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EFFETS DES PLANTATIONS D'ARBRES SUR LES COMMUNAUTÉS DE CARABES ET DE PETITS MAMMIFÈRES

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BS	Black spruce
CWD	Coarse woody debris
HL	Hybrid larch
HPO	Hybrid poplar
MNA	Minimum number alive
NRC	Naturally regenerated coniferous
NRD	Naturally regenerated deciduous
AIPL	Aire d'intensification de production ligneuse
FSC	Forest Stewardship Council
SM-YB	Sugar maple-Yellow birch
BF-YB	Balsam fir-Yellow birch
DBH	Diameter at breast height
Ha	Hectare
L	The transect length
d	Diameter of the CWD
PCA	Principal component analysis
Db-RDA	Distance-based redundancy analyses
PTCO	*Pterostichus coracinus*
PTAD	*Pterostichus adstrictus*
PTTR	*Pterostichus tristis*
CAIN	*Calathus ingratus*
PTPE	*Pterostichus pensylvanicus*
SYIM	*Synuchus impuctatus*

RÉSUMÉ

Afin de répondre à la demande croissante en bois, l'utilisation des plantations est en constante augmentation à travers le monde dont en Amérique du Nord. Les plantations forestières ont tendance à avoir une structure simplifiée comparée aux forêts naturelles car elles sont souvent monospécifiques et l'espacement entre les arbres est régulier. L'effet de cette simplification structurelle de l'habitat sur la faune est peu connu en Amérique du Nord. Le but de cette étude est de réaliser une première évaluation au Québec de l'impact des plantations de peupliers et mélèzes hybrides et d'épinettes noires sur les communautés de carabidés et de petits mammifères. Durant l'été 2015, en Haute-Mauricie, la diversité de ces communautés a été estimée dans sept plantations de peupliers hybrides et sept peuplements régénérés naturellement en peupliers faux-trembles après coupe (témoin). De plus la diversité des communautés de carabidés a été estimée dans cinq plantations de mélèzes hybrides, cinq plantations d'épinettes noires et cinq peuplements régénérés en forêt mixte après coupe (témoin). En plus de mesurer la diversité des communautés de carabidés et de petits mammifères, l'abondance ainsi que des variables démographiques ont été estimées chez le campagnol à dos roux (*Myodes gapperi*; espèce dominante dans les sites échantillonnés). La structure et la composition de la végétation, ont également été mesurées. Nous démontrons que les assemblages d'espèces de carabidés étaient différents entre les plantations et les peuplements régénérés naturellement, que ce soit en forêt feuillue ou résineuse. À l'inverse, l'abondance et les variables démographiques du campagnol à dos roux étaient similaires entre les plantations et les peuplements témoins. Cela suggère que pour le campagnol à dos roux, les plantations de peupliers hybrides offraient une qualité d'habitat similaire à celle rencontrée dans les peuplements régénérés naturellement. Cette similarité dans la qualité d'habitat serait expliquée par la présence d'éléments structuraux dans la strate arbustive et herbacée des plantations qui, bien qu'ils soient différents de ceux rencontrés dans les peuplements régénérés naturellement, remplissaient des fonctions similaires pour le campagnol à dos roux. Cependant, pour les carabidés, la présence de ces éléments structuraux ne semble pas suffisante pour que la qualité de l'habitat des plantations de peupliers hybrides soit équivalente à celle des peuplements régénérés naturellement en peupliers faux-trembles. Dans leur ensemble, les résultats de cette étude suggèrent que la complexité structurelle des strates herbacée et arbustive est une « keystone structure » (*sensu* Tews et al. 2004) qui influence à la fois les communautés de carabes et l'abondance des campagnols à dos roux. Ainsi, d'un point de vue appliqué, il semblerait important d'aménager les plantations de manière à assurer une certaine forme de complexité structurelle dans ces deux strates afin d'assurer le maintien de la diversité des carabes et des petits mammifères.

MOTS-CLÉS : Plantations; petits mammifères; carabidés; structure de la végétation; strate arbustive; strate herbacée

CHAPITRE I

INTRODUCTION

1.1 Importance et rôle des plantations

Les plantations, qui sont en plein essor, ont comme objectif de produire une plus grande quantité de bois sur une petite surface, et ce, en peu de temps(Carle et Holmgren, 2008 ; FAO, 2011). D'ici 2050, il est estimé qu'elles fourniront la moitié du bois de la production mondiale (Bauhus *et al.*, 2010). Elles sont décrites comme étant des forêts aménagées de façon intensive avec des arbres d'âge égal, présentant un espacement régulier et étant généralement monospécifique que ce soit indigène ou exotique (Varmola *et al.*, 2005). Au Québec, le nouveau régime forestier mis en place depuis avril 2013 prévoit que des *Aires d'intensification de production ligneuse* (AIPL) soient définies dans toutes les régions où l'on retrouve de la forêt publique productive (Laflèche et Cyr, 2013). À terme, c'est 15% du territoire forestier productif au Québec qui sera aménagé selon cet objectif d'intensification, de sorte à générer près de la moitié de la possibilité forestière annuelle (Réseau ligniculture Québec, s.d.).

1.2 Plantations et conservation de la biodiversité

Cette augmentation des plantations dans les forêts soulève des inquiétudes vis-à-vis leurs impacts sur la biodiversité. La raison est que par rapport à des forêts naturelles,

les forêts aménagées en plantation arborent généralement une structure et une composition végétales simplifiées qui représentent des habitats de moins bonne qualité pour de nombreuses espèces animales et végétales (Paillet *et al.*, 2010). Cela s'observe surtout lorsque les plantations sont composées d'espèces différentes de la forêt d'origine, d'arbres de la même espèce, d'âge similaire, plantés à égale distance, présentant une stratification verticale et horizontale uniforme et ayant un temps de rotation court (Carnus *et al.*, 2006 ; Hartley, 2002 ; Lugo *et al.*, 1993 ; Paillet *et al.*, 2010). Ces caractéristiques vont avoir des impacts sur la quantité de ressources biotiques et abiotiques disponibles à l'intérieur du peuplement ainsi que les caractéristiques physico-chimiques du sol ce qui peut restreindre la disponibilité de certains éléments de l'habitat dont dépendent d'autres espèces végétales (Barrette et Leblanc, 2013 ; Sebastià *et al.*, 2005 ; Standovár *et al.*, 2006). De plus, les plantations étant visées par des rotations courtes, toutes les superficies qu'elles occuperont sont d'emblées soustraites à la possibilité de devenir de vieilles forêts ou des forêts possédant de vieux arbres, des chicots et des débris ligneux.

Les plantations, via leur impact sur la structure et la composition des peuplements forestiers, influencent aussi la disponibilité de nourritures et d'habitats pour les communautés animales. Par exemple, les espèces d'oiseaux utilisant les plantations sont surtout des espèces associées à une strate arbustive dense, alors que les espèces spécialistes de vielles forêts et cavicoles n'y trouvent pas de sources de nourriture adéquates et les arbres matures requis pour la nidification (e.g. MacKay *et al.*, 2014 ; Riffell *et al.*, 2011). Il a notamment été démontré que les espèces qui dépendent du bois mort (e.g. coléoptères saproxyliques, petits mammifères, oiseaux cavicoles) seraient plus impactées par les plantations (où le bois mort est pratiquement absent dû à la préparation du terrain) que celles qui n'en dépendent pas (Paillet *et al.*, 2010). En plus, les plantations peuvent aussi indirectement, via la moindre diversité des plantes de sous-bois qui y poussent, avoir une forte influence sur les communautés animales qui lui sont associées (Bremer et Farley, 2010). En effet, il a été démontré que, globalement, la richesse spécifique de plusieurs taxons augmente avec la diversité des plantes (Castagneyrol et Jactel, 2012).

Toutefois, la perception générale que les plantations, lorsqu'elles remplacent une forêt, sont des « déserts biologiques » ne fournissant pas d'habitat adéquat pour la biodiversité est remise en cause (Bremer et Farley, 2010 ; Brockerhoff *et al.*, 2008a ; Quine et Humphrey, 2010). En effet, à l'échelle du peuplement, les impacts plus spécifiques des plantations sur la faune sont équivoques et dépendent en partie du groupe taxonomique étudié. Par exemple, la diversité des oiseaux et mammifères est généralement plus faible dans les plantations que les forêts naturelles, mais l'inverse est vrai pour les staphylins, une famille de coléoptères (Dauber *et al.*, 2010). De plus, la diversité des oiseaux et des carabes tend à augmenter avec l'âge des plantations de peupliers hybrides (Elek *et al.*, 2010 ; Riffell *et al.*, 2011), mais l'inverse a été observé pour les mammifères (Moser et Hilpp, 2003). Cette inconstance dans les résultats pourrait s'expliquer par notre compréhension limitée des relations existantes entre la composition et la structure des plantations et la diversité des communautés animales.

1.3 Les petits mammifères et les carabidés comme modèles biologiques

1.3.1 De bons bio-indicateurs

Les carabidés et les petits mammifères sont des groupes taxonomiques recommandés comme indicateurs de l'aménagement forestier, car ils sont relativement diversifiés en termes d'espèces (> 10 espèces par groupe), présents en grand nombre dans les forêts et facilement identifiables et capturables (e.g. Pearce et Venier, 2006 ; Pearce et Venier, 2005 ; Work *et al.*, 2008). Leur écologie est également bien connue et ils ont une fonction écologique importante dans les écosystèmes forestiers. D'un côté, les carabidés sont principalement des prédateurs qui régulent les populations de décomposeurs, et secondairement des granivores régulant la germination des plantes

(Lövei et Sunderland, 1996 ; Rainio et Niemelä, 2003). Leur forte biomasse fait qu'ils sont une source de nourriture importante pour de nombreux prédateurs tels les salamandres, petits mammifères et oiseaux (Lövei et Sunderland, 1996 ; Rainio et Niemelä, 2003). Les petits mammifères, quant à eux, disséminent les graines, spores et propagules des plantes vasculaires, bryophytes, lichens et champignons (Carey et Harrington, 2001). Ils participent à la décomposition de la matière organique et de la litière, régulent les populations d'invertébrés et servent de proies à plusieurs prédateurs terrestres et aviaires (Carey et Harrington, 2001). Finalement, comme ils ont une forte association avec les vieilles forêts et qu'ils répondent aux perturbations locales, ces deux groupes taxonomiques sont de bons indicateurs des conséquences des perturbations de celles-ci à court et long termes à l'échelle du peuplement (Pearce et Venier, 2006 ; Pearce et Venier, 2005).

1.3.2 Impacts des plantations sur la diversité des petits mammifères et carabidés

Généralement, les plantations, i.e. des peuplements arborant une composition et structure simplifiées, dont une faible quantité de bois morts relativement aux forêts naturelles, ne représentent pas un habitat d'aussi bonne qualité qu'une forêt naturelle pour la faune (Christian *et al.*, 1997). En effet, l'abondance des petits mammifères, lesquels dépendent des débris ligneux au sol (e.g. Etcheverry *et al.*, 2005) est souvent moindre dans les plantations comparativement aux forêts naturelles (Fauteux *et al.*, 2013). Le nombre d'espèces va également diminuer dans les plantations où les espèces généralistes vont dominer et les espèces spécialistes des vieilles forêts seront absentes ou en faible densité (Christian *et al.*, 1997). Par exemple, il a été observé que le campagnol des champs (*Microtus arvalis*) va seulement recoloniser une forêt 5 à 10 ans après une perturbation, comme une coupe à blanc suivie d'une plantation, et que le campagnol à dos roux (*Myodes gapperi*) y reviendra lorsque la végétation sera mature comme dans une vieille forêt (Pearce et Venier, 2005).

En plus, les vieilles forêts offrent une structure interne hétérogène créée par la végétation mature qui est recherchée par plusieurs espèces de carabidés. Ces espèces ne vont donc pas se retrouver dans des forêts qui ont un temps de rotation court, comme les plantations, car cette structure hétérogène n'a pas la chance de se mettre en place (Niemelä *et al.*, 1988). Par exemple, Cunningham *et al.*, 2005 ont observé une plus faible diversité structurelle des plantes de sous-bois accompagnée d'une plus faible diversité des carabidés dans les plantations comparé à des sites naturels. Il a également été démontré que la fermeture du couvert forestier était un facteur important affectant négativement la diversité spécifique et fonctionnelle des carabidés dans les plantations, et que la présence de trouées dans les plantations serait un attribut déterminant pour le maintien de la diversité des carabidés (Spake *et al.*, 2016). Il est donc probable que les plantations, à cause de leur structure interne simplifiée et l'absence de bois mort, amènent un changement dans la diversité et la composition des assemblages des petits mammifères et des carabidés.

1.4 Objectif principal de l'étude

Au Canada, de nombreux industriels forestiers détiennent la certification forestière (e.g. Forest Stewardship Council; FSC). Les gestionnaires de la certification FSC, à laquelle plusieurs compagnies adhèrent, ont émis des inquiétudes concernant l'impact potentiel des plantations sur la biodiversité. En plus, la littérature présente toujours des inconsistances quant aux effets des plantations sur la diversité animale ce qui rend une prise de position difficile. Peu d'études dans ce contexte ont été menées en forêt tempérée, mixte et boréale de l'Est canadien. Ainsi, l'objectif général de ce projet est de déterminer l'effet des plantations (peuplier et mélèze hybrides, épinette noire) sur la diversité des communautés de petits mammifères et de carabes en forêt mixte (Haute-Mauricie, Québec). De manière plus spécifique, ce projet va également déterminer quelles sont les caractéristiques internes du peuplement (e.g. structure et dans une moindre mesure, composition de la végétation) reliées aux plantations et aux peuplements régénérés naturellement qui expliquent les différences de diversité des communautés à l'étude.

