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CHAPITRE 1 : INTRODUCTION GÉNÉRALE

Contexte général

L'entrée en vigueur de la Loi sur l'aménagement durable du territoire forestier (c. A-18.1, Gouvernement du Québec 2017) en avril 2013 a entraîné plusieurs nouvelles modalités de gestion de la ressource forestière au Québec. Ainsi, c'est en adoptant la Stratégie d'aménagement durable des forêts (SADF) que le nouveau régime forestier québécois vise, par le biais d'orientations et d'objectifs spécifiques, une gestion favorisant le maintien de la diversité biologique et la durabilité des écosystèmes (Ministère des Forêts de la Faune et des Parcs 2015).

L'exploitation forestière dans l'est de l'Amérique du Nord au cours des dernières décennies a causé un écart grandissant entre les paysages aménagés et naturels (Cyr *et al.* 2009; Boucher *et al.* 2016). Les écarts jugés les plus problématiques quant à leurs impacts potentiels sur les attributs écosystémiques (*p.ex.* structure et composition des peuplements, organisation spatiale) constituent alors des enjeux écologiques auxquels la SADF doit s'adresser (Grenon *et al.* 2010). Cette nouvelle démarche s'appuie donc plutôt sur des principes d'écologie forestière beaucoup plus inclusifs qu'une foresterie uniquement axée sur la récolte de la matière ligneuse (Gauthier *et al.* 2009).

Le concept établi afin de répondre aux cibles et objectifs de la SADF est l'aménagement écosystémique. Ce principe vise à diminuer l'écart entre la forêt naturelle et la forêt aménagée en s'inspirant, par exemple, de perturbations naturelles comme les feux de forêt, les épidémies d'insectes et les chablis. En respectant la plage de variabilité générée par les perturbations naturelles (*c.-à-d.* intervalle, taille, sévérité; voir Bergeron *et al.* 2007), on peut s'attendre à ce que les espèces de la forêt boréale soient plus susceptibles d'être résistantes et résilientes aux pratiques forestières, puisqu'on y conserve une gamme d'éléments auxquelles elles sont adaptées (Attiwill 1994; Landres *et al.* 1999; Drapeau *et al.* 2016). Ainsi, c'est lors du processus de planification que les aménagistes ont recours à des solutions concrètes afin d'appliquer les principes d'aménagement écosystémique et de bien prendre en considération les différents enjeux écologiques d'un territoire (Jetté *et al.* 2012a; Ministère des Forêts de la Faune et des Parcs 2014). La SADF stipule d'ailleurs que les principaux enjeux écologiques au Québec sont, notamment, les changements dans la structure d'âge des forêts, la simplification de la structure interne des peuplements, ainsi que la raréfaction de certaines formes de bois mort (Ministère des Forêts de la Faune et des Parcs 2015).

Dynamique naturelle du bois mort en forêt boréale Québécoise

La forêt boréale continue de l'est de l'Amérique du Nord se classifie selon deux domaines bioclimatiques, soit la sapinière à bouleau blanc et la pessière à mousse, qui sont caractérisées par la nature de la végétation de fin de succession (Saucier *et al.* 2009). Les régimes de perturbations naturelles sont les principaux éléments conditionnant la structure et les fonctions écologiques des forêts (White et Pickett 1985; Franklin *et al.* 2002), et sont également à l'origine de la production de certaines formes de bois mort (Harmon *et al.* 1986; Franklin *et al.* 2007; Angers 2009).

En sapinière à bouleau blanc, ce sont principalement les épidémies d'insectes, dont la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana*), qui influencent la dynamique du bois mort (MacLean 1980; Morin *et al.* 2007). Les feux de forêt couvrent de petites superficies et cela permet généralement aux peuplements d'excéder la longévité des espèces d'arbres présentes (Gauthier *et al.* 2009). En pessière à mousse, ce sont les feux de grande envergure qui influencent majoritairement la disponibilité du bois mort tandis que les agents de perturbations secondaires agissent plutôt en toile de fond (De Grandpré *et al.* 2000; Harper *et al.* 2002; Pham *et al.* 2004). En effet, en l'absence de perturbations majeures dans ces deux domaines bioclimatiques, ce sont les épidémies légères, les chablis, les agents pathogènes ainsi que la sénescence naturelle qui assurent un apport relativement constant en bois mort, favorisant alors une structure forestière inéquienne (Desponts *et al.* 2004; Aakala *et al.* 2007; St-Denis *et al.* 2010). Bien qu'elles affectent de plus petites superficies, ces perturbations partielles façonnent tout de même la composition en bois mort de façon importante à l'échelle du paysage (McCarthy 2001).

De plus, chaque arbre a le potentiel de passer par différents stades de décomposition suite à sa mort et ainsi de persister longtemps dans l'écosystème. Bien qu'il existe de nombreux systèmes de classification du bois mort (*p.ex.* Thomas 1979; Imbeau et Desrochers 2002), tous se basent sur l'aspect visuel de l'arbre (*p.ex.* présence et couleur du feuillage, présence de brindilles et d’écorce, rupture de la cime, port de l’arbre) et sur la densité de la matière ligneuse (Angers *et al.* 2012a). Ainsi, la décomposition du bois peut s’amorcer dès la mort d’une branche ou de l’arbre entier, au stade sénescent ou chicot, et s’accélérer une fois tombé au sol, sous forme de débris ligneux (Yatskov *et al.* 2003; Angers *et al.* 2012a).

De même, la quantité et le type de bois mort présent sur un territoire sont conjoncturels de nombreux facteurs, dont l’intensité et la prévalence des perturbations, le temps écoulé depuis la mort, ainsi que l’espèce d’arbre (Angers 2009). Par exemple, une épidémie ou un feu de grande intensité produira un fort apport momentané de bois mort (Nappi *et al.* 2011), tandis que des évènements de plus faible intensité entraineront une mortalité décalée dans le temps, qui se reflètera alors par des stades de dégradation variées (Vaillancourt 2008; Nappi *et al.* 2010). La dynamique de trouée, qui est omniprésente en vieille forêt boréale (Bergeron *et al.* 1998; Pham *et al.* 2004; St-Denis *et al.* 2010), assure également une disponibilité constante de tous les stades de décomposition de bois mort (Desponts *et al.* 2004; Aakala *et al.* 2008), en plus de favoriser la croissance des arbres, et donc de permettre la présence de gros chicots (Aakala *et al.* 2007; Vaillancourt *et al.* 2008).

En forêt boréale, les feuillus intolérants favorisent un développement rapide de structures de grandes tailles (*p.ex.* chicots, cavités naturelles, débris ligneux), puisque ces essences ont une croissance plus forte que les résineux et sont plus susceptibles d’être affectés par divers agents pathogènes (Darveau et Desrochers 2001; Martin *et al.* 2004; Angers 2009). Cependant, la présence de ces attributs ne permet pas de combler toutes les fonctions écologiques liées au bois mort en forêt boréale, car de nombreuses espèces dépendent plutôt du bois mort issu de résineux (Saint-Germain *et al.* 2007; Tremblay 2009). De plus, les chicots de feuillus se dégradent plus rapidement que ceux de résineux et ont ainsi un taux de chute plus élevé (Angers *et al.* 2010; Angers *et al.* 2012b). Par exemple, le temps médian entre la mort et la chute (*c.-à-d.* demi-vie) des chicots de peuplier faux-tremble (*Populus tresmuloides*) est d’environ 15 ans, tandis qu’il peut atteindre plus de 25 ans pour le pin gris (*Pinus banksiana*) (Angers *et al.* 2010). Chez l’épinette noire (*Picea marianna*) et le sapin baumier (*Abies balsamea*), la demi-vie est estimée à 18.1 et 19.5 ans respectivement (Angers *et al.* 2010), mais ces valeurs augmentent en fonction du diamètre des chicots (Aakala *et al.* 2008).

Rôle écologique du bois mort

Le bois mort remplit de nombreuses fonctions écologiques au sein de tous les écosystèmes forestiers mondiaux (Stokland *et al.* 2012; Seibold *et al.* 2015). Au Québec, il est documenté qu'un peu plus de 90 espèces de vertébrés utilisent le bois mort pour diverses fonctions et à certains moments de leur cycle de vie (*p.ex.* nidification, alimentation, repos; voir Lang *et al.* 2015). Bien que l'utilisation du bois mort par la faune aviaire soit généralement la plus documentée (Imbeau et Desrochers 2002; Drapeau *et al.* 2009; Ouellet-Lapointe *et al.* 2015), il n'en demeure pas moins que plusieurs espèces d'autres groupes taxonomiques, tels que les invertébrés (Saint-Germain *et al.* 2006; Seibold *et al.* 2016), les mammifères (Trudeau *et al.* 2011; Fauteux *et al.* 2012) et les amphibiens (Otto *et al.* 2013; O'Donnell *et al.* 2014), sont étroitement associé à cette ressource. De plus, tant en stade chicot que débris ligneux, plusieurs espèces de bryophytes, de lichens et de champignons saprophytes croissent directement sur le bois mort (Söderström 1988; Boddy 2001; Kushnevskaya *et al.* 2007).

La figure 1 schématise ainsi les rôles qu'un résineux peut avoir sur différentes espèces boréales en fonction des stades de décomposition du bois. Dès lors, plusieurs organismes interagissent entre eux à de multiples niveaux afin de former un ensemble complexe et interdépendant. Par exemple, en s'alimentant des insectes saproxyliques qui se développent dans le bois mort debout et en excavant des cavités de nidification, les pics vont favoriser la dispersion de champignons contribuant à la dégradation de la matière ligneuse (Jackson et Jackson 2004; Cockle *et al.* 2012). Ultimement, leurs cavités de nidification seront réutilisées par une foule d'autres espèces, dont certaines incapables d'excaver elles-mêmes leurs abris pour la nidification ou pour le repos (*p.ex.* Martin et Eadie 1999; Aitken et Martin 2007; Trudeau *et al.* 2012; Robles et Martin 2014). Une fois au sol, les conditions d'humidité et de températures des débris ligneux en état de décomposition avancée peuvent être plus stables que celles du substrat environnant, ce qui favorise alors la germination de certaines essences forestières et créer un habitat adéquat pour de nombreux amphibiens (Harmon *et al.* 1986; McGee et Birmingham 1997; Stevens 1997). Enfin, en se décomposant totalement, le bois mort joue un rôle majeur dans la séquestration du carbone par le sol et influence également la disponibilité des éléments nutritifs présents dans la litière forestière (Laiho et Prescott 2004; Wiebe *et al.* 2014; Strukelj *et al.* 2018). Tous ces processus démontrent donc que les espèces dépendantes du bois mort se sont adaptées à traquer la disponibilité de cette ressource et à réagir continuellement aux variations temporelles et spatiales (Jonsson *et al.* 2005).

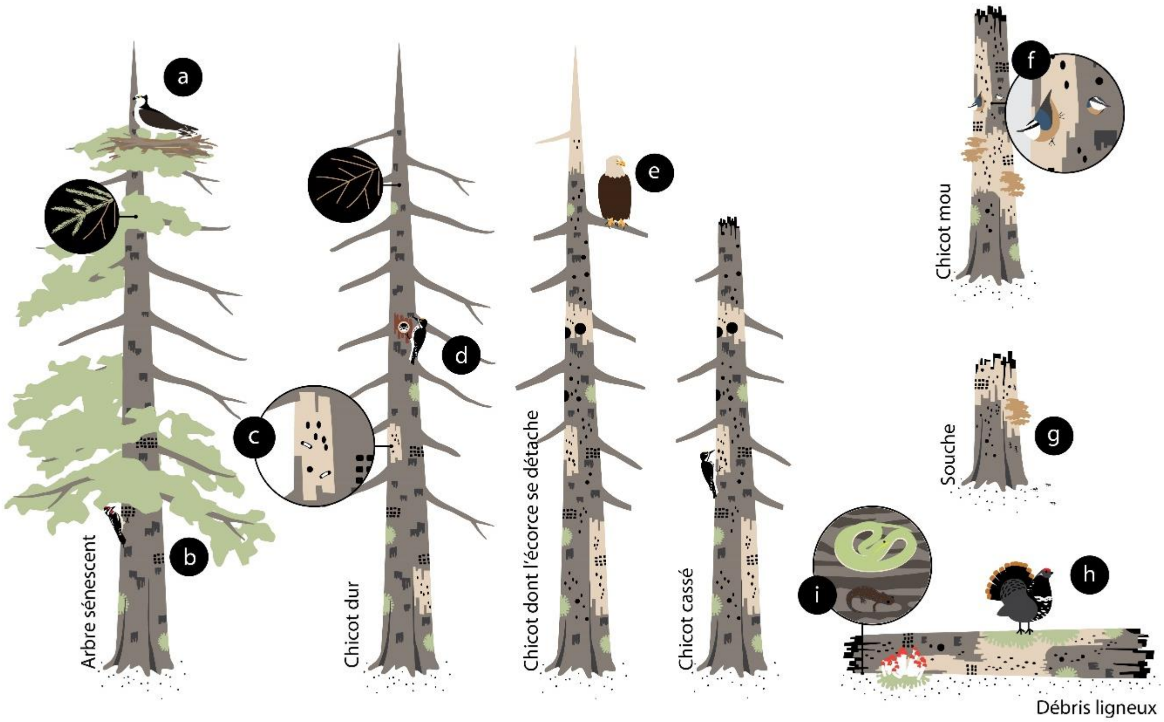

Figure 1. Exemples d'utilisateurs de différents types de bois mort en forêt boréale. a) Balbuzard pêcheur (*Pandion haliaetus*) nichant à la cime d'un vieil arbre, b) Pic maculé (*Sphyrapicus varius*) se nourrissant de sève, c) Insecte saproxyliques colonisant le bois, d) Pic à dos noir (*Picoides arcticus*) nichant dans sa cavité, e) Pygargue à tête blanche (*Haliaeetus leucocephalus*) utilisant un site de guet, f) Sitelle à poitrine rousse (*Sitta canadensis*) réutilisant une cavité, g) Champignon saprophyte décomposant le bois, h) Tétras du Canada (*Falcipennis canadensis*) sur un site de tambourinage, i) Amphibiens/reptiles utilisant les débris ligneux en état de décomposition avancé (adapté de Lang et al. 2015).

Enjeux écologiques liés au bois mort

Dans plusieurs écosystèmes mondiaux, il a été démontré que la diversité et la quantité de bois mort tendent à diminuer en raison de nombreux facteurs anthropiques (Siitonen 2001; Bouget *et al.* 2012; Lindenmayer *et al.* 2012). À titre d'exemple, plusieurs décennies de foresterie intensive ont entrainé une diminution importante de la quantité et de la diversité de bois mort au sein des forêts boréales Fennoscandinaves (Östlund *et al.* 1997; Linder et Östlund 1998; Siitonen 2001). Hekkala *et al.* (2016) résument d'ailleurs qu'il y a approximativement 5 à 7 m^3/ha de bois mort total dans les paysages aménagés, tandis que les forêts naturelles en comprennent entre 60 et 120 m^3/ha. Cette limitation de la ressource a ainsi contribué au déclin à grande échelle de nombreuses espèces associées au bois mort (Berg *et al.* 1994; Rassi *et al.* 2010).

Au Québec, bien que la situation générale soit moins dramatique qu'en fennoscandinavie, il est possible d'observer localement certains écarts dans les quantités de bois mort en lien avec l'aménagement forestier (Angers 2009; Côté *et al.* 2009). À cet égard, Tremblay *et al.* (2009) ont rapporté qu'une vieille pessière à mousse naturelle (>90 ans) comptait en moyenne 71,3 m^3/ha de bois mort total et que cette valeur diminuait à 29,7 et 18,1 m^3/ha respectivement dans les parterres de coupes récents (<5 ans) et les peuplements dénudés. Même si une comparaison directe entre les valeurs de bois mort observées dans les forêts fennoscandinaves et canadiennes ferait l'objet d'une étude en soit, les similitudes entre les deux milieux (*p.ex.* structure forestière, structure des populations d'oiseaux) rappellent qu'une foresterie intensive pourrait possiblement mener à des problèmes de conservation pour de nombreuses espèces locales associées au bois mort (Imbeau *et al.* 2001).

