UNIVERSITÉ DU QUÉBEC EN OUTAOUAIS

LA SIMPLIFICATION STRUCTURELLE DE LA VÉGÉTATION DANS LES PLANTATIONS DE PEUPLIER HYBRIDE MÈNE À DES DIFFÉRENCES DE COMMUNAUTÉS D'OISEAUX AVEC LES FORÊTS NATURELLES

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BA	Basal area
Cm	Centimeter
CWD	Coarse wood debris
d	Woody debris diameter
DBH	Diameter at breast height
db-RDA	Distance-based redundancy analysis
DF1	First discriminant function
DF2	Second discriminant function
DF3	Third discriminant function
FDR	False discovery rate
FSC	Forest Stewardship Council
G	Gini coefficient
H	Canopy height
Ha	Hectare
HPO	Hybrid poplar
km	Kilometer
L	Transect length
m	Meter
MA	Managed area
NS	Non-Significant
PCA	Principal Component Analysis
PC	Principal Component
PC1	First principal component
PC2	Second principal component
PC3	Third principal component

PEH	Peuplier hybride
PERMANOVA	Permutational multivariate analysis of variance
PERMDISP	Permutational analysis of multivariate dispersion
PNF	Parc national de Frontenac
PNMM	Parc national du Mont-Mégantic
PNMO	Parc national du Mont Orford
SDI	Shannon diversity index
Sel. Cut.	Selection cutting
SI	Structural index
SN	Stem number
V	Vegetation vertical inertia
y/o	Year old

RÉSUMÉ

Les plantations forestières comme celles de peuplier hybride (PEH), une espèce décidue couramment plantée en Amérique du Nord, sont de plus en plus utilisées pour répondre à la demande en bois à l'échelle mondiale. Ces plantations ont généralement une structure relativement simple et leur cycle de coupe est beaucoup plus court que celui des forêts naturelles (i.e., forêts matures ou régénérées naturellement après coupe). L'utilisation croissante des plantations soulève cependant des débats quant à la conservation de la biodiversité, notamment au Québec, car les plantations de PEH y sont jeunes et leurs effets sur la biodiversité peu documentés. Ainsi, l'objectif de cette étude est de déterminer l'effet des plantations de PEH en milieu forestier sur la diversité des communautés d'oiseaux. Durant l'été 2016, des inventaires d'oiseaux par points d'écoute ont été effectués afin de comparer la diversité des espèces se trouvant dans 34 peuplements situés dans les domaines de l'érablière à bouleau jaune et à tilleul (Estrie et Chaudière-Appalaches), soit dans 10 érablières matures (témoin) situées dans trois Parcs nationaux et 24 peuplements aménagés (plantations de PEH âgées de 1-3 ans (n=6); plantations de PEH âgées de 6-10 ans (n=6); peuplements régénérés naturellement après coupe (n=6) et érablières ayant subi une coupe de jardinage (n=6)). De plus, des relevés de végétation et une caractérisation du paysage avoisinant les peuplements ont été réalisés afin de déterminer le rôle relatif de la quantité d'attributs structuraux de la végétation, de l'hétérogénéité structurale de la végétation et de la composition du paysage avoisinant sur la diversité des communautés d'oiseaux. Nos résultats démontrent que les plantations arboraient une richesse spécifique aviaire similaire aux autres peuplements à l'étude. Toutefois, cette similarité s'accompagnait de différences d'assemblages d'espèces comparativement aux assemblages retrouvés en forêts matures non aménagées et régénérées naturellement. Ces dissimilarités dans l'assemblage des espèces étaient expliquées par des différences dans la quantité d'attributs structuraux de la végétation, combinée à des différences d'hétérogénéité structurale de la végétation et dans une moindre mesure, de différences de composition de paysage. Dans leur ensemble, nos résultats démontrent que les différences d'assemblages d'espèces seraient principalement dues à une simplification des attributs structuraux et de l'hétérogénéité structurale des arbres. D'un point de vue appliqué, ces résultats suggèrent qu'il serait important d'aménager les plantations de PEH de manière à y retrouver des arbres de différentes tailles (i.e., plantation inéquienne). Cela pourrait être possible en plantant plusieurs espèces d'arbre dont la croissance diffère (i.e., plantation multispécifique), ou de ne pas couper tous les arbres au sein de la plantation monospécifique afin de générer une hétérogénéité dans la taille des arbres d'une rotation à une autre.

MOTS-CLÉS : Plantation; peuplier hybride; biodiversité; assemblage d'espèces; communauté d'oiseaux; attribut structural; hétérogénéité structurale; composition du paysage

INTRODUCTION

Importance et rôle des plantations

Les plantations forestières sont de plus en plus utilisées à travers le monde pour augmenter et régulariser l'approvisionnement en bois (Carle et Holmgren, 2008; FAO, 2011). Ainsi, les plantations couvrent près de 7% de la superficie forestière mondiale et ce chiffre est appelé à augmenter dans les prochaines décennies (FAO, 2011; Payn *et al.*, 2015). En général, les plantations sont définies comme des forêts aménagées de façons intensives, composées d'une seule espèce d'arbres (indigène ou exotique), appartenant à la même classe d'âge (peuplement équienne) et espacées de façon régulière (Carnus *et al.*, 2006). L'aménagement intensif des plantations inclut, par exemple, la préparation de site pour améliorer les conditions du sol, le contrôle de la végétation compétitive et la fertilisation (Demarais *et al.*, 2017). Ainsi, les plantations sont principalement utilisées pour leur rendement ligneux élevé et généralement supérieur au rendement des forêts naturelles, ce qui permet des récoltes du bois sur de plus courtes rotations (Park et Wilson, 2007). De ce fait, la majorité des plantations (environ 76%) sont mises en place pour la production de bois (FAO, 2010). Actuellement, elles contribuent à plus de 15% de la production mondiale de bois et on prévoit prochainement atteindre 50% de la production (FAO, 2011). En effet, l'augmentation des superficies plantées et l'intensification des pratiques, notamment par l'utilisation des plantations d'espèces à croissance rapide (e.g. le peuplier hybride (*Populus spp.*)), sont au cœur de cette stratégie (Carle et Holmgren, 2008; FAO, 2011; Payn *et al.*, 2015). On reconnait internationalement que pour répondre à la demande future en bois, conjointement à l'augmentation de la population et la diminution des forêts primaires, les plantations avec différents degrés d'intensité joueront un rôle déterminant (Park et Wilson, 2007). Cette tendance se reflète également au Canada, 4^{e} pays en importance en terme de surface forestière plantée avec des plantations couvrant 3,7% de la surface forestière et en progression d'environ 4% depuis 1990 (Payn *et al.*, 2015).

Toutefois, leur utilisation fait l'objet de débat, car elles ont acquis une « mauvaise réputation » dans le passé résultant de la vision de monocultures intensives à grande échelle dans lesquelles la biodiversité est altérée, et cela au détriment des divers rôles écologiques positifs que peut jouer une plantation (Paquette et Messier, 2010). Or, les plantations devraient être vues dans un contexte plus large que simplement la production de bois, c'est à dire plutôt comme un outil pour la planification de l'aménagement des terres permettant l'atteinte d'objectifs de conservation (Hartmann *et al.*, 2010). Effectivement, les aménagements forestiers intensifs, telles les plantations, ont l'avantage de produire un volume de bois sur une fraction du territoire qu'utiliseraient des aménagements extensifs en forêt naturelle (i.e., en forêts matures ou en régénération naturelle après perturbation; Groupe d'experts sur la sylviculture intensive de plantations, 2013). Ainsi, l'augmentation de la production de bois sur une partie du territoire, par les plantations, peut permettre de consacrer une plus grande portion des forêts à la conservation ou de diminuer l'intensité des coupes sur le reste du territoire (Sedjo et Botkin, 1997).

Plantations et conservation de la biodiversité

Bien qu'elles ne couvrent encore qu'un faible pourcentage de la forêt dans le monde, l'utilisation croissante et intensive des plantations est une source d'inquiétude pour la conservation de la biodiversité (Brockerhoff *et al.*, 2008; Carnus *et al.*, 2006; Paquette et Messier, 2010). En effet, les écosystèmes forestiers sont d'importants réservoirs de biodiversité et on estime qu'ils abritent 80% des espèces terrestres (FAO, 2010). D'ailleurs, l'importance de maintenir, conserver et/ou restaurer cette biodiversité a été mise de l'avant au niveau commercial par la mise en place de système de certification forestière, comme la norme sociale et environnementale « *Forest Stewardship Council* » (FSC, Principe 6). Or, plusieurs études ont démontré que les plantations peuvent être moins diversifiées que les forêts naturelles pour plusieurs taxons (Bremer et Farley, 2010; Carnus *et al.*, 2006). En effet, en raison des pratiques sylvicoles associées aux plantations, ces dernières arborent souvent une quantité d'attributs structuraux de la végétation réduite comparativement aux peuplements régénérés naturellement (ex. réduction de l'étagement de la végétation, des différents couverts en sous-étage ou de l'abondance des chicots et d'arbres de gros diamètre) (Franklin *et al.*, 2002). De plus, les plantations sont généralement mises en place pour maximiser la production ligneuse d'une seule cohorte et minimiser la mortalité des arbres plantés, alors que les forêts naturelles offrent des conditions de croissance hétérogènes et la mortalité y est plus élevée. Par conséquent, la variation des différents attributs structuraux de la végétation (i.e. hétérogénéité structurale) à l'échelle du peuplement est généralement homogénéisée par rapport aux forêts naturelles ce qui fournit une plus faible diversité de niches écologiques pour les espèces végétales et animales (Groupe d'experts sur la sylviculture intensive de plantations, 2013). En somme, les altérations de ces caractéristiques (simplification et homogénéisation des attributs structuraux de la végétation) font que les plantations sont souvent des habitats de moindre qualité aux espèces forestières indigènes puisque les caractéristiques internes aux peuplements se sont éloignées de celle des forêts naturelles (Hartley, 2002; Paillet *et al.*, 2010). Subséquemment, la mise en place de plantations sur une grande partie du territoire à un potentiel élevé de simplification et homogénéisation du paysage forestier (Barrette *et al.*, 2014). Toutefois, les effets sur la biodiversité sont variables et dépendent entre autres du contexte (le type de couvert qu'elles remplacent et les alternatives potentielles aux plantations) et de multiples facteurs (espèce plantée, âge de la plantation, proportion du paysage couvert de plantation). Pour ces raisons, l'effet des plantations pour la conservation de la biodiversité fait l'objet de nombreux débats (Brockerhoff *et al.*, 2008; Carnus *et al.*, 2006; Hartmann *et al.*, 2010; D. Lindenmayer *et al.*, 2015; Stephens et Wagner, 2007).

Effet des plantations sur de la biodiversité animale

Il est bien connu que la simplification structurelle s'accompagne généralement d'effet sur la biodiversité (Paillet *et al.*, 2010). Les conséquences négatives de la simplification structurelle causées par la mise en place de plantations par rapport aux forêts naturelles ont été démontrées dans plusieurs études sur les oiseaux, mammifères et invertébrés (Martello *et al.*, 2018; Nájera et Simonetti, 2010; Ramírez et Simonetti, 2011). Plus spécifiquement, les plantations, via la simplification et l'homogénéisation du peuplement forestier, influencent la disponibilité des ressources pour l'alimentation et la reproduction des communautés animales. Par exemple, les espèces d'oiseaux utilisant les plantations sont surtout associées à une strate arbustive dense (Riffell *et al.*, 2011) alors que les espèces spécialistes des vieilles forêts et cavicoles n'y trouvent pas les sources de nourriture adéquates et les arbres matures requis pour la nidification (Bergner *et al.*, 2015; MacKay *et al.*, 2014). Néanmoins, avec la canopée qui se referme au fur et à mesure du développement de la plantation, cette dernière peut fournir un habitat pour les espèces forestières associées à un couvert fermé (Christian *et al.*, 1998). En effet, l'âge des plantations est un facteur important, puisqu'en vieillissant on observe que les plantations se complexifient et développent généralement une structure plus hétérogène (Hanowski *et al.*, 1997; Riffell *et al.*, 2011). Toutefois, les plantations accommodent souvent les espèces forestières qui peuvent bénéficier de plusieurs types de forêt pour leur reproduction et qui dominent souvent dans les environnements modifiés par l'homme au détriment des espèces spécialistes des forêts matures (Carnus *et al.*, 2006; Newbold *et al.*, 2015). De plus, les effets des plantations sur la diversité animale dépendent également du contexte spatial (e.g. la composition du paysage avoisinant) (Brockerhoff *et al.*, 2008). Néanmoins, l'information disponible sur l'effet des plantations sur la biodiversité animale au-delà de l'échelle du peuplement est très limitée (Carrara *et al.*, 2015). En général, pour les communautés d'animaux qui sont très mobiles, comme celle des oiseaux, l'assemblage des espèces dans les plantations serait principalement influencé par la composition du paysage avoisinant les plantations (Christian *et al.*, 1998). Par exemple, dans un paysage où l'on retrouve un fort couvert de forêts plantées, la présence dans les plantations des espèces associées aux forêts matures dépendrait de peuplements avoisinants peu ou pas aménagés (MacKay *et al.*, 2014). De plus, la composition du paysage avoisinant selon différentes classes d'âge de couvert forestier va influencer l'assemblage des espèces dans les plantations selon leur association à la succession végétale. En effet, quand une plantation est entourée d'une grande proportion de jeunes couverts forestiers, la présence d'espèces de début de succession est généralement observée dans la plantation (ou l'inverse si la proportion de couverts matures avoisinants est élevée) (Hagan *et al.*, 1997).

