aspen than other tree species (Table 2.4). All excavators were found to select large trees and were 10.9 to 11.7 times more likely to select a tree with each increase of 10 cm DBH (Table 2.4). The Red-breasted Nuthatch and the Downy Woodpecker selected dead trees and were 3.5 and 3.2 times more likely to select a tree with each increase of the decay stage (Table 2.4).

2.4.4 Nest tree use and selection along the age gradient

The proportion of nest cavities in aspens differed significantly between forest cover types. There was a greater proportion of nest cavities in aspens within deciduous forests than in conifer old-growth forests (generalized mixed models, $\beta = -2.5$, SE = 1.2, P = 0.04; Table 2.5). The mean nest tree DBH increased along the age gradient, although the differences between forest cover types using all excavator species grouped together was not significant. The Yellow-bellied Sapsucker was found to use larger trees in the conifer old-growth forests than in the deciduous forests (Table 2.5). Despite having a similar DBH distribution of live available aspen, the deciduous forests and the conifer old-growth forests differed dramatically in their nest trees DBH distribution (Figure 2.5). There was a gradual shift of abundance of nest trees from the 20-30 cm DBH category to the > 30cm DBH category along the time since fire age gradient (Figure 2.5). In the conifer old-growth, 84% of nests were in trees larger than 30 cm in DBH. No significant difference for decay stage use was found between the forest cover types (Table 2.5).

Live tree excavators selected large aspens in all forest cover types, but some variation in the probabilities of selection were found. The model, including all variables and interactions between *forest cover types* and *DBH* and *Decay*, had strong support ($W_i = 0.76$), although, the model excluding interactions between *forest cover type* and *Decay* was a close competitor (Table 2.2). Statistically significant differences in the probabilities of selecting trees as their DBH increases were found along the time since fire gradient. Predicted probabilities of nest tree selection for live tree excavators based on tree DBH derived from generalized mixed model multi-model inference results are shown in Figure 2.6. Live tree excavators had a higher probability of selecting trees as DBH increased in mixedwood and less importantly in conifer old-growth forests (Figure 2.6 and Table 2.6).

The dead tree excavators selected large degraded aspens in all three forest cover types. All models, except for the model that excluded interactions, were close competitors (delta AICc < 4) (Table 2.2). Following model averaging, none of the interactions were found to have an important influence (Table 2.6).

2.4.5 Abundance of nests along the age gradient and forest cover types

A total of 106 excavator's nests were found in 2009, 59 of which were Yellow-bellied Sapsucker, 17 were Downy Woodpecker, 16 were Red-breasted Nuthatch, 5 were Hairy Woodpecker, 8 were Northern Flicker and 1 was Pileated Woodpecker. There was a mean of 1.5 excavators per vegetation sampling stations in mixedwoods, 1.4 in deciduous forests and 0.93 in old-growth forests. The difference between forests cover types was marginally significant (Kruskal-Wallis $\chi^2_3 = 5.0$, df = 2, P = 0.08). However, when compared by age category (61-89, 90-186, 187-245 and > 245), the older forests (3 plots of 245 years since fire disturbance) differed significantly from younger forests (Kruskal-Wallis $\chi^2_3 = 14.3$, df = 3, P = 0.003, Tukey HSD test). At the species level, less Yellow-bellied Sapsucker nests were found in the conifer old-growth forests than in the two other forest cover types (Kruskal-Wallis $\chi^2_3 = 7.1$, df = 2, P = 0.03, Tukey HSD test). In addition, it was noted that Pileated Woodpecker's suitable cavities were rarely found in mature deciduous forests: only 2 out of 28 cavities were found in forests 61 years since fire disturbance.

Polynomial regressions were performed with all excavators' nests pooled together in order to verify the general trend of nest abundance along the age gradient. The Yellow-bellied Sapsucker was the only excavator for which we had an adequate nest sample size to verify the distribution trend at the species level. Quadratic polynomial regressions had a significantly better fit than a straight-line models (excavators pooled together: $F_{1,86} = 10.1$, $P = 0.002$ and Yellow-bellied Sapsucker: $F_{1,86} = 7.4$, $P = 0.008$). When pooled together, excavator's nests were found to follow a modal distribution along the age gradient ($F_{2,86} = 8.9$, $P < 0.001$, $r^2_{adj} = 0.15$; Figure 2.7). A very similar trend was found for the Yellow-bellied Sapsucker ($F_{2,86} = 8.4$, $P < 0.001$, $r^2_{adj} = 0.15$; Figure 2.7).

2.5 Discussion

The dynamics of nest tree selection by cavity excavators in the boreal mixedwood forest are directly linked to both large-scale natural disturbances (forest fires), and small-scale natural disturbances (ex: wind damage and insect outbreaks) that affect the abundance and distribution of quality cavity excavation substrates (Drapeau et al. 2009b, Nappi and Drapeau 2009). The nature of small-scale natural disturbances varies as the forest ages. In young and mature aspen-dominated stands, gaps are generally small and are mostly filled by shade intolerant species such as balsam fir (Kneeshaw and Bergeron 1998, Bergeron 2000). In conifer dominated old-growth forests, larger gaps, often created by spruce budworm outbreaks in balsam fir dominated stands, promote the growth of the white cedar and shade intolerant trees such as aspen (Kneeshaw and Bergeron 1998). Spruce budworm outbreaks in the studied old-growth sites may explain the persistence of aspen in the old-growth forests.

This study highlights the crucial importance of large trembling aspens with varying stages of decay infected by *Phelinus tremulae* for the conservation of cavity nesting communities in boreal mixedwood forests. We provide the first assessment of nest tree use and selection by cavity excavators along a well documented time since fire and compositional gradient (Bergeron and Dubuc 1989, Dansereau and Bergeron 1993) in eastern North American boreal mixedwood forest. Forest composition and structure changed considerably throughout the age gradient (61 to 245 years after the last fire). Forest canopy dominance varied from mature forests, where deciduous trees dominated the canopy, to old forests, where the canopy was mixed, to old-growth forests, where conifers mostly dominated the canopy. Along this gradual change in forest canopy composition, the overall abundance of nests seemed to follow a modal distribution. The highest nests abundances were located in old deciduous and mixedwood forest stands. Large aspen infected by heartrot (*Phelinus tremulae*) was identified as a key tree resource, and distribution of these along the age gradient is thought to explain in part the distribution in nest abundance. Nest tree selection by cavity excavators remained similar, even though this tree resource did not seem to be evenly distributed along the forest composition gradient. Our results thus corroborate our main prediction: cavity excavators used and selected a narrow spectrum of nesting tree characteristics and had limited nest site plasticity.

2.5.1 Nest tree use and selection

In mixedwood forests, numerous studies have reported that cavity excavators select large declining or dead trembling aspen as their nest tree (Li and Martin 1991, Dobkin et al. 1995, Martin et al. 2004, Savignac and Machtans 2006, Cooke 2009). This study reflects this strong association, as nest cavities were almost exclusively found in large trembling aspen with varying stages of decay. With less than 3% of total nests, degraded white birch was the second most used tree. The presence of heartrot by *Phellinus tremulae* in aspen plays a key role in the selection of live aspen trees by excavators (Kilham 1971, Hart and Hart 2001, Martin et al. 2004, Savignac and Machtans 2006, Cooke 2009). Almost all the living aspen nest trees and half the dead aspen nest trees sampled (nest trees of Yellow-bellied Sapsucker, Downy Woodpecker and Red-breasted Nuthatch) had fungal conks, although, only a very low proportion of available aspens were infected by the fungus (7% of > 20 cm in diameter). This strong selection for infected trees is likely related to the state of the preferred excavation substrate: a solid sapwood column with soft degraded heartwood (Kilham 1971, Conner et al. 1976). The association of *Phellinus tremulae* and trembling aspen seems to be a key factor for the existence and persistence of this rich cavity nesting community in boreal mixedwood forests, particularly for the Yellow-bellied Sapsucker.

All excavators selected trees larger than the mean diameter at breast height (DBH) of available trees and available aspen. There seemed to be a general preference for aspen > 30 cm in DBH. As with Martin et al. (2004), the mean nest tree diameter increased with the body size of the excavating species. Small excavators like the Red-breasted Nuthatch and the Downy Woodpecker had the lowest mean nest tree DBH (29-30 cm) and large excavators like the Pileated Woodpecker had the highest mean nest tree DBH (45 cm). Such a pattern is related to the minimum tree diameter required to excavate a suitable cavity. On the other hand, as proposed by Savignac and Machtans (2006), this may also be related to the minimum size for sufficient heartrot infection needed for excavation in aspen. Accordingly, there was a greater probability of detecting fungal conks on available aspen as DBH increased. This corroborates what is found in the literature: a greater proportion of aspens are infected as the age and size of trees increases (Basham 1958).

The Red-breasted Nuthatch and the Downy Woodpecker selected large dead aspens, despite their low availability. Only 5% of available large trees (> 20 cm DBH), all tree species confounded were dead or dying, whereas only 1.3% were large dead or dying aspens. Nests of Yellow-bellied Sapsucker, Hairy Woodpecker and Pileated Woodpecker were mostly found in live aspens. However, these excavators were not found to select a particular decay stage, as their use did not differ from what was available.

2.5.2 Plasticity of nest tree selection

Large aspen with varying stages of decay were strongly selected by live tree excavators (Yellow-bellied Sapsucker and Hairy Woodpecker) and dead tree excavators (Downy Woodpecker and Red-breasted Nuthatch) in all forest cover types. This strong selection highlights the crucial importance of this tree species for the excavation process and thus for the cavity nesting assemblages throughout the mature to old-growth forest gradient of the boreal mixedwood. While selecting the same excavation substrate, however, some variations in the probabilities of selection by live trees excavators were noted along the time since fire gradient.

Live tree excavators had the highest probability of selecting aspens as DBH increased in mixedwood followed by conifer old-growth forests. In deciduous forests where aspen basal area was the greatest, tree diameter was less indicative of nest tree selection. Despite a high abundance of large aspens in deciduous forests, live tree excavators did not seem to select the largest aspens. Likewise, in conifer old-growth where aspen had the lowest basal area and the highest mean diameter (marginally significant), DBH was, again, less indicative than in mixedwoods. However, in mixedwood forests, the diameter of aspen in mixedwood forests was a very good predictor of nest tree selection by live tree excavators even though large aspens had a lower availability in this forest cover type.

2.5.3 Abundance of nests

More cavity nesters were found in old aspen and mixedwood forests than in young to mature aspen forests (Hobson and Bayne 2000, Schieck and Song 2006). Western Canadian studies have shown that Yellow-bellied Sapsuckers were rarely detected in boreal mixedwood forests younger than 90 years old, and that the maximum density of nest trees for this species was in old aspen or mixedwood stands (> 90 years) (Savignac and Machtans 2006, Cooke 2009). We found a modal distribution of excavator nest densities along the age gradient (61 to 245 years after fire). High nest densities were located between 89 and 182 years after fire disturbance. This trend was found when all excavators' nests were pooled together and for Yellow-bellied Sapsuckers' nests. In addition, we found lower nest densities for pooled excavator nests and for Yellow-bellied Sapsucker nests in conifer old-growth forests than in deciduous and mixedwood forests. The modal distribution of nests along the age gradient may be explained by the combined availability of quality cavity excavation substrates as well as the availability of foraging substrates (Nappi 2009). Excavation substrates ranged from abundant aspens in deciduous forests to less abundant in mixedwoods and to even less abundant but larger aspens in conifer old-growth forests. Lower aspen basal area explains why there is a lower density of excavators' nests in conifer old-growth forests but does not explain the more or less higher densities found in old deciduous and mixedwood forests compared to mature deciduous forests. It has been documented that the proportion of heartrot by *Phellinus tremulae* in aspen increases with stand age (Basham 1958, Pothier et al. 2004). Basham (1958) reported that decayed merchantable volume went from 14% in the 41-60 age class to 41% in the 161-180 age class (Miller 1996). However, due to low sampling data and low overall infection rate, no differences in the proportion of infected aspen were found along the age gradient.

In addition to the distribution of quality excavation substrates, foraging substrates are an important factor to take into account to explain excavator nest distribution, as considerably more foraging trees are needed than nest trees (Imbeau and Desrochers 2002, Drapeau et al. 2009b). The occurrence of conifers in the canopy supplies a greater diversity of foraging substrates. A study by Nappi (2009) in the same study area showed that an important proportion of foraging activities by woodpeckers is done on conifers. Yellow-bellied Sapsuckers were shown to use white birch (41%) but also balsam fir (31%) as sap wells (Nappi 2009). Pileated Woodpecker used dead aspen (30%) but also balsam firs (21%) and white cedar (17%) (Nappi 2009).

2.5.4 Management Implications

Cavity excavators provide a critical link between trees and secondary cavity nesters, i.e. species that depend on cavities for reproduction and shelter but cannot excavate them. These species, which interact through creation, use and competition for cavities, form nest webs that are analogous to food webs (Martin et al. 2004). In the boreal mixedwood forests, the Yellow-bellied sapsucker is an important provider of cavities for small secondary cavity users and the Pileated Woodpecker is a keystone species providing cavities for large secondary cavity users (Bonar 2000, Conner et al. 2001, Savignac and Machtans 2006, Cooke 2009), this study: Chapter 3). Both of these species excavate in large trembling aspens infected by *Phellinus tremulae* (Kilham 1971, Savignac and Machtans 2006, Cooke 2009). As shown in this study, cavity excavators select this quality substrate even in conifer old-growth forests, where it is much less abundant. Therefore, large aspen showing signs of infection by *Phellinus tremulae*, as well as healthy aspen (> 20 cm DBH), should be maintained in partial cuts in order to supply immediate and future quality cavity excavation substrate in managed forests.