En effet, plusieurs facteurs inhérents à l'exploitation des forêts boréales limitent la disponibilité et le recrutement du bois mort (Gauthier *et al.* 2009). Dans les forêts équiennes matures, la récolte est souvent totale et la longueur des révolutions ne permet généralement pas la croissance d'arbres de fort diamètre en plus d'annuler la mortalité par sénescence (Desponts *et al.* 2002; Desponts *et al.* 2004; Roberge et Desrochers 2004). De plus, même si d'importantes superficies touchées par des feux ou des épidémies sont laissées intactes, les coupes de récupération de certains secteurs suite à une perturbation naturelle peuvent localement empêcher un apport massif de bois mort (Nappi *et al.* 2004; Nappi *et al.* 2011). Enfin, lors des interventions sylvicoles, le bois mort déjà présent est souvent éliminé par mesure de sécurité pour les travailleurs ou écrasé par la machinerie.

Pertinence de l'étude et objectifs généraux.

Dans certains contextes, l'aménagement compensatoire de l'habitat peut être utilisée afin de pallier à une problématique ciblée, ou tout simplement comme outil favorisant le développement durable d'un territoire (Morris *et al.* 2006). Ce concept vise à contrebalancer les effets négatifs d'un impact anthropique (*p.ex.* foresterie, urbanisation, secteur minier) en restaurant artificiellement certains éléments clés de l'habitat dans le but d'y rétablir des fonctions écologiques ciblées. En forêt boréale, les écarts grandissants entre les paysages naturels et aménagés peuvent donc localement entraîner des situations où le recours à de telles mesures peut être envisageable. Dans le cas du bois mort, il a été démontré que la création artificielle est possible afin d'obtenir un effet positif sur de nombreuses espèces associées (*p.ex.* Hane *et al.* 2012; Kilgo et Vukovich 2014; Ranius *et al.* 2014; Barry *et al.* 2017).

Diverses techniques ont été élaborées afin de créer des chicots ou de simuler certains attributs structuraux liés vieilles forêts. Certaines études ont eu recours au dynamitage (Bull et Partridge 1986), aux souches hautes (Ranius *et al.* 2014), à l'inoculation de champignons par arme à feu (Filip *et al.* 2004), au brûlage contrôlé (Toivanen et Kotiaho 2010) ou à l'installation de nichoirs (Aitken et Martin 2012). Le choix de la méthode peut évidemment dépendre de nombreux facteurs, dont le type et la quantité de bois mort nécessaire, les restrictions logistiques et les espèces visées. À titre d'exemple, l'annelage manuel des arbres permet de créer du bois mort qui restera sur pied relativement longtemps (Hallett *et al.* 2001), mais nécessite d'importantes ressources en terme de main-d'œuvre. En contrepartie, l'étêtage des arbres peut se faire plus rapidement à l'aide de machinerie forestière, mais puisqu'un tronc brisé peut être une porte d'entrée importante pour certains agents pathogènes, ce type de bois mort se décomposera plus rapidement (Weiss *et al.* 2018).

Bien que ces techniques aient largement été utilisées dans des contextes où la faible disponibilité du bois mort menace déjà la conservation d'espèces y étant associées (*p.ex.* Fennoscandinavie), peu d'études ont été menées dans les forêts boréales de l'est de l'Amérique du Nord (Boucher *et al.* 2012; Gagnon 2013; Thibault et Moreau 2016). Toutefois, la majorité des études orientent leurs recherches sur des espèces ou des groupes d'utilisateurs précis (*p.ex.* uniquement les insectes), ce qui limite l'étendue de l'interprétation en regard aux mécanismes écologiques interspécifiques (Seibold *et al.* 2015). Enfin, un nombre très limité d'aménagements compensatoires testent simultanément l'impact de différents types ou attributs de bois mort sur un même territoire (e.g. bois mort récent et cavités, Caine et Marion 1999).

Le présent projet contribue à combler ces lacunes en testant l'effet combiné de la supplémentation de bois mort debout et de cavités artificielles dans des peuplements forestiers d'épinettes noires de 50-70 ans sur deux grands groupes d'utilisateurs, soit les coléoptères saproxyliques et les vertébrés cavicoles (mammifères et oiseaux). Il est donc attendu que la supplémentation de chicots par annelage aura un effet positif sur les utilisateurs de bois mort récents tandis que l'addition de nichoirs permettra la nidification et le repos de certaines espèces cavicoles. À notre connaissance, il s'agit de la première expérimentation à grande échelle mettant en relation ces deux facteurs.

Les résultats de cette étude fourniront des pistes afin de déterminer si, dans un contexte où un problème de conservation relié au bois mort debout est identifié localement, il est possible d'agir rapidement et de rétablir les fonctions écologiques d'un territoire donné. Les connaissances acquises apporteront également des éléments supplémentaires pour les aménagistes afin d'adapter des méthodes représentatives des particularités régionales et logistiques. Ultimement, de telles méthodes pourraient en favoriser l'intégration dans des pratiques commerciales selon les principes de l'aménagement écosystémique.

CHAPITRE 2 : COMPENSATORY MEASURES FOR WILDLIFE CONSERVATION: TESTING THE EFFECT OF DEADWOOD AND CAVITY SUPPLY ON CAVITY USERS IN MANAGED BOREAL FOREST

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Abstract

In managed boreal forests, where clearcuttings tend to induce a change in the amount and diversity of standing deadwood, it is possible to simulate old-growth forest attributes to have positive effects on deadwood associated species. This study evaluates the short-term response of saproxylic beetles, foraging woodpeckers and secondary cavity users to snag and cavity supply in 50-70 years-old black spruce stands. In spring 2015, 8,000 black spruces have been girdled according to two spatial distributions (uniform and clustered treatments) and 450 nest boxes of 6 sizes have been disposed at 3 different distances from a forest edge. In late-spring 2015 and 2016, there was a significantly higher number of beetles captured at snag supply sites than at control sites as well as a general trend to capture more beetles in clustered treatments than in uniform treatments. We captured approximately 7-fold less beetles in 2016 (1 year after girdling) than in 2015 (few weeks after girdling). Very few woodpeckers foraging marks were observed in October 2015 (6 months after girdling) and in June 2016 (1 year after girdling), but in return, a large amount of foraging marks was detected in October 2016 (1 year and a half after girdling). Woodpecker foraged significantly more on girdled trees in clustered treatments than in uniform treatments and preferred bigger and recently dead girdled trees rather than live or dying girdled trees. Depending on the insect taxa analyzed, we found that various habitat variables at different scales influenced the number of beetles captured. Similarly, woodpeckers foraging mark presence was positively associated with the proportion of recent cuts (≤ 10 years) 1 km around sites. Only 5 Boreal chickadee pairs used nest boxes and occupied the two smaller box sizes located away from the forest edge. Our study failed to detect global changes within the forest bird community structure. Nevertheless, our study showed that structural enrichment as a compensatory measure could be an effective way to rapidly attract deadwood associated species within non-optimal forest stands. Further studies in eastern Canadian boreal forests should aim to develop more adaptive methods to facilitate their implementation in commercial activities and thus favor benefits at larger scales; especially where forest structures have been locally driven outside of their range of natural variability and that a conservation concern is identified.

Introduction

In boreal ecosystems, it is recognized that forest management decreases the proportion of old-growth stands (Östlund *et al.* 1997; Boucher *et al.* 2009; Cyr *et al.* 2009), and consequently, induces changes in the amount and diversity of standing deadwood (Fridman and Walheim 2000; Roberge and Desrochers 2004; Vaillancourt *et al.* 2008). Indeed, time interval between clearcutting rotations does not allow the development of deadwood structures similar to those observed in old-growth forests (Drapeau *et al.* 2009). In most accessible territories, salvage logging after a natural perturbation also limits the recruitment of large areas of deadwood (Nappi *et al.* 2004). It has been shown that forest management have already induced changes in the overall landscape and age structure of eastern Canadian forests (Cyr *et al.* 2009; Bouchard and Pothier 2011; Boucher *et al.* 2015), and that management and conservation targets implemented over the past few decades have proven to be insufficient to prevent habitat loss below minimum ecological thresholds (Imbeau *et al.* 2015). As a comparison, several plant, animal and fungus species in Fennoscandia are now threatened by the loss of old-growth forest attributes due to several decades of intensive forestry (Berg *et al.* 1994; Siitonen 2001, 2012). Given the similarities between Fennoscandian and northeastern Canadian boreal forests (*e.g.* forest-age structure, structure of bird assemblages; Imbeau *et al.* 2001), it is imperative to develop further tools to limit possibilities of such an outcome.

Ecosystem-based forest management has emerged as a possible solution to reduce the negative effects of forestry on ecosystem properties (Bergeron *et al.* 2007; Gauthier *et al.* 2009). By emulating the pattern of natural disturbances (*e.g.* wildfires, insect outbreaks, windthrows), one can assume that a smaller gap between natural and managed forest would help to maintain forest structures inside their historical range of natural variability to which animals are adapted (Harvey *et al.* 2002). Forestry practices aiming to increase the diversity of the internal structure of forest stands and to promote the availability of different types of deadwood could be an asset for the conservation of deadwood associated species (Drapeau *et al.* 2009; Boucher *et al.* 2016; Ibarra *et al.* 2017).

Many vertebrates and insects rely on standing deadwood (hereafter snags) at some part of their life cycle (Speight 1989; Siitonen 2001; Stokland *et al.* 2012), and those associations may differ from the type of deadwood produced. For instance, several saproxylic beetles are closely associated to specific habitat features (*e.g.* wildfires, Nappi *et al.* 2010), while other boreal species might be more opportunistic and rather forage or breed in unburned snags (Boucher *et al.* 2012). By digging galleries in the bark or the sapwood of recently dead trees, some aggregative beetles such as scolytids (Curculionidae) have a crucial effect on the dynamic of other species that use snags as foraging substrate (Murphy and Lehnhausen 1998; Drapeau *et al.* 2009; Edworthy *et al.* 2011). Indeed, some species such as the Black-backed (*Picoides arcticus*) and the American Three-toed (*P. dorsalis*) woodpeckers would prefer to forage on dying or recently dead trees rather than advanced-decay snags (Nappi *et al.* 2015; Tremblay *et al.* 2010, 2016; Cadieux and Drapeau 2017). Woodpeckers (primary cavity nesters), which also rely on snags to excavate cavities for nesting, are considered as keystone species in boreal ecosystems (Ouellet-Lapointe *et al.* 2015). Ultimately, woodpecker cavities will be used by many secondary cavity nesters/users – species unable to excavate themselves their shelter for nesting or roosting (Aitken and Martin 2007; Robles and Martin 2014). Other species such as chickadees and nuthatches (weak cavity excavators) frequently use existing cavities, but can create their own in well-decayed wood (Martin and Eadie 1999). Associations within nestwebs also depend on bird size, where large-bodied primary excavators would produce adequate cavities for larger secondary users such as owls and ducks (Martin *et al.* 2004). Furthermore, while feeding (*i.e.* by lifting the bark or pecking the wood), excavating or exploring, cavity users would favor the dispersal of wood decaying fungi, which will accelerate the decomposition rate of deadwood and provide further opportunities for species associated with highly decayed snags (Jackson and Jackson 2004; Cockle *et al.* 2012). Ultimately, fallen snags (coarse woody debris) would produce ideal habitat for many other organisms (see Stokland *et al.* 2012) and also have major implications for soil C sequestration and nutrient availability (Strukelj *et al.* 2018).

Some silvicultural practices, such as partial harvesting (Santaniello *et al.* 2017) or retention of both live and dead large trees in riverine and remnant linear forests (Remm *et al.* 2006; Vaillancourt *et al.* 2008) can allow a relative intake of deadwood at the landscape scale (Moussaoui *et al.* 2016). Nevertheless, those techniques are not always implemented in management strategies due to several economic or logistical restrictions, thus leading to a possible local lack of old-growth forest attributes (Angers 2009). In that context, artificial supply of snags could have positive effects on associated wildlife (Hane *et al.* 2012; Seibold *et al.* 2015; Thibault and Moreau 2016a). In other boreal ecosystems, is has been shown that high stump creation and tree girdling provide suitable habitat for saproxylic beetles (Ranius *et al.* 2014; Thibault et Moreau 2016a), and that tree topping favors foraging and nesting of primary cavity nesters (Barry *et al.* 2017). Is it also possible to enhance the availability of cavities using nest boxes if conservation concerns target secondary cavity nesters (Miller 2010; Robles *et al.* 2012). For example, it has been observed that the density of bird and mammal nests more than tripled after having tripled the availability of cavities (Aitken and Martin 2012); but such responses might not be instantaneous and would require a few years (Brawn and Balda 1988).

Many factors, such as the spatial distribution of snags at the stand scale, may also modify the degree of response of species targeted by mitigation measures. For instance, a high density of deadwood would increase the air concentration of volatile compounds (*e.g.* ethanol, α-pinene) necessary for its detection by saproxylic beetles (Saint-Germain *et al.* 2006). For certain species such as *Trypodendron lineatum*, the first beetles that attack a host emit aggregative pheromones (*e.g.* lineatin) which generates an exponential colonization (Nijholt 1979). By creating clustered deadwood, it is thus expected to maximize detectability of resource pulses by beetles in comparison to scattered snags within forest stands. A high density of saproxylic beetles would then become a highly profitable food source for predators (*e.g.* Picidae; Edworthy *et al.* 2011). Moreover, depending on specific preferences of secondary cavity users and habitat types, nest boxes occupancy as well as breeding parameters may be influenced by several factors such as wall thickness, physical dimensions of the box, orientation and shape of the entrance hole, placement height (Lambrechts *et al.* 2010; Møller *et al.* 2014) and distance from a forest edge (Kuitunen *et al.* 2003; Wiacek *et al.* 2014). For example, it is expected that small-bodied forest interior species (*e.g.* chickadees, nuthatches; Imbeau *et al.* 2003) would prefer nesting in small nest boxes located far from forest edges in order to maximize thermoregulation and limit predation risks. Finally, the habitat configuration at the landscape scale may also have a major influence on the effectiveness of structural enrichment strategies at local scale (Kroll *et al.* 2012). Indeed, occupancy at appropriate sites could remain low if the habitat in surrounding area is not suitable enough (Warren *et al.* 2005).

The main purpose of this project is to determine whether anthropogenic compensatory measures in managed boreal forest can emulate attributes of old-growth forest and thus favor the presence and reproduction of deadwood associated species. The first specific objective is to determine if snag supply based on two different distributions (uniform or clustered) can attract saproxylic beetles and bark insectivore birds while considering habitat variables at both local and landscape scales. The second specific objective is to assess if cavity addition using 6 sizes of nest boxes at 3 different distances from a forest edge can have an influence on associated species. Based on the detectability of resource pulses, our general hypotheses are that snag supply treatments will mainly favor the presence of species associated with recent deadwood and that this effect will be greater in sites with clustered snags. We also anticipate that one year after treatment, only a minority of nest boxes will be used, and that the overall structure of forest bird communities will not have changed significantly. We expect that a longer time frame is required to detect such changes within cavity user communities.

Methods

Study area

This study was conducted 150 km northwest of Lac Saint-Jean (Québec, Canada) (49°N, 71°W; Figure 1) in 2015 and 2016. This region is part of the balsam fir – white birch bioclimatic domain, which is characterized by mixedwood forests mainly composed of balsam fir (*Abies balsamea*) with white birch (*Betula papyrifera*), white spruce (*Picea glauca*), trembling aspen (*Populus tremuloides*) and black spruce (*Picea mariana*) (Saucier *et al.* 2009). Spruce budworm (*Choristoneura fumiferana*) outbreaks are the principal natural perturbations and greatly influence the forest composition (Morin *et al.* 2007). Fires are also relatively frequent, but normally cover small areas, with a mean historical cycle ranging from 600 to 1000 years (Chabot *et al.* 2009). The northern part of the study area is located at the limit of the black spruce – feather moss bioclimatic domain, where the major natural perturbations consist of larger forest fires, with a mean historical cycle of 247 years (Bélisle *et al.* 2013). The landscape composition of this bioclimatic domain is dominated by a mosaic of even-aged black spruce stands (Lefort *et al.* 2004). The general topography is undulating with valleys roughly oriented in a north-south axis. Clearcutting with protection of regeneration and soils is the most widely used harvesting technique in spruce stands. This method usually leaves small snags (DBH < 9 cm) in place if they do not represent a security concern for workers.