Objectif principal de l'étude

En Amérique du Nord, et particulièrement dans le sud du Québec, les plantations de peuplier hybride (PEH) sont de plus en plus utilisées en forêts aménagées pour des raisons économiques, i.e. pour les industries des pâtes et papiers (Fortier *et al.*, 2012; Park et Wilson, 2007). En effet, les plantations de PEH peuvent avoir une croissance très rapide et permettent des récoltes de bois en 15-20 ans. La compagnie Domtar, le partenaire industriel à ce projet, possède 160 000 ha de forêts privées en Estrie et en Beauce (Québec), dans lesquelles le PEH est un élément clé de leur stratégie d'aménagement et d'approvisionnement en fibre de leur usine de pâte et papier à

Windsor (Estrie, Québec). Depuis 1998, plus de 6 000 ha de plantations de PEH ont été mises en place et l'objectif est d'atteindre 8 000 ha d'ici 2020 (i.e., 5% de la superficie forestière exploitée). La diversité faunique dans les plantations de peupliers a surtout fait l'objet d'études dans les paysages agricoles (Moser et Hilpp, 2003, 2004), mais peu ont été menées dans des paysages forestiers où les plantations remplacent des forêts (Archaux et Martin, 2009; Christian *et al.*, 1998; Martín-García *et al.*, 2013). Ces études démontrent que les plantations de PEH peuvent fournir un habitat de qualité en milieu agroforestier, mais elles ont plutôt une fonction de milieu ouvert en milieu forestier. Ainsi les préoccupations concernant le maintien de la biodiversité sont particulièrement fortes, car les plantations de PEH étant généralement jeunes au Québec, leurs effets sur la biodiversité n'y sont pas encore bien documentés. De plus, Domtar et les gestionnaires de la certification FSC ont peu d'information concernant les effets potentiels des plantations de PEH sur la biodiversité en milieu forestier et les connaissances actuelles sont difficilement transposables aux forêts feuillues tempérées du sud du Québec où œuvre Domtar.

Ainsi, l'objectif principal de cette étude était de déterminer l'effet des plantations de PEH sur la diversité des communautés d'oiseaux (richesse en espèces, assemblage et traits biologiques). Pour cela, les communautés d'oiseaux rencontrées dans les plantations de PEH ont tout d'abord été comparées à celles habitant les forêts naturelles aménagées et non aménagées. Dans un deuxième temps, l'importance relative de la quantité des attributs et de l'hétérogénéité structurale de la végétation, ainsi que la composition du paysage avoisinant dans la structuration des communautés d'oiseaux ont été estimées afin de déterminer les facteurs responsables des différences de diversité d'oiseaux observées dans les plantations de PEH. Dans cette étude, nous avons utilisé les oiseaux comme proxy des effets des plantations de PEH sur la biodiversité, car 1) ils forment un assemblage riche en espèces utilisant une grande variété d'habitats, 2) ils sont sensibles aux changements environnementaux et 3) leur histoire de vie est bien documentée. Ainsi, les oiseaux sont de bons indicateurs de la capacité d'un habitat modifié à maintenir la biodiversité (Venier et Pearce, 2004). De plus, les oiseaux sont le groupe taxonomique le plus étudié pour déterminer les effets des plantations sur la biodiversité animale (Stephens et Wagner, 2007). Finalement, l'utilisation des traits biologiques décrivant les substrats utilisés pour la nidification ou les stratégies d'alimentation est pertinente pour comprendre l'influence du type d'habitat forestier sur les communautés d'oiseaux par groupe fonctionnel plutôt que basé sur la taxonomie (Canterbury *et al.*, 2000; De Graaf *et al.*, 1985).

L'effet des plantations de PEH sur la biodiversité animale en milieu forestier a été peu étudié au Canada. Par conséquent, cette étude permettra de fournir plusieurs connaissances inédites qui pourront être valorisées pour faire des plantations un meilleur outil pour la conservation de la biodiversité. De plus, les quelques études réalisées ont généralement déterminé l'effet des plantations de PEH sur la diversité animale en comparant les communautés animales entre des plantations et des forêts matures (Riffell *et al.*, 2011). Cependant, cette comparaison n'est pas forcément la plus pertinente puisque les plantations de PEH ne remplacent généralement pas des forêts matures et qu'il serait plus approprié de les comparer aux différentes alternatives d'utilisation des terres où se trouvent les plantations (Stephens et Wagner, 2007). Ainsi, dans cette étude, nous avons comparé les plantations de PEH à des forêts matures, mais aussi à deux autres pratiques sylvicoles largement utilisées dans le domaine forestier à l'étude afin de donner un portrait plus complet de l'effet des plantations de PEH sur la biodiversité animale en milieu forestier. Finalement, les études déjà réalisées se sont concentrées sur l'effet de la quantité des attributs structuraux de la végétation rencontrée dans les plantations sur la diversité animale (Riffell *et al.*, 2011). L'hétérogénéité structurale, une caractéristique pourtant importante de la végétation et qui est modifiée dans les plantations, n'est généralement pas étudiée pour comprendre l'effet des plantations sur la biodiversité animale (e.g. Hanowski *et al.*, 1997). Ainsi, cette étude va porter à la fois sur la quantité et l'hétérogénéité structurale de la végétation, afin d'avoir une compréhension plus précise des effets des plantations de

PEH sur la biodiversité animale. Ultimement, cela permettra aussi de mieux orienter les gestionnaires forestiers sur les aspects structuraux qui sont importants à considérer dans les plantations dans le but d'y maintenir la biodiversité animale.

CHAPITRE I

LOW QUANTITY AND HETEROGENEITY OF VEGETATION STRUCTURAL ATTRIBUTES IN HYBRID POPLAR PLANTATIONS DRIVE BIRD COMMUNITY DIFFERENCES WITH NATURAL FORESTS

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1.1 Introduction

Intensively managed plantations for high yield wood production are increasing worldwide (Carle et Holmgren, 2008; FAO, 2011). They now cover approximately 7% of the world's total forest area and produce nearly half of the commercial wood (Payn *et al.*, 2015). Half of these plantations are located in the temperate zone, where the increase has been the most rapid in the last decade (Payn *et al.*, 2015). Plantations are more productive than natural forests due to the use of fast-growing trees (e.g. hybrid poplar, HPO) and intensive management involving site preparation (e.g. fertilization, mounding) which also allows a shorter rotation between clear-cut harvesting (Fortier *et al.*, 2012).

Even though they still represent a small proportion of the world's forests, plantations are a source of concern for biodiversity conservation (Carnus *et al.*, 2006; Paquette et Messier, 2010). Many studies have shown that plantations can be less diverse than natural forests for many taxa (Bremer et Farley, 2010; Carnus *et al.*, 2006). Indeed, plantations are typically even-aged, even-spaced and monospecific with low vegetation structural attributes compared to naturally regenerated stands. Moreover, plantations are generally managed to reduce mortality and maximize growth whereas in natural forests, mortality is higher and growth more heterogeneous both of which contribute to vegetation structural heterogeneity. This simplification of vegetation structural attributes and homogenization of plantations compared to natural forests generally means a lower habitat quality for native forest species (Carnus *et al.*, 2006). Additionally, extensive deployment of plantations over a large portion of the land base has a high potential for simplifying and homogenizing entire forest landscapes (Barrette *et al.*, 2014). Hence, the effect of plantations on biodiversity is the subject of many debates (Brockerhoff *et al.*, 2008; Carnus *et al.*, 2006; Hartmann *et al.*, 2010; Stephens et Wagner, 2007) focusing on the fact that effects on biodiversity vary and depend on, among other things, which cover is being replaced, which species is planted, the age of the plantation and proportion of the landscape covered by plantations.

The structural simplification and homogenization of plantations negatively affect breeding and resource availability for many animal species. For example, cavity-nesting birds in mature forests do not find adequate food resources or nesting sites in plantations (MacKay *et al.*, 2014; Riffell *et al.*, 2011). Nonetheless, as the plantation matures, it can provide habitat for forest species associated with a closed canopy (Christian *et al.*, 1998). In addition, the effect of plantations on animal diversity also depends on the spatial context (e.g. composition and configuration) (Brockerhoff *et al.*, 2008; Hartmann *et al.*, 2010). However, the effect of the spatial context on biodiversity has rarely been evaluated (Carrara *et al.*, 2015).

In North-America, and particularly in southern Quebec, fast-growing hybrid poplar plantations are currently increasing in managed forest areas for economic purposes (i.e. pulp and paper industries) (Fortier *et al.*, 2012). Concerns about maintaining biodiversity in such plantations are particularly strong because their effects on biodiversity are not yet well documented in North-America, especially when hybrid poplar (HPO) plantations replace natural forests (Archaux and Martin, 2009, Christian et al., 1998, Martín-García et al., 2013). Therefore, this study will provide guidelines to make plantations a better tool for the biodiversity conservation. In addition, studies generally determined the effects of HPO plantations on animal diversity by comparing animal communities between plantations and mature forests (Riffell *et al.*, 2011). However, this comparison is not always relevant since HPO plantations do not generally replace mature forests. Therefore, it would be more appropriate to compare them with the different land-use alternatives where the plantations are located (Stephens et Wagner, 2007). Thus, in this study, we compared HPO plantations with mature forest but also with two silvicultural approaches largely used in the study area to provide a more complete picture of the effects of HPO plantations on animal biodiversity in forested area. Finally, previous studies focused on the effects of the quantity of vegetation structural attributes found in plantations on animal diversity (Riffell *et al.*, 2011). Structural heterogeneity, an important vegetation characteristic which is modified in plantations, is usually not taken into account to understand the effects of plantation on animal biodiversity (e.g. Hanowski *et al.*, 1997). Thus, this study will look at both the quantity and heterogeneity of the vegetation structure, in order to have a more precise understanding of the effects of the HPO plantations on animal biodiversity. Ultimately, this will also help to better guide forest managers on the structural aspects that are important to manage in plantations in order to maintain animal biodiversity.

In this study, we compare the short-term response of forest bird communities to various forest types, from hybrid poplar plantations to unmanaged forests. We use birds as a proxy for biodiversity effects because 1) they form species-rich assembly using a wide variety of habitats, 2) they are sensitive to environmental changes, and 3) their life histories are well known. Birds are known to be good indicators of the ability of an altered habitat to sustain biodiversity (Venier et Pearce, 2004).

The main objective was to test how community richness, species diversity, and biological traits respond to structural changes induced within HPO plantations. More specifically, we 1) determined how HPO plantations affect forest bird diversity (i.e. species richness, assemblage, and biological traits) according to tree maturation in plantations and habitat characteristics in managed and unmanaged natural forests, and 2) identified the relative role of stand level vegetation structural attribute and heterogeneity and landscape level composition surrounding plantations for forest bird community diversity.