We showed that the abundance of excavator nests along the age gradient followed a modal distribution. Although, potential nest trees are a prerequisite for the presence of breeding excavators, they are not the only important factor to consider. Forest management has to take into account the important role of foraging substrates (Drapeau et al. 2009b) for these cavity producers. Short rotation even-aged forest harvesting in boreal mixedwoods can have detrimental effects on cavity nesting assemblages, as young and mature deciduous forests would eventually replace old deciduous and mixedwood forests in the landscape. This does not leave enough time for 1) potential nest trees to become large, old and scenescent and 2) for conifers to occupy the canopy and provide a greater diversity of foraging substrate. Studies in western boreal mixedwood forests of Canada have reported that the Yellow-bellied Sapsucker is absent in forests younger than 50 years old and is rarely found in forests younger than 90 years (Savignac and Machtans 2006). However, in order to minimize the loss of merchantable wood volume mostly caused by heartrot (*Pheillinus tremulae*), it is recommended that rotation age for aspen stands be lower than 80 years (Basham 1991, Miller 1996). There is an obvious conflict between the need of cavity nesters for declining aspen trees and the economical need to harvest aspen stands before they decline. A balance between harvesting and conservation must be struck. We suggest retention of large patches of boreal mixedwood forests and old conifer forests representing the whole range of what was naturally present in the forest landscape. Another option that has been set forth by Bergeron and Harvey (1997) and Harvey et al. (2002) is to introduce partial cutting practices that may facilitate the transition from aspen to mixedwood stands and maintain senescent trembling aspen stems in the managed forest landscapes. Monitoring the status of woodpecker populations could be a key indicator to assess the efficiency of ecosystem management in such forests (Drapeau et al. 2009a, Gauthier et al. 2009).

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2.7 Figures

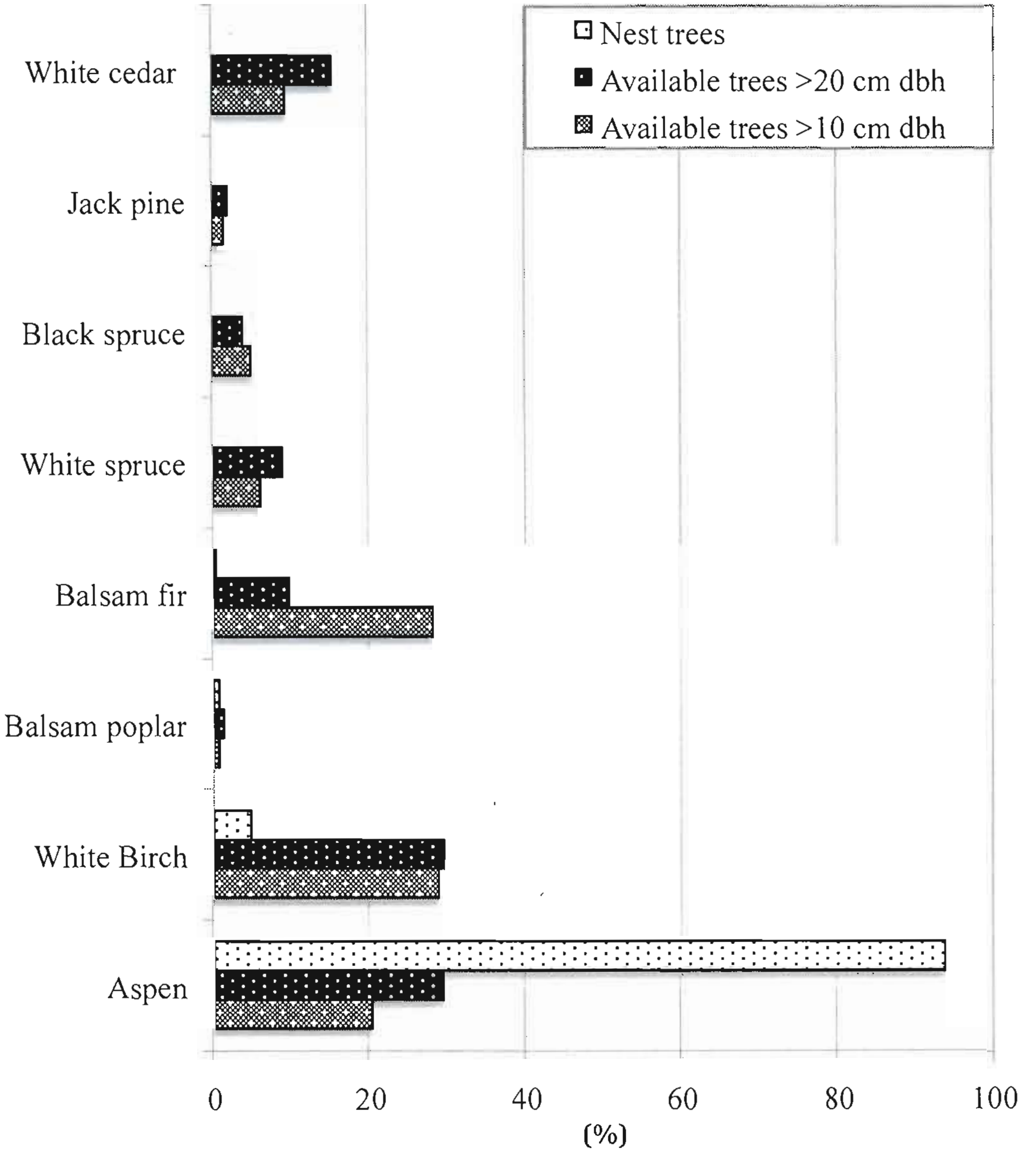

Figure 2.1: Nest tree use in relation with available trees species > 10 cm DBH and available trees species > 20 cm DBH.

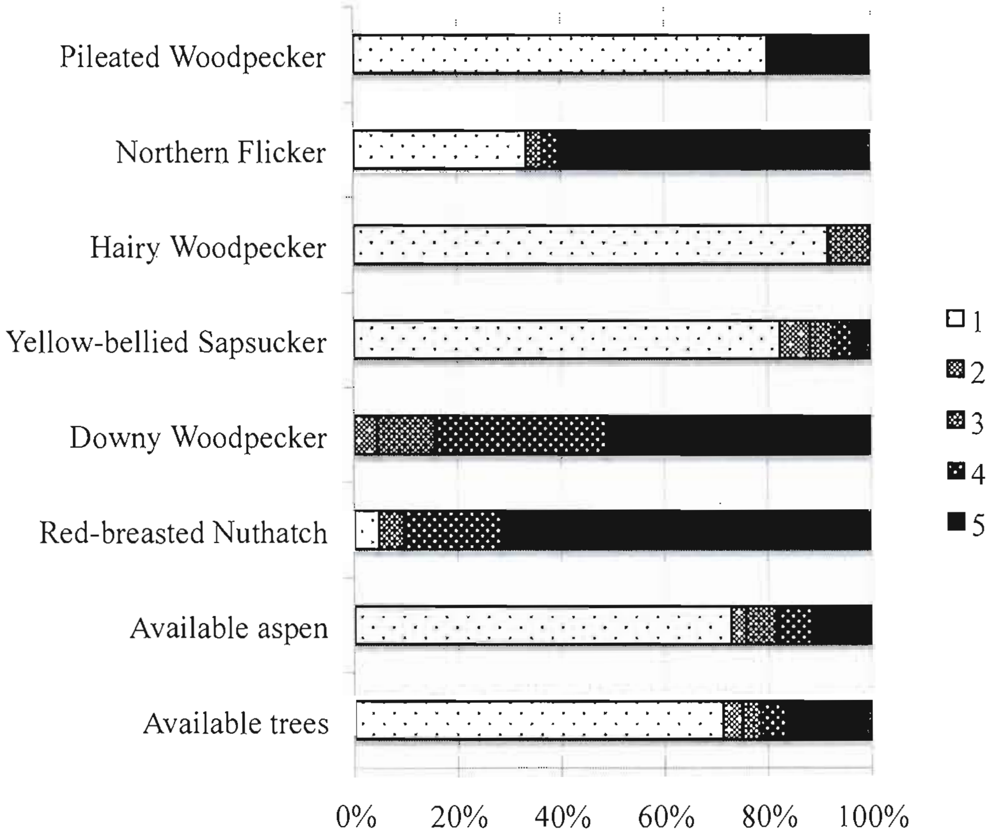

Figure 2.2: Nest tree decay stage use by excavator species in relation to available trees and available aspen trees decay stages. Tree decay is classified in 5 categories according to a modified version of Maser et al. (1979) (Nappi 2009): Decay 1 (alive, > 20% foliage); Decay 2 (declining, < 20% foliage); Decay 3 (recently dead, hard wood, firm bark cover); Decay 4 (moderate decay, soft wood, no dead foliage present, no small twigs, some branches remaining, usually intact top); Decay 5 (high decay, soft decomposed wood, very few branches, often broken top).

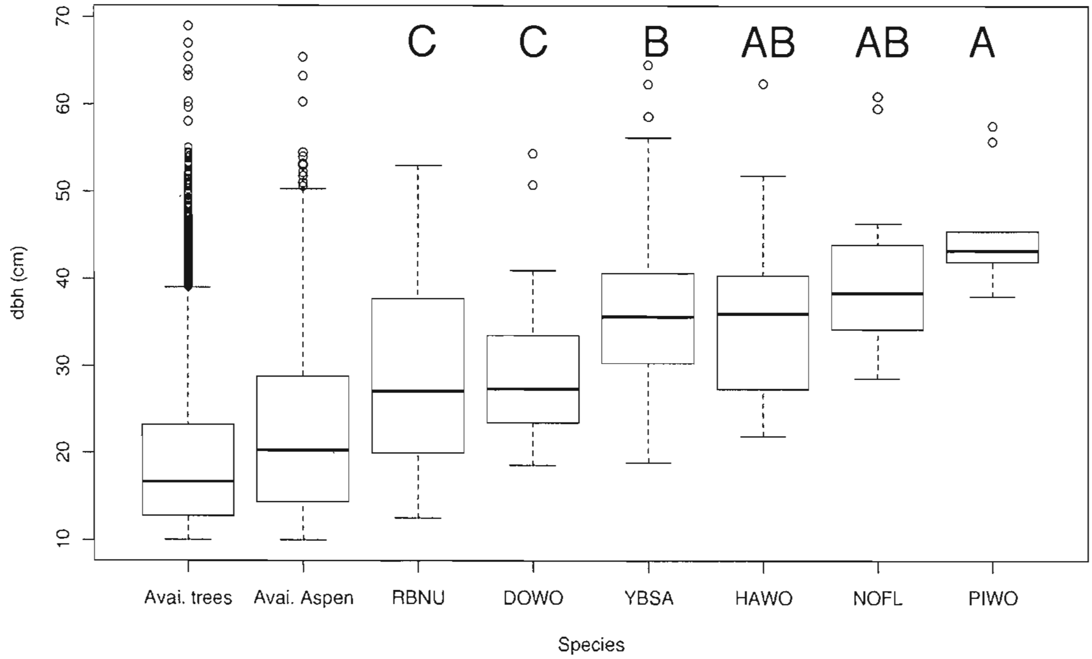

Figure 2.3: Nest tree DBH use in relation to available trees and available aspen trees DBH. Species not connected by the same letter are significantly different (Tukey HSD test, $\alpha < 0.05$). The species considered are the Red-breasted Nuthatch (RBNU), the Downy Woodpecker (DOWO), the Yellow-bellied Sapsucker (YBSA), the Hairy Woodpecker (HAWO), the Northern Flicker (NOFL) and the Pileated Woodpecker (PIWO).