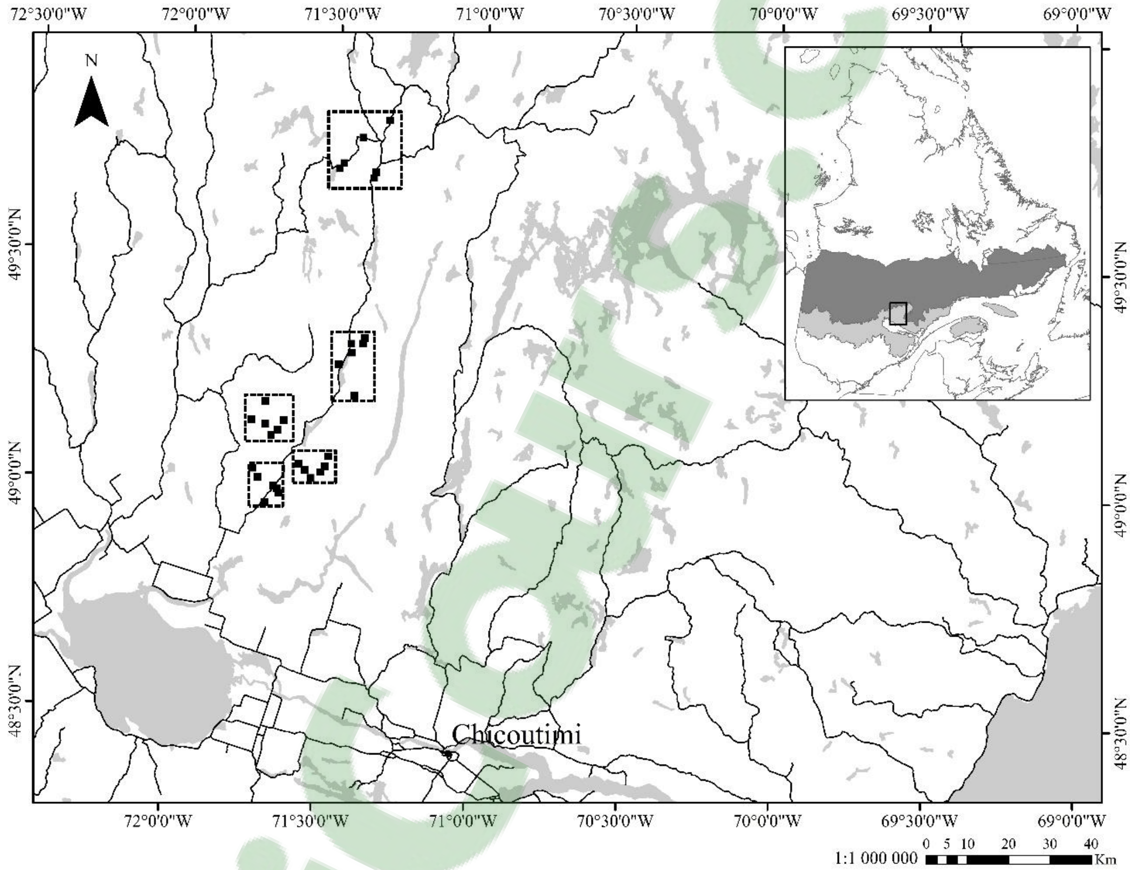

Figure 1. Map of the study area. Black squares represent experimental sites embedded in 5 experimental blocks. The panel shows the balsam fir – white birch (light grey) and the black spruce – feather moss (dark grey) bioclimatic domains.

Experimental design and data collection

Experimental design

The study area is composed of 5 experimental blocks, each containing 6 sites of 200 m by 200 m (4 ha.) spaced by 1.5 km from one another. Two different treatments were tested: cavity supply using nest boxes and deadwood creation using two spatial distributions of girdled trees. The location of a specific treatment as well as their interaction and a control, were assigned among sites of each block [uniform deadwood (DW1); clustered deadwood (DW2); cavities (CV); uniform deadwood with cavities (DW1CV); clustered deadwood with cavities (DW2CV); Control (CT)] (Figure 2). A forest stands selection has previously been performed using SQL queries on 1 : 20,000 digital forest maps (Ministère des Forêts de la Faune et des Parcs, Québec, Canada) in ArcGIS 9.3. Selection of forest stands (≥ 4 ha.) were made on 50 – 70 years old black spruce of all heights and had a canopy closure denser than 40%. The selection also included the presence of a forest road (of a width ranging from 3 to 5 m) crossing the stand and excluded any major watercourses or perturbations (*e.g.* fire, insect outbreak, cut block). A field validation was conducted for every site to ensure the adequacy between forest maps and actual stands.

Deadwood supply

Standing deadwood was created by girdling the trunk at breast height of healthy black spruce (n = 8,000) in May and June 2015. A total of 400 trees (DBH ≥ 9 cm) were girdled in sites with deadwood supply (i.e. 100 trees/ha.). This value was as a compromise between logistic constraints and the predicted probability of selection of nesting habitat by Black-backed Woodpeckers documented by Tremblay *et al.* (2015) in similar habitats (probability reaching 50% in stands with > 200 recently decayed snags/ha). In DW1 and DW1CV, each girdled tree was systematically distanced at 10 m from the other, while in DW2 and DW2CV, girdled trees were grouped in 4 clusters centralized on points distanced at 50 m from the other (Figure 2).

Cavity supply

To simulate cavities, 30 nest boxes of 6 different sizes were installed in June 2015 in every CV, DW1CV and DW2CV (n = 450; 7.5/ha.). In order to consider the edge effect on the use of nest boxes, the 3 larger sizes were disposed at 0 and 100 m to the road while the

3 smaller were installed at 0, 50 and 100 m (Figure 2). Nest boxes density was determined to test for different combinations of size/distance from the road, but is also consistent with the density of natural cavities in the balsam fir–white birch bioclimatic domain (11.2/ha, Ouellet-Lapointe *et al.* 2015). Each nest box was preferably facing east (except those along the forest road) while avoiding exposure to a dense lateral cover (Tremblay *et al.* 2015), and was installed at a height ranging from 2.5 to 4 m.

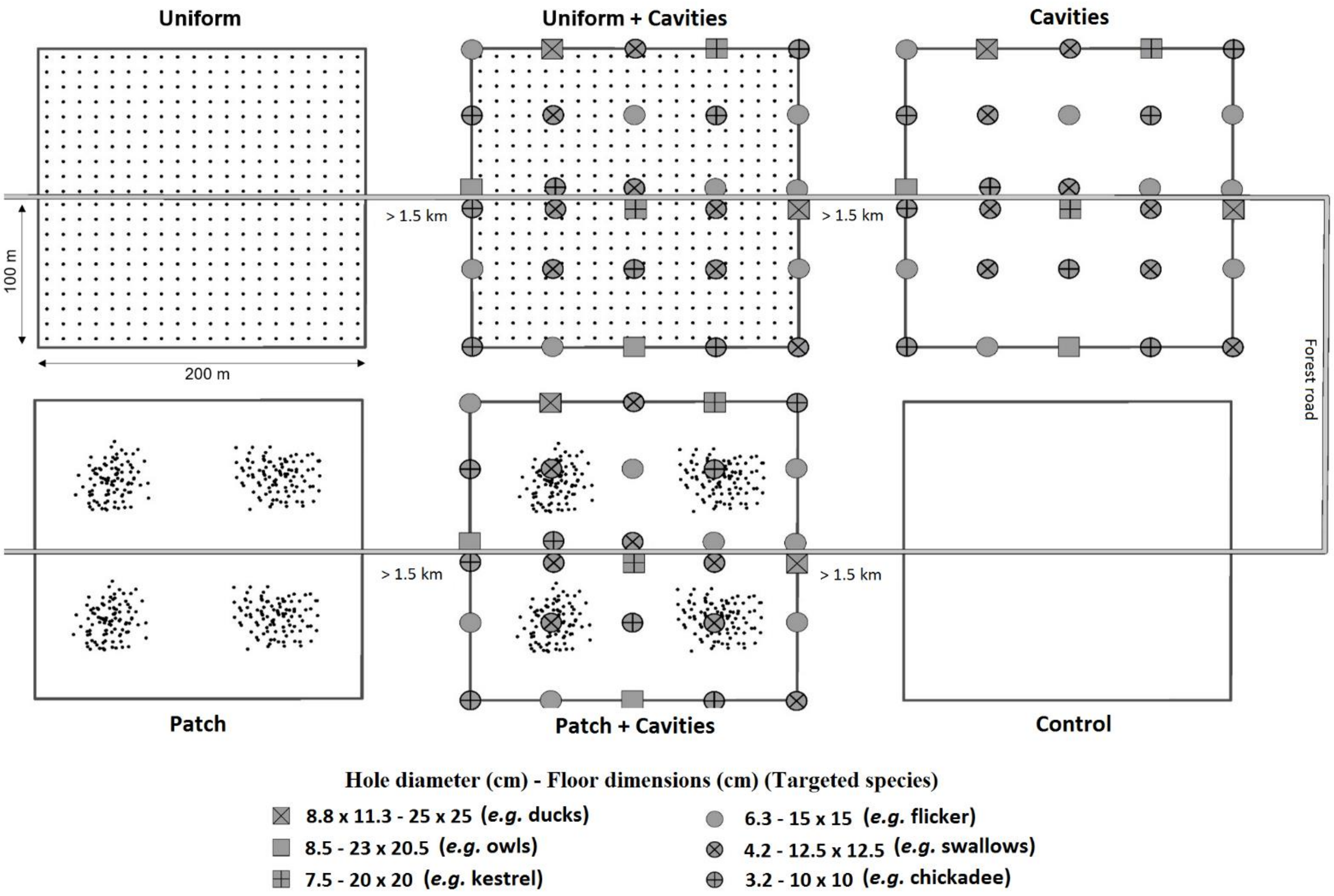

Figure 2. Visualization of the 6 experimental sites (*i.e.* every treatment combinations) within each experimental block (n = 5). Every black dot represent a girdled tree (n = 400/site) while nest boxes (n = 30/site) are represented by different symbols.

Insect survey

Saproxylic beetles were sampled using Trunk Window Traps (TWTs) installed on two girdled trees in every DW1, DW2, DW1CV, DW2CV and on two healthy trees in every CT (n = 50) (Kaila 1993; Boucher *et al.* 2012). The collecting containers were filled with ethanol [70%] and household vinegar (acetic acid) to preserve specimens. Traps were active for 4 weeks immediately after girdling (mid-june to mid-july 2015) and one year post-girdling (mid-june to mid-july 2016), which corroborates to the colonization period of several saproxylic species (Toivanen and Kotiaho 2010). A total of ten additional traps were distributed among CV in 2016 to act as a second control for deadwood supply. All samples were processed by the same observer and classified into 4 taxa (Cerambycidae, Curculionidae: Scolytinae [hereafter Scolytinae], Other Curculionidae [hereafter Curculionidae] and Cleridae). A second skilled observer reviewed all samples to identify insects at the lowest taxonomic level as possible for another research project.

Foraging marks survey

A subsample of 20 girdled trees was surveyed in every DW1, DW2, DWCV1 and DWCV2 in October 2015 (n = 400), with late addition of 20 other trees for the following sampling periods of June 2016 and October 2016 (total n = 780; one site having been harvested by mistake during the winter). The same trees were examined over time to detect any woodpeckers foraging marks (*i.e.* number of pecking marks or bark scaling surface on firsts 2 meters above the girdled section). Foraging marks were not assigned to specific species and were identified with paint at every sampling period to distinguish the old from the new ones. Because foraging marks observed on additional trees subsampled in June 2016 have not been painted during the first sampling period of October 2015, it was not possible to easily determine the period at which they were made. We therefore use the obvious color difference of sapwood (*i.e.* dark vs. light brown) between older and fresh foraging marks – as observed on the 400 trees that have been sampled at the first two periods – as a classification criterion. In October 2016, each subsampled girdled tree was classified as living (at least one new twig of the year), dying (no new twig, high proportion of red foliage) or dead (< 20% foliage remaining).

Bird survey

Point counts located at 50 m from the road were carried out in every site. A recording of unlimited radius was done for 15 minutes with an omnidirectional microphone (*Sennheiser ME 62*) and a recorder (*TASCAM DR-60D mkII*). Inventories were conducted between 5h00 and 10h00 on days without rain or wind (Ralph *et al.* 1995). A playback session located at the same place as the point count were performed immediately after using a MP3 player and a speaker (adjusted range of 100 m to only detect birds present within the site). Each bird species (respectively the Boreal Chickadee (*Poecile hudsonicus*), the Red-breasted Nuthatch (*Sitta canadensis*), the American Three-toed Woodpecker, the Black-backed Woodpecker, the Northern Flicker (*Colaptes auratus*), the Boreal Owl (*Aegolius funereus*) and the Northern Hawk Owl (*Surnia ulula*)) was called twice for 30 seconds; each time being followed by a listening period of 30 seconds. Bird survey was carried out according to a Before/After –Control/Impact design (Underwood 1994), where each point count and playback were conducted twice during the first three weeks of June 2015 (before treatment) and again at the same period of 2016 (after treatment). All recordings were processed by a single observer using spectrograms computed with the web application Avichorus (Environment and Climate Change Canada). Presence/absence of individual birds was noted at every 1-minute segment of each audio file. During point count, all species were noted, while in playback, only deadwood associated species or those undetected in the previous point count were considered. Different individuals of the same species were assessed only if several songs occurred simultaneously or near-simultaneously. The observer could replay recordings as many times as needed and refer to online sound libraries. Two skilled observers also reviewed every uncertain or unidentified bird songs.

Cavity survey

Every nest box was visited once during mid-June 2016. Those showing signs of use (*i.e.* vegetation debris, nest, bird presence) were followed every week to confirm nesting and determine productivity and survival rate. In order to measure the use of cavities outside of the breeding season, 27 motion-detector cameras (*SPYPOINT BF-8*, videos of 30 seconds, camera trigger set at 1-minute intervals) were randomly disposed to film 81 nest boxes of every size during the summer and spring of 2015. Cameras were set ON for 7 consecutive days in CV, DW1CV, DW2CV of blocks 1, 3, and 5.

Vegetation survey

Two circular plots of 11.28 m radius (400 m^2) were established 50 m from the center of every site to identify, count and measure the diameter of all trees (DBH ≥ 9 cm) using a digital distance measurer (*Haglof DME201*) and a caliper (± 0.05 cm). Saplings (DBH < 9 cm and height ≥ 1.5 m) were also assessed in the same way within five circular micro-plots (4 m^2) located in the center of the 400 m^2 plot and at the four cardinal points 11.28 m away from the center. Moreover, all standing dead trees (> 45°, Harmon and Sexton 1996) within a 20 m radius (1256 m^2), also centralized at the 400 m^2 plot, were counted, measured with a caliper and classified according to Imbeau and Desrochers (2002). Presence of woodpecker foraging marks was also noted. Digital forest maps were used to extract old-growth/perturbed as well as recently cut forest stands around every site according to different buffer widths (500, 1000, 2500 and 5000 m). These variables were included in different analyses (see description in Table 1).

Table 1. List and description of habitat variables.