1.2 Methods

1.2.1 Study area and experimental design

The study was conducted in the regions of Estrie and Chaudière-Appalaches (45°40'N 71°12'W) in the temperate deciduous forest of Quebec, Canada. The forest canopy is dominated by Sugar maple (*Acer saccharum)* and Yellow birch (*Betula alleghaniensis)*, and other common species such as American beech (*Fagus grandifolia*), Red maple (*Acer rubrum*), American ash (*Fraxinus americana*), Balsam fir (*Abies balsamea*) and Spruce (*Picea sp*). The region landscape is hilly and dominated by forests interspersed among agricultural land, lakes, and wetlands. The study was carried out in Domtar's private forest and three distinct nearby provincial parks (Parc national du Mont Orford (PNMO), Parc national de Frontenac (PNF) and Parc national du Mont-Mégantic (PNMM)). The 160 000 ha of Domtar's private forest are composed of mature (>50-year-old, 23%), developing (30-50-year-old, 32%) and young or regenerating forests (<30-year-old, 45%). HPO plantations are a key element of Domtar's management strategy; this private forest company is committed through the Forest Stewardship Council certification (FSC) to maintaining biodiversity (FSC 2012, Principle 6). Domtar started to plant Hybrid poplar (HPO) in 1998. In 2016, these plantations covered about 6 000 ha and Domtar's objective is to achieve 8 000 ha in the next few years (i.e. 5% of the total area of their private forest). There has been no commercial harvesting in National parks since their creations in 1938 (PNMO), 1987 (PNF) and 1994 (PNMM).

The sampling was conducted on 24 managed stands in the private forest areas and on 10 unmanaged forest stands distributed in the nearby National Parks (Figure 1.1). The 24 managed stands were distributed across six areas of Domtar's private forests, each one with 4 silvicultural treatments: 1) 1-3-year-old HPO plantations, 2) 6-10-year-old

HPO plantations, 3) 15-30-year-old forest stands originating from clearcutting (from 70 to 100% of the above-ground biomass harvested) that regenerated naturally (hereafter "naturally regenerated stands", and 4) 1-4-year-old stands after selection cutting (from 25 to 40% of the above-ground biomass harvested every 25 to 35 years) in mature maple forests (hereafter "stand managed by selection cutting"). The 15-30-year-old naturally regenerated stands were similar to 6-10-year-old HPO plantations in terms of tree height and diameter at breast height. Site preparation for HPO plantations included clearcutting, mounding, and fertilization. Three areas were selected in National parks as control representatives of unmanaged regional forests. Each control area consisted of three or four ≥60-year-old unmanaged sugar maple stands (PNMO: n=3 stands, PNF: n=4 stands, PNMM: n=3 stands). Thus, our 34 sampling stands were grouped in 9 areas (managed areas: n=6; National parks: n = 3) separated by a distance of 15 to 100 km. Within each area, the distance between sampling stands varied from 1.6 to 11 km, and each stand covered a minimum of 5 ha. The four silvicultural treatments were matched by area to account for local variations in the forest bird community.

1.2.2 Sampling of forest birds and their habitats

The presence of each bird species in each stand was monitored between May 24th and July 6th 2016 using a fixed-radius point count method of 30 meters (Bibby *et al.*, 1992). The point count began after a 2 minutes period of immobility and lasted for 10 minutes (Drapeau *et al.*, 1999). During this period, the presence of all birds seen or heard was recorded. Two point counts per stand were monitored 3 times during the breeding season between dawn and 8:00 a.m. Point counts were randomly selected to be at least 70 meters from each other and from any stand edges. To maximize the probability of detecting bird species, each point count was surveyed once during the early, middle and late stages of the breeding season and we alternated the survey among early, middle and late morning periods. Surveys were conducted by 2 observers on days without heavy wind and rain. Presence of each bird species at each point count station was expressed as a single detection for each species after 3 visits (n=68).

In each stand, forest bird habitat was characterized in a 400m^2 circular plot centered on the point count stations (N = 2) and on two randomly selected plots (more than 70 meters from each other, from point count station and from any stand edges) by measuring the composition and structure of the vegetation. In each circular plot, we recorded species and diameter at breast height (DBH) of all living trees ($\geq$9 cm DBH) and snags ($\geq$9 cm DBH). Living trees with DBH >22 cm were noted to identify potential habitats for cavity nesters and bark foragers. Canopy closure was measured using a convex densitometer held 1.30 m above ground (%). Canopy height was estimated by measuring a single representative tree using a clinometer. We visually estimated vegetation cover in classes (0-1%, 2-20%, 21-40%, 41-60%, 61-80%, and 81-100%) for 4 strata, including understory herbaceous cover, understory shrub cover, understory sapling cover, and overstory tree cover. Understory shrub and sapling cover, and overstory tree cover were estimated inside the 400 m^2 circular plot whereas herbaceous cover was estimated inside two 6.25 m^2 quadrats. These two quadrats were also used to characterize understory, by measuring and identifying saplings (DBH <9 cm) and recording shrub species. We estimated ground structure in the 400 m^2 circular plot by counting all tree stumps and by measuring coarse woody debris volume (CWD, m^3·ha^{-1}) with a diameter >9 cm lying on the ground along two 25 m transects placed on North-South and East-West axes (Ståhl, 1997; Van Wagner, 1968). The volume of woody debris (CWD) was estimated using the following equation (de Vries, 1973).

$$CWD = (\pi^2/8L) \times \sum d^2 \qquad \text{[Eq. 2.1]}$$

Where L is the transects total length (m) and d is the woody debris diameter (cm).

Based on this set of variables, we calculated three measures summarizing quantity of structural attributes. First, we adapted the index used by Holdridge (1967) to describe tree and sapling structural attributes in each plots. These attributes were defined by canopy height (H), respective basal area (BA) and stem number (SN). We calculated two structural index (SI) using the following equations:

$$SI_{Tree} = H \times BA_{tree} \times SN_{tree} \quad \text{[Eq. 2.2]}$$

$$SI_{Sapling} = BA_{sapling} \times SN_{sapling} \quad \text{[Eq. 2.3]}$$

Increasing SI_{Tree} or $SI_{Sapling}$ reflected higher amount of structural attribute for the respective strata when comparing sites.

Then, to describe the relative vertical distribution of vegetation in each plot, we computed an index of vegetation vertical inertia (V) using four different vegetation heights above ground (herbaceous = 0.25 m, shrub = 1.25 m, sapling =4 m, tree = 9 m) and associated vegetation covers (% as described above) for the fourth strata. The vegetation vertical inertia was based on the following equation (Doyon *et al.*, 2005):

$$V = \frac{0.25\times(\text{Herbaceous cover}) + 1.25\times(\text{Shrub cover}) + 4\times(\text{Sapling cover}) + 9\times(\text{Tree cover})}{(\text{Herbaceous cover}) + (\text{Shrub cover}) + (\text{Sapling cover}) + (\text{Tree cover})} \quad \text{Eq. 2.4]}$$

where 0.25, 1.25, 4, 9 were the respective constants for herbaceous, shrub, sapling and tree height (m). Increasing values indicate a distribution of the vegetation towards the higher strata.

Additionally, we characterized vertical diversity at the plot level by computing the Shannon diversity index (SDI) using the cover values (%) of each vegetation strata (varpart function in the vegan package in R, Oksanen et al. 2013). Thus, we obtained for each plot an SDI based on values of herbaceous cover, shrub cover, sapling cover, and tree cover. V and SDI measures give complementary information to describe structural attributes. V indicates where most of foliage biomass was located, whereas SDI indicates the relative distribution of foliage among different strata (i.e. vertical arrangement of the different cover types). Increasing SDI indicates higher quantity of overall vegetation cover and evenness among strata covers.

We also described the vegetation structural heterogeneity (i.e. within stands variation of structural attributes) by estimating the Gini coefficient (G) of statistical dispersion (Bradford et Kastendick, 2010). For each stand, G was computed for DBH, herbaceous cover, shrub cover, sapling cover and canopy closure using the following equations:

$$\text{G-DBH}=\frac{\sum_{i=1}^{n}(2i-n-1)x}{n^2\mu} \qquad \text{[Eq. 2.5]}$$

Where n is the number of trees in the plot, x is the diameter of tree i (cm) and μ is the mean tree diameter of the plot (cm)

and

$$\text{G-Vegetation cover or Canopy closure}=\frac{\sum_{i=1}^{n}(2i-n-1)x}{n^2\mu} \qquad \text{[Eq. 2.6]}$$

where n is the number of plots in the stand (= 4), x is the Canopy closure, Herbaceous cover, Shrub cover or Sapling cover (%) of plot i and μ is the mean Canopy closure, Herbaceous cover, Shrub cover or Sapling cover (%) of the stand. G varied between 0 and 1, where 0 expressed perfect equality between stand plots whereas 1 expressed perfect inequality.

Finally, we evaluated the composition of the surrounding matrix within 750 m radius circular buffers around each stand using digital forest cover data provided by territory managers (Domtar and Parks managers) and Quantum GIS (version 1.8.0). This radius was chosen to be large enough to be representative of area-demanding species, like

Picidea (Ouellet-Lapointe, 2010) and to avoid pseudo-replication (i.e. to create non-overlapping buffers). We estimated the proportion of: 1) ≤4-year-old HPO plantations, 2) ≥5-year-old HPO plantations, 3) different forest cover types (deciduous, mixed or resinous), 4) different forest types based on their age class: mature (>50-year-old), developing (30-50-year-old) and young or regenerating (<30-year-old), and 5) wetlands. The 5 year-old plantation threshold was used to distinguish open from tree-like plantations (Christian *et al.*, 1998). Furthermore, landscape composition has been identified as being the main factor influencing forest birds community on a mesoscale similar to our study (Barbaro *et al.*, 2007; Christian *et al.*, 1998). For this reason, we did not included any measure of landscape structure, although it could influence forest bird communities on a larger scale (Villard *et al.*, 1999)

1.2.3 Statistical analyses

We first performed a principal component analysis (PCA, rda function in the vegan package of R, Oksanen et al. 2013) to summarize bird habitat variation (i.e., environmental gradient) among our five stand types (n=136 sampling plots). Scores of the most important PCs, which were selected based on the broken stick model (screeplot function in the vegan package of R, Oksanen et al. 2013), were then entered into a discriminant function analysis to determine which environmental gradient (i.e., PC scores) differentiated our stand types (lda function in the MASS package of R, Brian et al. 2013). We evaluated the significance of environmental gradients based on a Wilk's lambda test (summary.manova function in the stats package of R, R Core Team 2013). We then carried out pairwise comparisons to identify which stand type was different (p-values were adjusted for multiple testing using a Holm's procedure). From all possible comparisons among the five stand types, only four were considered relevant for the analyses: 1) 1-3-year-old HPO plantations were compared with 6-10-

year-old HPO plantations, to quantify how habitat characteristics and their forest bird communities change with plantation maturation, 2) 6-10-year-old HPO plantations were compared with naturally regenerated stands, to assess effects of reforestation with HPO plantations, and 3) control forests (i.e., >60-year-old unmanaged mature forest) to evaluate the difference with the regional biodiversity control, and 4) control forests were compared with recent selections cutting in maple stand (1-4-year-old) to estimate the difference between a common and socially accepted cutting practice (contrary to HPO plantations that are less socially acceptable; Martineau & Bouthilier 2007) and regional habitat characteristics and bird species biodiversity control.

Bird species diversity was described in each stand (n=34) as the total number of species (species richness) detected at the two point count stations combined. We evaluated differences in species richness for each comparison previously described using four permutation analyses of variance (100,000 permutations; avop function in the lmPerm package of R; Wheeler & Torchiano 2016).

We tested whether species composition differed among stand types with a nonparametric permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) using a dissimilarity matrix calculated from Sorensen indices based on the bird species presence-absence (per station; n=68) data (adonis function in the vegan package of R; Oksanen et al. 2013). This analysis estimates the ratio of composition dissimilarity within a stand type to that of between stand types, and then tests its significance by permutations (n = 999). Permutations were restricted within each area to account for the lack of independence among stands located in the same area. A significant ratio may result from differences in dissimilarity among stand types, within a stand type or both. To distinguish the nature of the difference, we ran a complementary analysis, a permutational analysis of multivariate dispersion (PERMDISP, Anderson et al 2006) which tests whether composition dissimilarity within a stand type is homogeneous among stand types (i.e. a test of multivariate homogeneity of variance; betadisper function in the vegan package of R, Oksanen et al. 2013). A significant difference by PERMANOVA but not by PERMDISP indicated a difference in composition dissimilarity among stand types but not within stand types. If the difference was also significant with PERMDISP, this indicated that composition dissimilarity within stand types was not homogeneous. When the PERMANOVA or PERMDISP was significant (see the Results section), we carried out pairwise contrasts between the four pairs of stand types (comparisons 1 to 4 previously described) to identify which stand type was different and interpreted the nature of the difference in species composition. We adjusted p-value for multiple testing using Holm's procedure. To visualize the compositional differences among stand types and compositional dispersion of stand types from the community centroids, we used principal component ordination plots based on the species composition dissimilarity matrix. Contrary to the species richness analyses, rare species (species that were detected in fewer than 5 stands) were not included in the species assemblage analysis.