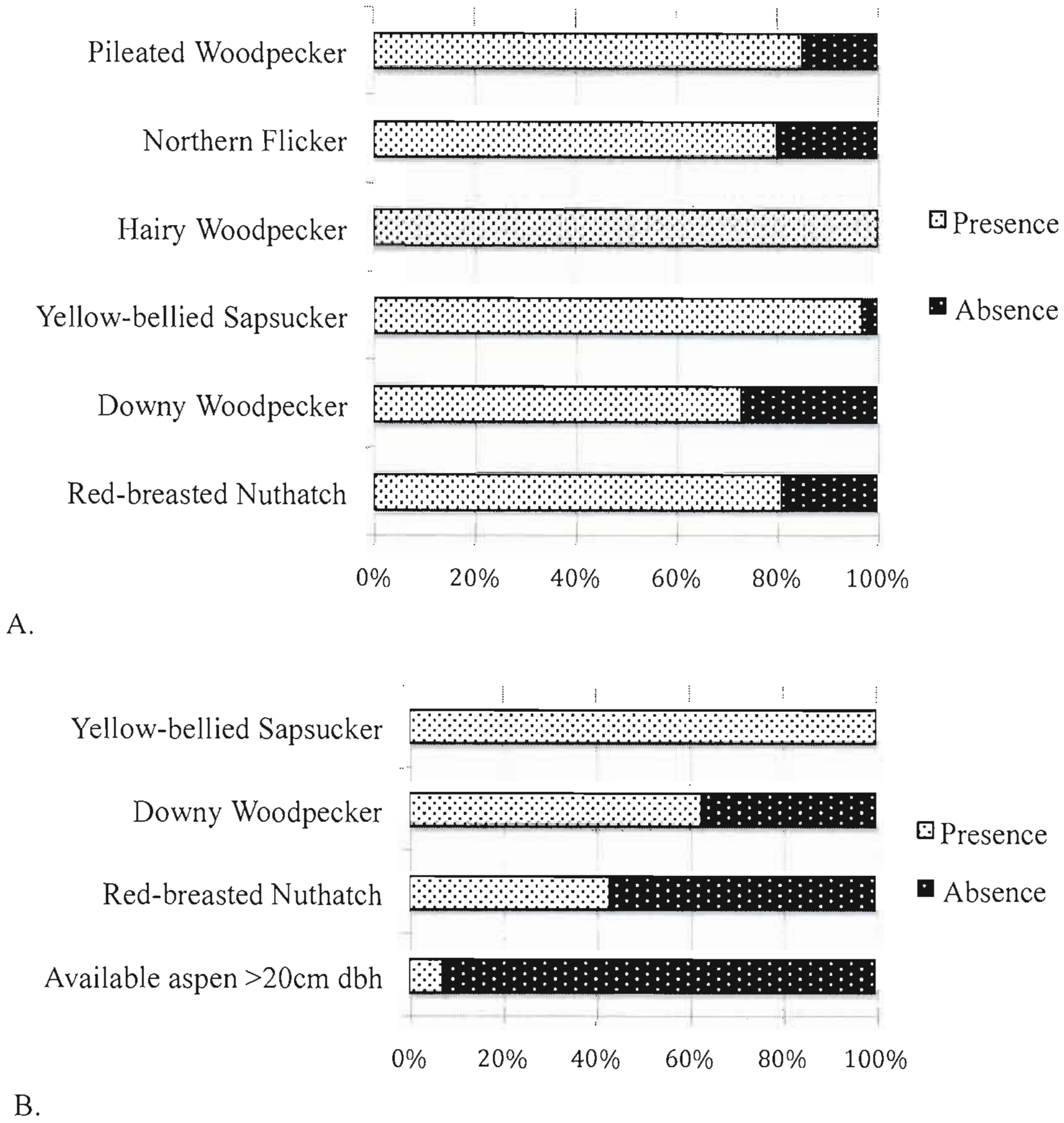

Figure 2.4: Proportion of aspen nest trees showing signs of fungal decay (A). Pileated Woodpecker and Northern Flicker unused cavities were pooled with used cavities. Proportion of aspen nest trees and available nest site aspens >20 cm DBH bearing fungal conks (*Phellinus tremulae* (Bondartsev Bondartsev & Borisov)(B).

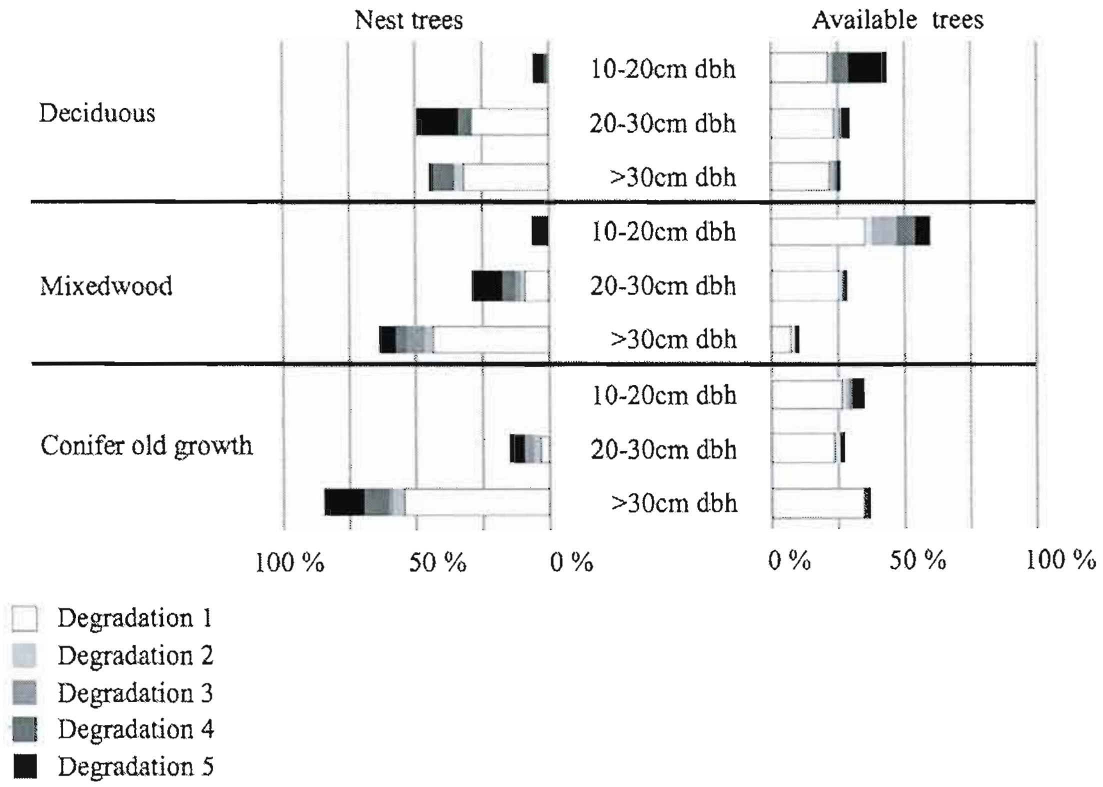

Figure 2.5: Proportion of aspen nest trees and available aspens for each forest cover type per DBH category. Decay stages are indicated by shades of grey, black being a highly degraded tree.

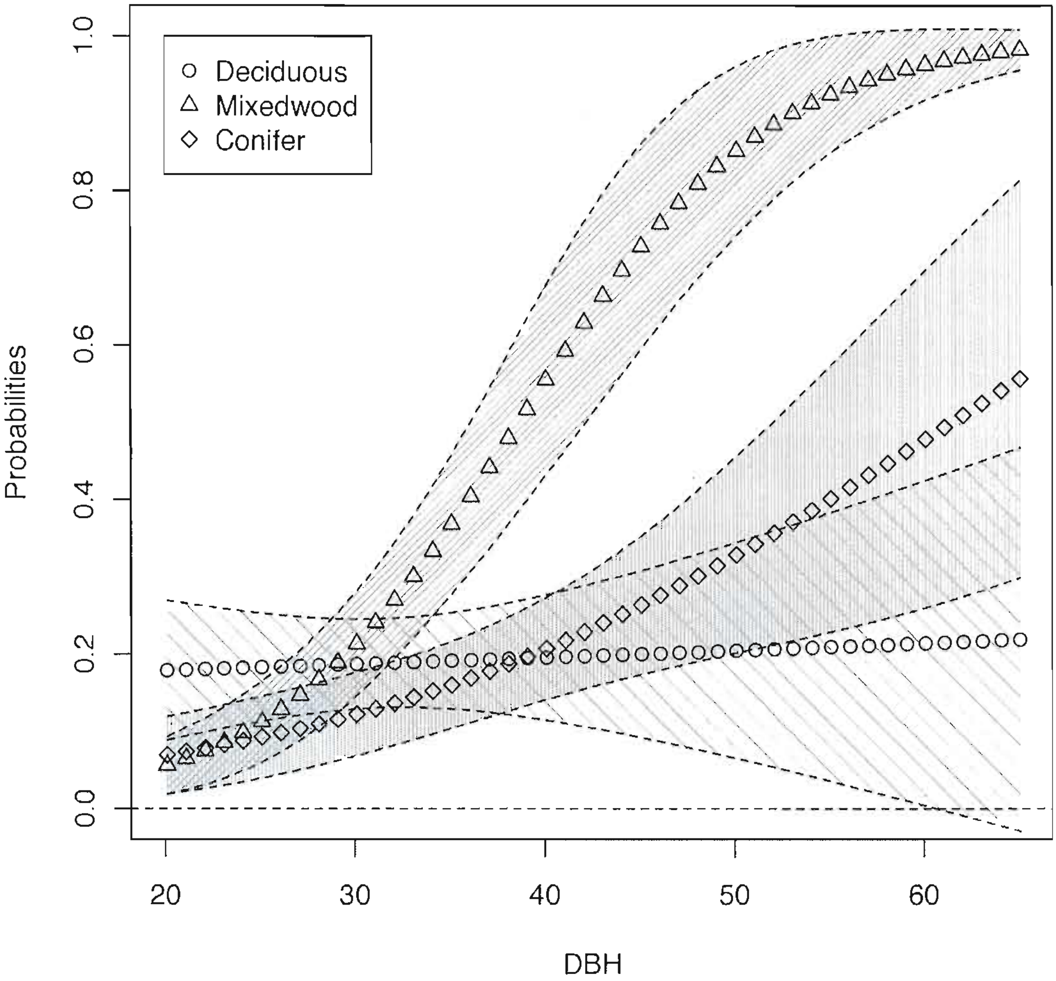

Figure 2.6: Predicted probabilities of nest tree selection for live tree excavators (Yellow-bellied Sapsucker and Hairy Woodpecker) based on large aspen DBH (> 20cm DBH) and derived from generalized mixed model multi-model inference results. Error bars represent the 95% confidence intervals for estimates.

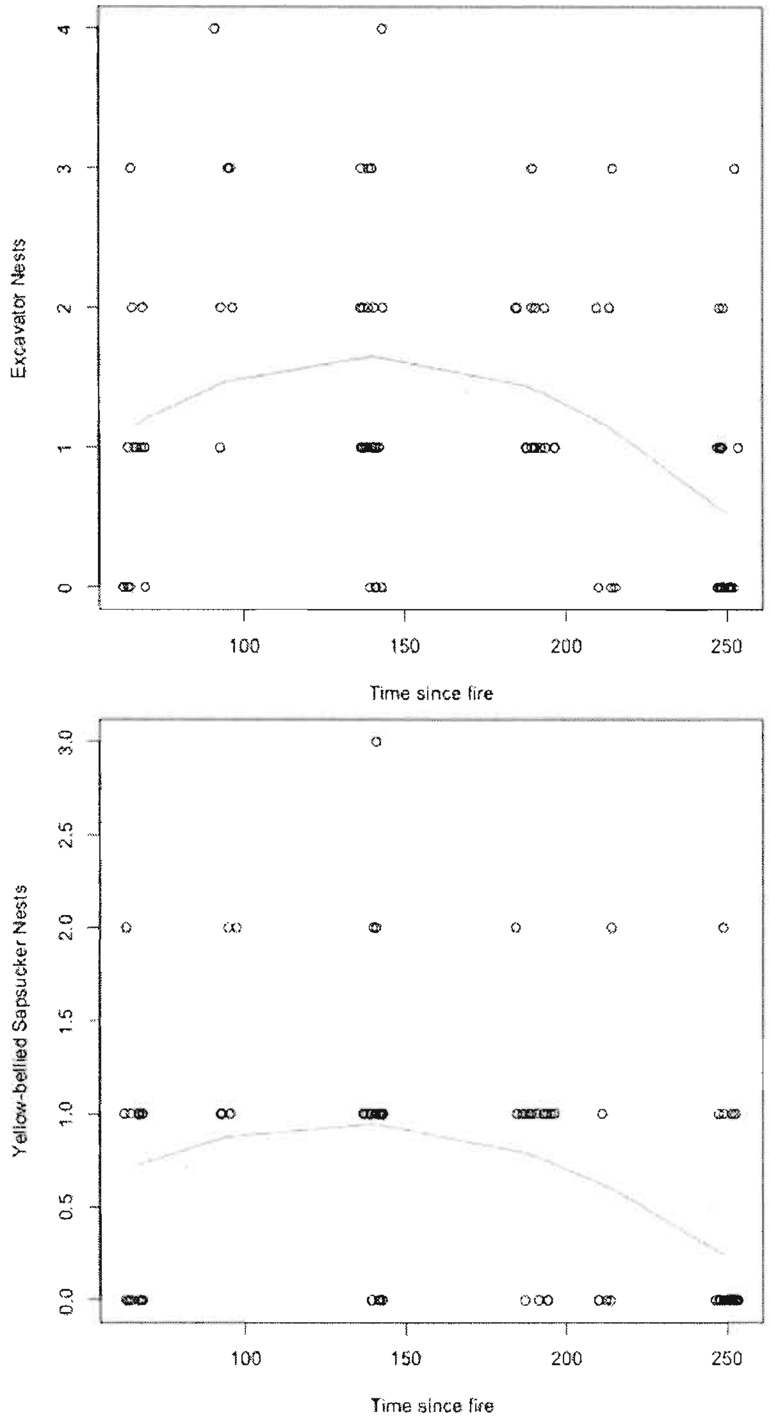

Figure 2.7: Nest abundances along the time since fire gradient for A; Excavators ($F_{2,86} = 8.9$, $P < 0.001$, $r^2_{adj} = 0.15$) and for B; Yellow-bellied Sapsuckers ($F_{2,86} = 8.4$, $P < 0.001$, $r^2_{adj} = 0.15$).

2.8 Tables

Table 2.1: Model selection results of nest tree characteristics influencing nest-tree selection by excavator species in the boreal mixedwood forests of eastern North America. Models are ranked from most plausible ($AIC_c = 0$) to least plausible. Only models with a $\Delta AIC_c \leq 4.00$ are listed. *K* is the number of model parameters. Akaike weight (W_i), is the weight of evidence in favor of model *i* being the best model among the models in the set. *Decay* could not be added for the Northern Flicker (NOFL) and for the Pileated Woodpecker (PIWO) because old unused cavities were pooled with active nest cavities.