Code	Habitat variable
Landscape scale	
RC	Recent cuts (% of the buffer zone) ≤ 10 years old interventions (excludes thinning)
MP	Major natural perturbations (% of the buffer zone) Severe insect outbreak, burn, windthrow or deterioration (≤ 40 years), affects ≥ 75% of the basal area of the stand
PP	Partial natural perturbations (% of the buffer zone) Partial insect outbreak, burn, windthrow or deterioration (≤ 40 years), affects ≤ 75% of the basal area of the stand
OF	Mature/Old-Growth stands (% of the buffer zone) ≥ 90 years-old even-aged or uneven-aged stands
DW	RC + MP + PP + OF
Site scale	
Sh.Dec	Density of deciduous shrubs per ha
Sh.Res	Density of coniferous shrubs per ha
Dw.3	Density of natural snags per ha (weakly decayed)
Dw.456	Density of natural snags per ha (moderately decayed)
Dw.78	Density of natural snags per ha (highly decayed)
Tr.Des	Density of deciduous trees per ha
Tr.Res	Density of coniferous trees per ha
DBH.mean	Mean DBH of trees within site
Tree scale	
DBH.Grd	DBH of girdled tree
MS.Grd	Mortality stage of girdled tree

Data analysis

Saproxylic beetles

We first compared the standardized number of captured saproxylic beetles (*i.e.* n/hour) according to deadwood supply treatments and the sampling year, including their interaction, using generalized linear mixed models (GLMMs) following a Gaussian distribution. Separate analyses were performed for every taxon (Cerambycidae, Scolytinae, Curculionidae and Cleridae) and also included the four landscape variables as fixed effects, at each spatial scale respectively (500, 1000, 2500 and 5000 m; Table 1). Response variables were either log-transformed or rank-transformed in order to normalize residuals (Conover and Iman 1981). Random effects were the sequential number of trap nested into the interaction of experimental site and block. The final model for every analysis was obtained through a stepwise selection method. Model averaging procedure was used to obtain parameter estimates if several models had an AIC_c difference (ΔAIC_c) < 2 (Burnham and Anderson 2002). Model selection and averaging were performed using the R-package "MuMin" (Barton 2016) and statistical significance of factors and their interactions was determined with "car" (John and Sanford 2011).

Foraging marks

We constructed a set of biologically relevant candidate mixed logistic models to predict the probability of presence of new woodpecker foraging marks on girdled trees based on deadwood supply treatment, sampling season, mean DBH of trees within vegetation plots, and landscape variables at different spatial scales. Random effects were subsampled girdled trees nested into the interaction of experimental site and bloc and retained variables in the final model were subsequently assessed using the lowest AICc value. Since the probability of detecting a new foraging mark decreases with the intensity at which a tree has been previously used, we then created a dummy variable that contains the proportion of the tree surface that has been used at the previous sampling period and included it in every analysis.

A different mixed logistic model was used on the 780 subsampled girdled trees surveyed in October 2016 (only moment with information about the degradation stage of trees) to determine which fine scale variables best explain the presence of new foraging marks on girdled trees. Random structure remained the same as in previous analyses while fixed effects were deadwood supply treatment and DBH, and their interaction, as well as the degradation stage of each girdled tree, respectively.

All GLMMs have been fitted using the R-package "lme4" (Bates *et al.* 2015) and we used the "lsmeans" R-package (Lenth 2016) to assess *posteriori* comparisons of least-squares means (α = 0.05).

Bird community

We used a removal model to take into account for the imperfect detectability of birds, given their presence, during the acoustic survey (Farnsworth *et al.* 2002). This method consists in dividing count period into several time intervals and creating an encounter history based on first detection. A bird detected on a given time interval is considered "removed " from the population and is not considered in following intervals. Conceptually, a bird counted during the second or subsequent time intervals must have been missed in the first one. The method also allows for heterogeneity (variation in detectability) within the population sampled. Thus, the most general model (Mc) estimates the total detectability ($\hat{p}$) by separating the population into two groups; group 1 being composed of birds that are easily detected and group 2 includes those that are more discrete. Otherwise, a more specific model (M) was used to estimate $\hat{p}$, assuming that all birds are members of group 2. We chose the model that better fit the data based on the lowest AIC value between Mc and M. As for any analysis of point count data, this method has for general assumptions that birds are not moving during count period and there is no double-counting of individuals. To reduce the violation of these assumptions, we only considered the firsts 10 minutes of point counts which we divided into 5 segments of 2 minutes. We pooled together all individuals detected during point counts (regardless of sites, sampling period or year) and we then constructed a first detection history while omitting every species with less than 5 occurrences. Given the low occurrence of certain species of interest (*i.e.* deadwood associated species), we also tried different combinations of species with *a priori* similar detection probabilities (Nichols *et al.* 2000). Playback data were analyzed in the same way, but completely independently from point counts, and only considered deadwood associated species. In order to standardize the time frame used to estimate detection probability, encounter histories of 6 minutes were made (3 segments of 2 minutes, each one being the playback of a different species), and the timing of the first segment varied based on the targeted species. For those who were actually called, the first segment was the moment of their first playback and count lasted for the next 6 minutes. For all non-called species (*i.e.* YBSS, PIsp, WOto; see Table 2 for species code), the first segment corresponded to the first playback of the Black-backed Woodpecker and count also lasted for the next 6 minutes. Every bird heard outside of these periods, respectively, was not retained for the analyses. All $\hat{p}$ have been computed using SURVIV code and equations given by Farnsworth *et al.* (2002).

In order to analyze relationships within the bird communities present in our study area, we used all counts of birds (15 min point counts + playback) in each experimental site of 2015 and 2016 and classified species according to 4 classes of functional traits, which are usually defined as features that affect overall fitness of a species (Violle *et al.* 2007). Based on Azeria *et al.* (2011), we regrouped species based on nest type, nest location, foraging and migratory behavior (see Table 2). We also discarded irrelevant species and those being more likely to violate assumption of closed population (*e.g.* Canada Goose (*Branta canadensis*), Common Raven (*Corvus corax*)). Species with less than 5 occurrences or having detection probability lower than 0.15 were also omitted for subsequent analyses (Cadieux and Drapeau 2017). We assessed the traits-environment-species relationship using RLQ analysis (Doledec *et al.* 1996) and the Fourth-Corner approach (Legendre *et al.* 1997). RLQ analysis produces simultaneous ordination of three matrices, each of them being analyzed by a different ordination method depending on the nature of the data. In our study, a Hill-Smith ordination was performed on the matrix R (fine scale habitat variables), a correspondence analysis was used for the matrix L (species) and a multiple correspondence analysis was made on the matrix Q (functional traits). In RLQ analysis, scores obtained from matrix L are used as link between R and Q matrices. We then applied the Fourth-corner tests to evaluate statistical significance of every functional trait—habitat variable associations according to a permutation procedure and the false discovery rate method to adjust *P*-values in order to account for type I error (see Dray *et al.* (2014) for details). Finally, as proposed by Dray *et al.* (2014), we combined both approaches to evaluate the global significance of the functional trait—environment variables relationships.

Table 2. Codes for bird species. Functional traits* are as follows. Foraging strategy: OM = Omnivore; SF = Seed forager; FI = Foliage insectivore; GI = Ground insectivore; BI = Bark insectivore; SA = Sap forager. Nest location: GN = Ground nester; CN = Canopy nester; SN = Shrub nester. Nest type: OC = Open-cup nester; CV = Cavity nester. Migration strategy: SDM = Short distance migrant; RES = Permanent resident; NEO = Long distance migrant.

Code	Common name	Latin name	Functional traits			
			For.	Nest loc.	Nest type	Migr.
TEWA	Tennessee Warbler	*Oreothlypis peregrina*	FI	GN	OC	NEO
RCKI	Ruby-crowned Kinglet	*Regulus calendula*	FI	CN	OC	SDM
WTSP	White-throated Sparrow	*Zonotrichia albicollis*	OM	GN	OC	SDM
NAWA	Nashville Warbler	*Vermivora ruficapilla*	FI	GN	OC	NEO
SWTH	Swainson's Thrush	*Catharus ustulatus*	FI	SN	OC	NEO
BBWA	Bay-breasted Warbler	*Setophaga castanea*	FI	CN	OC	NEO
CMWA	Cape May Warbler	*Setophaga tigrina*	FI	CN	OC	NEO
GCKI	Golden-crowned Kinglet	*Regulus satrapa*	FI	CN	OC	SDM
MAWA	Magnolia Warbler	*Dendroica magnolia*	FI	SN	OC	NEO
DEJU	Dark-eyed Junco	*Junco hyemalis*	OM	GN	OC	SDM
YRWA	Yellow-rumped Warbler	*Dendroica coronata*	FI	CN	OC	SDM
EVGR[†]	Evening Grosbeak	*Coccothraustes vespertinus*	*N/A*	*N/A*	*N/A*	*N/A*
PISI[†]	Pine Siskin	*Spinus pinus*	*N/A*	*N/A*	*N/A*	*N/A*
HETH	Hermit Thrush	*Catharus guttatus*	OM	GN	OC	SDM
WOto[†]	WOsp + PIsp + PIWO + YBSA		*N/A*	*N/A*	*N/A*	*N/A*
REVI	Red-eyed Vireo	*Vireo olivaceus*	FI	CN	OC	NEO
AMRO	American Robin	*Turdus migratorius*	OM	CN	OC	SDM
YBSA	Yellow-bellied Sapsucker	*Sphyrapicus varius*	SA	CN	CV	SDM
RBNU	Red-breasted Nuthatch	*Sitta canadensis*	BI	CN	CV	RES
WIWR	Winter Wren	*Troglodytes hiemalis*	GI	CN	CV	SDM
WOsp	Woodpecker sp.		BI	CN	CV	RES
GRAJ	Gray Jay	*Perisoreus canadensis*	OM	CN	OC	RES
PIWO	Pileated Woodpecker	*Dryocopus pileatus*	BI	CN	CV	RES
COYE	Common Yellowthroat	*Geothlypis trichas*	FI	GN	OC	NEO
RUGR	Ruffed Grouse	*Bonasa umbellus*	SF	GN	OC	RES
BOCH	Boreal Chickadee	*Poecile hudsonicus*	BI	CN	CV	RES
PIsp	Black-backed Woodpecker Am. Three-toed Woodpecker	*Picoides arcticus* *Picoides dorsalis*	BI	CN	CV	RES

* Functional traits were based on the peer-reviewed online database *Birds of North America* (Rodewald 2015). For species with functional traits that may belong to different categories, the most representative one has been selected.

[†] These species (or combinations of species) have not been retained for RLQ and fourth-corner analyses.

Results

Saproxylic insects

Overall, 24,828 saproxylic beetles were captured in 2015 compared to 3,805 in 2016, belonging to 44 species for 4 families/sub-families. In 2015, Cerambycidae, Cleridae, Curculionidae and Scolytinae accounted respectively for 1.1%, 1.0%, 1.2% and 96.7% of all samples, and respectively for 1.4%, 2.4%, 1.6% and 94.6% in 2016. In both years, *Trypodendron lineatum* was the most abundant species in traps, representing 88.5% (n = 21,983) of all species in 2015 and 74.6% (n = 2,839) in 2016 (see Annexe).

The interaction between deadwood supply treatments and year was highly significant for each of the 4 taxa analyzed (Table 3). Cerambycidae seemed to be positively influenced by the proportion of recent cuts and natural perturbations around sites. Curculionidae, Cerambycidae and Cleridae all seemed to be affected at some point by the amount of old forest. None of the landscape variable was retained in models for Scolytinae.

Overall, for the 4 insect taxa, there was significantly more beetles captured per day in deadwood supply treatments than in control sites, and this relationship was more pronounced in 2015 than in 2016 (Figure 3). Except for Cerambycidae in 2015, there was no significant difference between uniformly and clustered distributed deadwood on the number of beetles captured per day. For most of the insect taxa, there was significantly less captures per day in 2016 than in 2015 for a pairwise comparison of the same treatment.

Table 3. Interaction term of deadwood supply treatments and sampling year on the daily captures of saproxylic beetles from Type III Wald $\chi 2$ tests. Estimates (± 95% CI) from stepwise selection (and model averaging if several models had ΔAICc < 2) are reported for each landscape variables at 4 spatial scales (see Table 1 for variable name). Bold fond represents significant effects and N/As represent variables not retained through the selection process.

	Treatment * Year			**Variable**	**500**		**1000**		**2500**		**5000**	
	df	**Wald Chi-Square**	***P-value***									
Curculionidae[*]	*2*	11.27	*0.004*	RC	-1.44	[-4.98, 2.09]	-0.55	[-1.69, 0.59]	0.05	[-1.11, 1.21]	0.03	[-1.10, 1.16]
				MP	-0.37	[-3.79, 3.05]	0.16	[-0.95, 1.28]	-0.20	[-1.43, 1.03]	0.18	[-2.77, 3.12]
				PP	**-0.63**	**[-1.26, -0.01]**	-0.45	[-0.96, 0.05]	-0.59	[-1.38, 0.20]	-0.71	[-1.73, 0.31]
				OF		N/A	**0.48**	**[0.02, 0.93]**	0.44	[-0.16, 1.04]	-0.06	[-1.25, 1.14]
Cerambycidae[*]	*2*	11.19	*0.004*	RC	**2.82**	**[0.05, 5.59]**	**1.12**	**[0.16, 2.09]**	0.88	[-0.06, 1.82]	0.45	[-0.42, 1.32]
				MP	**2.40**	**[0.16, 4.63]**	0.75	[-0.17, 1.67]	0.60	[-0.55, 1.76]	-0.88	[-4.07, 2.30]
				PP		N/A		N/A	0.57	[-0.07, 1.21]	**0.98**	**[0.08, 1.88]**
				OF		N/A	-0.34	[-0.74, 0.06]	**-0.65**	**[-1.17, -0.13]**	-0.83	[-1.77, 0.10]
Cleridae[*]	*2*	11.40	*<0.001*	RC	-1.46	[-5.59, 2.67]	-0.34	[-1.60, 0.92]	0.23	[-1.05, 1.50]	0.05	[-1.28, 1.39]
				MP	1.44	[-2.03, 4.91]	0.60	[-0.62, 1.82]	0.41	[-1.10, 1.92]	-1.27	[-4.64, 2.09]
				PP		N/A		N/A		N/A	-0.20	[-1.41, 1.01]
				OF	0.44	[-0.03, 0.91]	**0.72**	**[0.20, 1.24]**	**0.80**	**[0.09, 1.51]**	0.37	[-0.85, 1.58]
Scolytinae[†]	*2*	14.60	*0.003*	RC		N/A		N/A		N/A		N/A
				MP		N/A		N/A		N/A		N/A
				PP		N/A		N/A		N/A		N/A
				OF		N/A		N/A		N/A		N/A

Response variables were rank (*) or log (†) transformed to meet assumptions of normality.