We evaluated the effect of the three components describing habitat characteristics, i.e. 1) a matrix of 11 variables describing vegetation structural attributes, 2) a matrix of 5 variables describing vegetation structural heterogeneity, and 3) a matrix of 7 variables describing the composition of the surrounding landscape (Table 1.1), on bird species assemblage using a distance-based redundancy analysis (db-RDA, Legendre & Anderson 1999) performed with the capscale function in the vegan package of R (Oksanen *et al.*, 2013). We used the dissimilarity matrix calculated from the Sorensen indices based on the bird species presence/absence (per station; n=68) data. Permutation tests (n=10 000) were used to evaluate the significance of the relationship between bird species assemblages and habitat characteristics. Based on this db-RDA and adjusted R^2, we used variation partitioning analyses (varpart function in the vegan package in R, Oksanen et al. 2013) to distinguish the overall variation in bird species assemblages attributable to each category of habitat characteristics as well as the shared variation explained by a combination of categories (Drapeau *et al.*, 2000).

Finally, and in order to increase our understanding of the differences in bird species assemblages among stand types, we investigated relationships between bird species traits and stand types using a fourth-corner analysis (fourthcorner function in the package ade4 of R, Dray et al. 2018). This method allowed the simultaneous analysis of three matrices (species presence/absence per station, species per traits, and stand types) and tests for significant relationships among all bird species traits and stands types in one single analysis (Dray et Legendre, 2008). All information about species traits was found online at the Cornell Lab of Ornithology "All About Birds" and the "Audubon Bird Guide" (last visited in December 2017). Biological traits focused on nesting substrates and foraging behavior related to distinct vegetation strata and structure (e.g. ground, shrubs, trees, cavities) to monitor the effect of stand type (Canterbury *et al.*, 2000; De Graaf *et al.*, 1985). Thus, we could classify groups of species rather than only a single species using a similar resource (guild) and show how stand types influence community composition on a broader scale. Permutation model 6 (n=9999) was chosen to reduce inflated type 1 error (Dray et Legendre, 2008). We applied a "FDR" method to adjust for multiple testing to avoid false positives.

1.3 Results

1.3.1 Habitat characterization

The results of the principal component analysis showed that the first three principal components accounted for 55.1% of the variation (30.8%, 13.3%, and 11.0%, respectively) in habitat characteristics (Table 1.1). The first principal component (PC1) represented a gradient ranging from plots with low to high quantity of structural attributes and heterogeneity associated with the canopy and DBH of trees (i.e., canopy closure, vegetation vertical inertia, basal area of larger trees, DBH heterogeneity; Table

1.1) together with a low to high proportion of mature forest but a high to low proportion of young forest in the surrounding matrix (Table 1.1). PC2 identified a gradient in the quantity and heterogeneity of structural attributes of the understory layer varying from plots with low to high sapling cover, sapling structural index, and shrub cover heterogeneity and high to low shrub cover and sapling cover heterogeneity (Table 1.1). PC3 represented a gradient from plots with a high canopy closure heterogeneity and proportion of ≥ 5-year-old HPO plantations in the surrounding landscape to plots with a high proportion of wetlands in the surrounding landscape (Table 1.1). The discriminant analysis based on the three principal components significantly separated the five stand types (Table 1.2). First and second discriminant functions explained 93.8% of the variation among plots (Figure 1.2). Habitat gradients represented by PC1 were more correlated with DF1 while PC3 and, to a lesser extent, PC2 were correlated with DF2 (Table 1.2). These three habitat gradients significantly discriminated stand types (Table 1.2). The first discriminant distinguished stands with a low (i.e., mainly 1-3-year-old and 6-10-year-old HPO plantations), an intermediate (i.e., mainly stands managed by selection cutting and naturally regenerated stands) and a high (i.e., unmanaged natural forests) quantity of structural attributes and heterogeneity associated with the canopy and DBH of trees, and proportion of mature forest in the surrounding landscape (Figure 1.2). The second discriminant makes the distinction between stands with a low (i.e., mainly 1-3-year-old HPO plantations and unmanaged natural forests) or a high (i.e., mainly 6-10-year-old HPO plantations and naturally regenerated stands) canopy heterogeneity and proportion of old HPO plantations in the surrounding landscape (PC3) and, to a lesser extent, sapling and shrub quantity and homogeneity of structural attributes associated with saplings and shrubs (PC2) (Figure 1.2).

1.3.2 Bird species richness and assemblages

A total of 52 bird species were detected in the 68 point count stations (see Supp. Table 1.1 for the complete list). The most common species (detected >50% of stands) were the Red-eyed Vireo (*Vireo olivaceus*), Ovenbird (*Seiurus aurocapilla*), Black-capped Chickadee (*Poecile atricapillus*), Hermit Thrush (*Catharus guttatus*), American Robin (*Turdus migratorius*), Veery (*Catharus fuscescens*) and Yellow-bellied Sapsucker (*Sphyrapicus varius*). On the other hand, 16 species which were present in fewer than 5 of the 34 stands were considered "rare" in our database and not included in multivariate analysis of species assemblages (1-3-year-old HPO plantations: n = 4; 6-10-year-old HPO plantations: n = 4; naturally regenerated stands: n = 4; unmanaged mature forest: n = 4; stands managed by selection cutting: n = 8).

Differences in bird species diversity and composition - Overall bird species richness in stands varied from 7 to 20 species (including rare species) and did not differ significantly between stand types for the four comparisons that we identified as relevant (Supp. Table 1.2 and Supp. Figure 1.2). However, this similarity in bird species richness was accompanied by a significant difference in bird species assemblages in the four comparisons (Table 1.3 and Supp. Figure 1.3). Differences were primarily due to composition dissimilarities among stand types (significant PERMANOVA) and not within a stand type (non-significant PERMDISP), except for the comparison between 1-3-year-old and 6-10-year-old HPO plantations. In the latter, species composition differences were also due to a more homogeneous species composition among younger plantations compared to older plantations (Table 1.4, Supp. Figure 1.3).

Young and older HPO plantations (comparison 1) shared 52% of all the species present in plantations (i.e., 27 species) while the other 13 species were specific to younger (2 species) or older (11 species) HPO plantations (see Supp. Figure 1.4). Common Yellowthroat (*Geothlypis trichas*) and White-throated Sparrow (*Zonotrichia albicollis*) were the most common species found in both plantation age classes. Lincoln's Sparrow (*Melospiza lincolnii*) was common only in young plantations whereas Red-eyed Vireo, American Redstart (*Setophaga ruticilla*) and Ovenbird were detected only in older plantations (Supp. Table 1.1). These species along with Black-capped chickadee were also highly detected in naturally regenerated stands (Supp. Table 1.1), which shared 66% of species with older plantations (i.e., 20 species over the 25 species; Supp. Figure 1.4). Finally, unmanaged mature forests shared more species with stands managed by recent selection cutting than with older plantations (i.e. 77% vs 52%, Supp. Figure 1.4). Yellow-bellied sapsucker, Black-throated Green Warbler (*Setophaga virens*), Black-throated Blue Warbler (*Setophaga caerulescens)*, White-breasted Nuthatch (*Sitta carolinensis*) and Brown Creeper (*Certhia americana*) were present in both unmanaged mature forests and stands managed by selection cutting but not in older plantations (except for Yellow-bellied sapsucker that was detected once in plantations see Supp. Table 1.1).

Drivers of the differences in bird species assemblages - Habitat characteristics explained 66.7% of the variation in bird species assemblages among the five stand types. Most of this variation (64.2%) was explained by the quantity of vegetation structural attributes (where 10.3% of the variation explained by this set of variables alone; Figure 1.3), with a significant proportion of this variation shared with variables describing vegetation structural heterogeneity (50.4%; d + g, Figure 1.3) and, to a lesser extent, composition of the surrounding landscape (28.3%; g + f, Figure 1.3). Vegetation structural heterogeneity and composition of the surrounding landscape alone had a small effect (<1% and 2% respectively; Figure 1.3) on bird community structure.

The fourth-corner analysis showed positive relationships between shrub nesters and 1-3-year-old HPO plantations (still significant after FDR correction; Table 1.5) and between ground nesters and naturally regenerated stands (not significant after FDR correction; Table 1.5). Regarding foraging traits, bark foragers tended to be negatively associated with 1-3-year-old and 6-10-year-old HPO plantations (not significant after FDR correction; Table 1.5). The other categories of traits were not related to any stand type.

1.4 Discussion

Effects of HPO plantations on forest bird diversity

Intensively managed systems, like tree plantations, generally modify bird diversity compared to natural forests (Riffell *et al.*, 2011; Stephens et Wagner, 2007). Unsurprisingly, HPO plantations hosted distinct species assemblages but a similar species richness when compared to the unmanaged mature forest. Differences in bird species composition were driven by more ground or shrub associates (e.g. Nashville Warbler (*Oreothlypis ruficapilla*), Common Yellowthroat, White-Throated sparrow), and by the reduced presence of bark and cavity nesting species (Yellow-bellied Sapsucker, Brown Creeper, *Sitta sp* and *Picoides sp)* in HPO plantations compared to the unmanaged mature forest. HPO plantations in forested areas also failed to maintain species assemblages and functional groups typically found in the stand type the plantation has replaced (i.e. young naturally-regenerated stands). According to our results, HPO plantations do not replace the habitat conditions provided by naturally regenerated forests. On the one hand, mature forest species (e.g. Black-throated Green Warbler, Black-throated Blue Warbler) and more specifically bark foragers (e.g. Black-and-white Warbler (*Mniotilta varia*), Yellow-bellied Sapsucker, Brown Creeper, *Picoides sp*) barely used plantations compared to naturally regenerating stands. Furthermore, HPO plantations were less associated to ground nesting species (e.g. Ovenbird and Hermit Thrush) than naturally regenerated stands. In addition, HPO plantations were composed of species like Chestnut-sided warblers (*Setophaga* *pensylvanica*), Common Yellowthroat and American Goldfinch (*Spinus tristis*). Those species are associated with shrub nesting guilds and were largely absent from naturally regenerated stands. Finally, the bird species turnover between 6-10-y/o HPO plantations and unmanaged forests was stronger (49% of species were exclusive to one forest type) than when plantations were compared with the naturally regenerated stands (34% were exclusive). Thus, since HPO plantations and unmanaged forests have a similar bird richness, it seems that the differences in species composition were mainly due to species turnover, rather than an impoverished subset of species (i.e. reduced number of species). This result is in contradiction with a recent study showing that differences in species composition between coniferous plantations in semi-deciduous forests and unmanaged forests were due to an impoverished subset of species in plantations (Iezzi *et al.*, 2018).

Drivers of differences in bird species assemblages

The "habitat heterogeneity hypothesis" assumes that structurally complex habitats provide more niches and thus increase species diversity (Bazzaz, 1975), as in birds (e.g. Hanowski et al. 1997, King & Degraaf 2000, Bergner et al. 2015, Renner et al. 2018). Studies have shown that structural attributes associated to vegetation cover, vertical diversity, snags, coarse woody debris, and larger trees are keystone structures for bird communities (e.g. Tews et al. 2004). HPO plantations had a low amount of structural attributes and low within stand variation of structural attributes associated to the canopy and DBH of trees compared to unmanaged mature forest. It is thus surprising that HPO plantations and unmanaged mature forests have similar bird species richness. The fact that plantations are not strict barriers for most species found in the natural forest (Iezzi *et al.*, 2018; Paviolo *et al.*, 2018) may explain this result. Many species found in plantations were also present in unmanaged forests (e.g. Blue Jay (*Cyanocitta cristata*), Rose-breasted Grosbeak (*Pheucticus ludovicianus*), Wood Thrush (*Hylocichla mustelina*), Red-breasted Nuthatch (*Sitta canadensis*), Hairy Woodpecker

(*Picoides villosus*) and Yellow-bellied Sapsucker). These ubiquist species contribute to higher species richness in plantations, which in turn may offset the negative effect of the reduced amount of structural attributes on species richness. However, our research revealed differences in bird species composition between HPO plantations and unmanaged mature forests, together with naturally regenerated stands, which were mainly explained by both the quantity and heterogeneity of vegetation structural attributes, and, to a lesser extent, by the surrounding landscape composition. Surprisingly, this result shows that, in our study, the quantity and heterogeneity of habitat structural attributes are important drivers of bird species assemblages, but not likely of species richness. Thus, this emphasizes the importance of assessing patterns of species composition which provide a more in depth assessment of communities than broad measures of species richness.