Le chapitre II a été rédigé en anglais et contient toutes les sections, à l'exception du résumé, d'un article soumis à une revue révisée par les pairs. Cet exercice a été fait à des fins pédagogiques pour permettre à l'étudiante de s'exercer à la rédaction rigoureuse en anglais.

Dans le cadre de ce projet de recherche, Justine Fontaine-Topaloff était responsable du volet visant à comprendre l'impact des plantations sur la diversité animale. Un second volet, dirigé par un stagiaire postdoctoral, visait à comprendre l'impact des plantations sur la diversité végétale. Ces deux volets ont été réalisés dans les mêmes sites. Justine Fontaine-Topaloff a participé à la sélection des sites en Haute-Mauricie durant l'été 2015, a réalisé l'échantillonnage des petits mammifères et carabidés, et la caractérisation des habitats des petits mammifères dans les sites feuillus. Le stagiaire postdoctoral a réalisé les inventaires de carabidés dans les sites résineux, ainsi que la caractérisation des habitats des carabidés dans les sites résineux et feuillus. Justine Fontaine-Topaloff a identifié les espèces de carabes et a analysé les données visant à déterminer l'impact des plantations sur la diversité animale, tandis que le stagiaire postdoctoral a analysé les données et publié les résultats décrivant l'impact des plantations sur la diversité végétale (Royer-Tardif *et al.*, 2017).

CHAPITRE II

EFFECT OF TREE PLANTATIONS ON SMALL MAMMAL AND GROUND BEETLE COMMUNITIES

2.1 Introduction

Forest plantations – a subset of planted forests that usually "are intensively managed with even age-class structure and regular spacing trees" (Varmola *et al.*, 2005), are expected to increasingly contribute to the world wood supply, reaching half of the global industrial production before 2040 (Bauhus *et al.*, 2010). They are usually composed of introduced or indigenous species and, for the same production area, they will generate an amount of wood that exceed by far the one produced by natural forest (Bauhus *et al.*, 2010). For example, hybrid poplar in appropriate conditions can produced up to 2.5 more wood in a third of the time it takes for indigenous species to produce the same amount (Ménétrier, 2008). However, the expansion of areas occupied by plantations raises concern about the conservation of forest biodiversity because fauna and flora are often impoverished in plantations compared to natural forest (Hartley, 2002).

When they replace degraded land, plantations can be seen as "lesser evil" and positively impact biodiversity but when they replace natural forest they are mostly perceived as a threat to biodiversity (Brockerhoff *et al.*, 2008b). Generally, animal diversity is positively correlated with plants diversity and plantations often host a less diverse plant community compared to natural forest (Bremer et Farley, 2010 ; Castagneyrol et Jactel, 2012). Moreover, even when site preparation is minimal, exotic tree species outcompete the understory plant community by rapidly modifying the light regime and the microclimate because of their high growth rate (Duan *et al.*, 2010). This retroaction could lead to a poorly developed understory layer with a lower diversity of plant species, a situation that has been observed in early forest plantations in Southern Quebec (Aubin *et al.*, 2008). However, as plantations age, they generally tend to develop a more complex structure (i.e., uneven canopy, patchy understory and presence of coarse woody debris (Cunningham *et al.*, 2005)), that may dampen ecological divergence with naturally regenerated forests.

Plantations, compared to natural forests, usually have lower plants species richness and habitat complexity leading to differences in the animal communities they support, like insect species assemblages (Cunningham *et al.*, 2005). For example, many ground beetle groups have a higher species richness and a different community composition in more complex habitat compared to simpler ones (Lassau *et al.*, 2005). Furthermore, numerous animal species respond positively to the presence of a developed understory (Lindenmayer et Hobbs, 2004). Notably, for example, species richness and abundance of medium sized mammals were higher in plantations with a well developed understory compared to plantations with no or barely developed understory (Simonetti *et al.*, 2013). Indeed, a well developed understory provides an habitat with a denser vegetation, which helps maintain shelter, food and refuge for small mammals, thus sustaining higher abundance and greater local diversity (Rosalino *et al.*, 2009).

Coarse woody debris (CWD) are considered a keystone structure in managed forests (Tews *et al.* 2004) since their presence or addition strongly benefit diversity and abundance of small mammals (Fauteux *et al.*, 2013) and the species richness and abundance of many arthropod species (Seibold *et al.*, 2016). CWD are also reported to be of critical importance in managed forests because it provides opportunities for many species like small mammals, amphibians and reptiles to hide, forage, nest and hibernate (Freedman *et al.*, 1996). In managed forest, the presence of CWD increased the small mammals abundance and positively influenced demographics variables such as the number of young (Loeb, 1999). Finally, CWD are particularly important to specialist arthropods of deadwood, which have been reported to be negatively impacted by management practices that removes a large proportion of slash (Kappes *et al.*, 2009).

Small mammal and ground beetle communities were monitored in forest plantations and compared to communities found in naturally regenerated forests of similar age growing on similar sites. Our objectives were to evaluate if such plantations may have deleterious effects on the biodiversity of these taxa and if these effects were associated with vegetation structure and to a lesser extent diversity. In North America, forest plantations and their impacts on biodiversity have been poorly studied (Christian *et al.*, 1998). There has been several studies that analyzed the effects on diversity of partial or clear cuts compared to unmanaged or mature forests, and more often in coniferous or boreal forests than in temperate forests. (Addison et Barber, 1997 ; Beaudry *et al.*, 1997 ; JL Pearce *et al.*, 2003). In the few studies where the effects of plantations on biodiversity have been studied in North America, hybrid poplar plantations dominate (Christian *et al.*, 1998 ; Moser *et al.*, 2002). In a meta analysis Riffell *et al.*, (2011), highlight the lack of information about other planted species in North America and suggest to compare plantations not only to mature forest but also to forest of similar age. The present study is the first to compare plantations of different species to naturally regenerated stands of the same age in the mixedwood forests of Quebec, Canada. In these forests, black spruce (*Picea mariana*) has been the most commonly planted native species in the last several decades, but interest has been increasing in the recent years for plantations of clones from hybrids of indigenous and exotic parental stock, specifically hybrid poplar and hybrid larch (Park et Wilson, 2007). Small mammals and ground beetles were investigated because they are relatively diverse, have a well documented ecology, are abundant in mixedwood forests, and because they respond rapidly to local changes in their environment (Lövei et Sunderland, 1996 ; Pearce et Venier, 2005 ; Rainio et Niemelä, 2003).

From the literature, we expected to confirm that the diversity and the abundance of small mammal species, and their demographic variables, would be negatively affected in plantations compared to regenerated stands, in particular because of a lower amount of CWD present. For ground beetles, we expected that the structural complexity of plantations would be different compared to regenerated stands and that this would affect community compositions by changing species identity and reducing the number of forest-associated species.

2.2 Materials and Methods

2.2.1 Study area

The study area is located near La Tuque in the Mauricie administrative region of Québec, Canada (Figure 2.1). It is part of the TRIAD functional zoning project (Messier *et al.*, 2009). More precisely, the study area is lying at the limits of the Sugar maple-Yellow birch (SM-YB) and the Balsam fir-Yellow birch (BF-YB) bioclimatic domains (Saucier *et al.*, 2009). The SM-YB domain is composed mainly of sugar maple (*Acer saccharum* Marsh.), yellow birch (*B. alleghaniensis* Britt.), white birch (*Betula papyrifera* Marsh.), red maple (*A. rubrum* L.), red spruce (*Picea rubens* Sarg.), and white pine (*Pinus strobus* L.), The BF-YB is composed mainly of balsam fir *(Abies balsamea* L.), jack pine (*Pinus banksiana* Lamb.), white birch, yellow birch, trembling aspen (*Populus tremuloides* Michx.), white spruce (*Picea glauca* [Moench] Voss) and white pine. Wildfire, insect outbreaks (*Choristoneura fumiferana* [Clemens]) and windthrow are the dominant natural disturbances in this area (Messier *et al.*, 2009). The average annual temperature is 3.5 °C, ranging from a minimum of -21 °C in January to a maximum of 25 °C in July. The average annual precipitation is 919 mm, including 186 cm of snow (Environment Canada, 2017).

2.2.2 Experimental Design

A total of 29 clear-cut stands were selected from previously deciduous (N=14) and coniferous (N=15) forest covers (Figure 2.1). The 29 stands were selected according to four criteria: (1) similar age and canopy closure (2) larger than 4 ha to limit edge effects, (3) absence of streams and roads, and (4) similar topography, drainage, soil texture, and soil depth. Some stands, particularly in the coniferous layout, where spatially aggregated because of harvest schedule and of the logistic constraints of site preparation before planting. A detailed description of all the stands is presented in table S1. The deciduous stands included seven naturally regenerated trembling aspen stands ("NRD stands" hereafter) and seven hybrid poplar plantations (P. *balsamifera* x *maximowiczii;* "HPO plantation" hereafter). The plantations were established in 2006, five to seven years after the clear-cuts. Competitive vegetation was removed mechanically using a clearing saw the year following planting. The coniferous stands included five naturally regenerated stands (16-years-old; "NRC stands" hereafter) dominated by a mixture of balsam fir, red maple, trembling aspen, and yellow birch, five stands planted with native black spruce ("BS plantation" hereafter; (25-years-old), and five hybrid larch (*Larix* X *eurolepis* Henry) plantations (16-years-old; "HL plantation" hereafter) developed from two parental species (*L. kaempferi* (Lamb.) and *L. decidua* Mill.) exotic to North America. Site preparation occurred only prior to planting black spruce by removal slash. Herbicide (hexazinone: Velpar L, 9 L/ha) was applied one year after planting. A mechanical vegetation control treatment was applied (2001-2002) to the hybrid larch plantations using a clearing saw.

2.2.3 Ground beetle sampling and habitat characterization

In each stand, ground beetles were sampled from June 1st to August 15, 2015 with six pitfall traps placed within three circular sampling plots of 100 m^2 (two traps per plot) randomly located in each stand at a minimum distance of 75 m of each other and of the stand edge. The two pitfall traps in each plot were randomly placed at a minimum distance of 5 m from each other and filled with 100 mL of a 40% ethanol solution with traces of household vinegar (5% acetic acid) to kill and preserve all insects. Pitfall traps were visited every two weeks and emptied and refilled with 100 mL of the preservative solution. Samples were preserved in 70% ethanol and placed in a cold room until identification. Identification of all the individuals to the species level has been done following the nomenclature of Larochelle (1976) and confirmed by Y. Bousquet, (Agriculture Canada). The number of individuals in the two pitfall traps were summed by species to obtain an estimate of their abundance. When pitfall traps in a plot were severely disturbed by bears, the plot was removed from the statistical analyses because richness and composition of the ground beetle communities were not accurately estimated (N=4, all in HPO plantations).

The habitat around the pitfall traps was characterized by measuring several attributes of the vegetation, as detailed in Royer-Tardif *et al.*, (2017). We focussed on structural and compositional attributes of the vegetation because both can be important for structuring ground beetle communities (Haddad *et al.*, 2001 ; Lassau *et al.*, 2005). Within each plot, all trees with a diameter at breast height (DBH) > 2 cm were identified to the species level and their DBH was recorded. Additionally, the shrub layer, defined as all woody stems with a height > 1 m and a DBH < 2 cm, was characterized along four transects (5.64 m long) extending from the center of each plot towards each cardinal direction (N, S, E, W). The density of each shrub species was recorded by counting each stem of each species in 8 circular microplots of 4 m^2 located at 1.6 and 4 m from the plot center along the aforementioned transects. Using data from the shrub and tree inventories, abundance of each tree and shrub species was expressed for each plot based on the sum of the basal area ($m^2.ha^{-1}$), and on stem densities, respectively. For each plot, canopy openness was averaged from eight hemispherical photographs (Nikon D300, equipped with a fisheye lens, EX Sigma) taken 1 m above the ground, one in each of the microplots. Photographs were analyzed using the *sky* package in R (Bachelot, 2016). The understory layer included herbs and ferns, as well as woody species smaller than 1 m in height. To record understory plant occurrence for each plot, a total of 16 quadrats (0.5 m^2) were sampled, four on each of the previously defined transects, at 1, 2.2, 3.4 and 4.6 m from the plot center. The proportion of ground covered by tree leaves, herbs, mosses and dead wood, was recorded in 10 x 10 cm quadrats at eight locations along the transects (1 and 3.4 m from the plot center and in each cardinal direction). This habitat characterization was not available in two plots located in hybrid larch plantations and black spruce plantations because data were lost.