Candidate model	Log likelihood	*K*	ΔAIC_c[a]	Akaike weight (W_i^d)
Red-breasted Nuthatch				
Model 1: Aspen, DBH, Decay[b]	-130.95	5	0.00	1
Downy Woodpecker				
Model 1: Aspen, DBH, Decay[b]	-133.84	5	0.00	1
Yellow-bellied Sapsucker				
Model 1: Aspen, DBH, Decay[b]	-357.57	5	0.00	0.74
Model 2: Aspen, DBH	-358.63	4	2.13	0.26
Northern Flicker				
Model 1: Aspen, DBH[b]	-118.71	4	0.00	1
Pileated Woodpecker				
Model 1: Aspen, DBH[b]	-86.97	4	0.00	1

[a] RBNU: minimum AIC*c* = 261.89; DOWO: minimum AIC*c* = 267.67; YBSA: minimum AIC*c* = 715.13; NOFL: minimum AIC*c* = 237.43; PIWO: minimum AIC*c* = 173.93.

[b] Global model.

Table 2.2: Model selection results of nest tree characteristics influencing nest-tree selection by live tree excavator species (Yellow-bellied Sapsucker and Hairy Woodpecker) and dead tree excavator species (Red-breasted Nuthatch and Downy Woodpecker) for three forest cover types (FCT) in the boreal mixedwood forests of eastern North America. Models are ranked from most plausible (AIC_c=0) to least plausible. Only models with a $\Delta AIC_c \leq 4.00$ are listed. *K* is the number of model parameters. Akaike weight (W_i), is the weight of evidence in favor of model *i* being the best model among the models in the set. The forest cover type (FCT) variable has three levels: 1) deciduous, 2) mixedwood and 3) conifer old-growth.

Candidate model	Log likelihood	*K*	ΔAIC_c[a]	Akaike weight (W_i)
Live tree excavators				
Model 1: DBH, Decay, FCT, FCT:DBH, FCT:Decay[b]	-313.70	10	0.00	0.76
Model 2: DBH, Decay, FCT, FCT:DBH	-314.84	8	2.27	0.24
Dead tree excavators				
Model 1: DBH, Decay, FCT, FCT:DBH, FCT:Decay[b]	-102.43	10	0.00	0.47
Model 2: DBH, Decay, FCT, FCT: Decay	-102.97	8	1.07	0.75
Model 3: DBH, Decay, FCT, FCT: DBH	-103.14	8	1.40	0.98

[a] Live tree excavators: minimum AIC*c* = 627.41; Dead tree excavators: minimum AIC*c* = 204.87.

[b] Global model.

Table 2.3: Habitat characteristics for three forest cover types: deciduous (61 to 89 years), mixedwood (135 years) and conifer old-growth (182 to 245 years). *n* is the number of plots of 0.06 ha sampled. Levels not connected by the same letter are significantly different (Tukey HSD test, $\alpha < 0.05$).

Variable	Deciduous forests (n=22)	Mixedwood forests (n=30)	Conifer old-growth forests (n=54)	*P*
Total basal area	31.7 ±9.4	32.5 ±8.2	31.4 ±10.7	0.822
Total dead tree basal area	4.9 ±3.3	6.6 ±3.2	6.9 ±3.3	0.426
Coniferous basal area	5.9 ±4.8 (B)	14.2 ±5.3 (AB)	18.1 ±10.8 (A)	0.024*
Deciduous basal area	25.7 ±7.8 (A)	18.3 ±7.9 (AB)	13.3 ±7.3 (B)	0.004*
Aspen basal area	15.5 ±10.2 (A)	9.3 ±7.4 (AB)	5.8 ±7.0 (B)	0.043*
Dead aspen basal area	3.1 ±3.3 (A)	1.7 ±2.2 (AB)	0.5 ±1.0 (B)	0.006*
Balsam fir basal area	3.6 ±2.4	4.8 ±2.7	5.2 ±2.6	0.488
Dead balsam fir on the ground basal area	0.8 ±1.4 (B)	1.6 ±0.9 (B)	3.7 ±1.9 (A)	0.002*
Mean tree DBH (SD)	17.4 ±2.4 (B)	19.8 ±2.6 (AB)	21.0 ±3.4 (A)	0.015*
Mean aspen DBH (SD)	25.3 ±7.4	23.4 ±7.8	32.2 ±11.16	0.125
Proportion of available nest site aspens >20 cm in DBH with fungal conks (%)[a]	3.6 ±6.7	7.8 ±14.4	7.2 ±15.6	0.383

[a] The proportion of available nest site aspens with fungal conks was averaged at the nest site and the differences between cohorts were tested with Kruskal-Wallis.

Table 2.4: Multi-model inference parameter estimates, confidence interval and odds ratio for nest tree selection by cavity excavators in the boreal mixedwood forests of eastern North America. Only statistically significant odds ratio are presented. Odds ratios were calculated for increases of one unit for *Aspen* and *Decay* and for increases of 10 cm for *DBH*.

Species	Variables	Model-averaged β estimates	95% lower confidence interval	95% upper confidence interval	Odds Ratio
Red-breasted Nuthatch	Aspen	3.17	2.28	4.07	23.92
	DBH	0.09	0.06	0.12	10.90
	Decay	1.25	0.93	1.56	3.47
Downy Woodpecker	Aspen	4.32	3.08	5.56	75.27
	DBH	0.09	0.06	0.12	10.90
	Decay	1.15	0.88	1.42	3.16
Yellow-bellied Sapsucker	Aspen	4.72	3.55	5.90	112.63
	DBH	0.10	0.09	0.12	11.10
	Decay	-0.13	-0.31	0.05	---
Northern Flicker	Aspen	2.96	1.74	4.18	19.25
	DBH	0.10	0.07	0.13	11.00
Pileated Woodpecker	Aspen	3.83	1.80	5.87	46.13
	DBH	0.16	0.12	0.20	11.70

Table 2.5: Nest tree characteristics for each species and for all species combined presented for different forest cover types. The proportion of aspen refers to the percentage of nest trees per plot that were aspen. Tree decay is classified in 5 categories according to a modified version of Maser et al. (1979) (Nappi 2009) and the median is presented. Difference between forest cover types for the proportion of aspen and the degradation stage were tested with generalized mixed models. Differences between cohorts for the DBH of nest trees were tested with an ANOVA with mixed models. The variable *plot* was added to the models as the random effect. Only probabilities smaller than 0.1 are presented.

Variable	Excavator Species	Deciduous forests	Mixedwood forests	Conifer old-growth forests	*P*
Proportion of aspen (SD)	All species	98.8	95.2	88.1	0.04*
	RBNU	83.3	80.0	81.8	---
	DOWO	100	95	80	---
	YBSA	100	100	94.1	---
	HAWO	100	100	100	---
	NOFL	100	100	72.7	---
	PIWO	100	100	92.9	---
DBH (SD)	All species	31.2 ±7.4	34.5 ±10.2	39.6 ±9.6	0.09
	RBNU	24.0 ±8.0 (B)	26.4 ±10.8 (AB)	36.8 ±9.3 (A)	0.06
	DOWO	25.5 ±5.3	30.5 ±9.7	32.0 ±5.2	---
	YBSA	31.8 ±6.4 (B)	37.0 ±7.8 (AB)	40.3 ±8.8 (A)	0.01*
	HAWO	28.9 ±5.8	41.6 ±6.7	36.1 ±11.3	---
	NOFL	34.3 ±6.7	35.4 ±7.2	40.8 ±11.7	---
	PIWO	43.5 ±6.7	44.9 ±9.5	45.8 ±8.5	---
Decay stage (range)	All species	1 (1-5)	1 (1-5)	2 (1-5)	---
	RBNU	5 (4-5)	5 (1-5)	5 (1-5)	---
	DOWO	5 (4-5)	4 (2-5)	5 (2-5)	---
	YBSA	1 (1-4)	1 (1-5)	1 (1-5)	---
	HAWO	1 (1-1)	1 (1-1)	1 (1-1)	---
	NOFL	4 (1-5)	1 (1-5)	5 (3-5)	---
	PIWO	1 (1-1)	1 (1-5)	1 (1-5)	---

Table 2.6: Multi-model inference parameter estimates, confidence interval and odds ratio for nest tree selection by live tree excavators (Yellow-bellied Sapsucker and Hairy Woodpecker) and dead tree excavators (Red-breasted Nuthatch and Downy Woodpecker) for three forest cover types (FCT). Only >20 cm DBH aspen were included in the analysis. Odds ratio are calculated for increases of one unit for *Decay* and for increases of 10 cm for *DBH*. Only statistically significant odds ratio are presented. *Forest cover type* (FCT) has three levels: 1) deciduous, 2) mixedwood and 3) conifer old-growth.

Excavators	Variables	Model-averaged β estimates	95% lower CI	95% upper CI	Odds Ratio
Live tree excavators	DBH	0.01	-0.04	0.05	---
	DBH: FCT 2	0.15	0.08	0.21	11.60
	DBH: FCT 3	0.06	0.00[a]	0.11	10.60
	Decay	-0.27	-0.61	0.08	---
	Decay: FCT 2	-0.04	-0.54	0.45	---
	Decay: FCT 3	0.35	-0.19	0.90	---
Dead tree excavators	DBH	-0.03	-0.13	0.06	---
	DBH: FCT 2	-0.06	-0.06	0.17	---
	DBH: FCT 3	0.08	-0.05	0.21	---
	Decay	1.54	0.83	2.24	4.65
	Decay: FCT 2	-0.41	-1.25	0.44	---
	Decay: FCT 3	-0.24	-1.14	0.67	---

[a] 0.002

CHAPITRE 3

NEST WEBS IN MATURE AND OLD BOREAL MIXEDWOOD FORESTS OF EASTERN NORTH AMERICA

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Cavity nesters are an important component of the diversity of vertebrates found in boreal mixedwood forests of eastern North America. They are dependent on adequate cavity-trees for nesting and roosting. However, the quality and quantity of these substrates can vary considerably between forest cover types and as the forest ages. Using a nest web approach, we compared functional structures and network properties of cavity nesting assemblages along an age gradient of naturally disturbed mixedwood boreal forest stands. Between 2003 and 2010, twelve 24 to 40 ha plots ranging from 61 to 245 years after fire were surveyed at the Lake Duparquet Research and Teaching Forest in Abitibi, Quebec, to detect cavities with active nests. This study provides the first comparison of nest webs along a time since fire gradient in a continuous large forest track of boreal mixedwood forest. Nest webs were composed of 5 primary cavity excavator species (woodpeckers), two weak cavity excavator species (nuthatches, chickadees) and 7 secondary cavity users (squirrels, passerines, ducks, birds of prey). Cavity nesting assemblages remained similar throughout the age gradient and the deciduous to coniferous cover type transition. Despite a lower abundance of nests, there was a greater complexity in the conifer old-growth nest web. Along the age gradient, we found a cavity nesting assemblage mainly structured around the trembling aspen, the Yellow-bellied Sapsucker and the Pileated Woodpecker. The trembling aspen harbored 95% of the cavity nests, despite its low availability (29%), particularly in old forests. Secondary cavity users selected excavated cavities (as opposed to naturally decayed) 99% of the time. They also had strong links to specific primary excavators. Contrary to nest webs in BC interior forests, the Northern Flicker was not an important cavity excavator in continuous tracks of boreal mixedwood forests. However, the Pileated Woodpecker was a keystone species; its cavities were the most exploited resource. The maintenance of large diameter trembling aspens covering a wide range of decay stages along the age and tree composition gradients allowed for a diverse cavity nesting assemblage across forest cover types.

Key words: Cavity-nesting birds, assemblage structure, changes in tree composition, age gradient, trembling aspen, Pileated Woodpecker, Yellow-bellied Sapsucker

3.1 Introduction

Cavity-nesting assemblages are composed of a wide array of vertebrates, birds and mammals that are associated by their dependence on tree cavities for reproduction and shelter. Cavity users can be structured in different guilds (Martin and Eadie 1999). Primary excavators (PCN) are woodpeckers that typically excavate a cavity for nesting on an annual basis. Secondary cavity nesters (SCN) are a more diverse group: passerines, birds of prey, ducks and mammals, which cannot excavate their own cavities and therefore depend on the availability of cavities. Weak excavators (WPCN) can excavate their cavities in soft or degraded wood or use already existing cavities. Assemblages are structured through the creation of cavities and the competition for their occupancy. This is often described as a nest web, a concept that serves to visually highlight the interactions between cavity nesting species and potential interdependencies (Martin and Eadie 1999).

The availability of cavity trees plays an important role in nest web structure, as cavity availability can limit population densities of cavity nesters, particularly secondary users (Newton 1994, Holt and Martin 1997). Cavities are either formed by the degradation of trees (natural cavities) or by excavator species. However, in most North American forest ecosystems where nest web studies were conducted, it was noted that excavators are the main architects of cavities and that the majority of reused cavities are woodpecker cavities (Martin et al. 2004, Blanc and Walters 2008, Cooke 2009). Accordingly, the excavation process is considered a keystone process (Bednarz et al. 2004) in the structuring of nest webs. A keystone species is defined as one that exerts a disproportional influence on its community or ecosystem compared to its relative abundance (Paine 1969, Power et al. 1996). In many studies, large cavity excavators like the Northern Flicker (*Colaptes auratus*) or the Pileated Woodpecker (*Dryocopus pileatus*) have been designated as keystone excavators

(Bonar 2000, Aubry and Raley 2002a, Martin et al. 2004, Blanc and Walters 2008, Cooke 2009). However, the roles of keystone excavators may vary as a function of the availability of excavation substrates. As suggested by Martin and Eadie (1999), nesting substrates availability may vary along forest succession, thus changing the nest web structure of cavity assemblages. Few nest web studies have yet evaluated such changes.