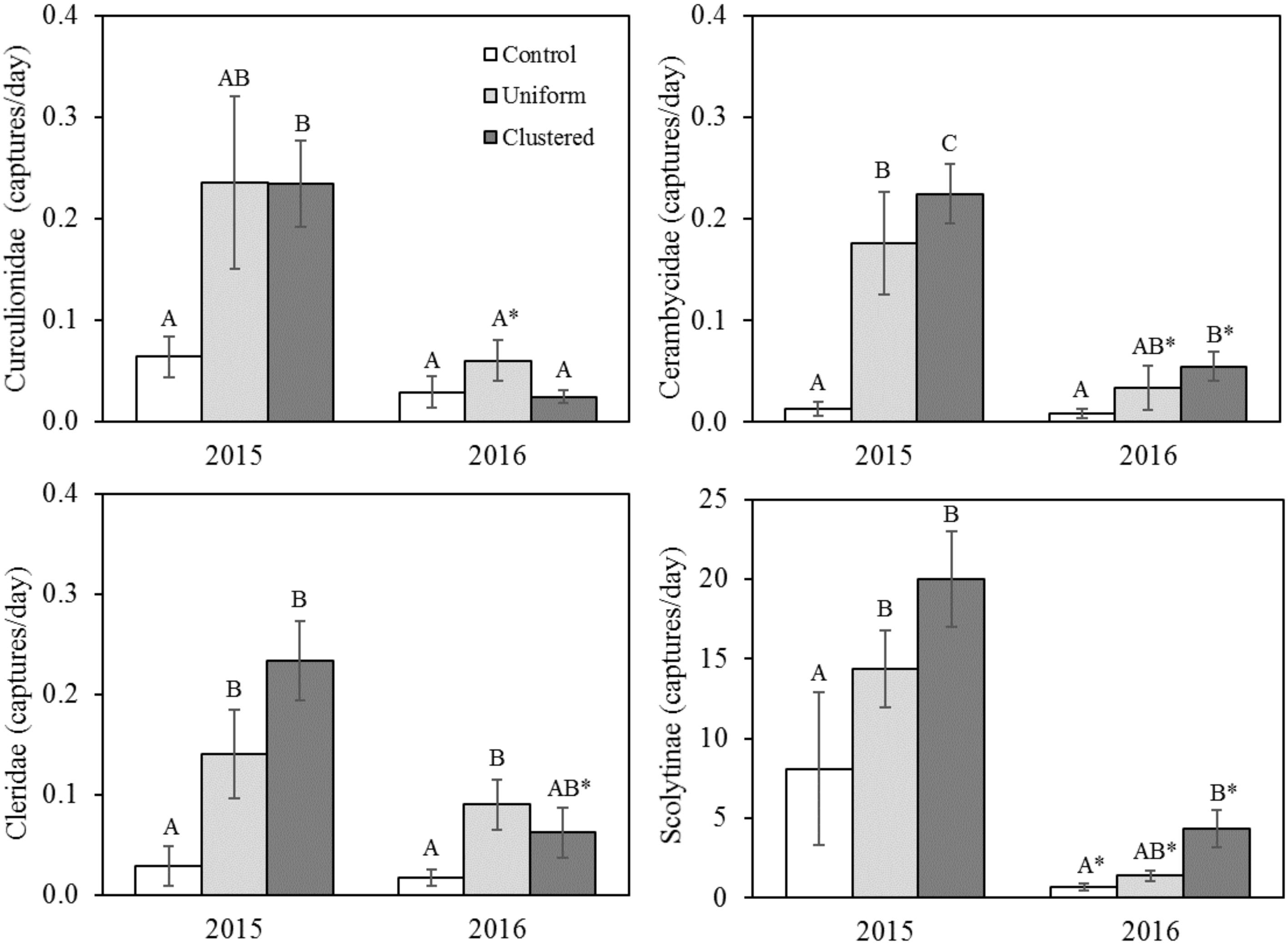

Figure 3. Mean capture (± SE) of Curculionidae, Cerambycidae, Cleridae and Scolytinae per day according to treatment and year. Different letters within a year indicate significantly different least-squares means among treatments, while asterisks represent significantly different least-squares means between years for the same treatment (α = 0.05).

Foraging marks

Overall, 17 months after girdling, 62.9% (n = 490) of subsampled trees were used by foraging woodpeckers (71.3% [n = 285] in clustered treatment and 54.1% [n = 205] in uniform treatment). According to the best model considering landscape variables and seasons (Table 4), there were highly significant effects of treatments and seasons on the probability of presence of new woodpecker foraging marks (Table 5, Figure 4). However, the interaction between these main effects was not significant. The proportion of recent cuts within a 1 km buffer around sites also revealed to have a highly significant positive effect on the probability of use of girdled trees, but differed depending on sampling season. For uniformly distributed deadwood treatment, Figure 5a shows that a high proportion of recent cuts 1 km around sites tends to increase the probability of use by woodpeckers, but more importantly in October 2015 and June 2016 than in October 2016. For clustered deadwood treatment, the same pattern occurs, but with higher probabilities for all seasons (Figure 5b).

Even though we did not collect data related to the degradation of girdled trees during the 2015 summer (few months after girdling), field observations allow to affirm that very few girdled trees showed visual signs of degradation during the foraging mark survey of October 2015. However, on the 780 girdled trees subsampled in October 2016, 74.1% were dead, 9.5% were dying, 13.1% were still alive and 3.3% were lost (identification tag was not found or had fallen). We found that the treatment as well as the DBH and the mortality stage of girdled trees all had significant effects on the probability of new woodpecker foraging marks. The effect of DBH, however, varied depending on treatment (Table 6). Indeed, the DBH of girdled tree affects the probability of presence of new woodpecker foraging marks more importantly in uniform treatment (Figure 6a) than in clustered treatment (Figure 6b).

Table 4. Set of biologically relevant candidate models to predict the probability of presence of new foraging marks on girdled trees. Reported are the number of parameters in the model (K), the log-likelihood (LL), the AIC corrected for small samples (AICc), the relative difference in AICc value compared to the top-ranked model (ΔAICc) and the Aikaike weight (wi).

Models	K	LL	AICc	ΔAICc	wi
Previous use + Treatment*Season + RC (1 km)*Season	12	-727.3	1478.7	0	1
Previous use + Treatment + Season + DBH.mean + RC (1 km) + MP (2.5 km)	10	-738.1	1496.2	17.56	0
Previous use + Treatment*Season + RC (1 km)	10	-740	1500.1	21.42	0
Previous use + Treatment*Season + RC (1 km)*Treatment	11	-739.5	1501.2	22.49	0
Previous use + Treatment*Season + DW (5 km)	10	-742.1	1504.3	25.61	0
Previous use + Treatment*Season	9	-743.7	1505.5	26.84	0
Previous use	4	-1080.7	2169.4	690.72	0

Table 5. Type III Wald $\chi 2$ tests for fixed effects on the probability of presence of new woodpecker foraging marks on girdled trees. Selected model represents the most parsimonious ($\Delta AICc < 2$) among set of candidate models accounting for landscape variables and sampling seasons (see Table 4).

Effect	*df*	χ^2	$Pr > \chi^2$
Treatment	1	10.27	0.001
Season	2	128.49	<0.001
RC (1 km)	1	17.08	<0.001
Treatment : Season	2	5.35	0.069
RC (1 km) : Season	2	23.84	<0.001

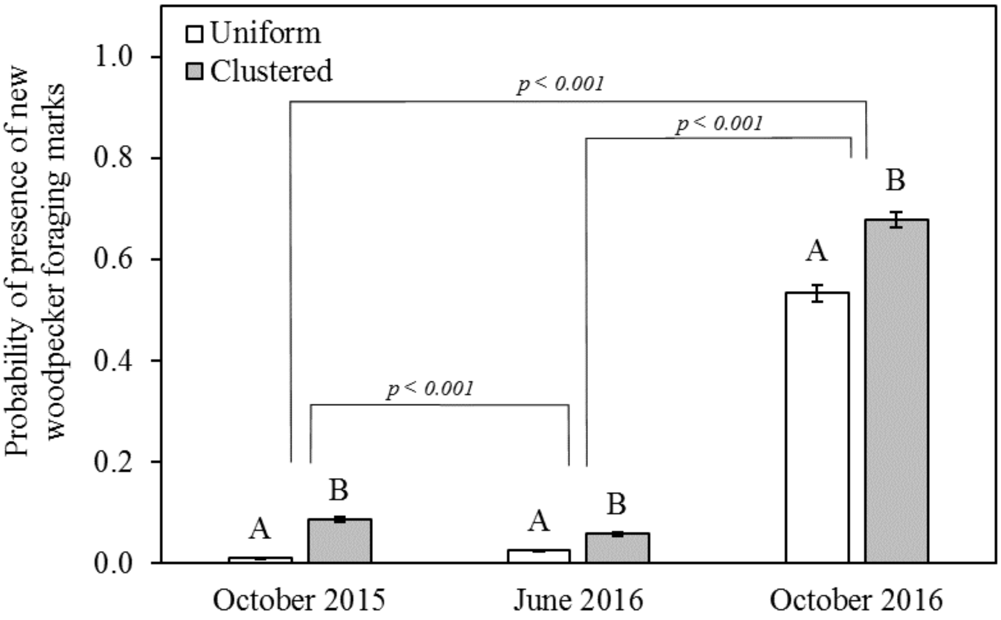

Figure 4. Predicted probability (± SE; back-transformed from the logit scale) of presence of new woodpecker foraging marks on girdled trees during the three sampling seasons. Different letters within a sampling season indicate significantly different least-squares means among treatments, while lines with associated p-value represent different least-squares means between sampling seasons, independently of treatments.

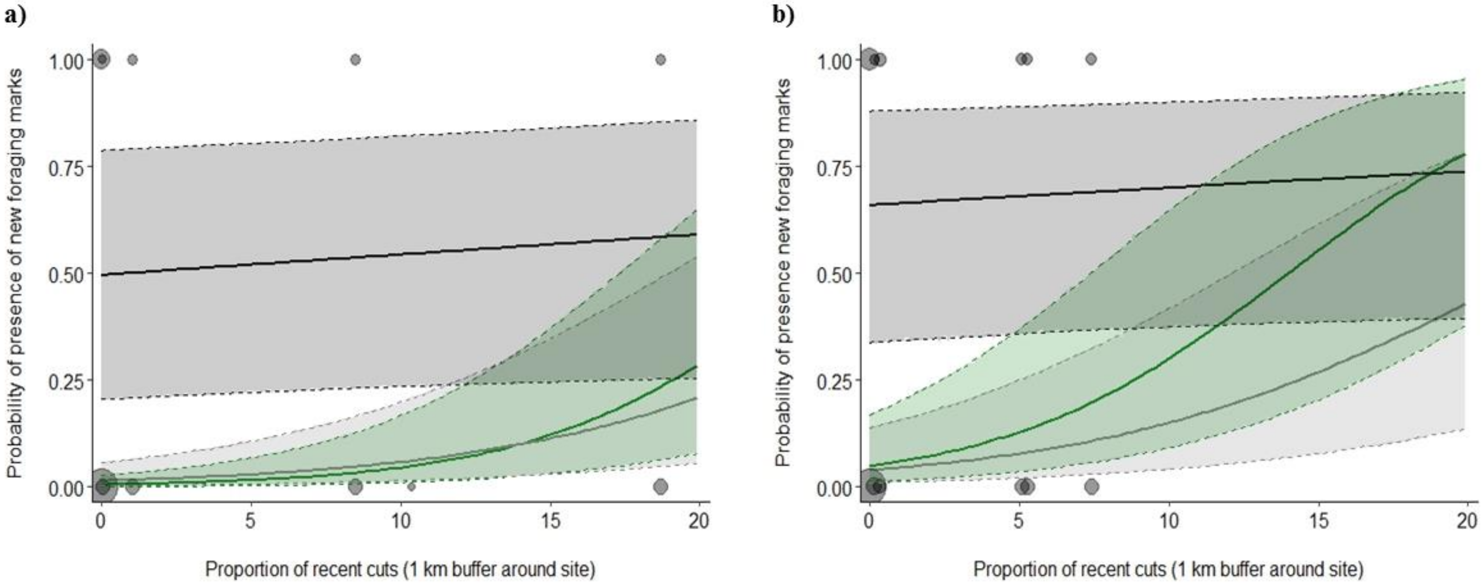

Figure 5. Projected probability of presence of new woodpecker foraging marks (± 95% CI) on girdled trees sampled in October 2015 (green lines), June 2016 (grey lines) and October 2016 (black lines) based on the proportion of recent cuts 1 km around sites for a) uniform treatment and b) clustered treatment. Grey dots represent the distribution of raw data, where bigger dots are related to more observations and superposed dots are darker.

Table 6. Type III Wald $\chi 2$ tests for fixed effects on the probability of presence of new woodpecker foraging marks on girdled trees. The model represents the complete set of fine scale variables for the 800 subsampled trees in October 2016.

Effect	*df*	χ^2	Pr > χ^2
DBH.Grd	1	9.18	0.002
Treatment	1	4.72	0.029
MS.Grd	2	72.23	<0.001
DBH.Grd : Treatment	1	4.03	0.045
MS : Treatment	2	3.86	0.145

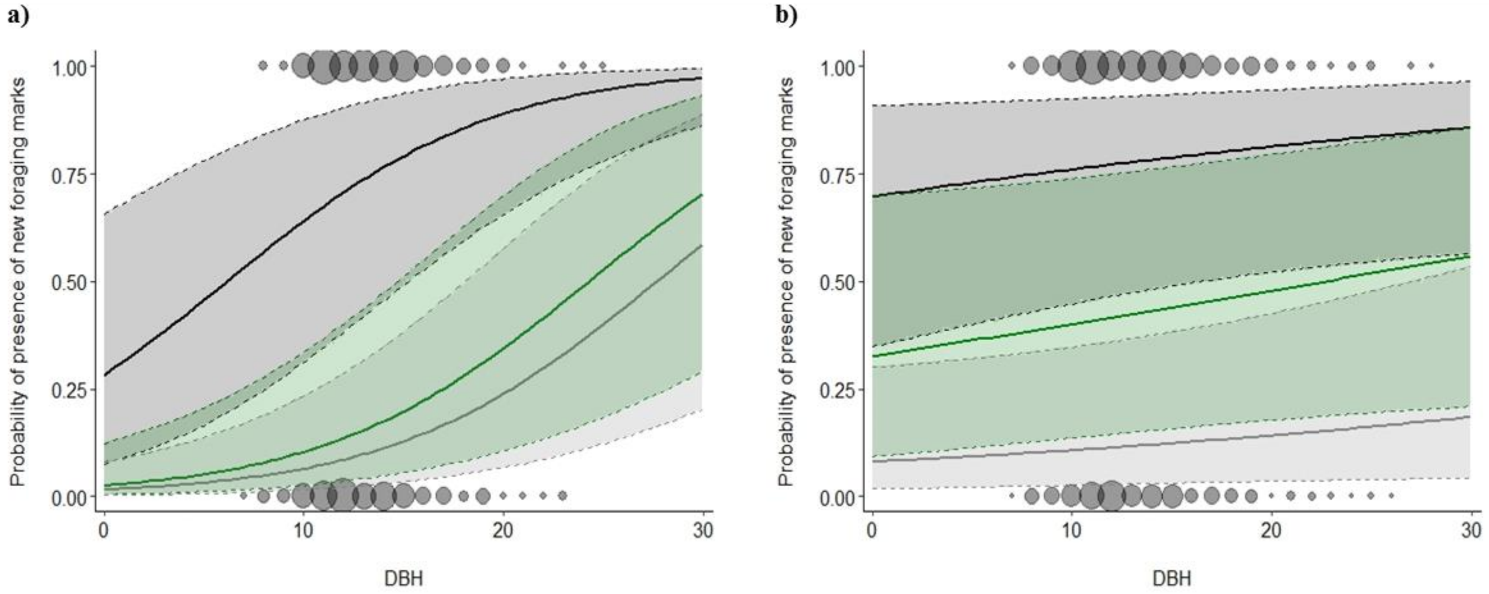

Figure 6. Projected probability of presence of new woodpecker foraging marks (± 95% CI) on girdled trees sampled in October 2016 based on the DBH of dead (black lines), dying (green lines) and live trees (grey lines) for a) uniform treatment and b) clustered treatment. Grey dots represent the distribution of raw data, where bigger dots are related to more observations and superposed dots are darker.

Bird survey

We recorded and identified a total of 884 birds from 50 species in 2015 and 858 birds from 42 species in 2016, representing an average (± SD) of 11.5 ± 2.8 and 12.3 ± 2.5 species per count period, respectively. In 2015, 6.67% (n = 59) of them were deadwood associated species compared to 9.67% (n = 83) in 2016. All species retained for detection probability evaluation had a $\hat{p} > 0.5$ (Table 7). More than one third of species required the use of the *Mc* model, suggesting that heterogeneity is an important component of their detectability. Detection probabilities were higher for the five species (or species groups) that we could have used playback data. For instance, Red-breasted Nuthatch had a null $\hat{p}$ because all the first detections occurred very late during point counts, but increased substantially during playback.

The first two axes of the RLQ analyses extracted 70.33% and 71.31% of the covariation between functional traits of birds and habitat variables, for 2015 and 2016 respectively (Table 8, Figure 7). In 2015, first axis was positively associated with bark insectivores, cavity nesters, residents, mean DBH of trees within site and recently decaying natural deadwood, and negatively associated with foliage insectivores, deciduous shrubs and open-cup nesters. Same global trends seemed to occur in 2016, but the first axis was highly positively associated with sap foragers and negatively associated with seed foragers. No relationship seemed to be evident between deadwood or cavity supply treatments and bird guilds associated with old forest attributes one-year *post*-treatment. Moreover, the fourth-corner analysis revealed that none of the bivariate associations was significant in 2015 and 2016. Finally, the combination of both approaches also showed that the global relationship of functional traits—habitat variables was not significant for both years (adjusted *p*-values of 0.792 and 0.085 for 2015 and 2016 respectively; based on 49,000 replicates).