2.2.4 Small mammal sampling and habitat characterization

We sampled small mammals in the five HPO plantations and the five NRD stands of the deciduous layout. No trapping was conducted in the coniferous layout because it was not logically possible for us to monitors live traps in all study sites simultaneously. Small mammals were trapped between June 8 and August 15 in 2015 along two 140 m parallel transects located at least 50 m apart of each other and from the stand edge. Live traps (7.7 x 8.8 x 23.0 cm; Sherman Traps, Tallahassee, Fla.) were placed every 10 m along each transect for a total of 30 traps per stand. These traps were baited with a piece of apple, cotton and peanut butter to provide humidity, nesting and food to each captured individual. Trapping lasted five consecutive days. Live traps were inspected and re-set at dawn daily. Before being released, captured animals were ear-tagged with a unique tag number, weighted, sexed and identified to the species according to Prescott et Richard, (2013). We estimated their abundance in each stand as the minimum number known alive (MNA) per 100 trap-nights corrected for sprung traps (Beauvais et Buskirk, 1999). The low number of captures (five sites had less than 10 captures) and recaptures in several sites (three sites had no recaptures) prevented us from using capture-recapture models (e.g. Teixeira *et al.*, 2017) to estimate species density in each stand.

The habitat (vegetation attributes) was characterized at each trap along the trapping transects within each stand. This characterization focussed on structural attributes of the vegetation, such as the coarse woody debris, because they are known to strongly influence small mammals abundance (e.g., Fauteux *et al.*, 2013 ; Teixeira *et al.*, 2017). Species and DBH of all the saplings and trees with a DBH > 1 cm were recorded in a 2 x 2 m quadrat centered on each live trap. The proportion of the ground covered by moss and sphagnum, dead leaves, graminoid and herbs was visually estimated within a 1 × 1 m quadrat centered on each trap. Canopy closure was estimated at each trap with a convex densiometer held 1 m above the trap. To further quantify cover availability around each trap, we estimated lateral visual obstruction caused by understory vegetation by observing a 0.4 x 1.5 m profile board separated in four 35cm segments of different colour (Nudds, 1977). Visual obstruction of each segment was estimated in 25% classes in opposite directions (north-south and west-east) from 4m away, the mid-distance being centered on the trap. We used the mean of the two readings in subsequent analyses. Finally, the volume of coarse woody debris (CWD) ($m^3.ha^{-1}$; length ≥ 1 m and diameter > 9 cm) was estimated at each trap using the line-intercept method (Ståhl, 1997) along a 4-m-long transect oriented north-south and centered on the trap. The diameter of each CWD was measured at the point of intersection with the transect and the volume was calculated using the following equation (de Vries, 1973): CWD volume=$\frac{\pi^2}{8\,L} \times \sum d^2$, where L is the transect length (m), and d is diameter of the CWD (cm).

2.2.5 Statistical analysis

We first summarized the variation in vegetation attributes (Table S2) among plantations and naturally regenerated stands with a principal component analysis (PCA) (R package Vegan; Oksanen et al. 2017). Three separate PCAs were performed on the vegetation datasets that characterize the habitats of small mammals (deciduous layout) and ground beetles (deciduous and coniferous layouts). Sphagnum, moss and graminoid covers were not included in the PCA analysis because of their low occurrence. A broken stick model was used to select the PCA axes that best summarized vegetation gradients (Borcard *et al.*, 2011). Then, we performed a mixed-effect one-way ANOVA (R package *nlme*, Pinheiro et al. 2017) on scores of each significant PCA axis to determine which vegetation gradients best described differences between plantations and naturally regenerated stands. Plot or transect were nested within stand and treated as random factors in the models to account for the lack of independence in the data. In the coniferous layout, if the ANOVA was significant, a post-hoc comparison of the three stands type (BS, HL and NRC) was run and p-values were adjusted with a Bonferroni correction.

For both the deciduous and coniferous layouts, differences in species diversity (expressed by species richness and by the exponential of the Shannon index) between plantations versus naturally regenerated were tested for ground beetles with a mixed-effect one-way ANOVA (R package *nlme*), with individual stands included as a random factor in the models. Again, if the ANOVA was significant in the coniferous layout, a post-hoc comparison of the three stands type (BS, HL and NRC) was run and p-values adjusted with a Bonferroni correction. For small mammals, only species diversity expressed by the exponential of the Shannon index species richness was tested because of the small number of species that were captured in each deciduous stand ($n \leq 2$ in 70% of stands). Differences in ground beetle communities between stand types were tested using a non-parametric MANOVA (R package *vegan*) based on the

Euclidean distances derived from Hellinger-transformed abundance matrices (PERMANOVA; Anderson, 2001). When a significant difference was found, pairwise comparisons (with p-values adjusted with a Bonferroni correction) was used to identify which communities differed between planted and naturally regenerated stands. Rare species (species that were present in less than 5 plots), which were located in plantations, were excluded from the non-parametric MANOVA (HPO plantations, n=4 species; BS plantations, n=1; HL plantations, n=6).

To explain the statistical differences in species composition between communities of ground beetles, the relationships between vegetation attributes and species composition were evidenced with a partial distance-based redundancy analyses (db-RDA; Legendre et Andersson, 1999) based on the Euclidean distances derived from Hellinger-transformed abundance matrices. A matrix of geographic coordinates of plots was added as a covariable in both analyses (coniferous and deciduous layout) to investigate the relationships between vegetation attributes and species composition once any potential spatial effect linked to stand location has been taken into account. This spatial effect may have been particularly important in the coniferous layout because each stand type (NRC, BS, HL) was spatially clumped in different areas (Figure 2.1). The significance of the db-RDA was tested with the *anova.cca* function where permutations (999 permutations) were ran at the within-stand level (R package *vegan*).

Such community analyses could not be performed on small mammal data because of the small number of species that were captured, and their generally low occurrences (Table S3). However, we investigated whether the abundance of red-backed vole, the most common species in our study, was different between HPO plantations and NRD stands, at both coarse (stand) and fine (trap) scales of resolution. At the coarse scale, abundance (minimum number alive, MNA) of voles estimated on each transect was first compared between HPO plantations and NRD stands with a negative binomial mixed-effect model (R package *glmmADMB*; Bolker *et al.*, 2012). The lack of independence among data from transects located in a same stand was included by adding stands as a random effect into the model. The count of trap-nights was also added as an offset variable into the model to control for differences in effort units among stands due to traps disturbed by bears in three stands. The offset variable makes model adjustments while being constrained to have a regression coefficient of 1 (Hilbe, 2011). Vegetation attributes that influenced vole abundances were then identified by including into the model scores of PCA axes (averaged per transect) that significantly summarized vegetation gradients. Scores of significant PCA axes were preferred to values of vegetation attributes because of the high number of vegetation variables (n = 9) compared to the dataset size (n = 20 transects).

At the fine scale, differences in trap (microhabitat) use by voles between HPO plantations and NRD stands were investigated by evaluating whether PCA scores of traps used by voles (niche location) were different between stand types. We used scores from the first PCA axis describing vegetation gradient that significantly discriminated stand types (see the *Results* section) and retained scores related to the trap used by the voles. We weighted the occurrence of each trap score by the number of captures of red-backed voles in the trap. For example, a trap with two captures was duplicated in the data set and a trap with one capture was included only once. The weighing assumes that the frequency of captures at a trap correlates with the red-backed vole preference for a microhabitat (Ale *et al.*, 2011). We then tested if the niche location (PCA scores of traps used by voles) was different between the HPO plantations and NRD stands using a linear mixed-effect model (R package *nlme*). The lack of independence among data from transects located in a same stand was included by adding transects nested in stands as a random effect into the model.

Demographic variables such as sex or young/adult ratios and individual body mass may be effected by vegetation attributes found in plantations (e.g., Loeb, 1999 ; Martin *et al.*, 2012). Consequently, differences between HPO plantations and NRD stands were tested for male/female and young/adult ratios estimated by transect (n=17, HPO = 8, NRD = 9). The individual body mass-length relationship (n=108) was tested using linear mixed-effect models (R package *nlme*). A binomial distribution was used for ratios and a gaussian distribution for the body mass data. Again, individual stands were considered as a random variable.

All statistical analyses were performed in the version 3.3.2 of the R software (R Development Core Team, 2017).

2.3 Results

2.3.1 Differences in habitat characteristics

More than half (54 %) of the variance in the vegetation attributes measured to characterize ground beetle habitats in the deciduous layout was explained by the two first principal components of the PCA (Figure 2.2a). However, only the scores of the first component (i.e., first axis; 31 % of the variance) differed significantly between HPO plantations and NRD stands (Table 2.1a and 2.1b). Compared to NRD stands, HPO plantations were characterised by a higher herb cover, density and richness of shrubs, whereas a higher basal area and percent of dead leaf and dead wood ground cover characterized the NRD stands (Figure 2.2a). In the coniferous layout, the first axis of the PCA explained 46% of the variance in vegetation attributes (Figure 2.2b). Scores of this first axis differed among stand types, more specifically between NRC stands and the two coniferous plantation types (Table 2.1c). They did not differ between BS and HL plantations (Table 2.1c). Compared to coniferous plantations, the NRC stands were characterized by a higher ground cover of dead leaf and dead wood, along with higher tree and shrub densities, and higher shrub diversity and richness, while the two plantations had a higher basal area (Figure 2.2b).

For small mammals in the deciduous layout, the first component of the PCA explained 29 % of the variance in vegetation attributes. Though the broken stick model indicated that none of the PCA axis was significant, we investigated whether scores of the first component differed between stand types and found significant differences between HPO plantations and NRD stands (Table 2.1d). Compared to NRD stands, the HPO plantations were characterised by a higher low-lying (<75 cm) lateral visual obstruction, probably due to the high cover by herbs, but also by a higher high-lying lateral visual obstruction (Figure 2.2c). NRD stands were characterized by larger volumes of CWD on the ground relatively to HPO plantations (Figure 2.2c).

2.3.2 Habitat effect on the ground beetle communities

As the result of a sampling effort of 11 492 trap-nights, a total of 7 533 ground beetle individuals from 28 species were captured in the 29 study stands (Table S3). In the deciduous and coniferous layouts, 2 046 individuals from 21 species and 5 487 individuals from 24 species were captured, respectively. Of all the captures, 95 % are represented by *Synuchus impunctatus* (Say) (39%), *Pterostichus coracinus* (Newman) (34 %), *Pterostichus pensylvanicus* (LeConte) (9 %), *Pterostichus tristis* (6 %), *Pterostichus adstrictus* (Eschscholtz) (4 %) and *Calathus ingratus* (Dejean) (3 %) (Table S3).

Ground beetle species richness was not different between plantations and naturally regenerated stands in both the deciduous and the coniferous layouts (Figure 2.3; Table 2.2a and 2.2c). However, in the deciduous layout, the exponential of the Shannon index revealed a significantly higher diversity in NRD stands compared to HPO plantations (Figure 2.3; Table 2.2b). In the coniferous layout, the exponential of the Shannon index was significantly higher in the BS relatively to HL plantations but did not differ between plantations and NRC stands (Figure 2.3; Table 2.2d).

Ground beetle species assemblages were significantly different between plantations and naturally regenerated stands in the deciduous layout (Figure 2.4a; Table 2.3a). Out of the 21 species captured in deciduous stands, 12 were present in both HPO plantations and NRD stands while five species were specific to HPO plantations (Table S3). Thus, only 57% of species were shared between HPO plantations and NRD stands. Vegetation attributes significantly explained 43% of the variation in ground beetles species assemblages (db-RDA: N = 38, DF = 14, F-value = 1.84, p-value = 0.001; Figure 2.5a). Geographical coordinates of the stands, included as a covariable in the analysis, explained only 6 % of the variation. Four groups of ground beetles were related to different vegetation attributes. *Pterostichus coracinus* (PTCO), *Pterostichus adstrictus* (PTAD), *Pterostichus tristis* (PTTR) and *Calathus ingratus* (CAIN) were more abundant in plots with a high cover of dead wood, dead leaf cover and a high basal area, and a low level of herb cover and tree species richness, characteristic of plots mainly found in NRD stands (Figure 2.5a). *Pterostichus pensylvanicus* (PTPE) was also more abundant in NRD stands, in plots having a low diversity and density of shrubs and offering a higher diversity and density of trees. Conversely, *Synuchus impuctatus* (SYIM) was more abundant in plots having a higher diversity and density of shrubs, i.e. in the HPO plantations (Figure 2.5a). The other species (centered on the axes) were not related to specific vegetation attribute or stand type (Figure 2.5a).

In the coniferous layout, ground beetles species assemblage also significantly differed between NRC stands and plantations, as well as between HL and BS plantations (Table 2.3b and 2.3c; Figure 2.4b). Out of the 24 species inventoried in coniferous stands, 11 were detected in the three stand types (NRC stands, BS and HL plantations) while one and three species were specific to BS and HL plantations, respectively (Table S3). Thus, and similarly to the deciduous layout, BS and HL plantations together shared only 54% of the species detected in the coniferous layout. But contrary to the deciduous layout, the vegetation attributes we measured did not allow to explain variation in the species assemblages (N = 43, DF = 12, p-value = 0.338, F-value = 2.20) (Figure 2.5b).