Landscape composition had a smaller influence (compared to stand structure) on bird species composition. This result is in accordance with other studies showing that within stand vegetation structure is the most important variable for explaining bird species composition (Hagan et Meehan, 2002; Iezzi *et al.*, 2018). This supports the idea that a species will not occupy a stand regardless of the surrounding landscape composition unless basic nesting and foraging structures within a stand are met (Warren *et al.*, 2005). At a larger scale, amount, localization and spatial arrangement of plantations are important issues that need to be addressed (Barrette *et al.*, 2014), but our study design was not planned for this purpose. Thus, further research is needed to evaluate how HPO plantations affect bird communities depending on the landscape surrounding these plantations on a larger scale.

Aspects to consider when evaluating effects of plantations on biodiversity

Diversity Components- Although bird species assemblages were different, 6-10-y/o HPO plantations were potential habitats for as many bird species as in unmanaged mature forests and naturally regenerated stands. Other studies have also reported these contrasting results (Clout et Gaze, 1984; Kwok et Corlett, 2000; Le Blanc *et al.*, 2010). These results demonstrate the importance for conservation purposes to consider several diversity components (i.e. species richness, species assemblages, and species biological traits). By considering these three diversity components, we were certain to retain the biological information necessary for evaluating the effects of HPO plantations on bird community diversity.

Comparison choice- An inappropriate choice of stand type to compare with the plantation can also generate confusion about the effect of plantation on biodiversity (Stephens et Wagner, 2007). Evaluation of biodiversity must consider which land use is modified by plantations and to what extent plantations can provide habitat for the species previously found on those sites (Brockerhoff *et al.*, 2008). In the particular context of this study, we think that the best comparison to quantify stand-level biodiversity change was to contrasts HPO plantations with naturally regenerated stands after a similar perturbation, i.e. clearcutting (comparison 2). This comparison indeed allowed to focus on the effect of the HPO plantation independent from the initial perturbation (clearcutting). We found that for stands having similar tree heights and DBH, HPO plantations shared only two-thirds (66%) of bird species with naturally regenerated stands. Nonetheless, the comparison with an unmanaged forest and the use of socially acceptable practices remained important to: 1) illustrate the contrast with regional forested areas in which plantations are established (older HPO plantations shared only 51% of species with the unmanaged forests) and 2) demonstrate if a plantation's effect on biodiversity is greater than what it is generally socially acceptable in the study region (e.g. effect of managing the forest by selection cutting). To that end, our study showed that a mature forest managed with selection cutting shared more species with unmanaged forest (77%) than older HPO plantations (51%). This greater similarity in bird species assemblages between a mature forest managed with selection cutting and an unmanaged mature forest may be explained by the fact that in our study, selective logging created an intermediate level of structure in the canopy (while this level was high and low in unmanaged forests and HPO plantations respectively). It benefited species associated with semi-open forest and clearings, i.e. Least Flycatcher (*Empidonax minimus*) and Eastern Wood-Pewee (*Contopus virens*) and species associated with early regenerated areas after logging, i.e. Mourning Warblers (*Geothlypis philadelphia*) and White-throated Sparrow. Remaining larger trees also contributed to greater amount and heterogeneity of structural attributes in the mature forest managed with selection cutting (compared to older HPO plantations) and probably explains why species composition in selection cutting is more similar to the unmanaged forest than the HPO plantations. Thus, our multiple comparisons indicated that HPO plantations in forested areas may sustain a different level of bird diversity depending on the benchmark with which they are compared.

Conservation Paradigm- The choice of conservation paradigm to be favored, i.e. maintain or maximize diversity, has a strong influence on the means of evaluating the success of a biodiversity management strategy (Bichet *et al.*, 2016), and the context of forest plantations is not an exception. Our results indicate that bird diversity is not maintained in HPO plantations (species composition and functional groups were different between plantations and natural forests). But HPO plantations do increase bird diversity in the landscape since 7 species were only detected in plantations and not in the other stand types (i.e. Song Sparrow (*Melospiza melodia*), Lincoln's Sparrow, Wilson's Snipe (*Gallinago delicata*), Swamp Sparrow (*Melospiza georgiana*), Red-winged Blackbird (*Agelaius phoeniceus*), Mallard (*Anas platyrhynchos*), Canada Warbler (*Cardellina Canadensis*)). However, most of these species are commonly found in surrounding ecosystems (e.g., wetlands and fields). Conserving the largest number of species can be appealing, but this approach is not always congruous with the effort of maintaining ecological integrity (Kareiva et Marvier, 2003). Moreover, concentrating conservation efforts on a simple number of species can be problematic as it does not consider species identity. For example, this could lead to considering the conservation of plantations composed of common (e.g. Red-eyed Vireo, Common Yellowthroat, White-throated Sparrow) and widespread species (e.g. Red-eyed Vireo, Black-capped Chickadee and Chestnut-sided warblers) as equivalent to the conservation of natural forest habitat composed of specialists (e.g. Brown Creeper, Black-throated green wabler, White-breasted Nuthatch). We thus used natural forests as a benchmark to base our evaluation of HPO plantations capacity to maintain a similar bird community.

Rotation time - Considering the fast growth rate of HPO plantations (Roy, 2018), one should expect a rapid change in the vegetation structural attributes of these plantations and consequently an equally rapid change in bird communities (Christian *et al.*, 1998; Hanowski *et al.*, 1997). In deciduous forest, the habitats provided for bird communities in young and older HPO plantations likely correspond to the early stages of vegetation successionnal process in deciduous forest (Hagan *et al.*, 1997). Thus, many early-successional bird species will probably benefit from plantations establishement and mid-age plantations at the expense of mature forest species. Subsequently, it is important to evaluate the effects of HPO plantations on bird communities in the fast growth dynamic of these plantations compared to the much slower growth dynamics of managed and unmanaged natural forests (Demarais *et al.*, 2017). Our results showed differences in bird species composition between 1-3-year-old and 6-10-year-old HPO plantations, along with an increase in 1) the quantity of vegetation structural attributes associated with canopy and 2) heterogeneity associated with both overstory and shrub cover. Hence, HPO plantations provided new nesting and foraging substrates (e.g. trees) in relatively few years (6 to 10 years), and appeared to benefit quickly to forest associated species (e.g. American Redstart, Veery, Ovenbird, Red-eyed Vireo) that were not usually supported by younger plantations. Furthermore, younger HPO plantations were dominated by a homogeneous assemblage of species using shrubs as a nesting substrate (i.e. Alder Flycatcher (*Empidonax alnorum*), Common Yellowthroat, Chestnut-sided Warbler, Lincoln Sparrow, Song Sparrow, White-throated Sparrow and American Goldfinch), while older HPO plantations hosted a heterogeneous mix of forest-associated species (see above) and a subset of species typically found in younger plantations (except Lincoln sparrow). These results are consistent with other studies reporting that maturing plantations with low maintenance contribute to plantation imperfections and consequently to a heterogeneous community assembly (Riffell *et al.*, 2011; Royer-Tardif *et al.*, 2018). These changes in bird diversity associated with HPO plantations over time are likely still in progress in our study sites since the plantations were relatively young and not likely to be harvested for another 10 years (Domtar, personal communication). Hence, it would be important to monitor birds in these plantations at the end of the rotation to assess how bird community diversity and composition fluctuated over the entire revolution. This information would increase our knowledge of the value of plantations for biodiversity, as current literature in North America has not documented vertebrate biodiversity response over a complete rotation of plantations (Demarais *et al.*, 2017).

Management Implications

Many tools and approaches have been proposed to manage biodiversity within intensively managed forests (Demarais *et al.*, 2017; Hartley, 2002; D. B. Lindenmayer *et al.*, 2006; McFadden et Dirzo, 2018). As other studies on forest plantations have proposed, our study suggests that managers interested in improving conditions for bird diversity in HPO plantations located in forested area should focus on local structural attributes rather than surrounding landscape composition. (Millan *et al.*, 2015). Consequently, future HPO plantations should be aimed at increasing within stand-level amount and heterogeneity of structural attributes associated to trees. Our results indicate that the low canopy closure, lack of large trees and homogenization of tree DBH in HPO plantations negatively affects bird diversity. We consider that retaining structure, such as large green trees within plantations after clearcutting, could play a critical role for bird species relying on older forest characteristics. Retention trees are important habitat features for many late-successional bird species as they provide cavity-bearing and foraging trees for the cavity-using community (Cadieux et Drapeau, 2017; Drapeau *et al.*, 2009; Maurer *et al.*, 1981; Vaillancourt *et al.*, 2008). Retentions trees could be maintained as biological legacies when the plantation is harvested (Hartley, 2002). Another possible approach for increasing quantity and heterogeneity of vegetation structural attributes would be to favour multi-species plantations. Hybrid poplar could be established with more slowly growing shade tolerant tree species as suggested by Paquette and Messier (2010).

On the other hand, HPO plantations in our study had a well-developed understory cover that may contrast with what is often found in other studies (e.g. Iezzi et al. 2018). This well-developed understory cover likely explains why shrub nester species were highly abundant in younger HPO plantations compared to natural forests. However, these species were not over-represented anymore in 6-10-year-old HPO plantations. This suggests that as HPO plantation growth, changes in understory cover allows to reduce the presence of shrub nester species in HPO plantation at a level similar to natural forests. Although understory cover seems not to be a source of concerns in terms of management for bird diversity, it can play an important role for other taxa, such as small mammals (Carrilho *et al.*, 2017). Since the response to forest plantations is variable between animal taxa (e.g. Iezzi et al., 2018), it would be important to extend this study to other taxa in order to have a more complete measure of the effect of HPO plantations. Thus, future research is needed that considers multi-taxa responses to HPO plantation management. This would also provide more specific guidance to forest managers with the ultimate goal of maintaining animal biodiversity in plantations.

1.5 Acknowledgments

We would like to thank our industrial partner, Domtar, for its support and logistics throughout the study. We are also thankful to the Mont Orford, Frontenac and Mont-Mégantic National Parks for the privileged access to their forests. Finally, this study would never have been possible without assistance in the field from Samuel Rosner and Alexandre Rodrigue.

1.6 Tables and figures

Table 1.1 Principal Component coefficients of habitat characteristics measured in 2016 at 136-point count stations located in 34 stands distributed in 5 stand types (1-3-year-old HPO plantations, 6-10-year-old HPO plantations, naturally regenerated stands, unmanaged mature forests and mature forests 1 to 4 years after selection cutting) in Southeastern Canada (Quebec). Habitat characteristics are organized according to the three components describing bird habitat: quantity of vegetation structural attributes, heterogeneity of vegetation structural attributes and surrounding landscape composition. These three principal components explain 30.8%, 13.3% and 11.0%, respectively, of the variation in bird habitat characteristics. Asterisks represent variables yielding the greatest contribution to each component (PC) based on the equilibrium contribution circle (see Supp. Figure 1.1).

Bird's habitat characteristics	PC1	PC2	PC3
Quantity of vegetation structural attributes			
Canopy closure (%)	*0.98	0.33	-0.64
Sapling cover (%)	0.24	*0.98	0.16
Shrub cover (%)	-0.51	*-0.79	0.05
Herbaceous cover (%)	-0.80	-0.36	0.05
Vegetation vertical inertia (m)	*1.09	0.32	-0.45
Shannon vertical diversity	-0.06	-0.58	-0.32
DBH>22cm basal area (m^2*/ha)*	*1.04	-0.38	0.32
Snags basal area (m^2*/ha)*	0.88	-0.29	0.28
Coarse wood debris (m^3*/ha)*	0.52	-0.16	0.45
Tree structural index	1.03	0.02	0.06
Sapling structural index	-0.08	*0.90	-0.31
Vegetation structural heterogeneity			
DBH gini dispersion	*1.16	-0.25	-0.01
Canopy closure gini dispersion	0.34	-0.28	*-0.88
Sapling cover gini dispersion	0.14	*-0.92	-0.26
Shrub cover gini dispersion	0.64	*0.68	-0.12
Herbaceous cover gini dispersion	0.35	-0.09	-0.50

Surrounding landscape attributes (%)			
≥5 y/o HPO plantations matrix proportion	-0.46	-0.11	*-0.92
≤4 y/o HPO plantations matrix proportion	-0.76	-0.09	0.53
Deciduous cover matrix proportion	0.71	-0.43	-0.39
Resinous cover matrix proportion	-0.36	0.22	0.29
Young forest cover matrix proportion	*-1.01	0.34	-0.50
Mature forest cover matrix proportion	*1.01	-0.33	0.48
Wetlands cover matrix proportion	0.43	0.46	*0.47

Table 1.2 Results of linear discriminant analysis showing loadings of the 3 habitat gradients (PC1, PC2 and PC3) for each discriminant function (DF1, DF2 and DF3) and significance of the Wilks' Lambda value. Values in bold represent the main habitat gradients contributing to discriminate sites among the 5 stand types (1-3-year-old HPO plantations, 6-10-year-old HPO plantations, naturally regenerated stands, unmanaged mature forests and mature forests 1 to 4 years after selection cutting).