Table 7. Detection probabilities ($\hat{p}$ ± SE) of birds (> 5 observations or counts) according to survey method (see Table 2 for species codes). Detection probabilities were estimated with the model having the lowest AIC value between *Mc* and *M* (Farnsworth et al. 2002).

Code	Detection propbability							
	Point counts				Playback			
	n	model	$\hat{p}$	SE	*n*	model	$\hat{p}$	SE
TEWA	233	*Mc*	0.95	0.05	-	-	-	-
RCKI	119	*Mc*	0.96	0.04	-	-	-	-
WTSP	110	*Mc*	0.79	0.18	-	-	-	-
NAWA	109	*Mc*	0.86	0.13	-	-	-	-
SWTH	105	*Mc*	0.92	0.07	-	-	-	-
BBWA	105	*Mc*	0.94	0.04	-	-	-	-
CMWA	89	*Mc*	0.92	0.07	-	-	-	-
GCKI	86	*Mc*	0.86	0.11	-	-	-	-
MAWA	73	*Mc*	0.60	0.44	-	-	-	-
DEJU	68	*M*	0.97	0.02	-	-	-	-
YRWA	61	*Mc*	0.67	0.34	-	-	-	-
EVGR	57	*M*	0.84	0.08	-	-	-	-
PISI	41	*M*	0.67	0.19	-	-	-	-
HETH	39	*Mc*	0.72	0.44	-	-	-	-
WOto	39	*M*	0.62	0.22	30	*M*	0.63	0.41
REVI	32	*M*	0.89	0.08	-	-	-	-
AMRO	20	*M*	0.64	0.29	-	-	-	-
YBSA	18	*M*	0.50	0.42	11	*M*	0.98	0.05
RBNU	16	*M*	0.00	0.88	41	*M*	0.98	0.02
WIWR	11	*M*	1.00	0.00	-	-	-	-
WOsp	9	*M*	0.57	0.52	7	*M*	0.97	0.08
GRAJ	7	*M*	0.98	0.03	-	-	-	-
PIWO	7	*M*	0.77	0.32	-	-	-	-
COYE	6	*M*	0.90	0.17	-	-	-	-
RUGR	5	*M*	0.88	0.21	-	-	-	-
BOCH	5	*M*	0.64	0.59	9	*M*	1.00	0.00
PIsp	5	*M*	0.98	0.05	-	-	-	-

Table 8. Results of the RLQ analyses and comparison with the separate ordination analyses (R, L and Q alone) in June 2015 and 2016.

Analysis	Spring 2015		Spring 2016	
	RLQ-axis 1	RLQ-axis 2	RLQ-axis 1	RLQ-axis 2
RLQ analysis				
Eigenvalue	0.016	0.005	0.020	0.013
Covariance	0.127	0.072	0.141	0.112
Correlation	0.129	0.093	0.141	0.133
R/RLQ (sd)	1.286	1.144	1.296	1.283
Q/RLQ (sd)	0.769	0.678	0.771	0.658
Explained variance (%) from separate ordinations				
R (Habitat variables, Hill-Smith)	21.03	16.16	21.00	16.93
L (Species, CA)	14.77	13.45	13.80	13.40
Q (Functional traits, MCA)	28.74	17.91	29.96	18.06
Inertia (Total variance explained)	53.19	17.14	43.63	27.68

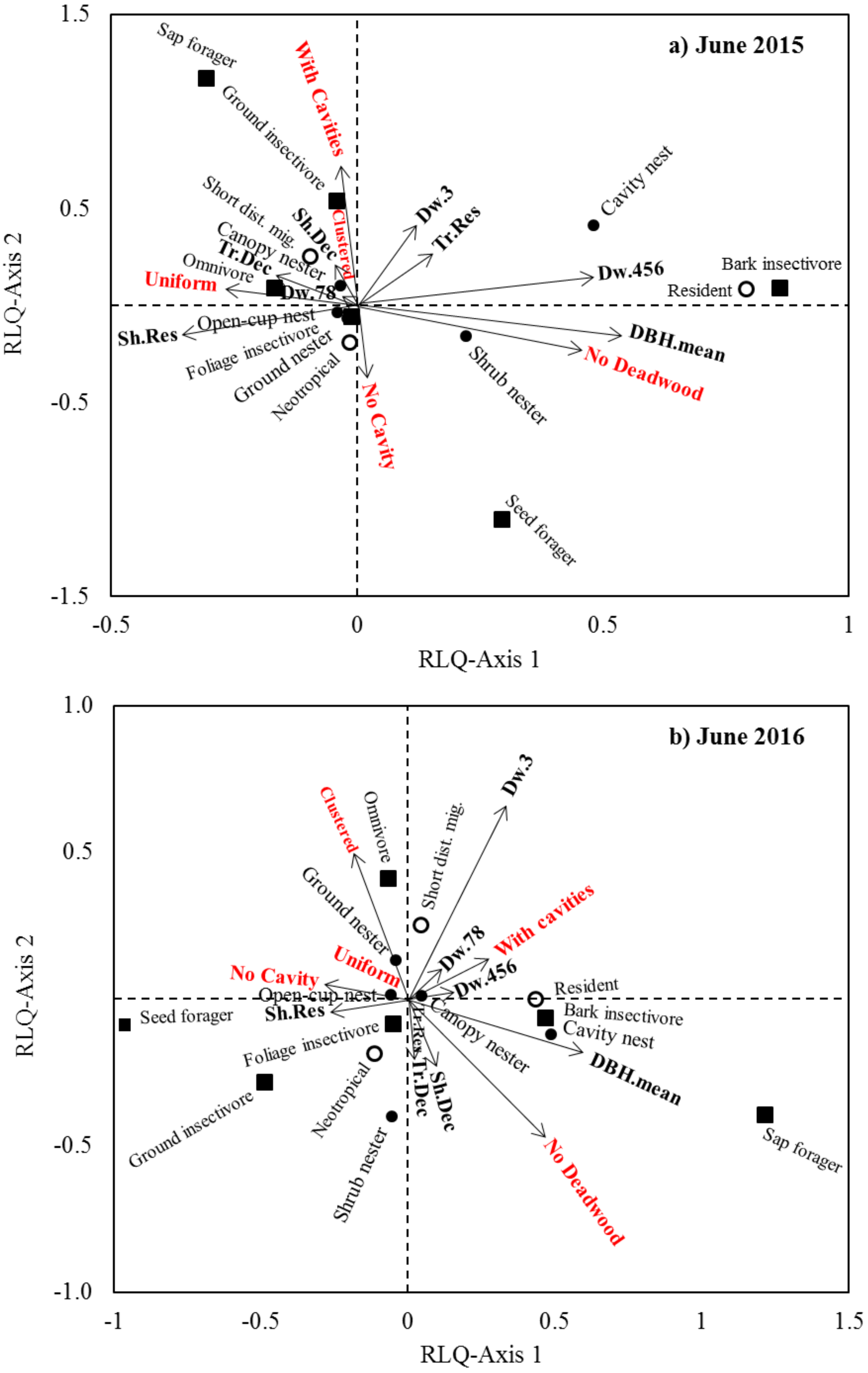

Figure 7. RLQ scores of habitat variables (bold font and arrows; treatments are in red) and functional traits (squares = foraging strategy; black dots = nest location and type; white circles = migration strategy) for a) 2015 and b) 2016. Note that scores for functional traits have been rescaled in order to fit in the same plot. Codes for habitat variables are shown in Table 1.

Cavity survey

On the 450 nest boxes installed in 2015, only 5 were used for nesting in June 2016, and all were used by the Boreal Chickadee. These birds occupied the two smaller nest boxes types and none of them was located on the edge of the road. All pairs successfully produced between 3 to 5 nestlings.

As revealed by monitoring cameras in summer and fall 2015, nest boxes of all types have been frequently used by other species outside the breeding bird season. For instance, we have recorded nest boxes used for roosting by red squirrel (*Tamiasciurus hudsonicus*), flying Squirrel (*Glaucomys sabrinus*) and deer Mouse (*Peromyscus maniculatus*). During the nest box survey of June 2016, we noted that 19 nest boxes (the 3 smaller sizes) were filled with vegetation debris, probably associated to squirrels. We also observed that 20.9% of nest box entrances (n = 94) were chewed by squirrels, often in order to enlarge the entrance (16.7% of the 3 larger sizes [n = 15] and 21.9% of the 3 smaller sized [n = 79]).

Discussion

Our study shows that tree girdling is an effective method to rapidly attract saproxylic beetles into 50-70 years-old even-aged black spruce forest stands. For every insect taxon sampled, except for Curculionidae (other than Scolytinae), there was a higher number of beetles captured at the treatment sites than at the control sites. We captured approximately 7-fold less beetles in 2016 (1 year after girdling) than in 2015 (few weeks after girdling), but the species composition remained almost the same. We also demonstrated that snag supply can attract foraging woodpeckers. Very few foraging marks (exclusively scaled bark) were observed in October 2015 (6 months after girdling) and in June 2016 (1 year after girdling), but in return, a large amount of foraging marks were detected in October 2016 (1 year and a half after girdling). Unlike what we might expect, the moment when we observed most foraging marks does not correspond to the moment when we captured most saproxylic beetles. That could be partly or concurrently explained by two factors: 1) beetle captures did not reflect the real colonization rate of girdled trees and 2) woodpeckers could have failed to detect beetles in 2015 even if there was a colonization.

Time lag between beetle captures and woodpecker foraging marks abundance

First, even if a larger number of beetles were captured in 2015, a weaker colonization success could have led to a lesser food supply for woodpeckers for that period, thus explaining the observation of only few foraging marks. Indeed, the use of flight-interception methods, such as trunk window traps, does not assess the actual colonization at the tree scale and substantial differences may occur between the number of flying beetles and those that oviposit (Boucher *et al.* 2012; Thibault and Moreau 2016b). Other methods, such as experimentally placing logs in rearing conditions, would have been useful to have a tree scale assessment of colonization (Saint-Germain *et al.* 2006; Thibault and Moreau 2016a).

The striped-ambrosia beetle, *Trypodendron lineatum*, is by far the most abundant species captured in 2015 and 2016. This wood-boring ambrosia beetle begins its spring dispersal flight when ambient temperature reaches 15.5°C, but mass flights occurs when mid day temperatures exceed 18°C (Chapman and Kinghorn 1958; Berryman 1988). Shortly after their dispersion, *T. lineatum* are highly attracted by ethanol produced by anaerobic metabolism of stressed or dying trees, and in a lesser extent, by low levels of the monoterpene α-pinene (Moeck 1970; Bauer and Vité 1975; Nijholt 1979). Once the first beetles have found a host, females will produce an aggregative pheromone (*i.e.* linetatin) to further attract dispersing mating males (Borden *et al.* 1979). After mating, females will bore their galleries approximately 2 cm into the sapwood to oviposit and then will feed from the symbiotic fungus they carry and that has been inoculated to the wood (Batra 1966). McIntosh and McLean (1997) estimated that *T. lineatum* (adults and their brood) would gradually exit their galleries (and the tree) after accumulation of 265 degree-days above a 13°C threshold after gallery establishment, leading to mid-july under meridional Canadian temperatures such as in the study area. Even if *T. lineatum* is highly associated with recently dead trees, it has been shown that they rather colonize timber killed at previous fall or winter than those killed the same spring (Dyer and Chapman 1965; Berryman 1988). These trees will have undergone ethanol production for a longer period of time and are more likely to have lower starch content in the sapwood and lower cell viability (Chapman and Dyer 1969). Moreover, conifers have a well-developed constitutive and induced defense system to prevent and counter bark attacks from beetles (Franceschi *et al.* 2005). By releasing large amount of resin and *de novo* synthesis or activation of chemicals (*e.g.* terpenoids, phenolics, enzymes, pathogenesis-related proteins), stressed trees can repel, flush out, or kill invading bark beetles (Franceschi *et al.* 2005). Indeed, it has been documented that *T. lineatum* can be deterred by high concentrations of turpentine oil (Nijholt 1973). Given that essential oils found in the bark of black spruce are mainly composed of turpentine-like compound (Francezon and Stevanovic 2017), fresh stressed girdled trees might have been more prone to counter saproxylic beetle invasion. Combined with inadequate physical characteristics of the too recently dying girdled trees, it may be plausible that colonization of 2015 did not occur representatively to the number of captured beetles. However, field observations allow to assert that there has been a certain degree of colonization, since several trees had frass (*i.e.* boring dust and feces cleaned out from the gallery) accumulated on the bark scales and at the base of the bole (Berryman 1988). Inversely, in 2016, more advanced degradation of girdled trees could have lowered defense mechanisms of trees and favored adequate sapwood characteristics, thus resulting in an important colonization of *T. lineatum* and in suitable foraging substrates for woodpeckers.

The second factor that could explain that foraging marks have not been detected the same year as the highest number of captured beetles is that, even if there was a colonization, woodpeckers could have failed to detect it in 2015. Although we did not directly assess it, the two main species that are likely to forage by bark scaling in our study area are BBWO and ATWO (Cadieux and Drapeau 2017). Both species forage almost exclusively on dying or recently dead trees (Nappi *et al.* 2015). In black spruce forests, Cadieux and Drapeau (2017) showed that *Picoides* bark scaling was significantly more frequent in > 90 years-old unpaludified stands than in 60-90 years-old stands, mainly because the formers are associated with higher structural diversity and high density of recently dead trees. Given that very few girdled trees showed visual signs of degradation during the first summer (*i.e.* red foliage) and the young age of forest stands (*i.e.* weak amount of natural deadwood; similar to younger stand surveyed by Cadieux and Drapeau (2017)), one can propose that woodpeckers were not primarily attracted by deadwood supply in 2015 because the habitat then seemed unsuitable (see Vergara *et al.* 2015). This is also consistent with the fact that most foraging marks were observed on recently dead girdled trees in October 2016, even if there were still live and dying girdled trees available.

Other time-related effects on the response of insects and birds to snag supply

Regardless colonization, differences in the number of captured saproxylic beetles between 2015 and 2016 also can be partly explained by several uncontrolled factors that may play a role in beetle activity, such as natural climatic variations or interannual changes in microhabitat characteristics (Berryman 1988; Seibold *et al.* 2016). Timing of sampling period could also have influenced the number of captures. For instance, early spring emergence in 2016 (*i.e.* before the installation of traps) could have led to a lower number of captures, but not necessarily a decreased colonization. However, given the unavailability of precise temperature data prior sampling periods, it is impossible to confirm such an affirmation.

The absence of woodpecker excavation marks during our survey suggests that they only fed on beetles present within or directly underneath the bark (*i.e.* mostly Scolytinae). BBWO most frequently excavate small holes to find wood-boring beetles but may also rely on scaling technique to access bark beetles (Tremblay *et al.* 2010, 2016). ATWO rather prefer feeding on bark beetles at any time (Nappi *et al.* 2015). Assuming a high insect colonization only in spring 2016 and given the fact that *T. linetaum* (adults and broods) remained in the sapwood of girdled trees until at least mid-july, it is more likely that the high proportion of new foraging marks detected in October 2016 is due to a high emergence rate of beetles during late-summer (13.3 beetles per successful gallery; Dyer 1963) combined with a high foraging activity during juvenile fall dispersion of woodpeckers (Tremblay *et al*. in prep.). Such a pulse in resource availability could thus have increased the cost-benefit ratio associated with foraging activities.

Moreover, low occurrence of new foraging marks on girdled trees in spring 2016, which covers the time frame between October 2015 and June 2016, could also be explained by different foraging ecology of woodpeckers during the breeding season. Indeed, it has been demonstrated that, during this period, Scolytinae were rare in BBWO diet and nestlings were rather provisioned with Cerambycidae (Tremblay *et al.* in prep.). One may suppose that Scolytinae are not enough energetically valuable in regard to other preys during the breeding season.