2.3.3 Habitat effect on the red-backed voles

A sampling effort of 1 365 trap-nights in the deciduous layout led to the capture of 150 different individuals (for a total of 266 capture/recapture events) belonging to five species (Table S3). Red-backed voles was the most abundant species with 80% of all captured individuals, whereas woodland jumping mouse (*Napaeozapus insignis* (Miller, 1891)), eastern chipmunk (*Tamias striatus* (Linnaeus, 1758)), a mouse species (*Peromyscus sp.*) and an unidentified species of shrew constituted the remaining captures.

Small mammal diversity (the exponential of the Shannon index; Figure 2.6; Table 2.2e) and red-backed vole abundance (HPO plantations: mean (± standard-error) = 7.52 ± 5.84, NRD stands: mean (± standard-error) = 8.89 ± 6.26) (Table 2.4a) did not differ between the HPO plantations and the NRD stands. Furthermore, red-backed vole abundance was not influenced by the vegetation gradient represented by the first axis of the PCA (Table 2.4b). However, at a finer scale, the niche location (scores of the first axis where the red-backed voles have been captured) differed between HPO plantations and NRD stands (Table 2.4c). This analysis showed that the niche location was more oriented towards microhabitats characterized by a higher volume of CWD in NRD stands, and a higher low-lying lateral obstruction in HPO plantations (Figure 2.7). Otherwise, there were no differences in the male/female ratio, the young/adult ratio or in the body mass of individuals between stand types (Figure 2.8; Table 2.5).

2.4 Discussion

Plantations have been shown to host different insect species diversity and communities composition compared to natural forest (Cunningham *et al.*, 2005). In agreement with the existing literature, our results concur that ground beetle species assemblage was different between plantations and natural stands in both the deciduous and the coniferous layouts. We have also found that species diversity differed among stand types, with the exponential of the Shannon index being higher in the NRD stands compared to the HPO plantations, and higher in the BS plantations compared to other coniferous stands. However, in the coniferous layout, differences in ground beetles species assemblages could not be associated with vegetation attributes. In the deciduous layout, the higher number of abundant species in the NRD stands (5 species) compared to HPO plantation (1 species) explained these differences in the exponential of the Shannon index. In NRD stands, the abundant species *Pterostichus coracinus*, *P. adstrictus*, *P. tristis* and *Calathus ingratus* were strongly associated with higher dead wood cover and dead leaf cover, as well as a high basal area. These species are all very common in natural forests and are known to be associated with the presence of CWD (Lindroth 1961, 1963, 1966, 1968, 1969a, 1969b). It is thus unsurprising to find these species preferentially in the NRD stands rather than in HPO plantations, i.e. where CWD volume was greater (compared to HPO plantations). *P. pensylvanicus*, another abundant species in NRD stands, was slightly associated with the diversity and density of trees but it normally prefers dead leaves, moss and the presence of alder (Lindroth 1961, 1963, 1966, 1968, 1969a, 1969b). This species association with tree density and diversity is unusual but its habitat preferences generally correspond better with the vegetation attributes found in the NRD stands than HPO plantations. On the other hand, *Synuchus impunctatus*, common in open habitats and among leaves and bushes (Lindroth 1961, 1963, 1966, 1968, 1969a, 1969b), was the most abundant species in the HPO plantations. This species was mainly associated to a high shrub density and diversity, and to a lesser extent to the presence of a high herb cover, which might provide this species the seeds it has been need to feed on (Pearce *et al.*, 2003). In our study, ground beetle communities in deciduous stands were associated to different vegetation attributes and most of them were structural in nature (*i.e.* dead wood on the ground cover, dead leaves cover, herbs cover, high basal area and trees and shrubs density). Association with vegetation composition (*i.e.* trees and shrubs diversity and trees richness) were less evident. Our hypothesis that the structural complexity of plantations would be different compared to the regenerated stands and that this would change community compositions is supported by our results, at least for the deciduous layout. For example, *Bembidion forestriatum* and *Dyschirius globosus* were found only in the HPO plantations and both species are associated to open and anthropogenic habitats (Lindroth 1961, 1963, 1966, 1968, 1969a, 1969b; Lövei et Sunderland, 1996 ; J. L. Pearce et Venier, 2006). As well, *P. punctatissimus* and *Platynus dencentis*, two speciesknown to be forest specialists, were only present in the NRD stands (Lindroth 1961, 1963, 1966, 1968, 1969a, 1969b; J. L. Pearce et Venier, 2006).

For the red-backed voles, there were no difference in male/female and adult/young ratio as well as the body mass and the abundance between the HPO plantations and the NRD stands. However, the niche used by the red-backed voles was not entirely the same in the two stand types. Indeed, the niche in the NRD stands was characterised by a higher amount of CWD while the HPO plantations have a well-developed understory layer. The positive relation between the red-backed voles and the amount of CWD is already well known in the literature (Freedman *et al.*, 1996) and is still relevant (Fauteux *et al.*, 2013). In plantations, understory development seems to be a key element to maintain small mammal populations (Carrilho *et al.*, 2017). The fact that there is no difference in abundance between the two stand types suggests that the well-developed understory in HPO plantations was a habitat of sufficient quality for the red-backed voles. Simonetti *et al.*, (2013) made similar observations in plantations in Chile where the abundance of medium sized mammals decreased when the understory was removed compared to plantations with a developed understory layer. As for CWD (Freedman *et al.*, 1996), a developed understory may lower small mammals predation (Falkenberg et Clarke, 1998 ; Melo *et al.*, 2013) by providing shelter (Rosalino *et al.*, 2009). Thus, in our study, as long as the function of shelter is fulfilled for red-backed voles, their populations will not be affected. Even if the presence of red-backed voles is strongly dependent on vegetation attributes, it can be difficult to determine a carrying capacity because red-backed voles can have large temporal fluctuation in population size that do not seem to be linked to structural elements or quality of the habitat (Pearce et Venier, 2005). However, the cyclic phenomena have not been studied in deciduous and mixedwood temperate forests of Quebec, but mainly in boreal forests (Fauteux *et al.*, 2015). Nevertheless, small mammals are considered a good bioindicator of forest management sustainability (Pearce et Venier, 2005).

2.5 Conclusion

This study is the first to compare plantations of different species to naturally regenerated stands of the same age in the mixedwood forests of Quebec, Canada. It has been found that ground beetle communities in plantations were different compared to their naturally regenerated counterparts, and that about 45% of species detected in plantations were not present in naturally regenerated stands (43% and 46% in the deciduous and coniferous layout respectively). However, we found no effect of plantations on the abundance or demographic variables of red-backed voles, the most common small mammal species in our study sites. One major result from this study was to evidence the importance of the structural attributes in the understory layer for both red-backed vole and ground beetles. Altogether, our results suggest that plantations should be managed in order to increase the structural complexity of the understory layer (see also Carrilho *et al.*, 2017). From our results, the make-up of the structural attributes in the understory may not need to be specific as long as the attributes have the same functional role. In our study, for example, CWD and a well-developed understory layer offering lateral visual obstruction appear to have played the same functional role for red-backed voles. This would mean that coarse woody debris and an understory layer offering lateral visual obstruction can be interchangeable attributes as each contribute to a critical habitat element for red-backed voles, which is the structural complexity of the understory layer in the forest. Accordingly, Tews *et al.*, (2004) suggest that structural elements that provide crucial resources, shelter or ‘goods and services’ for many species, should be considered as keystone structure as their presence in forest drives and supports animal diversity. Thus, in tree plantations, the structural complexity of the understory layer and not only coarse woody debris would be the keystone structure to manage in order to maintain animal biodiversity, at least for small mammals.

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Tables

Table 2.1. Results of linear mixed-models explaining the differences of habitat gradient (represented by scores of the axes of the principal component analysis realized on vegetation attributes; see text for details) between plantations and naturally regenerated stands of the deciduous and coniferous layouts for ground beetles and small mammals. In the deciduous layout, stand types were: hybrid poplar plantations (HPO) and naturally regenerated deciduous stands (NRD). In the coniferous layout, stand types were hybrid larch plantations (HL), black spruce plantations (BS) and naturally regenerated coniferous stands (NRC). N is defined by the number of observations and DF, by the degree of freedom.

Model	**Vegetation**	**N**	**Estimate ± standard error**	**DF**	**t or F value**	**p value**
	Ground beetles in deciduous layout					
a	Scores of axis 1 ~ stand type	42	0.97 ± 0.20	11	4.77	< 0.001
b	Scores of axis 2 ~ stand type	42	0.15 ± 0.31	11	0.49	0.632
	Ground beetles in coniferous layout					
c	Scores of axis 1 ~ stand type	43		2	51.18*	< 0.001
	Post-hoc comparisons (Bonferroni correction)					
	Scores of axis 1 ~ BS/HL	29	0.20 ± 0.17	8	1.18	0.815
	Scores of axis 1 ~ BS/CNR	29	1.31 ± 0.13	8	9.84	< 0.001
	Scores of axis 1 ~ CNR/HL	29	1.22 ± 0.16	8	7.21	< 0.001
	Small mammals in deciduous layout					
d	Scores of axis 1 ~ stand type	300	0.40 ± 0.08	18	4.93	< 0.001

Values followed by an * are F values. Values not followed by an * are t values.

Table 2.2. Results of linear mixed-models explaining the differences (represented by species richness ie number of species and the exponential of Shannon index) between plantations and naturally regenerated stands of the deciduous and coniferous layouts for ground beetles and small mammals. Due to the small number of species in each stand and their low occurrence, only the exponential of Shannon index was used for the diversity differences of small mammals (see text for details). In the deciduous layout, stand types were: hybrid poplar plantations (HPO) and naturally regenerated deciduous stands (NRD). In the coniferous layout, stand types were hybrid larch plantations (HL), black spruce plantations (BS) and naturally regenerated coniferous stands (NRC). N is defined by the number of observations and DF, by the degree of freedom.

Model	Diversity	N	Estimate ± standard error	DF	t or F value	p value
	Ground beetles in deciduous layout					
a	Species richness ~ stand type	38	1.53 ± 0.94	11	1.63	0.131
b	exp(Shannon) index ~ stand type	38	1.85 ± 0.63	11	2.97	0.013
	Ground beetles in coniferous layout					
c	Species richness ~ stand type	45		12	0.52*	0.605
	Exp(shannon) index ~ stand type	45		12	10.80*	0.002
d	**Post-hoc comparisons (Bonferroni correction)**					
	Exp(shannon) index ~ BS/HL	30	-1.86 ± 0.33	8	-5.65	0.002
	Exp(shannon) index ~ BS/NRC	30	-0.93 ± 0.40	8	-2.34	0.142
	Exp(shannon) index ~ HL/NRC	30	0.93 ± 0.47	8	1.97	0.250
	Small mammals in deciduous layout					
e	Exp(shannon) index ~ stand type	10	0.17 ± 0.39	8	0.45	0.667

Values followed by an * are F values. Values not followed by an * are t values

Table 2.3. Results of PERMANOVA analyses explaining species assemblage differences (based on the Euclidean distances derived from Hellinger-transformed ground beetle abundance dataset) for the ground beetle communities between plantations and naturally regenerated stands of the deciduous and coniferous layout. In the deciduous layout, stand types were: hybrid poplar plantations (HPO) and naturally regenerated deciduous stands (NRD). In the coniferous layout, stand types were hybrid larch plantations (HL), black spruce plantations (BS) and naturally regenerated coniferous stands (NRC). N is defined by the number of observations and DF, by the degree of freedom.

Model	**Species assemblage differences in deciduous layout**	**N**	**DF**	**F value**	**p value**
a	Hellinger distance matrix ~ stand type	38	1	9.84	0.001
	Species assemblage differences in coniferous layout				
b	Hellinger distance matrix ~ stand type	45	2	6.74	0.001
c	Post-hoc comparisons (Bonferroni correction)				
	Hellinger distance matrix ~ BS/HL	30	2	5.26	0.003
	Hellinger distance matrix ~ BS/NRC	30	2	6.77	0.003
	Hellinger distance matrix ~ HL/NRC	30	2	8.32	0.003

Table 2.4. Results of mixed-models explaining variation of the red-backed vole abundances (minimum number alive; MNA) according to a) the stand type and b) the vegetation gradient represented by scores of the first axis of the principal component analysis (see text for details) and at a finer scale, c) variation of the niche location of the red-backed voles (estimated as scores of the first axis of the principal component analysis where individuals have been captured; see the text for details), between hybrid poplar plantations and naturally regenerated stands in the deciduous layout. N is defined by the number of observations and DF, by the degree of freedom.

Model	**Coarse scale**	**N**	**Estimate ± standard error**	**DF**	**t or z value**	**p value**
a	MNA ~ stand type	20	1.87 ± 4.64	6	0.40	0.690
b	MNA ~ scores of axis 1	20	0.75 ± 7.29	6	0.10	0.920
	Fine scale					
c	Scores of axis 1~ stand type	177	0.26 ± 0.10	15	2.69*	0.017

Values followed by an * are t values. Values not followed by an * are z values.

Table 2.5. Results of linear mixed-models explaining the variation of the red-backed vole demographic variables (male/female ratio, adult/young ratio and body mass) between hybrid poplar plantations and naturally regenerated stands in the deciduous layout. N is defined by the number of observations and DF, by the degree of freedom.