Habitat gradient	Loadings		
	DF1	DF2	DF3
PC1	**-0.99**	-0.02	-0.05
PC2	0.02	-0.63	**0.78**
PC3	-0.13	**0.77**	0.62
Variables	Wilks' Lambda	F- stats approx.	P value
PC1+PC2+PC3	0.01	122.8	<0.001

Table 1.3 Results of a nonparametric permutational multivariate analyses of variance (PERMANOVA) evaluating differences of forest bird species assemblages among the stand types based on bird species presence-absence data at each station in forests of the Estrie and the Chaudière-Appalaches regions of Quebec, Canada. Stand types included: 1-3-year-old HPO plantations (n=12), 6-10-year-old HPO plantations (n=12), 15-30-year-old naturally regenerated stands (n=12), ≥60-year-old unmanaged mature forests (n=20) and mature forests 1 to 4 years after selection cutting (n=12). "df": degrees of freedom.

Variable	**df**	**Sum of square**	**Mean square**	**F-values**	**R^2**	**P-values**
Stand type	4	8.89	2.22	18.96	0.54	0.001

Pairwise comparisons	**F-values**	**R^2**	**Adjusted P-values**
			Holm correction
1-3-y/o HPO plantations vs *6-10-y/o HPO plantations*	40.28	0.65	0.004
6-10-y/o HPO plantations vs *Naturally regenerated stands*	9.54	0.30	0.004
6-10-y/o HPO plantations vs *Unmanaged mature forests*	33.0	0.52	0.004
1-4-y/o selection cutting vs *Unmanaged mature forests*	4.26	0.12	0.004

Table 1.4 Results of a nonparametric permutational multivariate analyses of dispersion (PERMDISP) comparing variation within stand types of forest bird species assemblages based on bird species presence-absence at each station in forests of the Estrie and the Chaudière-Appalaches regions of Quebec, Canada. Stand types included: 1-3-y/o HPO plantations (n=12), 6-10-y/o HPO plantations (n=12), 15-30-year-old naturally regenerated stands (n=12), ≥60-year-old unmanaged mature forests (n=20) and 1-4-year-old selection cutting (n=12)."df": degrees of freedom.

Variable	**df**	**Sum of square**	**Mean of square**	**F-values**	**P-values**
Stand types	4	1.16	0.29	7.39	0.001

Pair comparisons	**F-values**	**Adjusted P-values**
		Holm correction
1-3-y/o HPO plantations vs *6-10-y/o HPO plantations*	8.25	0.035
6-10-y/o HPO plantations vs *Naturally regenerated stands*	1.09	0.614
6-10-y/o HPO plantations vs *Unmanaged mature forests*	33.0	0.261
1-4-y/o selection cutting vs *Unmanaged mature forests*	4.26	0.614

Table 1.5 Synthesis of the results of the fourth-corner analysis for bird species assemblages in which species traits are related to stand types. Only significant relationships at the 5% significance level are shown. White rectangles indicate negative significant relationships, dark grey indicates positive significant relationships and light grey background indicates non-significant results. The asterisk shows the relationships that are still significant after FDR correction.

		Stand types				
Birds traits	**Categories**	1-3–y/o HPO plantations	6-10–y/o HPO plantations	Naturally regenerated stands	Unmanaged mature forests	1-4-y/o selection cutting
Nesting substrat	*Ground*			■		
	Shrub	■ *				
	Living tree					
	Cavity					
Foraging behavior	*Ground forager*					
	Flycatcher					
	Foliage gleaner & hovering					
	Bark forager	□	□			

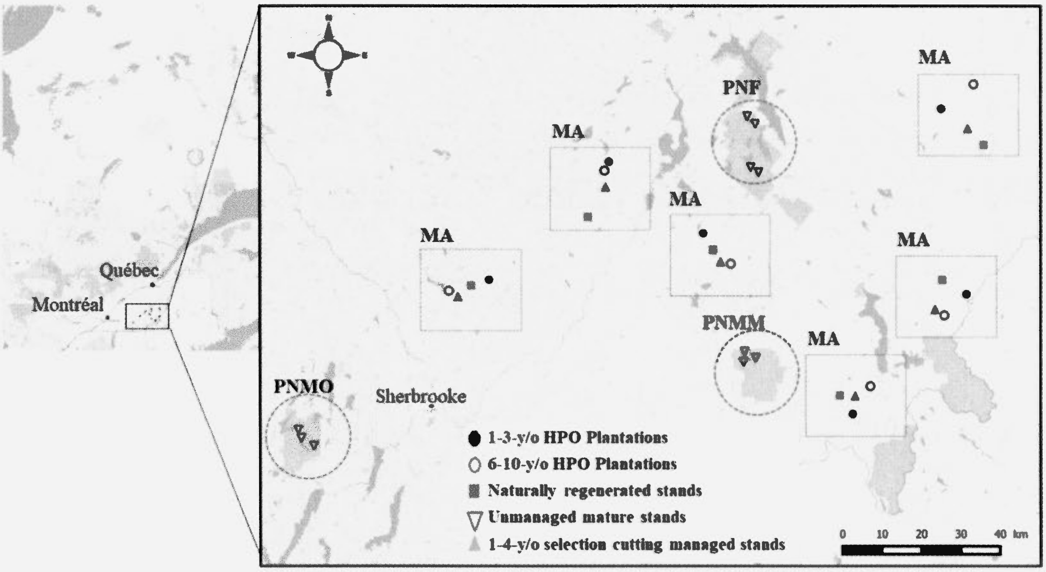


Figure 1.1 Study area and location of the unmanaged and managed stands in the regions of Estrie and Chaudière-Appalaches in the temperate deciduous forest of Quebec, Canada. Circles encompass control areas (PNMO: Parc National du Mont-Orford, PNF: Parc National de Frontenac, PNMM: Parc National du Mont-Mégantic) and the rectangles include the six managed areas (MA: Managed area).

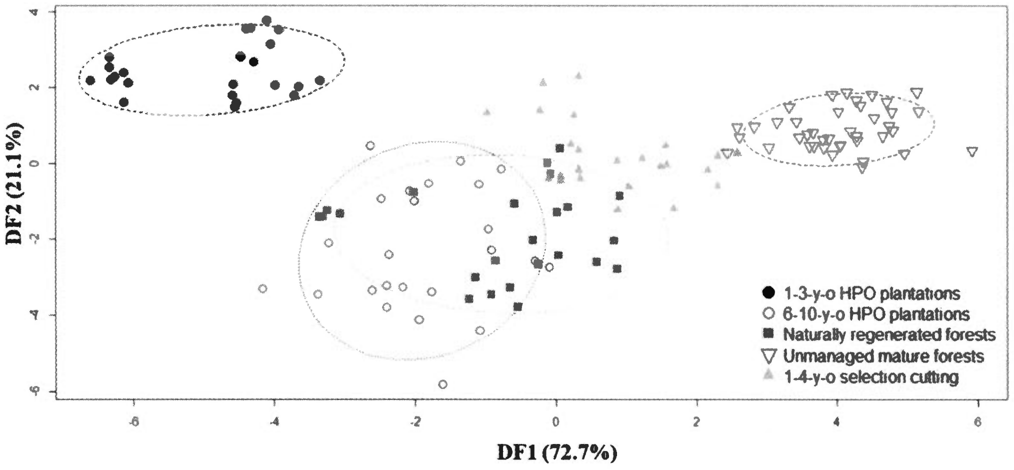


Figure 1.2 Results of a discriminant analysis showing differences in habitat characteristics among the 5 stand types (1-3-year-old HPO plantations (n=24), 6-10-year-old HPO plantations (n=24), naturally regenerated stands (n=24), unmanaged mature forests (n=40) and managed mature forests 1 to 4 years after selection cutting (n=24)). Discriminant functions 1 and 2 explained 72.7% and 21.1%, respectively, of variation among stand types.

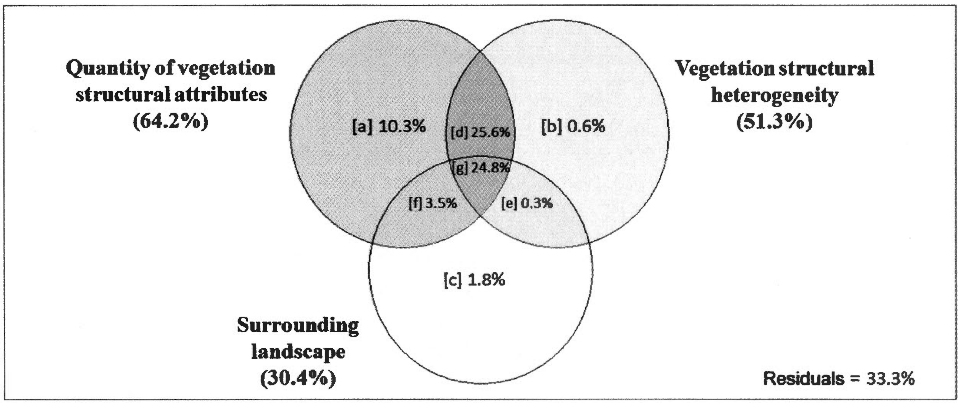


Figure 1.3 Illustration of bird species assemblage variation partitioning for three sets of explanatory variables (quantity of vegetation structural attributes, vegetation structural heterogeneity and composition of the surrounding landscape) using distance-based redundancy analysis ordination (db-RDA) on bird species presence-absence dissimilarity matrix calculated from Sorensen indices (n=68). Individual variation explained by each set of variables (a, b and c) and shared variation explained by two (d, e and f) or three (g) sets of variables are illustrated.

1.7 Supplementary material

Supp. Table 1.1 List of forest bird species detected in 1-3-year-old HPO plantations (1-3-y/o HPO, n=6), 6-10-year-old HPO plantations (6-10-y/o HPO, n=6), 15-30-year-old severe cut naturally regenerated stands (Nat. reg., n=6), ≥60-year-old unmanaged sugar maple stands (Umn., n=10) and 1-4-year-old selection cutting in maple stands (Sel. Cut., n=6) during the summer of 2016 in temperate deciduous forests of the Estrie and the Chaudière-Appalaches regions of Quebec, Canada. Values indicate the percentage of stands where the species was detected.