Differences between snag supply treatments

Except for Cerambycidae in 2015, we did not find any significant difference between uniformly and clustered distributed snags on the number of saproxylic beetles captured. This result contrasts with our expectations since the density of recent deadwood could increase the concentration of volatiles and thus favor the detection of suitable habitat patches by saproxylic beetles (Lindelöw *et al.* 1992; Saint-Germain *et al.* 2006; Park and Reid 2007). Based on the size of experimental sites (4 ha) and the relatively low distances between girdled trees in uniformly distributed snags treatments (10 m), it is possible that the difference in the concentration of volatiles released by snags at the stand scale was not enough to induce a change in their detectability by saproxylic beetles. Saint-Germain *et al.* (2006) reported that even if beetles in flight orient themselves toward habitat patches using host volatiles, they land on random trees and then perform final selection in a trial-and-error fashion. However, regardless statistical significance, we did observe a general trend to capture more beetles in clustered treatments.

Unlike saproxylic insects, woodpecker foraged more on girdled trees in clustered treatments than in uniform treatments. Most woodpeckers forage by sequentially visiting trees (Tingley *et al.* 2014; Nappi *et al.* 2015) and it is expected that each time that a bird moves to another foraging substrate, its quality should be higher than the quality of all available trees (Fretwell and Calver 1969; Rosenzweig 1981). Foraging decisions may be based on information gathered across multiple spatio-temporal scales, as demonstrated for Magellanic woodpeckers (*Campephilus magellanicus*; Vergara *et al.* 2016). Indeed, this species acts as *locally-informed forager* and uses visual cues from the immediate vicinity to select individual tree, whereas time spent to forage on the same tree is rather influenced by long-time memory of tree availability along foraging routes or within their home range (*i.e. route-informed forager*) and tree-level attributes (*e.g.* DBH, decay stage). Based on these foraging strategies, woodpeckers in our study area could have been more likely to find girdled trees in clustered than in uniform treatments because they were closer from one another and would have intensively use them given that foraging substrate was more abundant in those treatments than in their foraging route.

Effect of spatial scale on snag use

We found that various habitat variables at different scales influenced the number of beetles captured from the 4 taxa analyzed. Such varied response patterns between species groups have often been found in managed boreal forests (Olsson *et al.* 2012; Rubene *et al.* 2017). In this study, the number of Cerambycidae captured was positively affected by natural perturbations and recent cuts at different scales around sites. Boucher et al. (2016) suggested that several burn-associated species found in low number in green forests may benefit from high quality burned ecotones by increasing their populations. Clearcut areas can also leave variable quantities of stumps that may be used by saproxylic insects (Ranlund and Victorsson 2018). On the other hand, the opposite effect of old-growth forests on Cerambycidae occurrence may be linked to the higher proportion of more decayed snags within those stands, which are less suitable for stressed-host species due to the reduced inner bark moisture (Hanks 1999). Thus, smaller populations of such species around experimental sites could reduce the number of beetles available to be attracted by snag supply treatments. We observed inverse response for Curculionidae, which were positively affected by surrounding old-growth stands and negatively affected by natural perturbations. Béland (2017) found that *Pissodes dubius (striatulus)* – the most captured Curculionidae species in this study – is associated with live trees highly defoliated by the hemlock looper (*Lambdina fiscellaria*), whereas Wall (1988) linked this species with trees recently killed by the spruce budworm. This could partly support the positive effect of old-growth forests around sites, since these habitats could present similar forest attributes, but also contradicts the negative effect of natural perturbations. However, only limited information is available in regard of this species and such results suggest that clear interpretation might be difficult when analyzing various habitat factors, especially with limited dataset (n = 279). Scolytinae were not impacted by any of the landscape variables. Because of the disproportionate response of *T. lineatum* to host tree abundance (Park and Reid 2007), the addition of fresh snags at treatment sites could have led to a marginal effect of forest composition at a broader scale. Finally, the two Cleridae species detected (*Thanasimus undatulus* and *Thanasimus dubius*) are natural predators of bark beetles, so it is most likely that their presence is mainly linked to that of Scolytinae rather than for any landscape variables (Nappi *et al.* 2010). Indeed, Cleridae are attracted by the pheromones of their prey as well as monoterpenes emitted by dying trees (Bakke and Kvamme 1981; Chénier and Philogène 1989). By improving connectivity between habitats rich in Scolytinae, old-growth forest stands may also have acted as corridor, and thus partly explain the positive effect on the number of captures within sites.

Woodpeckers foraging mark presence was positively associated with the proportion of recent cuts (≤ 10 years) 1 km around sites. These results are similar to those obtained by other studies in unburned boreal forests, where BBWO tend to establish their home ranges in areas with high proportions of recent cuts and often nest in residual snags (Tremblay *et al.* 2009; 2015). It has also been shown that ATWO use clear-cut edges as movement corridors (Gagné *et al.* 2007). More open habitat around experimental sites may have favored movements amongst fine-scale habitat components within woodpeckers' home range (*e.g.* open nesting habitats towards denser foraging habitats) and increased the probability of detecting girdled trees. This explanation might be more accurate during fall 2015 and spring 2016, when girdled trees are thought to have been less suitable or less attractive for woodpeckers, than in fall 2016. During the first two periods, woodpeckers were possibly seeking food in a more exploratory way. In return, the principal driver of foraging habitat selection in fall 2016 was more likely the abundance of saproxylic beetles at sites, which could have encouraged woodpeckers to wander more widely in search of high quality patchy food resources (Tingley *et al.* 2014), thus partly explaining why the proportion of recent cuts around sites seemed to be less important.

At fine scale, in October 2016, the probability of presence of new woodpecker foraging marks was associated with recently dead trees of bigger size. These results are consistent with many other studies on foraging behavior of boreal woodpeckers (*e.g.* Imbeau and Desrochers 2002; Gagné *et al.* 2007; Tremblay *et al.* 2010; Nappi *et al.* 2015). Indeed, bigger trees are more likely to inhabit high density and diversity of saproxylic beetles (Nappi *et al.* 2003; Saint-Germain *et al.* 2004; Brin *et al.* 2010). However, the size of girdled trees was less important in clustered snag treatments since woodpecker would be more likely to forage on closer suitable trees than to systematically search for bigger ones. In other forests close to our study area, foraging BBWO and ATWO tend to select trees having a mean DBH ± SE of 18.3 ± 0.4 cm and 19.2 ± 0.5 cm respectively (Imbeau and Desrochers 2002; Tremblay *et al.* 2010). Given a mean DBH of 13.49 ± 0.1 for the 780 subsampled girdled trees, one can assume that girdling bigger trees would be more suitable for foraging woodpeckers. A substantial proportion of girdled trees (13.6%) were not dead even 1.5 years after girdling. It has been shown that girdled trees can live and even continue to grow for 1-2 years before the roots die from lack of photosynthate (Raffa and Berryman 1982).

Effect of cavity supply

Only 5 BOCH pairs used nest boxes (1.1 % of boxes available) and occupied the two smaller box sizes located away from the forest edge. The selection of small-sized nest boxes by chickadees has also been observed in nest-site limitation experiment (Aitken and Martin 2012). In this system, chickadees nest primarily in natural cavities excavated by small to medium-bodied species, even though most of available natural cavities were excavated by large-bodied woodpeckers (Aitken *et al.* 2002; Aitken and Martin 2007). Indeed, nesting in larger cavities may cause higher predation rate (Moeed and Dawson 1979; Robertson and Rendell 1990; Aitken *et al.* 2002).

Nest boxes occupancy in this study contrasts with that of other cavity supply studies in different forest systems (Cockle *et al.* 2010; Robles *et al.* 2012). For instance, Aitken and Martin (2012) observed that 10 % of their nest boxes were occupied by cavity nesters (birds or squirrels) the year after their installation in > 80-year-old mixed coniferous forests of Western Canada. Similarly, Miller (2010) detected the presence of secondary cavity users in 26 out of 320 nest boxes (8 %) within the first year after their addition in 40-year-old pine plantations. Very few studies have assessed cavity supply efficiency in eastern boreal forests, but an experiment in diversified balsam fir—white birch forests showed that between 1.3 and 11.5 % of 150 pairs of large-sized boxes were used annually by the Northern saw-whet owl (*Aegolius acadicus*) from 2006 to 2011 (Gagnon 2013). In that study, occupancy varied among years, with the first year having the most detections, and nest boxes were also used by several other species (Séguy 2014; J. Gagnon, pers. comm.). Other studies noted that nest boxes occupancy tends to increase with time since installation (Brawn and Balda 1988; Miller 2010; Cuatianquiz Lima and Macias Garcia 2016), suggesting that we might expect more use in upcoming years. In fact, nest box reuse among birds is common (Ficken *et al.* 1996; Steenhof and Peterson 2009), especially after a successful nesting (Aitken *et al.* 2002), but is highly variable depending on species (Hayward and Hayward 1993; Stanback and Rockwell 2003).

Several experimental studies showed that some cavity-nesting species appear to be limited by cavity availability and quickly respond to nest-sites manipulation, but that may depend on stand age, food availability and landscape features (see Newton 1994). For example, Hayward *et al.* (1993) reported that Boreal owls will use nest boxes in young forest stands when mature /old-growth forests are not available, but otherwise, they will avoid them. Given the low proportion of nest boxes used at our sites, one can think that nesting habitat for cavity users is not limiting at the landscape scale. However, based on 5km buffer around sites, only ca. 25 % of the surrounding habitats likely contain high quantity of deadwood (*i.e.* > 90 years-old stands or natural perturbations). Thus, even though > 90 years-old balsam fir stands may comprise high proportions of snags (33 % of all stems, 8 % are large dead stems; Vaillancourt *et al.* 2008), the impact of extensive harvesting may limit the availability of large snags at the landscape scale, and thus raise concerns about the sustainability of local populations of large cavity users (Côté *et al.* 2009; Edworthy and Martin 2013).

The use of nest boxes by red squirrels and northern flying squirrels as roosting sites is common (Patterson *et al.* 2007; Trudeau *et al.* 2012; Priol *et al.* 2014). However, given their capability to construct bolus nests in the tree canopy and to use underground burrows (Benhamou 1996), squirrels may not be limited by cavity availability (Ransome and Sullivan 2004). On the other hand, Aitken and Martin (2012) hypothesized that squirrels' preference for large-sized boxes and the enlargement of the entrances of smaller boxes may indicate a shortage of suitable large-sized den sites in their study area. This statement does not seem to be applicable to our study, since only the three smaller sizes were used for roosting and that larger nest boxes were chewed almost as much as the smaller ones.

Effect on global avian community

Bird assemblages characterized during our study are similar to what we might expect for boreal forests at these latitudes of eastern Canada (Lemaître *et al.* 2012; Desrochers and Drolet 2017; Zhao *et al.* 2017). The use of audio recordings allowed us to minimize observer-related biases (Sauer *et al.* 1994; Kendall *et al.* 1996; Shonfield and Bayne 2017) while adequately accounting for imperfect detectability of birds. In fact, detection probabilities estimated at our sites were on average higher than those from traditional point counts for the same species in similar habitats (Cadieux and Drapeau 2017; Desrochers and Drolet 2017). Celis-Murillo *et al.* (2009) also estimated higher detection probabilities when listening to audio files collected by a soundscape recording system versus data obtained by a field observer. Indeed, the use of recordings allows the observer to replay and visualize sonograms and to cross-validate songs with other experts or databases, thus enhancing the ability to detect and identify birds. Detection probabilities were increased when species were called, which also corroborates with other studies using both silent and playback approaches (Baumgardt *et al.* 2014; Rae *et al.* 2015). However, given the low occurrences of some species during bird surveys, such as woodpeckers, one must be careful when interpreting their high detection probabilities outside of the objectives of this study.

Our study failed to detect significant associations between birds' functional traits and habitat variables, but the RLQ ordination helps to visualize possible trends within dataset. For example, sap foragers and bark insectivores were associated with the presence of larger trees and higher amount of recently dead trees within sites, which have often been documented (Nappi *et al.* 2003; Tremblay *et al.* 2010; Cadieux and Drapeau 2017), but no treatment seemed to have an impact on singing breeding birds. The low occupancy of nest boxes in spring 2016 can explain the poor relationship with cavity nesters. On the other hand, given the high use of girdled trees by foraging woodpeckers, we should have expected a certain relationship between bark insectivores and deadwood supply treatments. However, because foraging marks have mostly been detected in October 2016 instead of

June 2016, one can assume that the attraction of bark insectivores only occurred after the point count survey. The absence of link in our analysis may be due to a timing issue according to methods rather than a true absence of effect.

Conclusion

Several studies assessed the unique effect of deadwood supply (Boucher *et al.* 2012; Thibault and Moreau 2016a; Barry *et al.* 2017) or cavity supply (Miller 2010; Aitken and Martin 2012; Trudeau *et al.* 2012) on deadwood associated species, but to our knowledge, very few have tested the impact of both at the same time (Caine and Marion 1999). Furthermore, structural enrichment experiments often measure the effects on a relatively restrained number of species. Here, we found that snag supply can quickly attract saproxylic beetles and foraging boreal woodpeckers in 50-70 years old black spruce stands but, in return, that nest boxes did not attract secondary cavity users as much as expected, at least one year after their installation. Nevertheless, even though immediate use of artificial cavities was low, pulses of dual resources (food and nest sites) may enhance overall habitat quality for secondary cavity users (Ransome and Sullivan 2004; Aitken and Martin 2012; Norris and Martin 2012).

With the implementation of ecosystem based management approaches to reduce the gap between managed and natural boreal forests, Québec's forest planners should aim to limit the simplification of the internal structure of forest stands as well as the rarefaction of certain types of deadwood (Jetté *et al.* 2012). To achieve that, researchers highlighted the importance of leaving a greater variety of forest remnants in terms of width, composition and structural attributes (Vaillancourt *et al.* 2008; Moussaoui *et al.* 2016). Similarly, in black spruce forests, Tremblay *et al.* (2015) recommended the protection of ~50 ha. patches of old irregular forest stands embedded in at least 30% of remnant productive forests within agglomeration of cutblocks. The use of extensive sylvicultural treatments, such as partial cutting, may also provide suitable habitat for deadwood associated species (Nappi *et al.* 2015). Nevertheless, when forest structures have been locally driven outside of their range of variability and that a conservation concern is identified, structural enrichment as a compensatory measure could be an effective way to palliate such deficits. If a problem occurs at a larger scale, for example, snag creation could even be integrated to actual forest practices (*e.g.* at the time of thinning entries, see Thibault and Moreau 2016a). Since those strategies can quickly become expensive, managers should prioritize their actions based on highest ecological benefits. Here we have shown that compensatory measures oriented toward early successional saproxylic beetles and foraging boreal woodpeckers should aim to create snags by girdling black spruces in several clusters and to choose the largest trees available. As they decay, created snags would remain suitable for those species over the firsts few years and would then become suitable for many other species afterward (*e.g.* primary and secondary cavity users, late-successional saproxylic organisms). Even though no minimal threshold has been identified in this study, it is expected that larger amount of snags would be required in highly managed landscapes. However, too many snags at local scale could lower occupancy of individual snag, as resource would become more abundant than colonizing rate (Ibarzabal *et al.* Unpublished data). Further studies in eastern Canadian boreal forests should aim to test different structural enrichment strategies (*e.g.* killing methods, target species, optimal quantities) according to different levels of management intensity. More adaptive methods could thus facilitate their implementation in commercial activities and favor benefits at larger scales.