Demographic variables	**N**	**Estimate ± standard error**	**DF**	**t or z value**	**p value**
Male/Female ratio ~ stand type	17	-0.26 ± 0.28	14	-0.91	0.363
Young/Adult ratio ~ stand type	17	-0.40 ± 0.50	14	-0.80	0.426
body mass-length relationship ~ stand type	108	0.37 ± 0.64	7	0.58*	0.581

Values followed by an * are t values. Values not followed by an * are z values

Figures

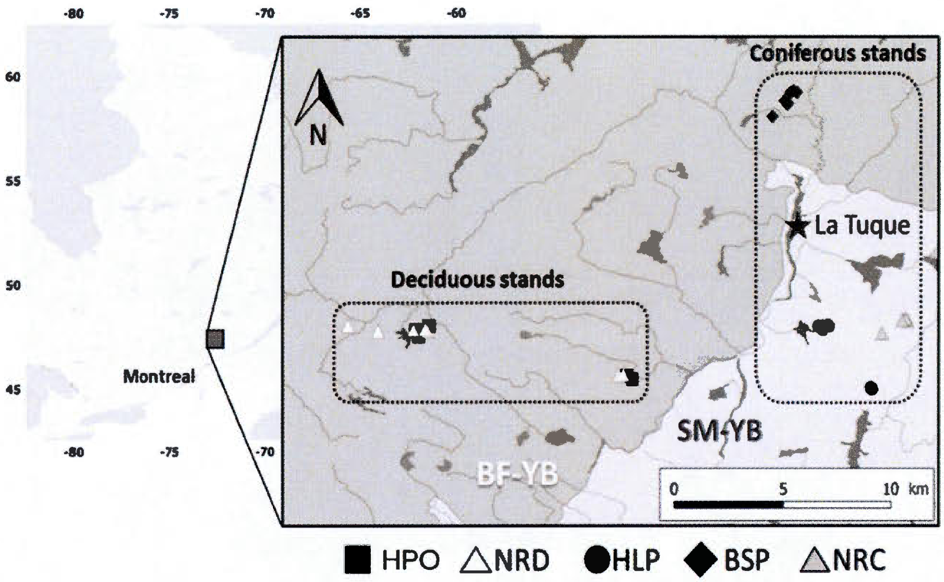

Figure 2.1. Study area and locations of the deciduous and coniferous forest stands, near La Tuque (Mauricie, Québec). HPO: hybrid poplar plantations; NRD: naturally regenerated deciduous stands; HLP: hybrid larch plantations; BSP: black spruce plantations; NRC: naturally regenerated coniferous stands. BF-YB and SM-YB: Balsam fir-Yellow birch and Sugar maple-Yellow birch bioclimatic domains, respectively.

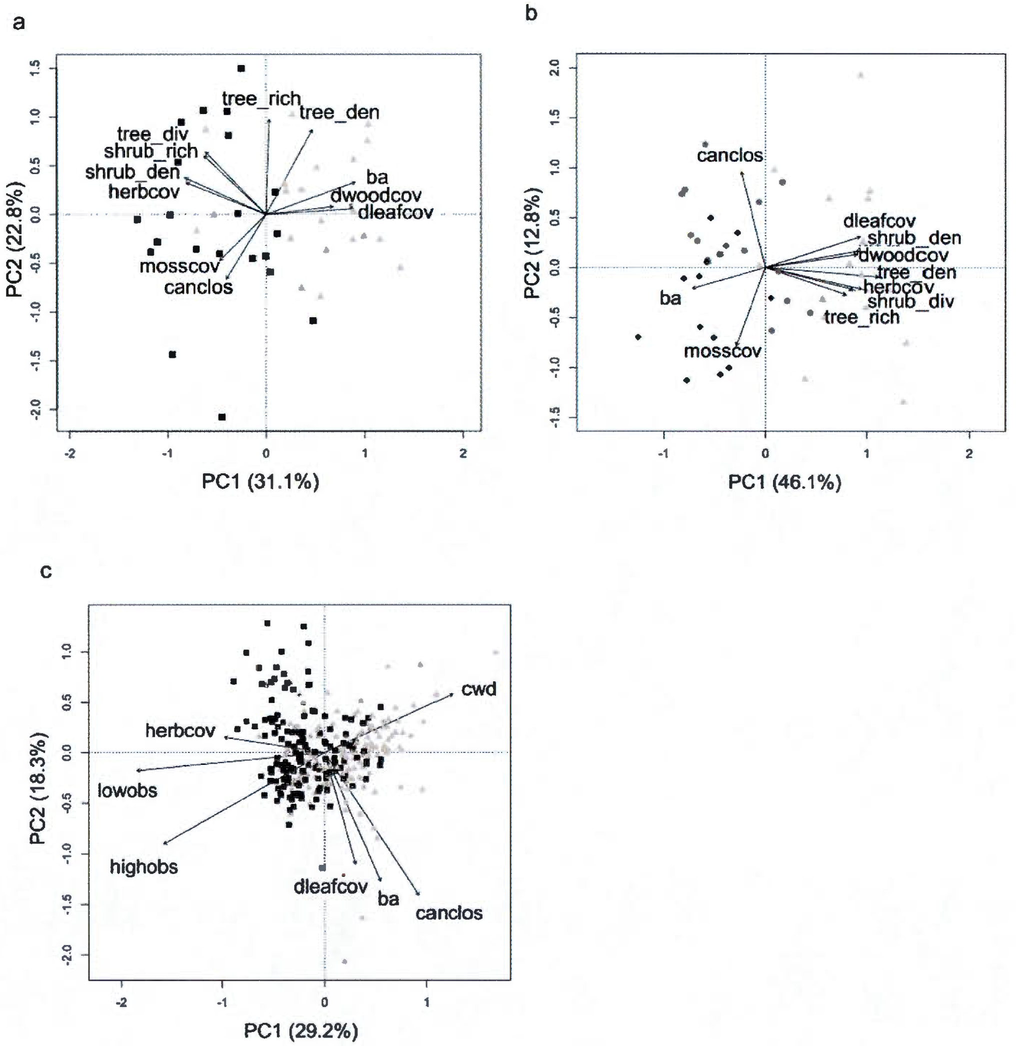

Figure 2.2. Principal component analysis summarizing habitat gradient (based on vegetation attributes) in stands for a) ground beetles in the deciduous layout, b) ground beetles in the coniferous layout, and c) small mammals in the deciduous layout. Black filled squares: hybrid poplar plantations. Grey filled circle: hybrid larch plantations. Black filled diamonds: planted black spruce stands. Grey filled triangles: naturally regenerated stands. All the explanations of the vegetation attributes acronym are listed in table S2.

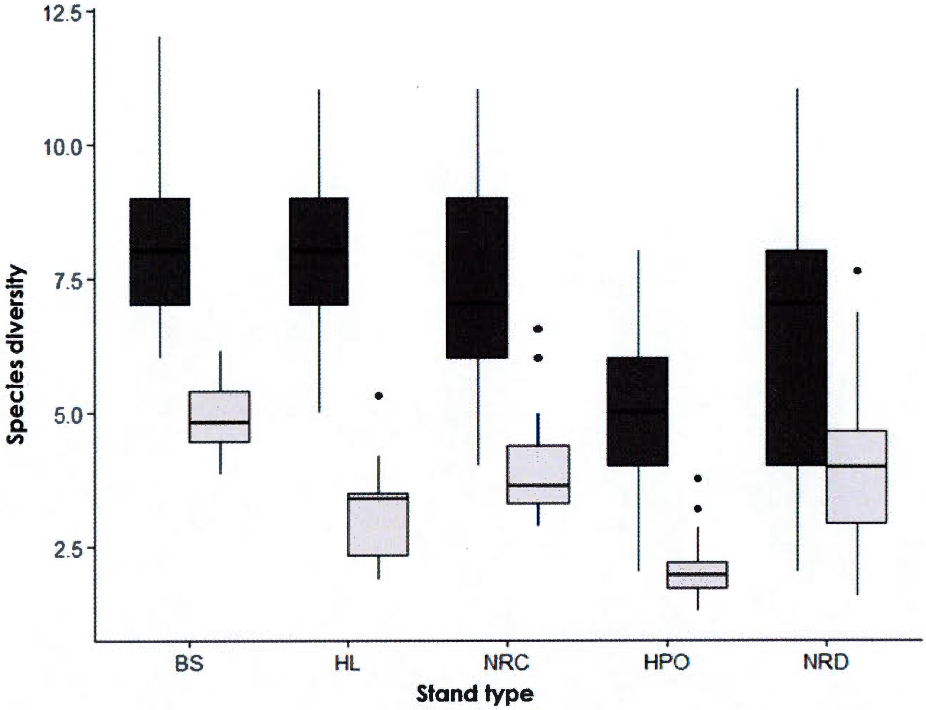

Figure 2.3. Boxplot of ground beetles species richness (dark gray boxplot) and exponential of Shannon index (light gray boxplot) in plantations and naturally regenerated stands of the coniferous and deciduous layout. BS: black spruce plantations, HL: hybrid larch plantations, NRC: naturally regenerated coniferous stands, HPO: hybrid poplar plantations and NRD: naturally regenerated deciduous stands. In each box, the middle line represents the median while the ends are the first and third quartiles. The whiskers include the data points that are within a factor of 1.5 times the interquartile range above the third quartile and bellow the first quartile. All the points beyond the whiskers are plotted individually.

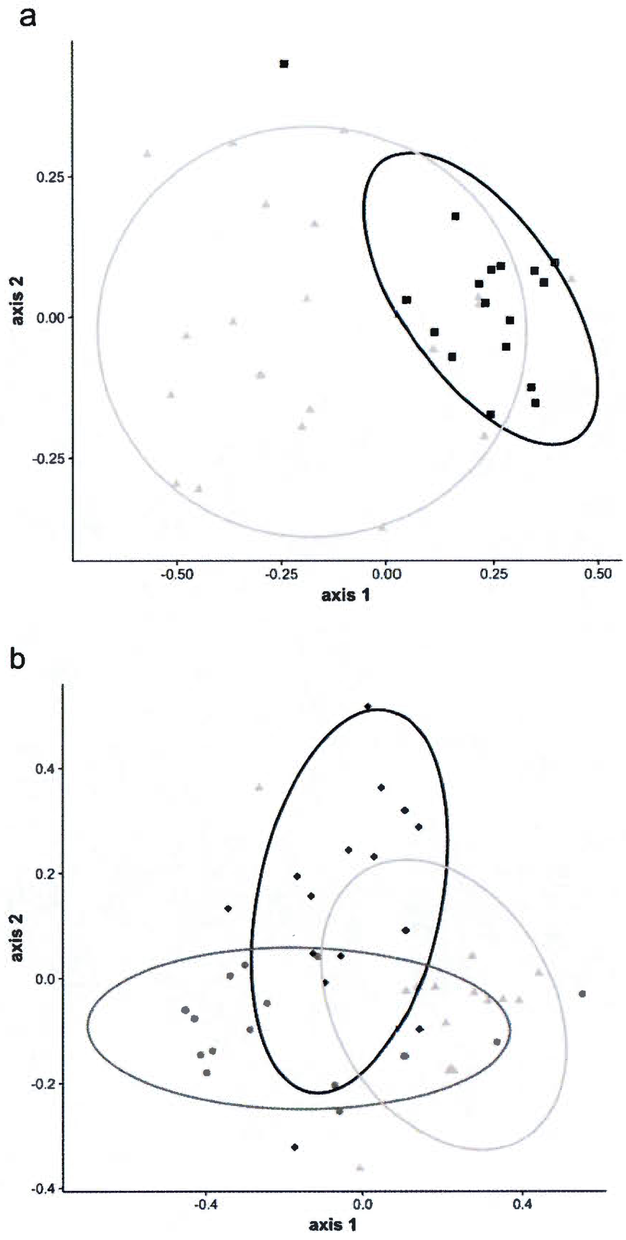

Figure 2.4. Result of PERMANOVA analyses explaining species assemblage differences (based on the Euclidean distances derived from Hellinger-transformed ground beetles abundance dataset) for the ground beetle communities in a) the deciduous layout and b) the coniferous layout. Black filled squares: hybrid poplar plantations. Grey filled circle: hybrid larch plantations. Black filled diamonds: planted black spruce stands. Grey filled triangles: naturally regenerated stands. The ellipse included 80% of the variability accounted by the first two axis.