An ideal study for evaluating nest webs along forest succession would require detailed knowledge of natural disturbances and the resulting age structure of forest landscapes under investigation. Such information is rare and can be obtained through studies of disturbance history reconstruction using dendrochronological (Bergeron et al. 2004) or paleological approaches (Cyr et al. 2009) to reconstruct the past disturbance events and their footprint on forest cover types. We had such an opportunity at the southern fringe of the boreal mixedwood forest in northwestern Québec where a detailed fire reconstruction study was conducted in an area not affected by timber harvesting (Bergeron 1991, Dansereau and Bergeron 1993). Using this precise information on time since last fire, we selected permanent study plots (20 to 40 ha) that covered the range of forest cover types from deciduous stands often dominated by trembling aspen (*Populus tremuloides*) and white birch to mixedwood and coniferous stands where these intolerant tree species are gradually replaced by conifers such as white spruce, balsam fir and white cedar (Bergeron and Harvey 1997). These changes in composition and structure along time since disturbance considerably reduce the abundance of trembling aspen, a tree species known to be strongly selected by primary excavators in mixedwood forests of western North America (Dobkin et al. 1995, Aitken and Martin 2004, Martin et al. 2004, Savignac and Machtans 2006, Cooke 2009). Likewise, changes in tree species composition of forest cover types lead, however, to a higher diversity of nesting tree substrates that could increase and affect the nest web structure of cavity assemblages in older forests. The interactions between cavity nesting species and the structure of the cavity nesting community within nest webs are also likely to be affected by the change in composition and structure along the age gradient of naturally disturbed boreal mixedwood forests. Quantification of network properties allows comparisons of nest web structure in different forest cover types (Blanc and Walters 2007).

In this paper, we document and compare how the change in nest tree availability influences the nest web structure by looking at (1) nest tree occupancy by excavating birds, (2) interspecific interactions between excavators and secondary users, (3) the cavity-providing role of excavators and (4) network characteristics of cavity nesting assemblages along an age gradient of naturally disturbed eastern North American boreal mixedwood forests.

3.2 Methods

3.2.1 Study area

This study was done in the boreal mixedwood forest of northern Quebec in the balsam fir-white birch bioclimatic domain, located in the northern Clay Belt of Quebec and Ontario. This region is characterized by clay soils and low rocky hills (Robitaille and Saucier 1998). The average annual temperature is 0.6 °C and the average total annual precipitation is 822.7 mm (Environment Canada 2008). The study site is located within the conservation area of the Lake Duparquet Research and Teaching Forest (LDRTF; at the southern fringe of the boreal forest in Québec (48°30' N, 79°22' W). The are spans ~2000 ha and contains a complex natural forest mosaic formed by different forest cover types and by a variety of natural disturbances (Harvey 1999). Fire history at the LDRTF is well documented (Bergeron 1991, Dansereau and Bergeron 1993) and includes eight major fires that have occurred over the last three centuries. Young and mature forests are dominated by early succession tree species: paper birch (*Betula papyrifera*), trembling aspen and jack pine (*Pinus banksiana*). In our study area, trembling aspen and white birch mostly dominated these stands; hence they were named "decidous forests". Old forests ("mixedwood forests") are characterized by mixed stands where balsam fir (*Abies balsamea*), black spruce (*Picea mariana*) and white spruce (*Picea glauca*) share the forest canopy with the deciduous species. Old-growth stands ("conifer old-growth forests") are dominated by coniferous species where the white cedar (*Thuja occidentalis*) becomes more abundant (Bergeron and Harvey 1997, Harvey et al. 2002). Over the last century, the balsam fir-dominated stands were severely affected by three spruce budworm outbreaks, the most recent being between 1970 and 1987 (Morin et al. 1993). These outbreaks reduced the abundance of large balsam firs, killing as much as 75% of firs of more than 15 cm in DBH in the study area (Bergeron et al. 1995).

3.2.2 Field methods

Between 2003 and 2010, we collected data on cavity nesters in 12 sampling plots ranging from 24 to 40 ha in size (totalizing 448 ha). The time since the last fire was calculated using 2005 as a point of reference, and ranged from 61 to 245 years. Forests younger than 150 years after fire disturbance were joined to represent the deciduous and mixedwood forests and forests older than 150 years after fire disturbance were joined to represent the conifer old-growth forests. This grouping was done in order to examine the impact of the deciduous to coniferous change in canopy dominance, which might play an important role in the structure of the cavity nesting community, and to increase nest sample sizes in order to enable the comparison of network characteristics.

In each sampling plot, rectangular shaped vegetation-sampling stations measuring 600 m^2 (10 m X 60 m) were distributed 200 m apart in each plot (112 in total). Six of them were located on rocky cliffs and were not used in analyses in order to limit the variation in the vegetation data. Three variables were used to characterize the available trees: tree species, decay stage and diameter at breast height (DBH). The vegetation-sampling plots were sampled in 2005 and all trees having a DBH greater than 10 cm were characterized. Tree decay was classified based on visual appearance in 5 categories according to a modified version of Maser et al. (1979) (Nappi 2009): Decay 1 (alive, >20% foliage); Decay 2 (declining, <20% foliage); Decay 3 (recently dead, hard wood, firm bark cover); Decay 4 (moderate degradation, soft wood, no dead foliage present, no small twigs, some branches remaining, usually intact top); Decay 5 (high degradation, soft decomposed wood, very few branches, often broken top).

This study is based on data compiled from studies on cavity nesters, which took place between 2003 and 2010 in the study site and in the surrounding areas. Nest search effort and data collection protocols varied between years but were relatively constant between plots sampled. Nest searches were conducted between the beginning of May and the middle of July, from sunrise to 14h00 under adequate conditions, without significant rain or wind >20km/h. Observers walked along transects and used visual and auditory cues that would indicate the presence of an occupied cavity: breeding-bird behavior, begging nestlings or wood chips on the ground. Also, trees containing cavities were tapped to detect occupants. From mid-May to early July in 2003 and 2004, data on cavity nesters were collected as part of a study on the foraging ecology of woodpeckers (Nappi 2009), which consisted of surveying transects with 100 m buffers on each side covering 224 ha in the deciduous and mixedwood forests and 220 ha in the conifer old-growth forests. In 2005, data on cavity nesters was collected in all the plots covering 224 ha in the deciduous and mixedwood forests and 220 ha in the conifer old-growth forests. In 2009 data was collected on transects having a buffer zone of 50 m on each side to increase the detection power of active nests. The nest search covered 180 ha in both forest type covers. All trees with occupied cavities were marked with an aluminum tag and geo-referenced. When possible, the excavator of the cavity was visually identified. If no excavator was present at the site, we identified the excavator with the size and characteristics of the cavity. If there was a doubt, the excavator remained unidentified. These cavities were then inspected with a camera mounted on a telescopic pole

(TreeTop Peeper$^{(tm)}$, Sandpiper Technologies, Manteca, California) to determine the state of the cavity: non-completed excavation, suitable cavity or occupied cavity. A cavity was considered "occupied" if it contained at least one egg or nestling (Martin et al. 2004), or if a mammal was inside the cavity. For nests that were not accessible with the telescopic pole and camera (higher than 15.24 m) and for nests that were in cavities with an opening too small for the camera (ex: some of the Red-breasted Nuthatch nests), we used nesting clues (behavior of adult cavity nesters) to confirm the state of the cavity. In addition, nests discovered during other studies or found by chance within a continuous boreal mixedwood forest setting, but outside the sampling plots, were also characterized and geo-referenced.

In order to increase the detection of cavity nesters that reuse cavities, which can be more elusive, inspections of existing cavities were done at least once a year from 2008 to 2010. Since it would have been too difficult to visit every cavity found, a selection of cavities to inspect was made by taking into consideration the origin of the cavity (excavated or non-excavated and excavator species) and the amount of field effort required to inspect the cavity (height of the cavity and access distance).

To further investigate the importance of large cavities for cavity nesters, all large cavities visually detected during the 2009 nest search were subsequently inspected with a camera on a telescopic pole. Large cavities were defined as being cavities excavated by the Northern Flicker, the Pileated Woodpecker or natural cavities (non-excavated) that were of greater or equal size.

3.3 Statistical analyses

3.3.1 Characterization of forest cover types

Descriptive statistics were compiled to characterize the different forest cover types along the age gradient. All normally distributed habitat variables were tested using one-way ANOVAs with mixed models and a Tukey HSD test for multiple comparisons. Non-normally distributed variables were $\log_{10}$ transformed to fit the requirements or were analyzed with a Kruskal-Wallis test. A significance level of $\alpha = 0.05$ was used in all tests. The variable *plot* was added in the mixed models in order to account for the hierarchical structure of the sampling design. The basal area was first averaged at the vegetation sampling station.

3.3.2 Keystone excavator species

In order to identify potential keystones excavators we 1) compared the cavities provided by each excavator species that were reused by other cavity nester species and 2) took into account the nesting abundance of each excavator species (Blanc and Walters 2008). To quantify the cavity-providing importance of each excavator, a ratio of reused cavity was calculated. The amount of cavities excavated by the excavator and reused by other species was divided by the total amount of reused cavities excavated by all excavators (((E - N) / Total cavity reuse) * 100), where N is the number of nests found and E is the number of excavated cavities that were used by the excavator and by other cavity nesters. A negative ratio meant that the excavator species reused more cavities excavated by other excavators than it provided cavities to the community.

3.3.3 Nest web characteristics

Cavity nesting community characteristics were described and compared along the age gradient using two perspectives: interactions at the species level and network characteristics at the community level.

Nest webs were constructed using only nests for which the excavator and the tree species were identified. These nests include reuse of cavities. At the species level, the interactions between species and the strength of these interactions are described and compared for the complete boreal mixedwood nest web and along the age gradient using two nest webs representing the deciduous and mixedwood forests and the conifer old-growth forests. The complete boreal mixedwood nest web (CBM) was created as a reference for the complexity and diversity of the cavity nesting community at the forest scale. It is composed of all the nest data that were collected in the sampling plots and its surroundings (in a continuous boreal mixedwood forest setting) from 2003 to 2010. The deciduous and mixedwood and the conifer old-growth nest webs were constructed using only nests found in the study site and during years of similar nest search effort (2003-2005 and 2009). At the community level, quantitative aspects were characterized by species richness, number of links, mean link strength and nest to link ratio. The number of links was calculated by summing all connections between species in the nest web but did not include links between natural cavities and tree species. Linkage strength was calculated separately for two levels: the tree to excavator level and the cavity reuse level. The linkage strength between a tree species and an excavator was defined as the proportion of an excavator's nests located in a tree species. The linkage strength for cavity reuse by SCN, WPCN or PCN was calculated as the proportion of total nests located in cavities not excavated by the species in question. Mean nest web link strengths were calculated using links between species that had a sufficient sample size ($n >= 3$).

3.4 Results

3.4.1 Characterization of forest cover types

Aspen, white birch, balsam fir and white cedar dominated the landscape across forest cover types (Figure 3.1). Along the age gradient, forest vegetation was found to follow a deciduous to coniferous forest cover transition. Conifer basal area and mean tree DBH increased along the age gradient, whereas deciduous basal area, aspen basal area and dead aspen basal area decreased (Table 3.1). In the case of total basal area, total dead basal area and mean aspen DBH, no significant differences were found (Table 3.1).

3.4.2 Importance of large cavities

Large suitable cavities were rare in the study site, as only 65 were found in ~360 ha during the 2009 nest search. The majority of large cavities and all large reused cavities were excavated (Table 3.2). There seemed to be a preference for the cavities made by the Pileated Woodpecker's cavities, as 38% of cavities created by this excavator were occupied by other cavity nesting species. In comparison, only 7% of the Northern Flicker's cavities were reused by other cavity nesting species (Table 3.2).

3.4.3 Nest webs

The complete boreal mixedwood nest web (CBM) contained 357 nests and is illustrated in (Figure 3.2A). The D&M nest web contained 167 nests and represents 47% of nests contained in the CBM (Figure 3.2B; Table 3.2). The COG nest web had 101 nests and represented 28% of nests contained in the CBM (Figure 3.2C; Table 3.2). The CBM had more nests than the D&M and COG combined because, unlike the others, it included all nests found from 2003 to 2010. The D&M and COG only contain nests found in years where a similar search effort was made in the field (2003-2005 and 2009).

All excavators had strong links with the trembling aspen. It was a key species for nesting, harboring 95% of nests despite its low availability in old forests (Figure 3.1). The second most excavated tree species was the white birch. The excavator that used the most varied excavation substrate was the Red-breasted Nuthatch (*Sitta canadensis*), which has links with up to five tree species (Figure 3.2). All occupied natural cavities were in the trembling aspen (Figure 3.2). Natural cavities were rarely used; only two occupied natural cavities were found, one of which contained the only Common Grackle's (*Quiscalus quiscula*) nest found (Figure 3.2).

Most small-bodied SCN had strong links with the Yellow-bellied Sapsucker (*Sphyrapicus varius*) cavities (Figure 3.2). This species was the dominant excavator with the highest relative nest abundance and was the supplier of numerous small cavities used by small-bodied SCN. However, the northern flying squirrel (*Glaucomys sabrinus*) also had medium links to the Downy Woodpecker (*Picoides pubescens*) cavities (Figure 3.2).

All of the large-bodied SCN had strong links with the Pileated Woodpecker cavities. The majority (83%) of Common Goldeneye (*Bucephala clangula*) nests and 86% of Northern Saw-Whet Owl (*Aegolius acadicus*) nests were in cavities excavated by the Pileated Woodpecker (Figure 3.2). In addition, the Northern Saw-Whet Owl and the Common Goldeneye had medium links to the Northern Flicker cavities (Figure 3.2). Overall, large-bodied SCN reused almost exclusively Pileated Woodpecker cavities (Figure 3.2). The Pileated Woodpecker was a keystone excavator because it provided the greatest proportion of cavities used by other cavity nesting species relative to its nesting abundance (Figure 3.3). More than one third of reused cavities were excavated by the Pileated Woodpecker despite its low relative nest abundance (< 2%; Figure 3.3).