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Annexe. List of saproxylic beetles captured

Family	**Genus**	**Species**	**Authority**	**2015**	***%***	**2016**	***%***
Cerambycidae	*Acmaeops*	*proteus*	(Kirby)	19	*0.08*	6	*0.16*
	Asemum	*striatum*	(Linnæus)	7	*0.03*	0	*0.00*
	Clytus	*ruricola*	(Olivier)	7	*0.03*	4	*0.11*
	Evodinus	*m. monticola*	(Randall)	6	*0.02*	1	*0.03*
	Meriellum	*proteus*	(Kirby)	1	*0.00*	1	*0.03*
	Monochamus	*s. scutellatus*	(Say)	19	*0.08*	15	*0.39*
	Phymatodes	*testaceus*	(Linnæus)	0	*0.00*	1	*0.03*
	Pogonocherus	*penicillatus*	LeConte	5	*0.02*	3	*0.08*
	Rhagium	*inquisitor*	(Linnæus)	6	*0.02*	9	*0.24*
	Tetropium	*cinnamopterum*	Kirby	183	*0.74*	8	*0.21*
	Trachysida	*mutabilis*	(Newman)	1	*0.00*	0	*0.00*
	Xylotrechus	*undulatus*	Say	12	*0.05*	4	*0.11*
				266	***1.07***	**52**	***1.37***
Cleridae	*Thanasimus*	*undatulus*	(Say)	230	*0.93*	89	*2.34*
	Thanasimus	*dubius*	(Fabricius)	8	*0.03*	1	*0.03*
	Zenodosus	*sanguineus*	(Say)	0	*0.00*	1	*0.03*
				238	***0.96***	**91**	***2.39***
Curculionidae	*Hylobius*	*congener*	Dalla Tore, Schenkling & Marshall	55	*0.22*	14	*0.37*
	Hylobius	*warreni*	Wood	7	*0.03*	3	*0.08*
	Pissodes	*dubius* (*striatulus*)	Randall ((Fabricius))	239	*0.96*	40	*1.05*
	Pissodes	*nemorensis*	Germar	10	*0.04*	0	*0.00*
	Pissodes	*rotundatus*	LeConte	0	*0.00*	1	*0.03*
	Rhyncolus	*macrops*	Buchanan	0	*0.00*	3	*0.08*
	-	*sp.*	-	1	*0.00*	0	*0.00*
				312	***1.26***	**61**	***1.60***
(Scolytinae)	*Crypturgus*	*borealis*	Swaine	2	*0.01*	2	*0.05*
	Dendroctonus	*rufipennis*	(Kirby)	19	*0.08*	2	*0.05*
	Dryocoetes	*affaber*	(Mannerheim)	65	*0.26*	63	*1.66*
	Dryocoetes	*autographus*	(Ratzeburg)	332	*1.34*	130	*3.42*
	Dryocoetes	*betulae*	Hopkins	51	*0.21*	77	*2.02*
	Dryocoetes	*caryi*	Hopkins	247	*0.99*	88	*2.31*
	Gnathotrichus	*materiarius*	(Fitch)	0	*0.00*	1	*0.03*
	Ips	*latidens*	(LeConte)	1	*0.00*	6	*0.16*
	Ips	*pini*	(Say)	1	*0.00*	0	*0.00*
	Orthotomicus	*caelatus*	(Eichhoff)	3	*0.01*	2	*0.05*
	Polygraphus	*rufipennis*	(Kirby)	1303	*5.25*	377	*9.91*
	Scolytus	*piceae*	(Swaine)	3	*0.01*	3	*0.08*
	Trypodendron	*lineatum*	(Olivier)	21983	*88.54*	2839	*74.61*
	Xyleborus	*sayi*	(Hopkins)	2	*0.01*	11	*0.29*
				24012	***96.71***	**3601**	***94.64***
Total				**24828**	***100.00***	**3805**	***100.00***

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CHAPITRE 3 : CONCLUSION GÉNÉRALE

Retour sur le projet et synthèse des résultats

Un des grands défis en foresterie au Québec est de favoriser des aménagements qui assureront la durabilité des écosystèmes. La SADF oriente donc certaines de ses actions dans le but de limiter l'écart entre la forêt naturelle et aménagée et de maintenir des habitats de qualité pour des espèces qui sont sensibles à l'aménagement forestier (Ministère des Forêts de la Faune et des Parcs 2015). Pour ce faire, la SADF prévoit d'inclure, dans les plans d'aménagement forestier, une analyse locale des enjeux écologiques – dont le bois mort – en fonction des exigences de certaines espèces particulières, et ultimement, de mettre en œuvre des solutions adaptées. Dans ce contexte, il est donc impératif de développer des connaissances scientifiques qui pourront servir de base décisionnelle aux aménagistes lors des planifications tactiques et opérationnelles (Jetté *et al.* 2012b; Ministère des Forêts de la Faune et des Parcs 2014a, b).

Ce projet d'aménagement compensatoire avait pour but de tester l'impact de la création artificielle de bois mort et de cavités en forêt boréale aménagée sur les espèces fauniques y étant associée. Bien que l'ajout d'attributs structuraux liés au bois mort ait fait l'objet de nombreuses études dans divers écosystèmes mondiaux (*p.ex.* Miller 2010; Robles *et al.* 2012; Lambrechts *et al.* 2013; Kilgo et Vukovich 2014), peu d'entre elles ont été réalisées en forêt boréale de l'est de l'Amérique du Nord. De plus, la majorité de ces recherches sont orientées sur un seul groupe d'utilisateur de bois mort, ou encore, étudient les liens avec une seule forme d'attribut structurel (Seibold *et al.* 2015).

Ainsi, notre dispositif expérimental nous a permis de documenter les liens qui existent entre divers groupes taxonomiques associés au bois mort debout en fonction de différents types d'attributs structuraux (chicots récents et cavités). L'application d'un tel dispositif dans de jeunes peuplements résineux de 50-70 ans, intégrés dans un paysage forestier aménagé, permet de compenser une situation où il peut y avoir un certain manque de bois mort à l'échelle fine tout en ayant une quantité variable à plus grande échelle. Le fait de considérer divers éléments spatiaux (*c.-à-d.* répartition spatiale des aménagements compensatoires, perturbations forestières autour des sites expérimentaux) nous a également permis de déterminer comment ces facteurs peuvent influencer la réponse de la faune à de tels traitements.

Globalement, les aménagements effectués ont permis d'attirer – à divers degrés – de nombreuses espèces associées au bois mort. Pour tous les taxons d'insectes échantillonnés, nous avons capturé plus d'individus dans les sites avec création de bois mort que dans les sites témoins. Les marques d'alimentation présentes sur les arbres récemment morts nous permettent également d'affirmer que l'addition de chicot peut rapidement attirer les espèces de pics se nourrissant des insectes présents dans/sous l'écorce. Il semble également y avoir davantage de coléoptères saproxyliques et de marques d'alimentation de pics dans les traitements où le bois mort est groupé que dans ceux où il est distribué uniformément; cet effet n'est cependant pas statistiquement significatif pour les insectes. Le nombre de Curculionidés, de Cérambycidés et de Clearidés capturés varie en fonction des caractéristiques du paysage liées à la présence naturelle de bois mort (*c.-à-d.* coupes récentes, vieilles forêts, perturbations naturelles majeures et partielles), et ce à différentes échelles spatiales. Aucune de ces variables ne semble cependant influencer le nombre de Scolytinés capturés. La présence de marques d'alimentation de pics est quant à elle positivement associée à une plus grande proportion de coupes récentes 1 km autour des sites expérimentaux. La présence de ces marques est d'autant plus associée, à petite échelle, à des chicots morts récemment qui présentent un plus grand diamètre.

L'utilisation des cavités artificielles (nichoirs) a cependant été relativement faible, une année après leur installation. Au total, des 450 nichoirs disponibles, seulement 5 ont été utilisés pour la nidification de mésanges à tête brune, et 19 ont été utilisés comme site de repos pour l'écureuil roux et/ou le grand polatouche. De surcroit, aucun changement global dans les populations d'oiseaux forestiers entre la saison de reproduction avant-aménagement et celle après-aménagement n'a été détecté. Les résultats obtenus nous permettent toutefois d'affirmer que de tels aménagements peuvent être bénéfiques très rapidement si le but premier est d'attirer les insectes saproxyliques associés au bois mort récent ainsi que leurs prédateurs. Pour la faune cavicole, il apparaît que d'autres facteurs limitent le degré et la rapidité de réponse à un apport anthropique en sites de nidification ou de repos.

Contributions appliquées du projet

Compte tenu des ressources importantes reliées à la confection et l'installation des nichoirs, en plus du temps requis pour anneler une grande quantité d'arbres, un dispositif semblable à celui présenté dans cette étude pourrait être réplicable dans un nombre limité de situations. À titre d'illustration, la pose de 450 nichoirs et l'annelage de 8000 arbres ont nécessité un effort total de près de 800 heures*personnes. Néanmoins, la reproductibilité demeure envisageable dans un contexte où une problématique de conservation en lien avec des espèces associées au bois mort est documentée sur un petit territoire. Il peut s'agir, par exemple, d'un territoire structuré (Cuatianquiz Lima et Macias Garcia 2016), d'une forêt d'étude ou d'enseignement (Thibault et Moreau 2016), d'un petit secteur ayant subi une perturbation anthropique majeure (Caine et Marion 1999), ou même d'une zone assurant la connectivité entre deux milieux de qualité (Schiegg 2000; Ranius *et al.* 2016).

Par ailleurs, Gundersen *et al.* (2017) ont démontré à l'aide d'un sondage à grande échelle, que les participants évaluaient à la hausse des images de forêt dont les caractéristiques reliées au bois mort avaient été effacées par ordinateur. Cependant, une fois informés sur le rôle écologique de ces attributs, les participants amélioraient l'impression qu'ils avaient de cette ressource et de son utilité dans l'écosystème. Ce type d'intervention pourrait donc être applicable dans un milieu touristique à des fins de sensibilisation, et potentiellement avoir un impact favorable sur l'opinion publique envers certaines pratiques sylvicoles (Gundersen *et al.* 2017).

Contributions théoriques du projet

Avant d'adopter des stratégies sylvicoles tenant compte de l'enjeu écologique du bois mort, il importe de se poser les questions adéquates en fonction de la région à l'étude (Angers 2009). D'abord, il faut déterminer quel régime de perturbation prédomine dans le secteur et quel patron de recrutement de bois mort cela engendre (*p.ex.* % de mortalité, distribution spatiale et temporelle, type de bois mort créé). Ensuite, il est également indispensable de définir quelles sont les caractéristiques de bois mort les plus importantes pour la région (*p.ex.* espèce, stade de décomposition, taille), et s'il y a présence d'espèces sensibles à cette ressource. Enfin, il importe d'avoir une bonne compréhension des régimes d’aménagement en vigueur et de l’influence qu’ils peuvent avoir sur le bois mort (*p.ex.* présence, patron de recrutement, distribution diamétrale). Si certaines formes de bois mort – ou leurs espèces associées – sont impossibles à maintenir par un aménagement conventionnel (*p.ex.* Vanderwel *et al.* 2009; Vanderwel *et al.* 2011; Ruel *et al.* 2013), il peut être utile de se baser sur des résultats provenant d’études expérimentales afin de développer de nouvelles stratégies.

Par exemple, considérant les résultats obtenus lors de ce projet, il pourrait être envisageable de créer artificiellement de petites agglomérations de bois mort debout – par étêtage ou par annelage – au moment des différentes entrées de coupes partielles ou d’éclaircies commerciales (Thibault et Moreau 2016). La même stratégie pourrait être adoptée dans le cas de coupes plus intensives, telles que les coupes totales, en créant de petits groupes de chicot à même les séparateurs de coupes ou en conservant des agrégats de souches hautes dans les parterres de coupes (Ranius *et al.* 2014). Peu importe les manœuvres retenues, il serait avantageux de cibler des arbres de grande taille, puisqu’ils peuvent répondre aux besoins écologiques d’un plus grand nombre d’espèces (Vaillancourt *et al.* 2008). Enfin, la mise en place d’un réseau de nichoirs pourrait s’avérer utile dans les paysages forestiers les plus intensivement aménagés, notamment dans les endroits offrants des opportunités d’interprétation de la nature ou de science citoyenne (*p.ex.* pourvoiries, Z.E.C., réseaux publics d’observation d’oiseaux). Toutefois, tel que démontré dans cette étude ainsi que dans de nombreuses autres (Warren *et al.* 2005; Kouki *et al.* 2012; Kroll *et al.* 2012), il importe de considérer la composition forestière à l’échelle du paysage lors de la planification d’une intervention visant l’enjeu écologique du bois mort, puisque certaines variables peuvent influencer le degré de réponse de plusieurs espèces associées.

Limites et améliorations

Plusieurs suggestions peuvent être émises suite à ce projet. D’abord, il serait nécessaire de couvrir une période temporelle beaucoup plus importante afin de pouvoir décrire correctement la réponse des espèces cavicoles à l’ajout de nichoirs. Il a en effet été documenté que l’utilisation de telles structures peut évoluer en fonction du temps depuis l’installation (Brawn et Balda 1988; Miller 2010). Il en va de même avec les espèces qui ont utilisé le bois mort artificiel. Puisque nous avons principalement attiré des espèces associées au bois mort récent, nous pouvons supposer qu'elles délaisseront ces chicots au profit de nouvelles espèces à un rythme proportionnel à la décomposition de la matière ligneuse (Saint-Germain *et al.* 2007; Cadieux et Drapeau 2017).

Par ailleurs, il serait intéressant de tester différentes quantités de ces attributs afin de déterminer des valeurs seuils auxquelles il est possible d'associer, à grande échelle, un degré minimal de réponse. À cet égard, Ibarzabal *et al.* (données non-publiées) ont observé une augmentation de la richesse spécifique d'insectes saproxyliques colonisateurs dès qu'une petite quantité d'arbres annelés était présente dans le peuplement. En augmentant la quantité d'arbres annelés, cette valeur a rapidement atteint un plateau avant de diminuer de façon significative. Ces résultats suggèrent donc que les insectes saproxyliques sont très efficaces pour détecter les arbres morts, mais que la ressource peut devenir rapidement surabondante et ainsi diminuer le nombre d'espèces observées par arbre.

Bien que nous ayons pu documenter l'effet de la supplémentation de bois mort et de cavités à l'échelle du peuplement, aucun de nos résultats ne nous permet de déterminer l'effet de telles interventions à l'échelle du paysage. Ainsi, en étudiant cette problématique selon un contexte spatial élargi, il pourrait être possible de définir le type d'action à entreprendre afin de maximiser les effets positifs : plusieurs petits groupes de chicots épars sur le territoire versus une concentration des efforts dans quelques zones prioritaires.

Une certaine mise en garde s'impose quant à l'utilisation de mesures compensatoires pour répondre à des enjeux écologiques. Bien qu'elles procurent un recrutement rapide de diverses formes de bois mort, ces méthodes devraient se limiter à des contextes de restauration d'habitat. Une gestion passive de la ressource (*c.-à-d.* sans création artificielle d'habitats) pourrait tout autant assurer une disponibilité et une diversité adéquate de bois mort à l'échelle du paysage (Tremblay *et al.* 2007; Angers 2009). En conséquence, les aménagistes pourraient prévoir, là où c'est possible, de préserver le bois mort ou les gros arbres moribonds déjà en place lors des interventions (Watt et Caceres 1999), de cibler certains habitats pour la protection d'éléments clés (c.-à-d. peupliers qui formeront de gros chicots, pins gris qui formeront des chicots longévifs; Angers *et al.* 2010), de laisser intact des séparateurs de coupes plus grands et plus âgés (Vaillancourt *et al.* 2008; Tremblay *et al.*

2015) ou d'établir davantage de secteurs de conservation totale. De plus, les aménagistes ont recours à diverses méthodes, telle que la modélisation du bois mort à grande échelle (*p.ex.*Venier *et al.* 2015) afin de raffiner, en amont, les directives d'aménagement forestier.

Finalement, bien que la compréhension de la dynamique des écosystèmes boréaux se soit grandement améliorée au cours des dernières décennies (Engelmark 1999; Bergeron *et al.* 2006), plusieurs questions demeurent quant aux conséquences que nos actions peuvent avoir sur les processus écologiques (Gauthier *et al.* 2009). Il est donc impératif d'aménager le territoire forestier selon des stratégies adaptatives qui sont en accord avec les nouvelles connaissances scientifiques dans le but d'établir des cibles de gestions représentant des niveaux d'altérations socialement et écologiquement acceptables. Le tout s'insère ainsi dans une volonté d'aménagement écosystémique visant la réduction de l'écart entre les forêts naturelles et aménagées, tout en facilitant la certification écologique des forêts commerciales.

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