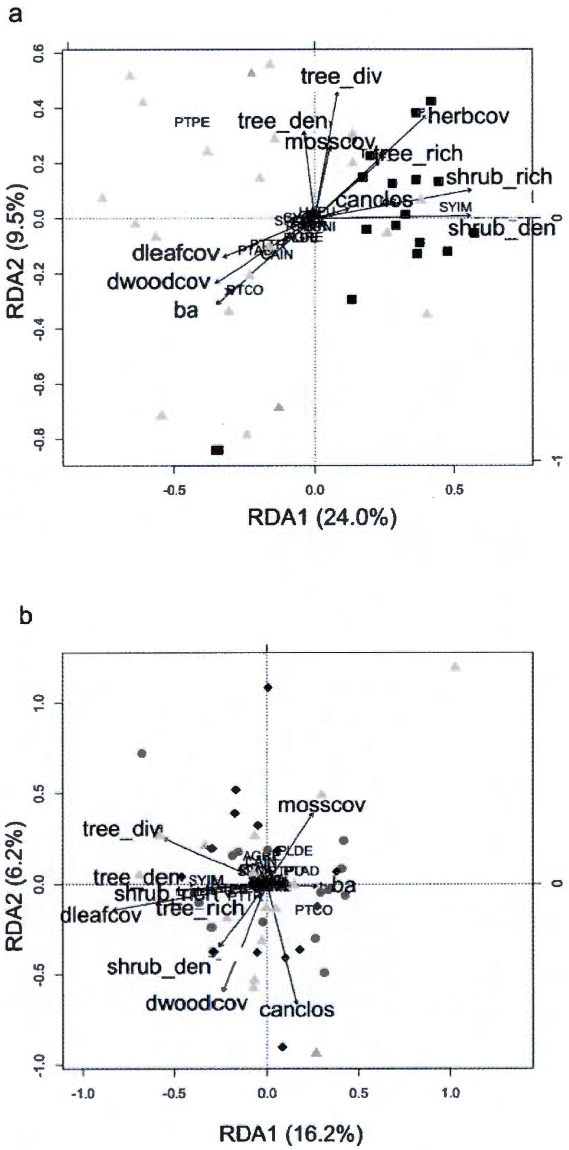

Figure 2.5. Result of RDA explaining the effect of vegetation variables on ground beetles species assemblages in a) the deciduous layout and b) the coniferous layout. Black filled squares: hybrid poplar plantations. Grey filled circle: hybrid larch plantations. Black filled diamonds: planted black spruce stands. Grey filled triangles: naturally regenerated stands. Explanations for the acronyms of vegetation attributes and ground beetles species names are listed in tables S1 and S2 respectively.

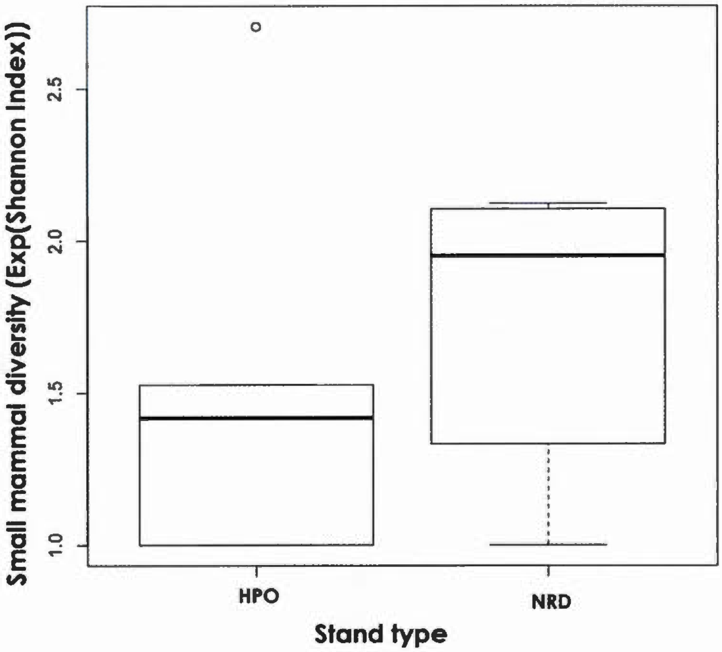

Figure 2.6. Boxplot of Shannon index of the small mammal communities in hybrid poplar plantations (HPO) and naturally regenerated deciduous (NRD) stands. In each box, the middle line represents the median while the ends are the first and third quartiles. The whiskers include the data points that are within a factor of 1.5 times the interquartile range above the third quartile and bellow the first quartile. All the points beyond the whiskers are plotted individually.

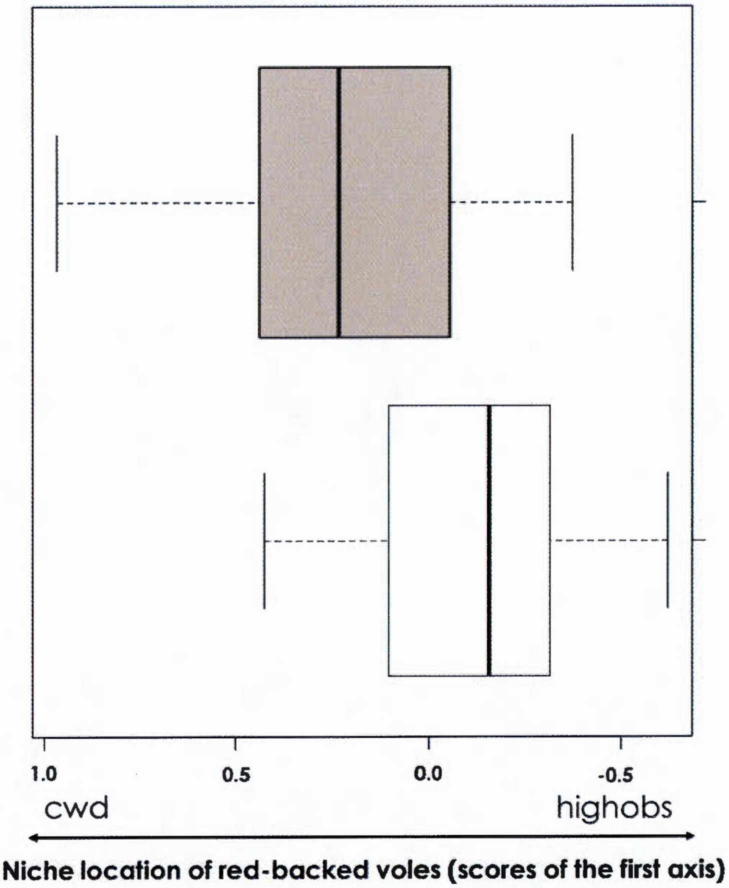

Figure 2.7. Boxplot of the niche location (scores of the first principal component PC1 estimated from a PCA based on the vegetation attributes measured in small mammal habitats; see the Methods section for more details) of red-backed voles in hybrid poplar plantations (HPO) and naturally regenerated deciduous (NRD) stands. White boxplot: hybrid poplar plantations. Grey boxplot: naturally regenerated deciduous stand. Each boxplot represents scores variation of traps in which at least one red-backed vole was captured. In each box, the middle line represents the median while the ends are the first and third quartiles. The whiskers include the data points that are within a factor of 1.5 times the interquartile range above the third quartile and bellow the first quartile. All the points beyond the whiskers are plotted individually. The arrow represents the vegetation gradient described by PC1. The HPO plantations were characterised by a high visual lateral obstruction (highobs) while a high volume of coarse woody debris (cwd) was associated to NRD stands.

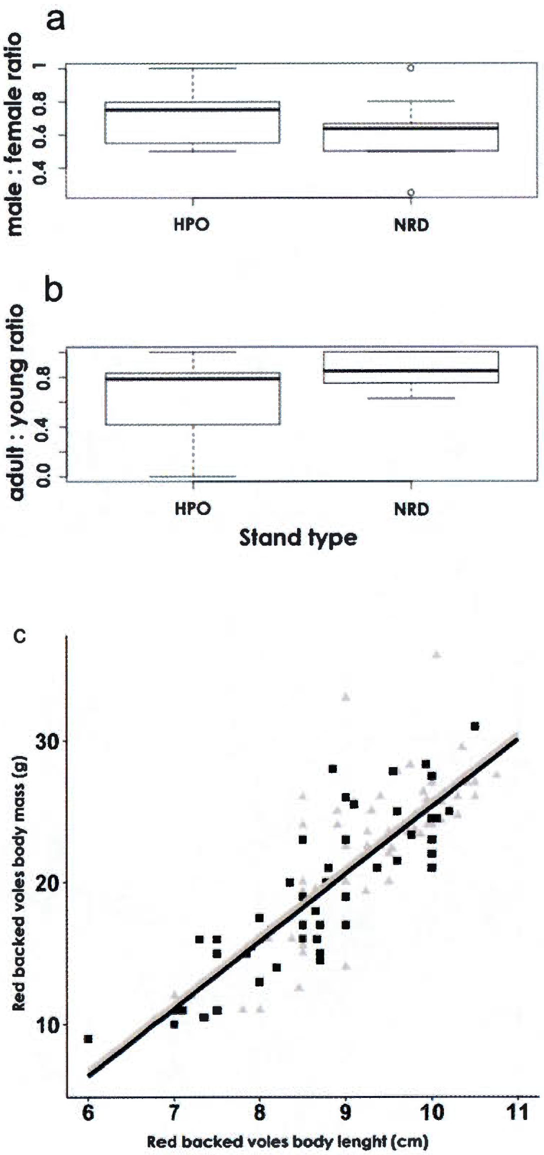

Figure 2.8. Variation of the demographic variables for the red-backed voles between the hybrid poplar (HPO) plantations and the naturally regenerated deciduous (NRD) stands for a) the male/female ratio, b) the adult/young ratio and c) the body mass (controlled for the body length). Black filled squares and gray filled triangles represent HPO plantations and NRD stands respectively. In each box (figure panels a and b), the middle line represents the median while the ends are the first and third quartiles. The whiskers include the data points that are within a factor of 1.5 times the interquartile range above the third quartile and bellow the first quartile. All the points beyond the whiskers are plotted individually.

Supplementary material

Table S1. Average stand characteristics and environmental conditions reported in Haute-Mauricie (Quebec, Canada) during the summer 2015, in deciduous naturally regenerated stands (NRD), hybrid poplar plantations (HPO), coniferous naturally regenerated stands (NRC), hybrid larch plantations (HL) and black spruce plantations (BS). Values are based on vegetation attributes that were measured to characterize ground beetle habitats.

Variable	**NRD**	**HPO**	**NRC**	**HL**	**BS**
Number of stands	7	7	5	5	5
Age (years)	13-17	9	16	16	25
Trees and saplings (>2cm DBH)					
Density (stem ha^{-1})	17886 ± 4083	13200 ± 5710	14253 ± 4900	5223 ± 2912	4169 ± 1033
Plantation density (stem ha^{-1})	NA	1014 ± 314	NA	1200 ± 314	1521 ± 504
Mean tree DBH (cm)	4.10	5.90 ± 2.30	4.50 ± 0.80	14.50 ± 1.90	13 ± 0.80
Total basal area (m^2 ha^{-1})	19.30 ± 7.20	8 ± 3.10	20.30 ± 4.10	24.10 ± 4.20	28.40 ± 4.80
Three most abundant tree species (average % of basal area)	P. tremuloides (100)	Hybrid poplar (100)	A. rubrum (22) A. balsamea (15)	Hybrid larch (81) B. papyrifera (7)	P. mariana (71) A. balsamea (9)

			P. pensylvanica (14)	P. tremuloides (4)	A. saccharum (6)
Species richness	7.70 ± 2	7.20 ± 1.80	7.70 ± 1.80	6.70 ± 2	5.90 ± 1.70
Diversity (^1D)	3.65 ± 1.24	4.15 ± 0.99	3.72 ± 0.95	2.04 ± 0.88	2.50 ± 1.11
Shrubs					
Density (stem ha^{-1})	17202 ± 13291	33899 ± 16038	7708 ± 5103	2792 ± 2003	792 ± 687
Species richness	5.90 ± 2.30	7.50 ± 2.10	4.80 ± 2.10	3.10 ± 1.50	1.50 ± 1.10
Diversity (^1D)	3.53 ± 1.44	4.52 ± 1.48	3.64 ± 1.48	2.58 ± 1.02	1.71 ± 0.76
Canopy openness (%)	22.90 ± 5	25 ± 6.90	11.80 ± 2	11.90 ± 1.50	11.70 ± 1.10

Table S2. List of vegetation attributes that were measured to characterize small mammal and ground beetle habitats.

Vegetation attributes	Acronym
Small mammals	
Canopy closure (%)	canclos
Low-lying lateral Obstruction (0-75 cm; %)	lowobs
High-lying lateral Obstruction (75-150 cm; %)	highobs
Herb cover (%)	herbcov
Dead leaf cover (%)	dleafcov
Coarse wood debris volume (m^3/ha)	cwd
Basal area (m^3/ha)	ba
Ground beetles	
Herb cover on the ground (%)	herbcov
Dead leaf cover (%)	dleafcov
Dead wood cover (%)	dwoodcov
Moss cover (%)	mosscov
Basal area (m^3/ha)	ba
Tree density (stem ha^{-1})	Tree_den
Tree species richness	Tree_rich
Tree diversity based on basal area	Tree_div
Canopy closure (%)	canclos
Shrub density (stem ha^{-1})	Shrub_den

Shrub richness	Shrub_rich

Table S3. Species names, acronym and abundance of small mammals (number of different individuals) and ground beetles that were captured during the summer 2015 in Haute-Mauricie (Quebec, Canada), in hybrid poplar plantations (HPO), deciduous naturally regenerated stands (NRD), hybrid larch plantations (HL), black spruce plantations (BS) and coniferous naturally regenerated stands (NRC). *Species defined as rare in our dataset (species present in less than 5 plots).