Cavity reuse was observed in almost every excavating species (> 10), but not with the Hairy Woodpecker (*Picoides villosus*) or the Pileated Woodpecker. The Red-breasted Nuthatch was the excavator with the highest proportion of nests in cavities excavated by another excavator species (13%). This species had an intermediate link with Downy Woodpecker cavities (Figure 3.2). Two nests of this species were found in Downy Woodpecker's cavities that had been used by this excavator the same year.

Overall, the D&M and COG were similar; they had a similar strong link pattern and they shared the same excavator species (Figure 3.2). All excavators had a strong link with the trembling aspen. The small-bodied secondary cavity users had strong links with the Yellow-bellied Sapsucker cavities, except in the COG where they seemed to use wider cavity resources. All large-bodied SCN had strong links with the Pileated Woodpecker cavities. In both nest webs the Northern Flicker had medium links with the Pileated Woodpecker cavities. The two cavity nesting communities shared a similar relative abundance of excavator species (Figure 3.3A). The Yellow-bellied Sapsucker was the dominant excavator with ~60% of nests found.

The cavity nesting network complexity seemed to increase along the age gradient (Table 3.3). Complexity properties of networks, such as species richness, number of links, mean link strength and nest to link ratio increased as the forest age increased (Table 3.3). Despite the fact that we found 40% fewer nests in the COG than in the D&M, this nest web had more links (26 vs 20) and more species (17 vs 13, including tree species) (Table 3.3).

3.5 Discussion

Nest web studies are important to detect potentially critical interactions for species that use tree cavities, as identification of keystone or umbrella species is needed to guide forest management and conservation efforts. In the last decade, there has been an increase of interest in interactions and connections in cavity nesters studies (Bednarz et al. 2004, Blanc and Walters 2007), for they are at the core of the nest web concept. On a more fundamental note, interactions may have gained importance in a long-lasting ecological debate relating diversity with ecological stability (MacArthur 1955, May 1973, McCann 2000). In recent years, it has been proposed that the relationship between diversity and stability would be better explained with direct analyses of interactions between species than by the broad measure of species richness (McCann 2000). The comparison of nest web characteristics allows us to weigh the influence of forest composition and structure on the functional structure of cavity nesting assemblages.

Our study provides the first comparison of nest webs along a natural forest age and compositional gradient. The nest web analysis allowed us to detect fine-scale differences and intricacies in the cavity nester assemblage along the age gradient. Cavity nesting assemblages remained similar throughout forest cover changes. However, despite a lower abundance of nests, we found a greater complexity in the conifer old-growth nest web. Throughout this gradient, we found a cavity nesting community mainly structured around trembling aspen, Yellow-bellied Sapsucker and Pileated Woodpecker.

To date, numerous studies have shown that cavity-nesting assemblages are strongly linked to trembling aspen in ecosystems where this tree species is naturally present (Li and Martin 1991, Dobkin et al. 1995, Martin et al. 2004, Cooke 2009). Our study reflected this key association, as 95% of nests were in trembling aspen despite its decreasing availability along our age gradient. Also, excavators played an essential role in providing cavities to secondary cavity nesters. As in other studies in North America (Martin et al. 2004, Blanc and Walters 2008, Cooke 2009), natural cavities did not seem to play an important role in this cavity nesting assemblage, harboring less than 1% of nests.

Over the course of numerous studies on cavity nesters, an important pattern has emerged: only one or sometimes two excavator species provide the bulk of reused cavities (Aitken et al. 2002, Bednarz et al. 2004, Blanc and Walters 2008). Studies in various ecosystems have shown that large cavity-providing species such as the Northern Flicker and the Pileated Woodpecker are often identified as keystone excavators, providing cavities for multiple secondary cavity nesters (Martin et al. 2004, Blanc and Walters 2008, Cooke 2009). In our study site, large suitable cavities were a rare (0.2 cavities/ha), but prized, resource. The cavity density for both large-cavity excavators was very similar. However, there was a strong preference for the Pileated Woodpecker's cavities. The majority of cavities reused by large-bodied SCN, and more than one third of all observed reused cavities were excavated by this species. In this study, we show that the Northern Flicker is not an important cavity-providing species in continuous eastern North American boreal mixedwood forests with low entropic disturbance. A lower presence of open woodland habitat, differences in secondary cavity nesters (SCN) species composition and lower availability of large degraded aspen may explain why this excavator's role differed in our system compared to what was found in western Canadian studies. First, most of SCN identified as having strong links with the Northern Flicker in western Canadian studies are open woodland habitat species: Tree Swallow (*Tachycineta bicolor*), European Starling (*Sturnus vulgaris*), Mountain Bluebird (*Sialia currucoides*) and American Kestrel (*Falco sparverius*). Most of these species are commonly found in the studied region but not in our continuous forest plots setting. Second, slight differences in SCN species composition have a big impact on the structure of the community. The Bufflehead (*Bucephala albeola*), a small-sized *Anatidae* (half the weight of the Common Goldeneye and Barrow's Goldeneye (*Bucephala islandica*), was identified in studies by Cooke (2009) and Martin et al. (2004) as having strong links with Northern Flicker cavities. This species is commonly found in some parts of western Canadian forests (Gauthier 1993) but is uncommon in our study region (Gauthier and Aubry 1995). Finally, the functional roles of cavity-providing species might also be influenced by the availability of excavation substrates. The Northern Flicker is not a strong excavator and tends to excavate its cavities in soft degraded wood (Martin et al. 2004). However, the availability of large degraded aspen was low in the continuous boreal mixedwood forests. The majority of available aspen trees were alive (76%) and only 17% of available aspens of more than 20 cm in DBH were dead or dying.

In our natural continuous boreal mixedwood study sites, the Northern Flicker cavity-providing role was unimportant. It became an important species in remnant habitats (riparian buffers and cutblock separators) in managed forest landscapes nearby (Ouellet-Lapointe 2010). On the other hand, excavators that had the ability to excavate in live aspens were the most influential in providing cavities. The cavities of live tree excavators such as the Yellow-bellied Sapsucker and the Pileated Woodpecker were the most reused. These two species created over 57% of all cavities used, and 78% of cavities reused by SCN. In fact, a majority of SCN nests were in live aspen trees (64% of nests). The Yellow-bellied Sapsucker was the dominant excavator with the highest relative nest abundance. While it plays an important role in supplying cavities used by small-bodied SCN, this excavator was not considered a keystone excavator. Its importance was not disproportional to the abundance of its cavities in the environment. Because it provided the greatest proportion of cavities used by other cavity nesting species relative to its low relative nesting abundance, the Pileated Woodpecker was found to be a keystone excavator and it maintained its status across the natural time since fire age gradient. A number of studies have also found this species to be a keystone excavator (Bonar 2000, Aubry and Raley 2002b, Martin et al. 2004, Cooke 2009), but to our knowledge this is the first time the functional role of this species has been confirmed across a mature to old forest age gradient.

3.5.1 Nest webs along the age gradient

Even though aspen was significantly less abundant in conifer old-growth forests, this tree species was still the main nest tree and contributed to the persistence of a complex cavity nesting assemblage. The functional structure of cavity nesting assemblages remained similar along the age and forest compositional gradient. In both mature and in old-growth forests, the trembling aspen, Yellow-bellied Sapsucker and Pileated Woodpecker were important species that structured the community of cavity nesters in boreal mixedwood forests.

Nest web complexity was, however, higher in older forests. Despite having 40% fewer nests, it had a higher number of links, lower mean link strength and greater species richness. This greater complexity is partially accounted for by tree species use diversification by cavity excavators. Indeed, the aspen and dead aspen availability decreased along the succession, coinciding with the increase in the number of links with other tree species. Hence, almost all excavators ($n > 3$) had at least one more link with other tree species in the conifer old-growth forests. Accordingly, the mean link strength was lower (although not significant) in the conifer old-growth nest web, indicating the use of a greater diversity of cavity resources. Although the abundance of nests was lower in conifer old-growth forests, this habitat might support a greater diversity of cavity nesting species. On the other hand, the differences in complexity were subtle and more research is needed in order to further understand the role of old-growth boreal mixedwood forests for cavity nesting communities.

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3.7 Figures

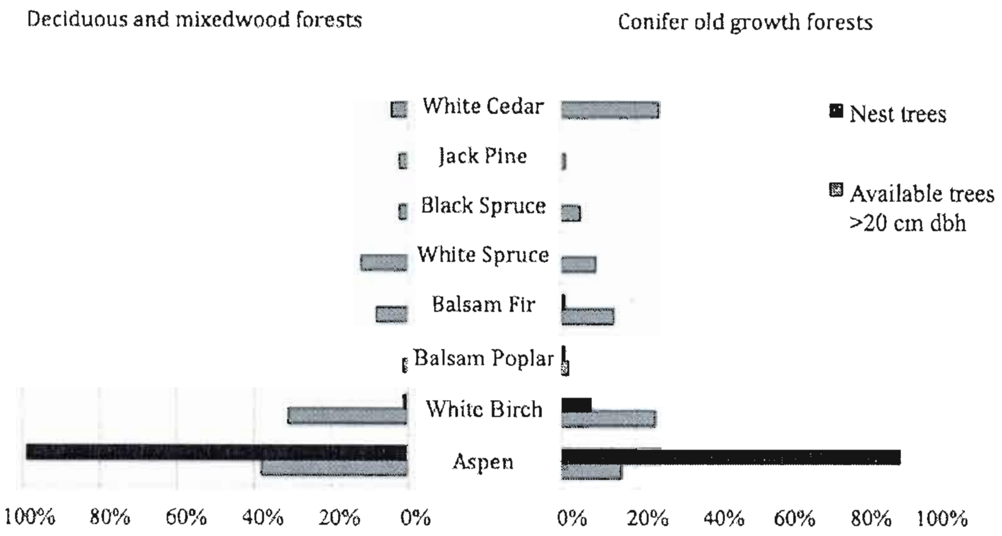
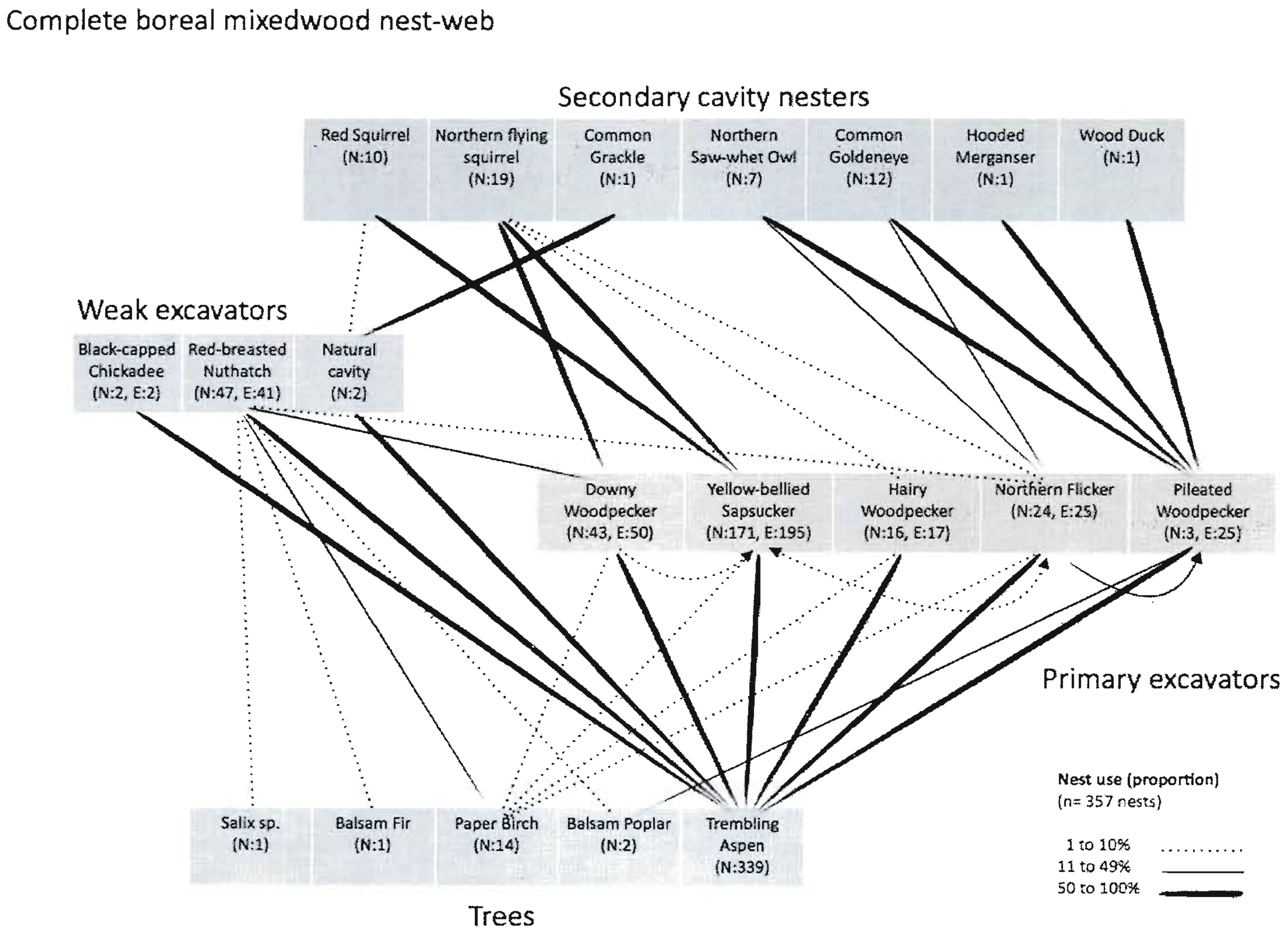