		Occupied stand (%)					
Species name	**Code**	**Total**	**1-3-y/o HPO**	**6-10-y/o HPO**	**Nat. reg.**	**Unm.**	**Sel. cut.**
Red-eyed Vireo *(Vireo olivaceus)*	REVI	79.4	0.0	83.3	100.0	100.0	100.0
Ovenbird *(Seiurus aurocapilla)*	OVEN	73.5	0.0	83.3	100.0	90.0	83.3
Hermit Thrush *(Catharus guttatus)*	HETH	55.9	0.0	50.0	100.0	80.0	33.3
Black-capped Chickadee *(Poecile atricapillus)*	BCCH	55.9	16.7	66.7	100.0	50.0	50.0
Veery *(Catharus fuscescens)*	VEER	52.9	33.3	83.3	50.0	50.0	50.0
American Robin *(Turdus migratorius)*	AMRO	52.9	33.3	50.0	50.0	70.0	50.0
Yellow-bellied Sapsucker *(Sphyrapicus varius)*	YBSA	52.9	0.0	16.7	33.3	100.0	83.3
Black-throated Green Warbler *(Setophaga virens)*	BTGW	50.0	0.0	0.0	50.0	100.0	66.7

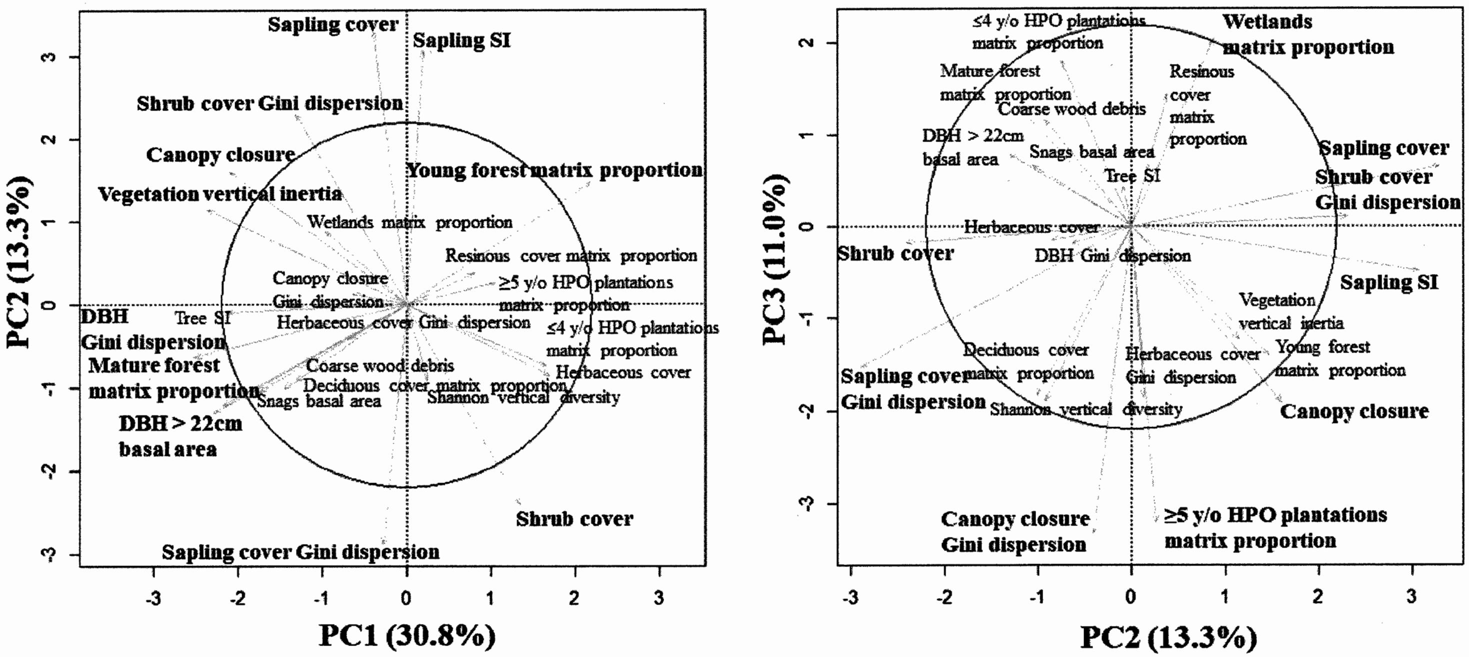
Black-throated Blue Warbler *(Setophaga caerulescens)*	BTBW	47.1	0.0	0.0	33.3	100.0	66.7
White-throated Sparrow *(Zonotrichia albicollis)*	WTSP	41.2	83.3	66.7	33.3	0.0	50.0
Cedar Waxwing *(Bombycilla cedrorum)*	CEDW	38.2	66.7	33.3	16.7	30.0	50.0
American Redstart *(Setophaga ruticilla)*	AMRE	38.2	0.0	83.3	50.0	30.0	33.3
Chestnut-sided Warbler *(Setophaga pensylvanica)*	CSWA	35.3	100.0	50.0	0.0	10.0	33.3
Common Yellowthroat *(Geothlypis trichas)*	COYE	35.3	100.0	83.3	16.7	0.0	0.0
Hairy Woodpecker *(Picoides villosus)*	HAWO	35.3	0.0	16.7	16.7	50.0	83.3
American Goldfinch *(Spinus tristis)*	AMGO	29.4	83.3	50.0	0.0	20.0	0.0
Brown Creeper *(Certhia americana)*	BRCR	29.4	0.0	0.0	16.7	60.0	50.0
Rose-breasted Grosbeak *(Pheucticus ludovicianus)*	RBGR	26.5	16.7	16.7	50.0	20.0	33.3
Ruby-throated Hummingbird *(Archilochus colubris)*	RTHU	26.5	33.3	0.0	0.0	40.0	50.0
Mourning Warbler *(Geothlypis philadelphia)*	MOWA	26.5	66.7	33.3	0.0	0.0	50.0
Red-breasted Nuthatch *(Sitta canadensis)*	RBNU	26.5	0.0	16.7	16.7	40.0	50.0
Ruffed Grouse *(Bonasa umbellus)*	RUGR	23.5	16.7	66.7	33.3	0.0	16.7
Alder Flycatcher *(Empidonax alnorum)*	ALFL	23.5	100.0	16.7	16.7	0.0	0.0
Black-and-white Warbler *(Mniotilta varia)*	BAWW	23.5	0.0	33.3	50.0	30.0	0.0
White-breasted Nuthatch *(Sitta carolinensis)*	WBNU	23.5	0.0	0.0	0.0	60.0	33.3

Song Sparrow *(Melospiza melodia)*	SOSP	20.6	100.0	16.7	0.0	0.0	0.0
Blue Jay *(Cyanocitta cristata)*	BLJA	20.6	0.0	16.7	50.0	20.0	16.7
Least Flycatcher *(Empidonax minimus)*	LEFL	20.6	0.0	0.0	0.0	20.0	83.3
Eastern Wood-Pewee *(Contopus virens)*	EAWP	20.6	0.0	0.0	0.0	10.0	100.0
Winter Wren *(Troglodytes hiemalis)*	WIWR	20.6	0.0	0.0	16.7	40.0	33.3
Nashville Warbler *(Oreothlypis ruficapilla)*	NAWA	17.6	0.0	50.0	50.0	0.0	0.0
Lincoln's Sparrow *(Melospiza lincolnii)*	LISP	14.7	83.3	0.0	0.0	0.0	0.0
Wood Thrush *(Hylocichla mustelina)*	WOTH	14.7	0.0	16.7	0.0	40.0	0.0
Scarlet Tanager *(Piranga olivacea)*	SCTA	14.7	0.0	0.0	0.0	30.0	33.3
Northern Flicker *(Colaptes auratus)*	NOFL	14.7	16.7	33.3	16.7	10.0	0.0
Downy Woodpecker *(Picoides pubescens)*	DOWO	14.7	0.0	0.0	16.7	30.0	16.7
Wilson's Snipe *(Gallinago delicata)*	WISN	11.8	33.3	33.3	0.0	0.0	0.0
Swamp Sparrow *(Melospiza georgiana)*	SWSP	11.8	33.3	33.3	0.0	0.0	0.0
Purple Finch *(Haemorhous purpureus)*	PUFI	11.8	0.0	0.0	33.3	10.0	16.7
Great Crested Flycatcher *(Myiarchus crinitus)*	GCFL	8.8	0.0	0.0	0.0	20.0	16.7
Red-winged Blackbird *(Agelaius phoeniceus)*	RWBL	5.9	33.3	0.0	0.0	0.0	0.0
Northern Parula *(Setophaga americana)*	NOPA	5.9	0.0	0.0	0.0	10.0	16.7

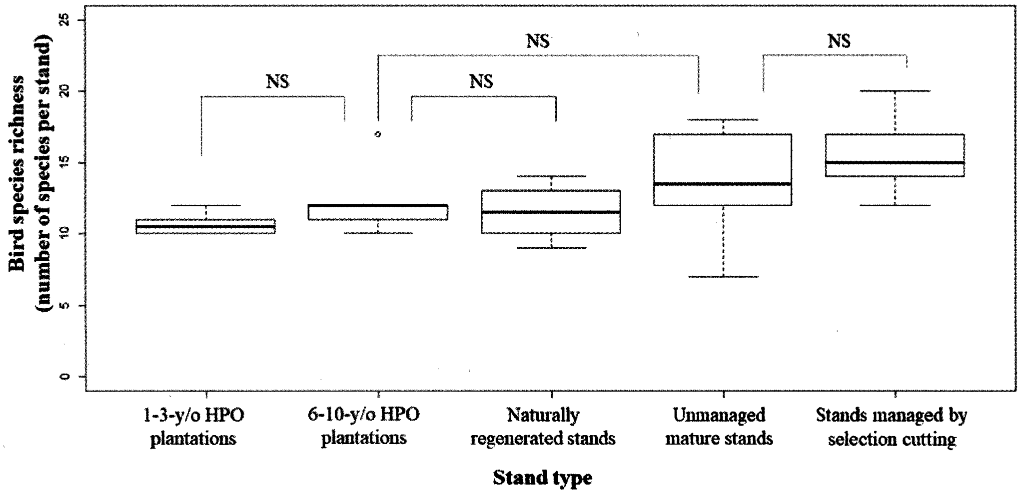
Blackburnian Warbler *(Setophaga fusca)*	BLBW	5.9	0.0	0.0	0.0	0.0	33.3
Northern Waterthrush *(Parkesia noveboracensis)*	NOWA	5.9	0.0	16.7	0.0	0.0	16.7
Broad-winged Hawk *(Buteo platypterus)*	BWHA	5.9	0.0	0.0	0.0	20.0	0.0
Mallard *(Anas platyrhynchos)*	MALL	2.9	16.7	0.0	0.0	0.0	0.0
Swainson's Thrush *(Catharus ustulatus)*	SWTH	2.9	0.0	0.0	0.0	0.0	16.7
Dark-eyed Junco *(Junco hyemalis)*	DEJU	2.9	0.0	0.0	0.0	0.0	16.7
Canada Warbler *(Cardellina canadensis)*	CAWA	2.9	0.0	16.7	0.0	0.0	0.0
Yellow-rumped Warbler *(Setophaga coronata)*	YRWA	2.9	0.0	0.0	16.7	0.0	0.0
Tennessee Warbler *(Oreothlypis peregrina)*	TEWA	2.9	0.0	0.0	16.7	0.0	0.0
Common Grackle *(Quiscalus quiscula)*	COGR	2.9	0.0	0.0	0.0	0.0	16.7

Supp. Table 1.2 Differences in bird species richness (n=34) according to stand type for the four comparisons using a permutation analysis of variance. Stand type included: 1-3-year-old HPO plantations (n=6), 6-10-year-old HPO plantations (n=6), 15-30-year-old naturally regenerated stands (n=6), ≥60-year-old unmanaged mature forests (n=10) and 1-4-year-old selection cutting in managed mature forests (n=6).

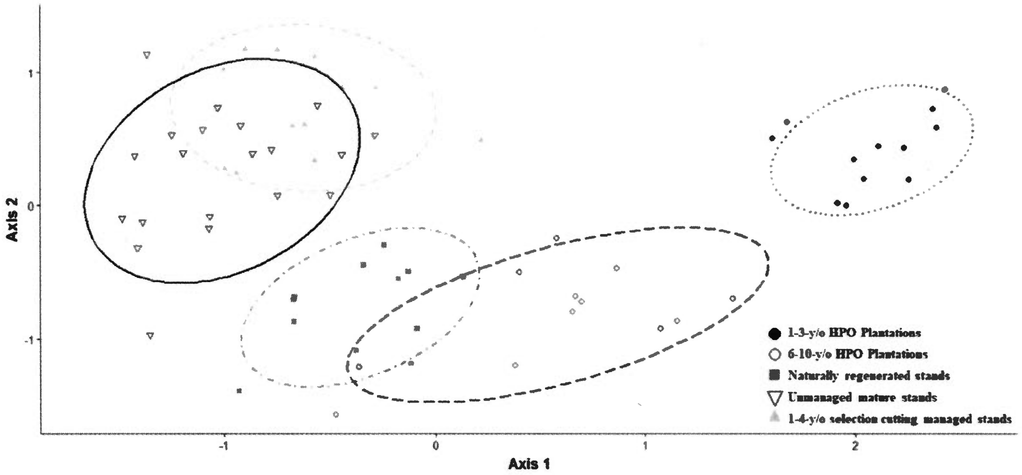
Treatment comparisons	**Source**	**df**	**Sum of square**	**Mean of square**	**F-values**	**P-values**
1-3-y/o HPO plantations vs 6-10-y/o HPO plantations	Stand type	1	8.33	8.33	2.23	0.20
	Residuals	5	18.67	3.73		
6-10-y/o HPO plantations vs Naturally regenerated stands	Stand type	1	2.08	2.08	0.91	0.38
	Residuals	5	11.42	2.28		
6-10-y/o HPO plantations vs Unmanaged mature forests	Stand type	1	9.20	9.20	0.86	0.37
	Residuals	14	150.20	10.73		
1-4-y/o selection cutting vs Unmanaged mature forests	Stand type	1	9.60	9.60	0.85	0.37
	Residuals	14	158.40	11.31		