Species name	Acronym	HPO	NRD	HL	BS	NRC
Ground beetles						
**Agonum fidele*	AGFI	0	0	1	0	0
Agonum retractum	AGRE	9	18	35	29	51
**Bembidion fortestriatum*	BEFO	1	0	0	0	0
Bembidion wingatei	BEWI	1	0	7	2	0
Calathus ingratus	CAIN	13	88	5	88	11
Calosoma frigidum	CAFR	1	1	4	0	0
**Carabus nemoralis*	CANE	0	0	1	0	0
Cymindis cribricollis	CYCR	4	6	4	3	3
**Dyschirius globosus*	DYGL	1	0	0	0	0
Harpalus pleuriticus somnulentus	HAPL	0	0	0	1	0
Harpalus fulvilabris	HAFU	1	2	0	2	0
Loricera pilicornis	LOPI	0	0	0	2	0
**Notiophilus aeneus*	NOAE	1	0	1	1	0
**Patrobus longicornis*	PALO	0	0	3	0	0
Platynus decentis	PLDE	0	10	35	22	40

Poecilus lucublandus	POLU	0	1	0	0	0
Pterostichus adstrictus	PTAD	5	31	112	166	23
Pterostichus coracinus	PTCO	60	136	1404	441	504
**Pterostichus melanarius*	PTME	0	0	5	0	0
**Pterostichus mutus*	PTMU	1	0	12	0	0
Pterostichus pensylvanicus	PTPE	69	289	101	73	116
Pterostichus punctatissimus	PTPU	0	4	1	8	3
Pterostichus tristis	PTTR	9	35	99	84	236
Sphaeroderus canadensis	SPCA	0	4	4	0	11
Sphaeroderus nitidicollis brevoorti	SPNI	5	3	0	0	0
Sphaeroderus stenostomus lecontei	SPST	4	16	0	11	10
Synuchus impunctatus	SYIM	757	460	325	413	965
Trechus apicalis	TRAP	0	0	3	4	2
Small mammals						
Myodes gapperi		51	59			
Napaeozapus insignis		5	0			
Unidentified shrew species		4	2			
Tamia striatus		2	1			
Peromyscus sp		0	26			

CHAPITRE III

CONCLUSION

Nos résultats montrent l'importance de la complexité structurelle à l'intérieur des forêts dans le maintien de la diversité animale. En effet, une quantité élevée de débris ligneux au sol ainsi qu'une strate arbustive développée sont des éléments clés expliquant la composition des communautés de carabes et aidant au maintien des populations de campagnols à dos roux dans les plantations de peupliers hybrides. La strate arbustive développée permettait aux plantations de peupliers hybrides d'offrir un habitat de qualité similaire aux peuplements régénérés naturellement (qui comprenait des débris ligneux au sol) pour le campagnol à dos roux, car aucune différence d'abondance ou de variables démographiques entre les deux traitements n'a été détectée. Ces résultats concordent avec ceux de Simonetti, Grez, & Estades (2016) qui soutiennent qu'une strate de sous-bois bien développée à l'intérieur d'une plantation fournit un habitat de qualité qui contre-balancerait les effets négatifs de la plantation sur la faune locale. Pour ce qui est des carabidés, le développement de la strate de sous-bois ainsi que la présence d'éléments structuraux au sol étaient également les éléments qui expliquaient la composition des communautés dans le dispositif feuillu. Cependant, les assemblages d'espèces retrouvés entre les peuplements des deux dispositifs étaient tous différents ce qui laisse supposer que les habitats des différents types de plantations (HPO, BS et HL) et des deux types de peuplements régénérés naturellement (NRD et NRC) divergeaient. La disponibilité et la variabilité de la lumière, qui sont intimement reliées au développement de la strate arbustive, semblent être importantes pour expliquer la diversité des carabidés retrouvés à l'intérieur des forêts (Mueller *et al.*, 2016 ; Schowalter, 2017). Le fait que les plantations de peupliers hybrides n'ont pas d'impact sur les populations de campagnols à dos roux, mais amènent des différences de composition dans les communautés de carabidés renforce l'importance d'utiliser plusieurs groupes taxonomiques dans les études. De plus, ces résultats suggèrent deux choses : 1- les plantations de peupliers hybrides représentent des habitats de qualité similaire aux peuplements régénérés naturellement en peuplier pour le campagnol à dos roux à condition que la strate de sous-bois y soit bien développée; 2- les plantations, qu'elles soient décidues ou résineuses, ne semblent cependant pas fournir un habitat de qualité comparable aux peuplements régénérés naturellement pour les carabes.

Dans une revue de littérature, Tews et al. (2004) ont voulu relier la diversité faunique à l'hétérogénéité de l'habitat et ont constaté que plusieurs éléments ont une influence sur la diversité faunique. Ces constats les ont amenés à mettre de l'avant un nouveau concept : les « keystone structure » qui sont des éléments spatiaux qui fournissent ressources, abris et « biens et services » cruciaux non pas à une seule espèce mais à un ensemble d'espèces simultanément. De ce fait, la diminution de ces « keystone structure » aurait des conséquences pour plusieurs groupes taxonomiques. En adoptant une approche basée sur le rôle fonctionnel de la structure physique des éléments de l'habitat, plusieurs « keystone structure » pourraient être définies. Cela rendrait la comparaison des études beaucoup plus facile et la portée des conclusions plus grande, car elles pourraient s'étendre à tous les groupes taxonomiques associés à la « keystone structure » comparativement à seulement les bioindicateurs choisis. D'un point de vue appliqué, il pourrait être plus facile pour les gestionnaires forestiers de cibler des « keystone structure » et de s'assurer que leur présence, sous la forme qui est la plus adaptée à la forêt visée, est maintenue afin de minimiser les impacts des pratiques sylvicoles sur la biodiversité.

LISTE DE RÉFÉRENCES

Addison, J. A. et Barber, K. N. (1997). *Response of soil invertebrates to clear-cutting and partial cutting in a boreal mixedwoo d forest in Northern Ontario. Environmental Research and Assessment Project Canadian Forest Service.*

Ale, S. B., Morris, D. W., Dupuch, A. et Moore, D. E. (2011). Habitat selection and the scale of ghostly coexistence among Arctic rodents. *Oikos, 120*(8), 1191–1200. http://dx.doi.org/10.1111/j.1600–0706.2010.18933.x

Anderson, M. J. (2001). A new method for non parametric multivariate analysis of variance. *Austral ecology, 26*(2001), 32-46. http://dx.doi.org/10.1111/j.1442-9993.2001.01070.pp.x

Aubin, I., Messier, C. et Bouchard, A. (2008). Can plantations develop understory biological and physical attributes of naturally regenerated forests? *Biological Conservation, 141*(10), 2461-2476. http://dx.doi.org/10.1016/j.biocon.2008.07.007

Bachelot, B. (2016). Canopy Openness Analyzer Package, (version 1.0), 1-6. Récupéré de https://cran.r-project.org/package=Sky

Barrette, M. et Leblanc, M. (2013). *La sylviculture intensive de plantations dans un contexte d'aménagement écosystémique – Rapport du groupe d'experts.*

Bauhus, J., Van der Meer, P. et Kanninen, M. (2010). *Ecosystem goods and services from plantation forests. The Earthscan Forest Library* (Earthscan). London, UK : [s.n.].

Beaudry, S., Duchesne, L. C. et CôTé, B. (1997). Short-term effects of three forestry practices on carabid assemblages in a jack pine forest. *Canadian Journal of Forest Research, 27*(12), 2065-2071. http://dx.doi.org/10.1139/cjfr-27-12-2065

Beauvais, G. P. et Buskirk, S. W. (1999). Modifying estimates of sampling effort to account for sprung traps. *Wildlife Society Bulletin, 27*(1), 39-43. http://dx.doi.org/10.2307/3783938

Bolker, B., Skaug, H., Magnusson, A. et Nielsen, A. (2012). Getting started with the glmmADMB package, (version 0.6.5), 1-12. Récupéré de glmmadmb.r-forge.r-project.org/

Borcard, D., Gillet, F. et Legendre, P. (2011). *Numerical ecology in R.* [s.l.] : Springer

Science & Business Media. http://dx.doi.org/10.1007/978-0-387-78171-6

Bremer, L. L. et Farley, K. a. (2010). Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. *Biodiversity and Conservation*, *19*(14), 3893-3915. http://dx.doi.org/10.1007/s10531-010-9936-4

Brockerhoff, E. G., Jactel, H., Parrotta, J. a., Quine, C. P. et Sayer, J. (2008a). Plantation forests and biodiversity: Oxymoron or opportunity? *Biodiversity and Conservation*, *17*(5), 925-951. http://dx.doi.org/10.1007/s10531-008-9380-x

Brockerhoff, E. G., Jactel, H., Parrotta, J. A., Quine, C. P. et Sayer, J. (2008b). Plantation forests and biodiversity: Oxymoron or opportunity? *Biodiversity and Conservation*, *17*(5), 925-951. http://dx.doi.org/10.1007/s10531-008-9380-x

Brose, U. (2003). Bottom-up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity? *Oecologia*, *135*(3), 407-413.

Carey, B. A. et Harrington, A. C. (2001). Small mammals in young forests: implications for management for sustainability. *Forest Ecology and Management*, *154*, 289-309. http://dx.doi.org/10.1016/S0378-1127(00)00638-1

Carle, J. et Holmgren, P. (2008). Wood from Planted Forests, A Global Outlook 2005-2030. *Forest Products Journal*, *58*(12), 6-18.

Carnus, J.-M., Parrotta, J., Brockerhoff, E. G., Arbez, M., Jactel, H., Kremer, A., Lamb, D., O'Hara, K. et Walters, B. (2006). Planted Forests and Biodiversity. *Journal of Forestry*, *104*(2), 65-77.

Carrilho, M., Teixeira, D., Santos-Reis, M. et Rosalino, L. M. (2017). Small mammal abundance in Mediterranean Eucalyptus plantations: how shrub cover can really make a difference. *Forest Ecology and Management*, *391*, 256-263. http://dx.doi.org/10.1016/j.foreco.2017.01.032

Castagneyrol, B. et Jactel, H. (2012). Unraveling plant-animal diversity relationships: A meta-regression analysis. *Ecology*, *93*(9), 2115-2124. http://dx.doi.org/10.1890/11-1300.1

Christian, D. P., Collins, P. T., Hanowski, J. M. et Niemi, G. J. (1997). Bird and small mammal use of short-rotation hybrid poplar plantations. *Journal of Wildlife Management*, *61*(1), 171-182. http://dx.doi.org/10.2307/3802426

Christian, D. P., Hoffman, W., Hanowski, J. M., Niemi, G. J. et Beyea, J. (1998). Bird and mammal diversity on woody biomass plantations in North America. *Biomass and Bioenergy*, *14*(4), 395-402. http://dx.doi.org/10.1016/S0961-9534(97)10076-9

Cunningham, S. A., Floyd, R. B. et Weir, T. A. (2005). Do Eucalyptus plantations host an insect community similar to remnant Eucalyptus forest? *Austral Ecology, 30*(1), 103-117. http://dx.doi.org/10.1111/j.1442-9993.2005.01429.x

Dauber, J., Jones, M. B. et Stout, J. C. (2010). The impact of biomass crop cultivation on temperate biodiversity. *GCB Bioenergy, 2*(6), 289-309. http://dx.doi.org/10.1111/j.1757-1707.2010.01058.x

de Vries, P. G. (1973). A general theory on line intersect sampling: with application to logging residue inventory. *Meded. Landbouwhogeschool Wagening, 73*(11), 1-23.

Duan, W., Ren, H., Fu, S., Wang, J., Zhang, J., Yang, L. et Huang, C. (2010). Community Comparison and Determinant Analysis of Understory Vegetation in Six Plantations in South China. *Restoration Ecology, 18*(2), 206-214. http://dx.doi.org/10.1111/j.1526-100X.2008.00444.x

Elek, Z., Dauffy-Richard, E. et Gosselin, F. (2010). Carabid species responses to hybrid poplar plantations in floodplains in France. *Forest Ecology and Management, 260*(9), 1446-1455. http://dx.doi.org/10.1016/j.foreco.2010.07.034

Environment Canada. (2017). *Canadian Climate Normals: 1981-2010 Climate Normals & Averages*. Récupéré le 20 mai 2017 de http://climate.weather.gc.ca/climate_normals/index_e.html

Etcheverry, P., Ouellet, J.-P. et Crête, M. (2005). Response of small mammals to clear-cutting and precommercial thinning in mixed forests of southeastern Quebec. *Canadian Journal of Forest Research, 35*(12), 2813-2822.

Falkenberg, J. C. et Clarke, J. A. (1998). Microhabitat Use of Deer Mice: Effects of Interspecific Interaction Risks. *Journal of Mammalogy, 79*(2), 558-565. http://dx.doi.org/10.2307/1382986

FAO, food and agriculture organization of the U. N. (2011). *State of the world's forests 2011*. Rome.