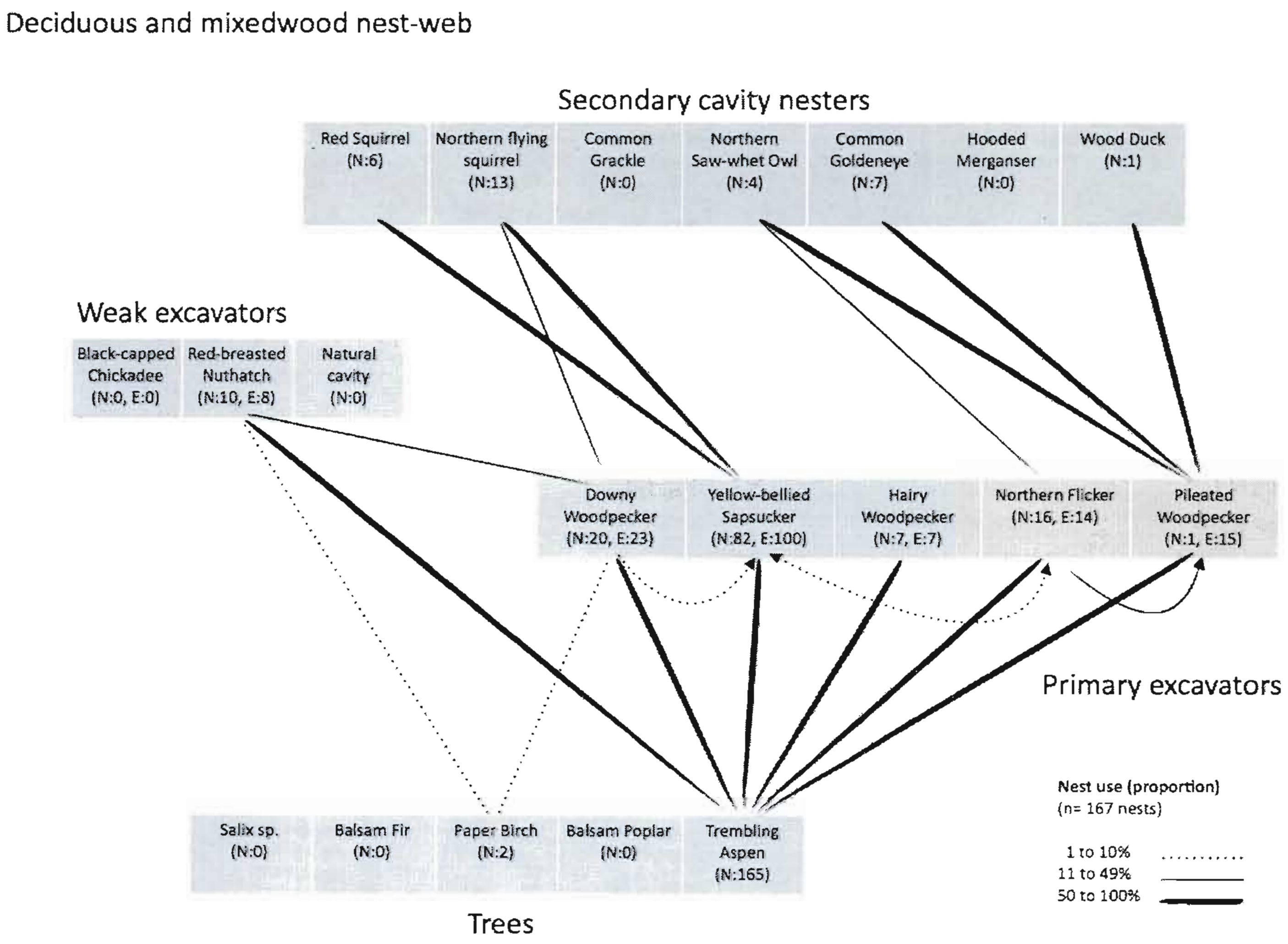
Figure 3.1: Nest tree use in relation with available trees species >20 cm DBH in the deciduous and mixedwood forests and in the conifer old-growth forests.

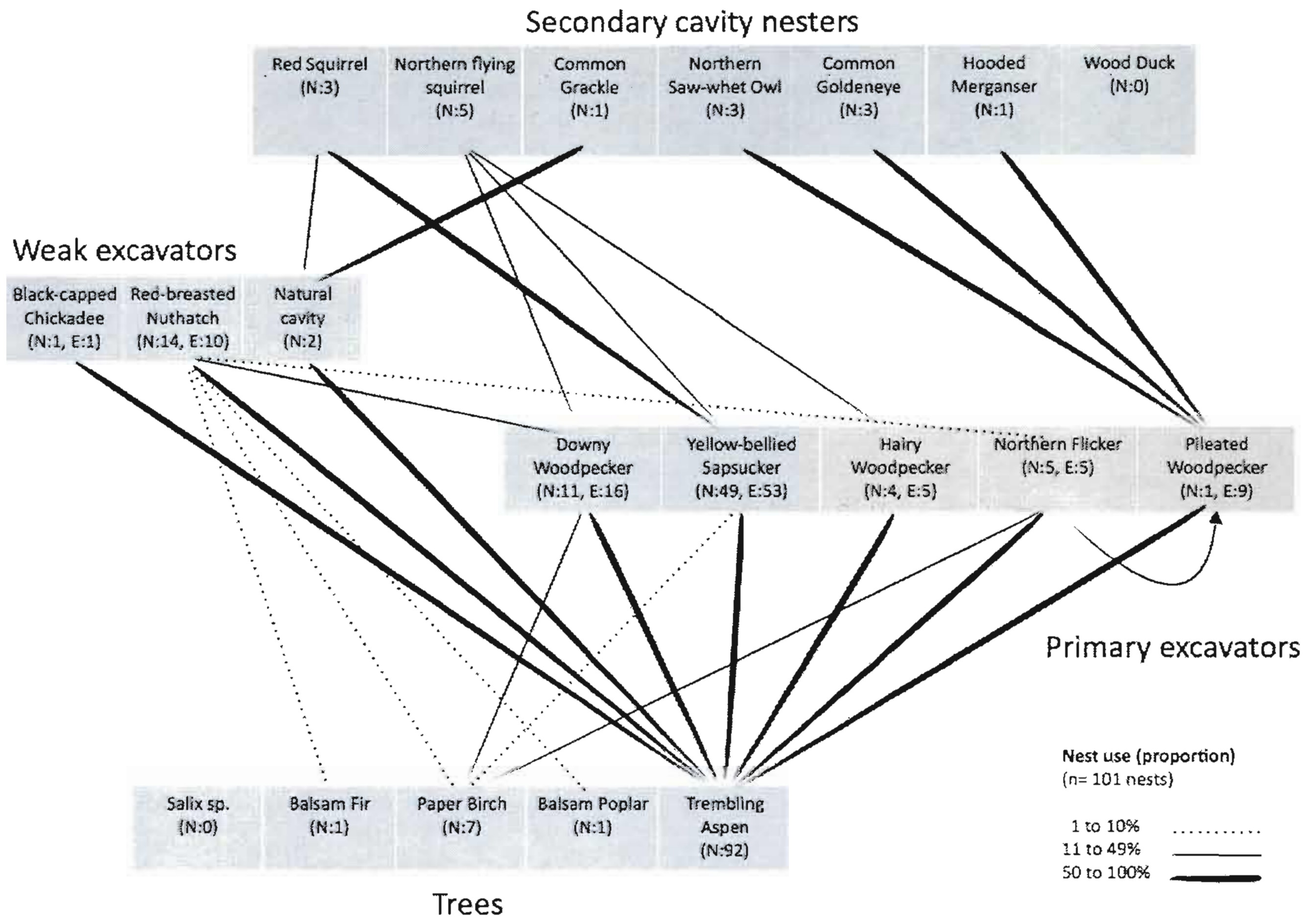
Figure 3.2: A) Complete boreal mixedwood nest web, B) Deciduous and mixedwood nest web and C) Conifer old-growth nest web in Abitibi, Québec. Nest data were collected from 2003 to 2010. Lines between species represent the use of cavity resource. N is the number of nests found and E is the number of excavated cavities that were used by the excavator and by other cavity nesters. Links between the excavator level and the tree level represent the proportion of nests found in the tree species and the links between secondary cavity nesters, excavators and natural cavities represent the proportion of nests found in reused cavities.

A.


Complete boreal mixedwood nest-web
Secondary cavity nesters
Red Squirrel (N:10)
Northern flying squirrel (N:19)
Common Grackle (N:1)
Northern Saw-whet Owl (N:7)
Common Goldeneye (N:12)
Hooded Merganser (N:1)
Wood Duck (N:1)
Weak excavators
Black-capped Chickadee (N:2, E:2)
Red-breasted Nuthatch (N:47, E:41)
Natural cavity (N:2)
Downy Woodpecker (N:43, E:50)
Yellow-bellied Sapsucker (N:171, E:195)
Hairy Woodpecker (N:16, E:17)
Northern Flicker (N:24, E:25)
Pileated Woodpecker (N:3, E:25)
Primary excavators
Salix sp. (N:1)
Balsam Fir (N:1)
Paper Birch (N:14)
Balsam Poplar (N:2)
Trembling Aspen (N:339)
Trees
Nest use (proportion)
(n= 357 nests)
1 to 10%
11 to 49%
50 to 100%

B.

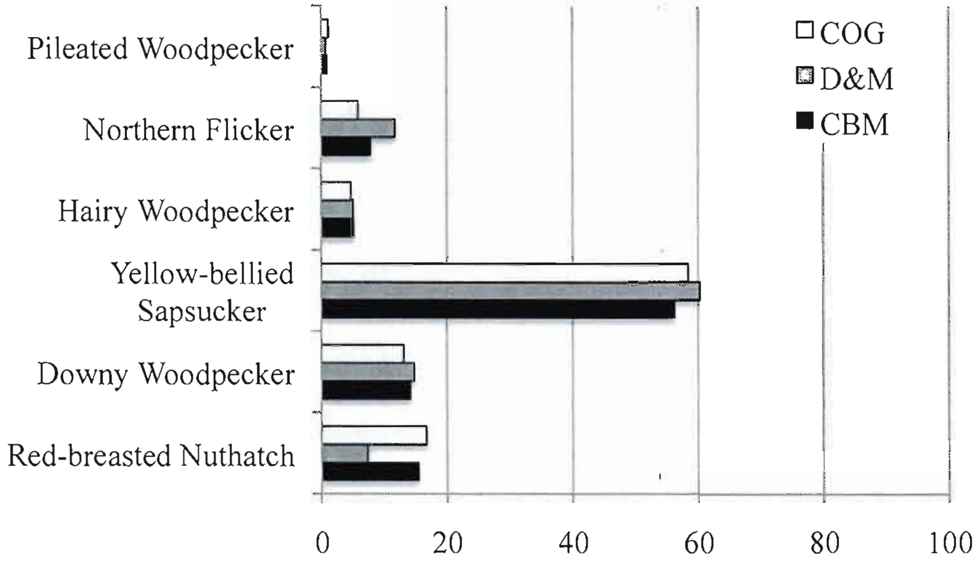

Deciduous and mixedwood nest-web
Secondary cavity nesters
Red Squirrel (N:6)
Northern flying squirrel (N:13)
Common Grackle (N:0)
Northern Saw-whet Owl (N:4)
Common Goldeneye (N:7)
Hooded Merganser (N:0)
Wood Duck (N:1)
Weak excavators
Black-capped Chickadee (N:0, E:0)
Red-breasted Nuthatch (N:10, E:8)
Natural cavity (N:0)
Downy Woodpecker (N:20, E:23)
Yellow-bellied Sapsucker (N:82, E:100)
Hairy Woodpecker (N:7, E:7)
Northern Flicker (N:16, E:14)
Pileated Woodpecker (N:1, E:15)
Primary excavators
Nest use (proportion)
(n= 167 nests)
1 to 10%
11 to 49%
50 to 100%
Salix sp. (N:0)
Balsam Fir (N:0)
Paper Birch (N:2)
Balsam Poplar (N:0)
Trembling Aspen (N:165)
Trees



Conifer old-growth nest-web

C.

A.



B.

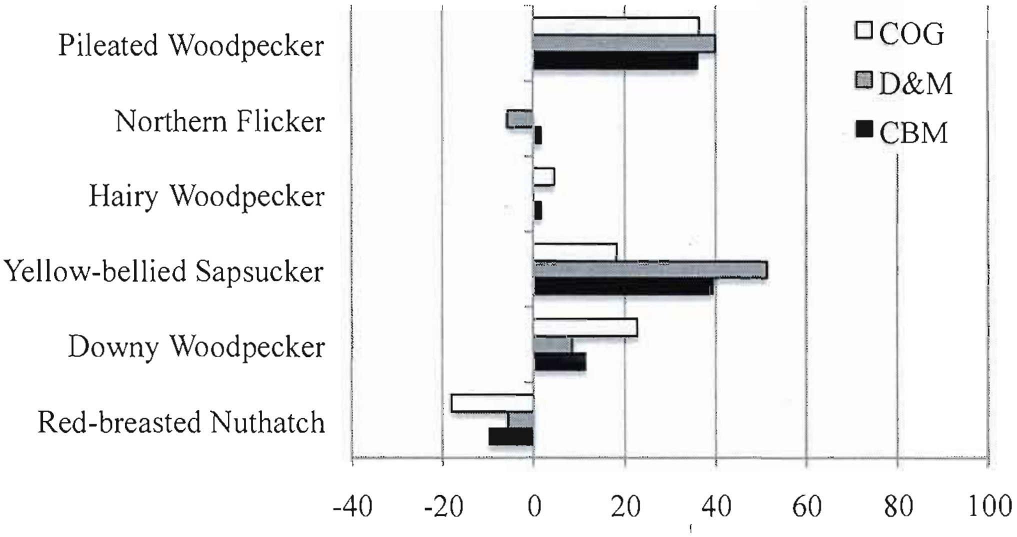


Figure 3.3: Relative excavator nest abundance (A) and proportion of reused cavities excavated (B). In B, the ratio of reused cavities was calculated using the total amount of the excavator's nests divided by the total amount of nests of all species found in cavities excavated by this excavator. A negative ratio meant that the excavator species reused more cavities excavated by other excavators than it provided to the community.