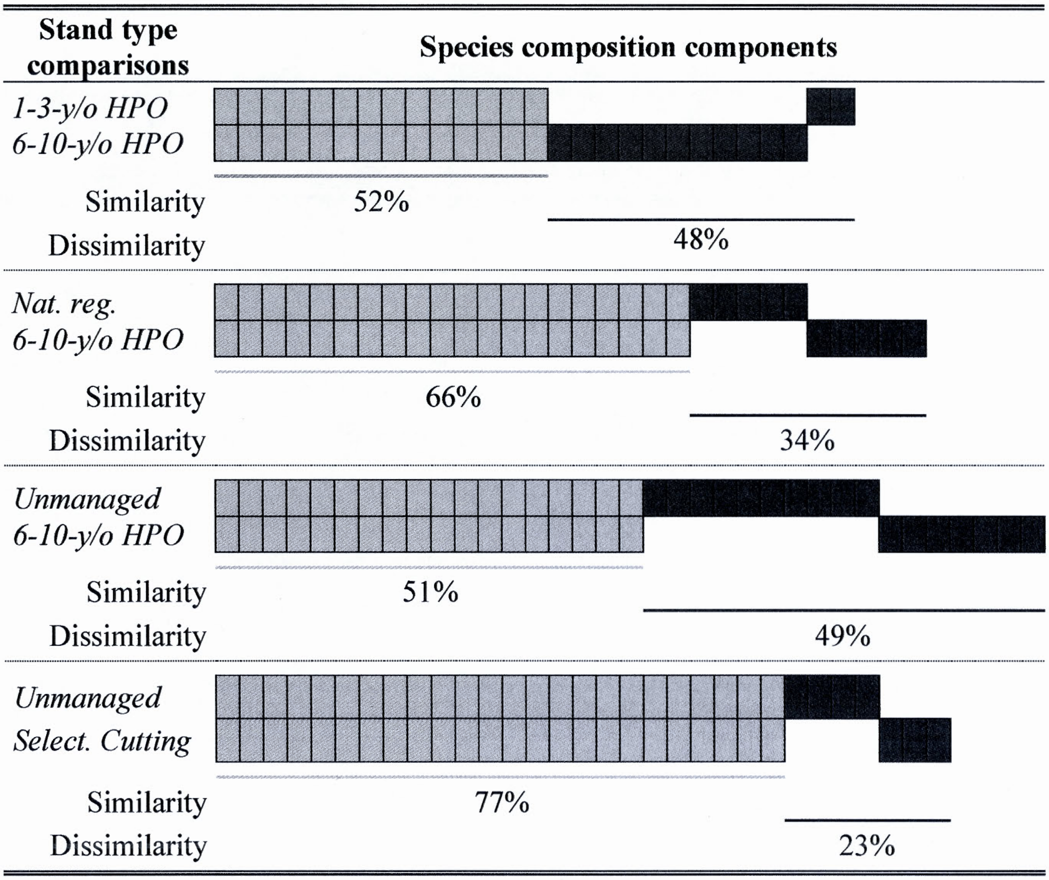
Supp. Figure 1.1 Illustration of the three principal components (and percentage of the variance explained by each component) that summarize habitat gradients measured in 136 stations located in 1-3-year-old HPO plantations (n=6), 6-10-year-old HPO plantations (n=6), 15-30-year-old naturally regenerated stands (n=6), ≥60-year-old unmanaged mature forests (n=10) and 1-4-year-old selection cutting in managed mature forests (n=6). The circle represents the equilibrium contribution of the variables on each axis.



Supp. Figure 1.2 Variation of bird species richness among 1-3-year-old HPO plantations (n=6), 6-10-year-old HPO plantations (n=6), 15-30-year-old naturally regenerated stands (n=6), ≥60-year-old unmanaged mature forests (n=10) and 1-4-year-old selection cutting in managed mature forests (n=6). "NS" indicates nonsignificant differences between the two stand types based on a permutation analysis of variance with alpha threshold of 0.05. Only relevant pairwise comparisons are shown (see the text for details).



Supp. Figure 1.3 Ordination plots of the principal coordinates analysis (based on dissimilarity matrix calculated from Sorensen indices) representing dissimilarity in bird species assemblage patterns among the five stand types (n=68) in temperate forests of the Estrie and the Chaudière-Appalaches regions of Quebec, Canada. Stand types included: 1-3-year-old HPO plantations (n=12), 6-10-year-old HPO plantations (n=12), 15-30-year-old naturally regenerated stands (n=12), ≥60-year-old unmanaged mature forests (n=20) and managed mature forests 1 to 4 years after selection cutting (n=12). The ellipses enclose 80 % of the variability in compositional differences accounted for by the first two axes.



Supp. Figure 1.4 Illustration of differences in bird species composition among the 4 stand types (each rectangle represents a bird species). Total number of species per stand type (filled rectangles), species similarity estimated as the number of species that were common to both stand types (light grey) and dissimilarity in terms of total species that were unique to both stand types (dark grey). Stand types included: 1-3-year-old HPO plantations (n=6), 6-10-year-old HPO plantations (n=6), 15-30-year-old naturally regenerated stands (n=6), ≥60-year-old unmanaged mature forests (n=10) and 1-4-year-old selection cutting in managed mature forests (n=6).

CONCLUSION

Ce projet de recherche révèle l'importance du rôle de la quantité d'attributs structuraux et de l'hétérogénéité structurale de la végétation à l'échelle du peuplement pour maintenir la composition des espèces d'oiseaux forestiers. En effet, les plantations de PEH à l'étude étaient l'habitat potentiel d'autant d'espèces d'oiseaux que les forêts naturelles aménagées ou non. Toutefois, nos comparaisons indiquent que les plantations de PEH en milieu forestier peuvent soutenir un niveau de diversité, en termes de composition en espèces et traits fonctionnels, qui diffèrent selon à quoi elles sont comparées. Notamment, des différences plus importantes dans la composition en espèces sont observées entre les plantations de PEH et les forêts régénérées naturellement, ainsi qu'entre les plantations de PEH et les forêts matures non aménagées, qu'entre ces dernières et des coupes qui sont généralement mieux acceptées socialement, i.e. coupes sélectives en forêts matures. D'un point de vue des traits fonctionnels, les plantations de PEH (jeune ou moins jeunes) abritaient moins d'espèces d'oiseaux s'alimentant sur l'écorce des arbres que les autres types forestiers, mais les jeunes plantations présentaient plus d'espèces nichant dans la strate arbustive. Ces différences, en termes de composition en espèces et de traits fonctionnels, au sein des plantations par rapport aux forêts naturelles seraient principalement dues à une plus faible quantité et hétérogénéité d'attributs structuraux associés aux arbres. D'un point de vue appliqué, ces résultats suggèrent qu'il serait important d'aménager les plantations de PEH en milieu forestier de manière à y retrouver des arbres de différentes tailles (i.e., plantation inéquienne) pour diminuer leur écart de composition en espèces aviaires avec les forêts naturelles. Cela pourrait être possible en plantant plusieurs espèces d'arbre dont la croissance diffère (i.e., plantation multispécifique), ou par le maintien d'arbres au sein de la plantation monospécifique au moment de la coupe afin de générer une hétérogénéité dans la taille des arbres d'une rotation à une autre (Hartley, 2002; Paquette et Messier, 2010).

De plus, cette étude montre l'importance de considérer plusieurs composantes de la diversité des communautés d'oiseaux (richesse spécifique, composition en espèces et en traits fonctionnels) pour faire une évaluation éclairée de l'effet des plantations sur la biodiversité. Dans un contexte d'aménagement écosystémique, le choix de paradigme de conservation devrait se baser sur la capacité des plantations de PEH à maintenir une composition en espèces et en traits comparable aux forêts naturelles plutôt que de maximiser le nombre d'espèces. En effet, l'aménagement écosystémique vise à réduire les écarts entre la forêt aménagée et la forêt naturelle. Or, nos résultats démontrent que les plantations favorisent la présence de plusieurs espèces qui ne se trouvent pas dans les forêts naturelles (aménagées ou pas). Par conséquent, valoriser les plantations par le fait qu'elle maximise le nombre d'espèces augmenterait l'écart avec les forêts naturelles. Finalement, nos résultats montrent que des changements rapides (en quelques années seulement) dans la structure de la végétation se produisent au sein des plantations et entrainent des changements rapides dans la composition en espèces d'oiseaux (et en traits) qui y sont associés. Il est donc important d'évaluer l'effet des plantations de PEH selon leur contexte très dynamique comparativement à la dynamique plus lente des forêts naturelles aménagées et non aménagées. Ainsi, notre étude montre l'importance de plusieurs facteurs qui sont à considérer lors de l'évaluation de l'effet des plantations sur la biodiversité, 1) le choix du peuplement contrôle, 2) les composantes de la diversité à gérer, 3) le choix de paradigme de conservation à privilégier et 4) le temps de rotation.

Pistes futures de recherche :

Plusieurs aspects relatifs aux plantations de PEH sont encore à étudier afin d'en faire des habitats dans lesquels la biodiversité est maintenue. En effet, à l'échelle du territoire forestier productif, il a été recommandé au Québec de limiter à 5% le territoire forestier couvert par les plantations (Groupe d'experts sur la sylviculture intensive de plantations, 2013). Cette recommandation, faite par un comité d'experts, nécessite cependant d'être validée par des données scientifiques. Bien que nous ayons exploré l'effet de la proportion du paysage avoisinant (i.e., dans un rayon de 750 m) couvert de plantations de PEH sur la diversité des communautés d'oiseaux, notre design expérimental n'était pas adapté pour tester les effets potentiels de la quantité, la localisation et l'arrangement spatial des plantations sur la biodiversité. Ainsi, de futurs travaux de recherche seraient nécessaires pour évaluer comment la quantité de plantations de PEH dans le paysage, ainsi que la localisation et l'arrangement des plantations de PEH, affectent la diversité des communautés d'oiseaux.

De plus, notre étude permet d'identifier l'importance de la quantité et de l'hétérogénéité des attributs structuraux de la végétation comme moteur principal des différences des communautés d'oiseaux avec les forêts naturelles, mais ne permet pas de dissocier le rôle relatif de la quantité et de l'hétérogénéité des attributs structuraux. Cette distinction est pourtant essentielle à faire puisque les conséquences en termes d'aménagement ne sont pas les mêmes. Par ailleurs, comme révélé par une récente revue de la littérature (McFadden et Dirzo, 2018), il y a actuellement une lacune dans l'identification de valeurs seuils, tel que la quantité de structure ou de legs biologiques, requises à l'échelle de la plantation pour maintenir la biodiversité. Il serait donc également souhaitable, que ce soit pour la quantité et l'hétérogénéité des attributs structuraux, de déterminer les valeurs seuils (à l'échelle de la plantation) nécessaires au maintien de la biodiversité dans les plantations de PEH situées un paysage forestier aménagé.

D'autre part, nous avons étudié l'effet des plantations de PEH sur la diversité des oiseaux dans des plantations qui venaient d'être mises en place (après 1-3ans) jusqu'à des plantations âgées de 6-10 ans, i.e. des plantations qui ont un âge moyen si on considère le fait qu'elles seront coupées à l'âge de 15-20 ans. Sachant que la quantité et l'hétérogénéité des attributs structuraux de la végétation vont continuer à évoluer dans les plantations de 6-10 ans, il serait nécessaire de caractériser la diversité des communautés d'oiseaux à la fin de la rotation (après 15-20 ans) afin d'estimer si des différences de diversité existent toujours avec les peuplements naturels (aménagés et non aménagés). Cette information est, à notre connaissance, absente de la littérature qui touche l'Amérique du Nord (Demarais *et al.*, 2017).

Finalement, cette étude s'est concentrée sur les oiseaux puisqu'ils sont généralement de bons bio-indicateurs de la réponse de la biodiversité aux perturbations de l'habitat. Cependant, la réponse aux plantations en milieu forestier étant variables entre taxons animaliers (e.g. Iezzi *et al.*, 2018), il serait important d'étendre cette étude à d'autres groupes fauniques afin d'avoir une estimation plus complète de l'effet des plantations de PEH sur la biodiversité animale. Cela permettrait également de fournir des lignes directrices plus précises aux gestionnaires forestiers dans le but ultime de maintenir dans sa totalité la biodiversité animale dans les plantations.

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