Fauteux, D., Cheveau, M., Imbeau, L. et Drapeau, P. (2015). Cyclic Dynamics of a Boreal Southern Red-Backed Vole Population in Northwestern Quebec. *Journal of Mammalogy, 96*(3), 573-578. http://dx.doi.org/10.1093/jmammal/gyv062

Fauteux, D., Mazerolle, M. J., Imbeau, L. et Drapeau, P. (2013). Site occupancy and spatial co-occurrence of boreal small mammals are favoured by late-decay woody debris. *Canadian Journal of Forest Resources, 43*, 419-427. http://dx.doi.org/dx.doi.org/10.1139/cjfr-2012-0397

Freedman, B., Zelazny, V., Beaudette, D., Fleming, T., Johnson, G., Flemming, S., Gerrow, J. S., Forbes, G. et Woodley, S. (1996). Biodiversity implications of changes in the quantity of dead organic matter in managed forests. *Environmental*

Reviews, *4*(3), 238-265. http://dx.doi.org/10.1139/a96-013

Haddad, N. M., Tilman, D., Haarstad, J., Ritchie, M. et Knops, J. M. N. (2001). Contrasting Effects of Plant Richness and Composition on Insect Communities : A Field Experiment. *The american naturalist*, *158*(1), 19.

Hartley, M. J. (2002). Rationale and methods for conserving biodiversity in plantation forests. *Forest Ecology and Management*, *155*(1), 81-95. http://dx.doi.org/10.1016/S0378-1127(01)00549-7

Hilbe, J. M. (2011). Negative binomial regression. *Cambridge University Press.*

Kappes, H., Jabin, M., Kulfan, J., Zach, P. et Topp, W. (2009). Spatial patterns of litter-dwelling taxa in relation to the amounts of coarse woody debris in European temperate deciduous forests. *Forest Ecology and Management*, *257*(4), 1255-1260. http://dx.doi.org/10.1016/j.foreco.2008.11.021

Laflèche, V. et Cyr, G. (2013). *Identification des propositions d'aires pour l'intensification de la production de matière ligneuse.*

Larochelle, A. (1976). *Manuel d'identification des carabidae du Québec.* [s.l.] : [s.n.].

Lassau, S. A., Hochuli, D. F., Cassis, G. et Reid, C. A. M. (2005). Effects of habitat complexity on forest beetle diversity: do functional groups respond consistently? *Diversity & Distributions*, *11*(1), 73-82. http://dx.doi.org/10.1111/j.1366-9516.2005.00124.x

Legendre, P. et Anderson, M. J. (1999). Distance-based redundancy analysis: Testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs*, *69*(1), 1-24. http://dx.doi.org/10.2307/2657192

Lindenmayer, D. B. et Hobbs, R. J. (2004). Fauna conservation in Australian plantation forests – a review. *Biological Conservation*, *119*(2), 151-168. http://dx.doi.org/10.1016/j.biocon.2003.10.028

Lindroth, C.H., 1961, 1963, 1966, 1968, 1969a, 1969b. The ground-beetles (*Carabidae*, excl. *Cicindelinae*) of Canada and Alaska, Part 2. Opusc. Entomol. Suppl. 20,1-200; 24,201-408; 29,409-648; 33, 649-944; 34, 945-1192; 35, I-XLVIII.

Loeb, S. C. (1999). Responses of small mammals to coarse woody debris in a southeastern pine forest. *Journal of Mammalogy*, *80*(2), 460-471. http://dx.doi.org/10.2307/1383293

Lövei, G. L. et Sunderland, K. D. (1996). Ecology and behavior of ground beetles (COLEOPTERA: CARABIDAE). *Annual Review of Entomology*, *41*(1), 231-256. http://dx.doi.org/doi.org/10.1146/annurev.en.41.010196.001311

Lugo, A. E., Parrotta, J. A. et Brown, S. (1993). Loss in species caused by tropical deforestation and their recovery through management. *Ambio, 22*(2/3), 106-109. http://dx.doi.org/10.1016/0006-3207(94)90633-5

MacKay, A., Allard, M. et Villard, M.-A. (2014). Capacity of older plantations to host bird assemblages of naturally-regenerated conifer forests: A test at stand and landscape levels. *Biological Conservation, 170,* 110-119. http://dx.doi.org/10.1016/j.biocon.2013.12.023

Martin, P. S., Gheler-Costa, C., Lopes, P. C., Rosalino, L. M. et Verdade, L. M. (2012). Terrestrial non-volant small mammals in agro-silvicultural landscapes of Southeastern Brazil. *Forest Ecology and Management, 282,* 185-195.

Melo, G. L., Miotto, B., Peres, B. et Cáceres, N. C. (2013). Microhabitat of small mammals at ground and understorey levels in a deciduous, southern Atlantic forest. *Anais da Academia Brasileira de Ciencias, 85*(2), 727-736. http://dx.doi.org/10.1590/S0001-37652013000200017

Ménétrier, J. (2008). Le peuplier hybride au Québec : une révolution, une évolution ! *Le naturaliste canadien, 132*(1), 46-54.

Messier, C., Tittler, R., Kneeshaw, D. D., Gélinas, N., Paquette, A., Berninger, K., Rheault, H., Meek, P. et Beaulieu, N. (2009). TRIAD zoning in Quebec: Experiences and results after 5 years. *Forestry Chronicle, 85*(6), 885-896. http://dx.doi.org/10.5558/tfc85885-6

Moser, B. W. et Hilpp, G. K. (2003). Wintering raptor use of hybrid poplar plantations in northeastern Oregon. *J Raptor Res, 37*(4), 286-291.

Moser, B. W., Pipas, M. J., Witmer, G. W. et Engeman, R. M. (2002). Small mammal use of hybrid poplar plantations relative to stand age. *Northwest Science, 76*(2), 158-165.

Mueller, K. E., Eisenhauer, N., Reich, P. B., Hobbie, S. E., Chadwick, O. a., Chorover, J., Dobies, T., Hale, C. M., Jagodziński, A. M., Kałucka, I., Kasprowicz, M., Kieliszewska-Rokicka, B., Modrzyński, J., Roz˙en, A., Skorupski, M., Sobczyk, Ł., Stasińska, M., Trocha, L. K., Weiner, J., Wierzbicka, A. et Oleksyn, J. (2016). Light, earthworms, and soil resources as predictors of diversity of 10 soil invertebrate groups across monocultures of 14 tree species. *Soil Biology and Biochemistry, 92,* 184-198. http://dx.doi.org/10.1016/j.soilbio.2015.10.010

Niemelä, J., Haila, Y., Halme, E., Lahti, T., Pajunen, T. et Punttila, P. (1988). The distribution of carabid beetles in fragments of old coniferous taiga and adjacent managed forest. *Annales Zoologici Fennici, 25*(2), 107-119.

Nudds, T. D. (1977). Quantifying the Vegetative Structure of Wildlife Cover. *Wildlife Society Bulletin, 5*(3), 113-117.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E. et Wagner, H. (2017). Community Ecology Package. *R package*, (Version 2.4-3). Récupéré de https://cran.r-project.org/web/packages/vegan/index.html

Paillet, Y., Bergès, L., HjÄltén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R. J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., SebastiÀ, M. T., Schmidt, W., Standovár, T., TÓthmérész, B., Uotila, A., Valladares, F., Vellak, K. et Virtanen, R. (2010). Biodiversity differences between managed and unmanaged forests: Meta-analysis of species richness in Europe. *Conservation Biology*, *24*(1), 101-112. http://dx.doi.org/10.1111/j.1523-1739.2009.01399.x

Park, A. et Wilson, E. R. (2007). Beautiful Plantations: Can intensive silviculture help Canada to fulfill ecological and timber production objectives? *Forestry Chronicle*, *83*(6), 825-839. http://dx.doi.org/10.5558/tfc83825-6

Pearce, J. L. et Venier, L. a. (2006). The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: A review. *Ecological Indicators*, *6*(4), 780-793. http://dx.doi.org/10.1016/j.ecolind.2005.03.005

Pearce, J. et Venier, L. (2005). Small mammals as bioindicators of sustainable boreal forest management. *Forest Ecology and Management*, *208*(1), 153-175. http://dx.doi.org/10.1016/j.foreco.2004.11.024

Pearce, J., Venier, L., McKee, J., Pedlar, J. et McKenney, D. (2003). Influence of habitat and microhabitat on carabid (Coleoptera: Carabidae) assemblages in four stand types. *The Canadian Entomologist*, *135*(3), 337-357.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., EISPACK, Heisterkamp, S. et Van Willigen, B. (2017). Linear and Nonlinear Mixed Effects Models Description. *R package*, *version 3.*, 1-336. Récupéré de https://cran.r-project.org/package=nlme

Prescott, J. et Richard, P. (2013). *Mammifères du Québec et de l'est du Canada* (3e édition). [s.l.] : Éditions Michel Quintin.

Quine, C. P. et Humphrey, J. W. (2010). Plantations of exotic tree species in Britain: irrelevant for biodiversity or novel habitat for native species? *Biodiversity and Conservation*, *19*(5), 1503-1512. http://dx.doi.org/10.1007/s10531-009-9771-7

R Development Core Team. (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing : Vienna, Austria. Récupéré de https://www.r-project.org/

Rainio, J. et Niemelä, J. K. (2003). Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity and Conservation*, *12*(3), 487-506. http://dx.doi.org/10.1023/A:1022412617568

Réseau ligniculture Québec. (s.d.). *Réseau ligniculture Québec*. Récupéré le 19 décembre 2015 de http://www.rlq.uqam.ca/LigniculturеQc_fr.php

Riffell, S., Verschuyl, J., Miller, D. et Wigley, T. B. (2011). A meta-analysis of bird and mammal response to short-rotation woody crops. *GCB Bioenergy*, *3*(4), 313-321. http://dx.doi.org/10.1111/j.1757-1707.2010.01089.x

Rosalino, L. M., Rosário, J. do et Santos-Reis, M. (2009). The role of habitat patches on mammalian diversity in cork oak agroforestry systems. *Acta Oecologica*, *35*(4), 507-512. http://dx.doi.org/10.1016/j.actao.2009.03.006

Royer-Tardif, S., Paquette, A., Messier, C., Bournival, P. et Rivest, D. (2017). Fast-growing hybrids do not decrease understorey plant diversity compared to naturally regenerated forests and native plantations. *Biodiversity and Conservation*, 1-25. http://dx.doi.org/10.1007/s10531-017-1452-3

Saucier, J. P., Robitaille, A. et Grondin, P. (2009). Cadre bioclimatique du Québec. Dans *Écologie forestière, Manuel de foresterie* (2e éd., p. 186-205). [s.l.] : Ordre des ingénieurs forestiers du Québec.

Schowalter, T. (2017). Arthropod diversity and functional importance in old-growth forests of north america. *Forests*, *8*(4). http://dx.doi.org/10.3390/f8040097

Sebastià, M. T., Casals, P., Vojniković, S., Bogunić, F. et Beus, V. (2005). Plant diversity and soil properties in pristine and managed stands from Bosnian mixed forests. *Forestry*, *78*(3), 297-303.

Seibold, S., Bässler, C., Baldrian, P., Reinhard, L., Thorn, S., Ulyshen, M. D., Weiß, I. et Müller, J. (2016). Dead-wood addition promotes non-saproxylic epigeal arthropods but effects are mediated by canopy openness. *Biological Conservation*, *204*, 181-188. http://dx.doi.org/10.1016/j.biocon.2016.09.031

Simonetti, J. A., Grez, A. A. et Estades, C. F. (2013). Providing Habitat for Native Mammals through Understory Enhancement in Forestry Plantations. *Forest Ecology and Management*, *27*(5), 117-1121. http://dx.doi.org/10.1111/cobi.12129

Spake, R., Barsoum, N., Newton, A. C. et Doncaster, C. P. (2016). Drivers of the composition and diversity of carabid functional traits in UK coniferous plantations. *Forest Ecology and Management*, *359*, 300-308. http://dx.doi.org/10.1016/j.foreco.2015.10.008

Ståhl, G. (1997). Transect relascope sampling for assessing coarse woody debris: the case of a π/2 relascope angle. *Scandinavian Journal of Forest Research*, *12*(4), 375-381. http://dx.doi.org/10.1080/02827589709355426

Standovár, T., Ódor, P., Aszalós, R. et Gálhidy, L. (2006). Sensitivity of ground layer vegetation diversity descriptors in indicating forest naturalness. *Community Ecology*, *7*(2), 199-209.

Teixeira, D., Carrilho, M., Mexia, T., Köbel, M., Santos, M. J., Santos-Reis, M. et Rosalino, L. M. (2017). Management of Eucalyptus plantations influences small mammal density: Evidence from Southern Europe. *Forest Ecology and Management*, *385*, 25-34. http://dx.doi.org/10.1016/j.foreco.2016.11.009

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M. et Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, *31*(1), 79-92. http://dx.doi.org/10.1046/j.0305-0270.2003.00994.x

Varmola, M., Gauthier, D., Lee, D., Montagnini, F., Saramaki, J., Cao, Y., Lucca, M. Di, Giller, P., Goudie, J. W., Iremonger, S., Kelly, D. L., Mitchell, F. J. G., Halloran, J. O., Park, D. K., Park, Y. D. et Vanhanen, H. (2005). Forests in the Global Balance – Changing Paradigms. Dans International Union of Forest Research Organizations (IUFRO) (dir.), , *17* (p. 117-136). Helsinki : [s.n.].

Work, T. T., Koivula, M., Klimaszewski, J., Langor, D., Spence, J., Sweeney, J. et Hébert, C. (2008). Evaluation of carabid beetles as indicators of forest change in Canada. *The Canadian Entomologist*, *140*(4), 393-414.