3.7 Tables

Table 3.1: Habitat characteristics for the four forest age categories: mature to old-growth forests, at the Lake Duparquet Research and Teaching Forest in Abitibi, Québec. The data was collected in July of 2005. In parentheses, *n* is the number of plots of 0.06 ha sampled. Levels not connected by the same letter are significantly different (Tukey HSD test, $\alpha < 0.05$).

Variable	61-89 years (n=26)	135 years (n=30)	182-208 years (n=26)	245 years (n=30)	*P*
Total basal area	29.9 ±10.6	32.5 ±8.2	27.5 ±7.7	33.0 ±12.4	0.45
Total dead tree basal area	4.6 ±3.1	6.6 ±3.2	6.0 ±3.0	7.8 ±3.3	0.26
Coniferous tree basal area	7.3 ±6.1 (B)	14.2 ±5.3 (B)	13.5 ±6.8 (B)	21.5 ±11.8 (A)	0.001*
Deciduous tree basal area	22.6 ±9.5 (A)	18.3 ±7.9 (AB)	14.0 ±7.6 (AB)	11.6 ±7.2 (B)	0.03*
Aspen basal area	13.3 ±10.2 (A)	10.7 ±6.9 (AB)	10.3 ±7.1 (AB)	8.5 ±6.1 (B)	0.04*
Dead aspen basal area	3.3 ±3.1 (A)	2.6 ±2.3 (AB)	1.7 ±1.2 (AB)	1.5 ±1.1 (B)	0.02*
Mean tree DBH (SD)	17.4 ±2.4 (B)	19.8 ±2.6 (AB)	20.2 ±3.3 (AB)	21.8 ±3.3 (A)	0.01*
Mean aspen DBH (SD)	25.3 ±7.4	23.4 ±7.8	30.9 ±11.1	34.3 ±12.5	0.25

Table 3.2: Large cavity survey and systematic inspections done at Lake Duparquet Research and Teaching Forest in Abitibi, Québec in 2009.

	Natural cavities	Northern Flicker cavities	Pileated Woodpecker cavities	Total
Cavities visually detected during nest search	14	45	92	151
Suitable cavities	4	29	32	65
Number of cavities used by SCN	0	2	12	14
Proportion of cavities used by SCN (%)	0	7	38	22

Table 3.3: Networks characteristics of the Complete boreal mixedwood, the Deciduous and mixedwood and the Conifer old-growth nest webs.

	Complete boreal mixedwood	Deciduous & mixedwood	Conifer old-growth	*P*
Sample size	357	167	101	
Tree species	5	2	4	
Cavity nesting species	14	11	12	
Links	35	20	26	
Strong links	13	11	12	
Medium links	7	5	9	
Weak links	13	4	5	
Mean link strength	40	61	51	0.37
Link strength between Excavators and Trees	50	81	56	0.21
Nests to links ratio	0.10	0.12	0.27	

CONCLUSION GÉNÉRALE

Cette étude montre que les peupliers faux-tremble de grand diamètre sénescents et morts sont une ressource essentielle pour la faune cavicole tout au long du vieillissement de la forêt boréale mixte. Tous les excavateurs ont sélectionné ce substrat d'excavation de qualité, malgré une baisse de disponibilité de celui-ci au long du gradient d'âge. Suivant cette baisse de disponibilité, l'abondance des nids d'excavateurs de cavités était plus basse dans les forêts anciennes (182 à 245 ans). Cependant, le réseau formé par les utilisateurs de cavités y était plus complexe.

Dans ce mémoire, nous avons caractérisé la dynamique de la faune cavicole le long d'un gradient de temps depuis le dernier feu en forêt boréale mixte. Dans le deuxième chapitre, nous avons déterminé les caractéristiques des arbres de nidification utilisés et sélectionnés par les oiseaux excavateurs, ainsi que la plasticité de cette utilisation et sélection au long d'un gradient d'âge. Dans le deuxième volet, nous avons documenté la structure fonctionnelle des réseaux d'utilisateurs de cavités, identifié les espèces « clé de voûte » du système, et comparé la structure fonctionnelle des forêts décidues et mixtes à celle des forêts anciennes avec une analyse de réseaux.

4.1 Sélection d'arbres de nidification par les oiseaux excavateurs

Tous les oiseaux excavateurs de cavités ont fortement sélectionné le peuplier faux-tremble de grand diamètre sénescent ou mort. Le peuplier faux tremble était l'essence utilisée pour 95 % des nidifications, le bouleau à papier fut la deuxième essence la plus utilisée pour moins de 3 % des nidifications. Les excavateurs ayant un faible pouvoir d'excavation ont sélectionné les arbres morts et les excavateurs ayant une forte capacité d'excavation ont utilisé en majorité les arbres vivants. Par contre, le Pic flamboyant se démarque en utilisant autant des arbres vivants que morts. Bien que l'état de dégradation des arbres utilisés diffère selon les espèces excavatrices, une caractéristique importante commune à la majorité des arbres de nidification des excavateurs de bois vivant et des excavateurs de bois mort est la présence de signes d'infections fongiques et, plus précisément, des carpophores du champigon Phellinus tremulae indiquant la carie blanche. En effet, presque toutes les cavités creusées dans le tremble vivant et plus de la moitié des cavités excavées dans le tremble mort étaient infectées par Phellinus tremulae. Ce champignon pourrit le bois du cœur de l'arbre lorsque celui-ci est encore vivant et facilite grandement l'excavation par les pics (Basham 1991, Hart et Hart 2001, Jackson et Jackson 2004). Tous les excavateurs ont sélectionné les arbres de grand diamètre. La taille moyenne des arbres de nidification a augmenté en fonction de la taille des excavateurs. La Sittelle à poitrine rousse (Sitta canadensis) et le Pic mineur (Picoides pubescens) utilisent les arbres de plus petits diamètres (moyenne de 29 cm), tandis que le Grand Pic utilise les plus grands (moyenne de 45 cm). Cependant, il est important de rappeler que même les plus petits excavateurs utilisaient des arbres dont le diamètre dépassait le diamètre moyen des arbres disponibles.

4.2 Les réseaux d'utilisateurs de cavités

Le réseau d'utilisateurs de cavités pour la forêt boréale mixte de l'ouest du Québec est composé de cinq excavateurs primaires, de deux excavateurs faibles et de sept utilisateurs secondaires. Cette communauté est principalement structurée autour de trois espèces : le peuplier faux-tremble, le Pic maculé (Sphyrapicus varius) et le Grand Pic. Le peuplier faux-tremble est l'essence d'arbre clé de ce système, portant 95 % des cavités de nidification malgré sa faible disponibilité dans l'environnement (29 %). La presque totalité (99 %) des cavités réutilisées fut excavée (comparée aux cavités provenant de la dégradation de l'arbre). Le Pic maculé et le Grand Pic sont responsables pour l'excavation de 58 % de toutes les cavités utilisées et de 78 % des cavités réutilisées par les utilisateurs secondaires. Le Pic maculé est l'excavateur dominant et joue un rôle important en fournissant des cavités qui sont réutilisées par les petits utilisateurs secondaires. Cela dit, son influence n'est pas disproportionnée à son abondance relative. Le Grand Pic, n'ayant qu'une très faible abondance relative, fournit des cavités de grande taille qui sont réutilisées par les utilisateurs secondaires de grande taille. Vu sa faible abondance relative et le fort taux de réutilisation de ses cavités, le Grand Pic a été désigné comme une espèce clé de voûte. Le Pic flamboyant n'est pas un pourvoyeur important de cavités pour la communauté cavicole de la forêt boréale mixte continue. Ce résultat diffère des autres études sur les réseaux d'utilisateurs de cavités effectuées principalement en milieux ouverts ou incorporant des sections de forêts aménagées (Martin et al. 2004, Blanc et Walters 2008, Cooke 2009).

4.3 La dynamique de la faune cavicole le long d'un gradient d'âge en forêt boréale mixte

La sélection d'arbres de nidification et la structure fonctionnelle des réseaux d'utilisateurs de cavités sont demeurées très semblables le long du gradient de temps depuis le dernier feu. Cependant, un nombre plus élevé de nids d'oiseaux excavateurs ont été trouvés dans les forêts mixtes, l'abondance des nids présentant une distribution modale le long du gradient d'âge. Nous émettons l'hypothèse que cette distribution est associée, du moins en partie, à une variation dans la disponibilité du substrat d'excavation de qualité et associée, encore une fois en partie, à une plus grande disponibilité et diversité de substrats d'alimentation dans les forêts mixtes. En effet, les peupliers faux-trembles voient leur abondance relative diminuer des forêts décidues, aux forêts mixtes pour atteindre de très faibles valeurs dans les forêts résineuses anciennes. Toutefois, les diamètres des trembles sont en moyenne plus grands dans les forêts résineuses anciennes. De plus, l'arrivée des conifères dans la voûte forestière est bénéfique et mène à une plus grande diversité de substrat d'alimentation.

La plasticité de l'utilisation et de la sélection des arbres de nidification peut être considérée faible, car l'utilisation et la sélection étaient semblables dans les trois différents couverts forestiers. Cependant, certaines tendances ont été notées. Les excavateurs d'arbres vivants (Pic maculé et Pic chevelus) avaient de plus grandes probabilités de sélectionner un arbre à mesure que son diamètre augmente dans les forêts mixtes et dans les forêts âgées résineuses. Contrairement à ce qui prévalait dans les vieilles forêts, les excavateurs de bois vivant des forêts décidues ne semblaient pas sélectionner les plus gros peupliers.

Le long du gradient de temps depuis le dernier feu, les réseaux d'utilisateurs de cavités se partagent des types de liens forts semblables et ont les mêmes espèces d'excavateurs de cavités. Par contre, les réseaux d'utilisateurs de cavités des forêts anciennes sont plus complexes que ceux des forêts décidues et mixtes. En effet, malgré une plus faible abondance de nids (40 % de moins), les réseaux des forêts anciennes ont une plus grande diversité d'espèces, plus de liens et une force moyenne des liens plus faibles que ceux des forêts décidues et mixtes. La variation du substrat d'excavation de qualité en combinaison avec une plus grande diversité d'espèces et une plus grande abondance de bois mort sur pied pourrait expliquer une partie de la complexité accrue retrouvée dans le réseau des forêts anciennes.

4.4 Implications pour l'aménagement forestier

Cette étude montre l'importance de la présence de peupliers faux-trembles de grands diamètres sénescents ou morts et montrant des signes d'infection fongique tout le long du gradient d'âge allant de forêts décidues matures aux forêts conifériennes anciennes. Cette ressource est fortement sélectionnée par les oiseaux excavateurs et les utilisateurs secondaires ont des liens forts avec les cavités excavées par certains excavateurs, principalement le Grand Pic et le Pic maculé. Il est donc important que les gros peupliers faux-trembles infectés par *Phellinus tremulae,* ainsi que des peupliers en santé (> 20cm DHP) soient maintenus à la fois dans les habitats résiduels d'agglomérations de coupes ou dans des secteurs où des coupes partielles adaptées pour maintenir des attributs clés d'habitats, dont les arbres sénescents et morts.

Nous avons trouvé une distribution modale des cavités de nidification le long du gradient de temps depuis le dernier feu, les vieilles forêts décidues et mixtes étant les plus utilisées par les oiseaux excavateurs. En effet, la plupart des excavateurs de cavités en forêt boréale sont associés aux vieilles forêts (Imbeau et al. 2001, Drapeau et al. 2003, Savignac et Machtans 2006, Schieck et Song 2006, Cooke 2009). Quoique indispensables pour la présence d'oiseaux excavateurs reproducteurs, les arbres de nidification potentiels ne sont pas le seul facteur important dont il faut tenir compte. L'aménagement forestier doit aussi prendre en compte l'importance des arbres d'alimentation (Drapeau et al. 2009, Nappi 2009) pour ces oiseaux. Dans un contexte d'aménagement forestier où l'objectif principal consiste à récolter la forêt à rendement soutenu sur de courtes révolutions, les vieilles forêts décidues et mixtes ainsi que les forêts conifériennes anciennes sont graduellement remplacées par des forêts décidues jeunes et matures. Ceci ne laisse pas assez de temps 1) pour un vieillissement des arbres de nidification potentiels, afin qu'ils soient de grand diamètre et sénescents et 2) pour que les conifères occupent la canopée et fournissent une plus grande diversité de substrat d'alimentation.

Afin de rétablir un compromis entre les besoins de la faune cavicole et les besoins pour l'industrie forestière, nous suggérons la rétention de grands massifs forestiers représentant la variabilité naturelle anciennement retrouvée dans le paysage forestier. Une autre option serait l'introduction de coupes partielles, qui faciliterait la transition des peuplements décidues aux peuplements mixtes (Bergeron et Harvey 1997, Harvey et al. 2002).

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