



Sélection de l'habitat diurne des chauves-souris dans un contexte d'aménagements sylvicoles en forêt boréale

Thèse

François-Henri Fabianek

Doctorat en sciences forestières

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Québec, Canada

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RÉSUMÉ COURT

La petite chauve-souris brune (*Myotis lucifugus*) et la chauve-souris nordique (*Myotis septentrionalis*) nichent dans des arbres durant l'été et devraient être affectées par les aménagements sylvicoles. Mon premier objectif était d'évaluer les variables impliquées dans la sélection des arbres gîtes des chauves-souris en forêt boréale. Mon second objectif était d'évaluer la proportion et la répartition spatiale de ces variables dans le paysage forestier aménagé. J'ai, lors du premier chapitre, réalisé une synthèse quantitative de 34 études portant sur la sélection des arbres gîtes des chauves-souris cavicoles en Amérique du Nord. Pour évaluer la sélection des arbres gîtes des chauves-souris du genre *Myotis* à la forêt Montmorency (Québec, Canada), j'ai comparé les arbres et les peuplements sélectionnés par 22 mâles suivis à des points aléatoires. Le diamètre et la hauteur des arbres, l'ouverture de la canopée et la densité de chicots étaient les variables les plus importantes à considérer pour les chauves-souris du genre *Myotis*. J'ai généré des cartes d'habitat diurne potentiel à travers la partie méridionale du massif des Laurentides à partir de ces résultats. Les sommets semblaient avoir un moindre potentiel pour les chauves-souris du genre *Myotis* et la sapinière apparaissait plus propice pour la chauve-souris nordique, comparée à la petite chauve-souris brune. Favoriser ou maintenir des îlots de végétation de 0,1 hectare comprenant un minimum de 10 chicots devrait préserver les arbres gîtes de ces espèces. Augmenter la proportion de parcelles résiduelles surannées devrait également contribuer à préserver les habitats diurnes potentiels des chauves-souris à travers la partie méridionale du massif des Laurentides.

RÉSUMÉ LONG

Jusqu'à présent, l'écologie des chauves-souris en forêt boréale n'était pas étudiée au Québec. La petite chauve-souris brune (*Myotis lucifugus*) et la chauve-souris nordique (*Myotis septentrionalis*) nichent dans des arbres en été et pourraient être affectées par les aménagements sylvicoles en forêt boréale. Mon premier objectif était de trouver dans la littérature les principales variables impliquées dans la sélection des arbres gîtes des chauves-souris cavicoles. Mon second objectif était de trouver les variables impliquées dans la sélection des arbres gîtes des espèces du genre *Myotis* en forêt boréale aménagée. Mon troisième objectif était de déterminer la proportion et la répartition spatiale des habitats diurnes potentiels à travers la partie méridionale du massif des Laurentides. Ma synthèse quantitative se base sur 34 études réalisées en Amérique du Nord. Le diamètre des arbres apparaissait comme étant un élément clé à considérer dans la sélection des arbres gîtes des chauves-souris cavicoles, particulièrement à des latitudes nordiques. J'ai suivi par télémétrie 22 chauves-souris mâles capturées dans différents secteurs de la forêt Montmorency (Québec, Canada). J'ai comparé les arbres et les peuplements sélectionnés par les chauves-souris à des points aléatoires pour évaluer la sélection des arbres gîtes. Les chicots avec un stade intermédiaire de détérioration étaient principalement sélectionnés. Le diamètre et la hauteur des arbres, l'ouverture de la canopée et la densité de chicots étaient les variables les plus importantes à considérer dans la sapinière (*Abies balsamea*) à bouleau blanc (*Betula papyrifera*) de l'Est-du-Québec. J'ai utilisé ces résultats pour générer des cartes d'habitat diurne potentiel des espèces du genre *Myotis* à travers la partie méridionale du massif des Laurentides. Les sommets avaient un moindre potentiel pour les chauves-souris du genre *Myotis*. La sapinière à bouleau blanc apparaissait plus propice pour la chauve-souris nordique, comparée à la petite chauve-souris brune. Favoriser ou maintenir des arbres de gros diamètre et des îlots de végétation de 0,1 hectare comprenant un minimum de 10 chicots devrait préserver les arbres gîtes des espèces du genre *Myotis* en forêt boréale aménagée du Québec. Augmenter la proportion de parcelles résiduelles surannées permettrait de préserver les habitats diurnes potentiels des chauves-souris du genre *Myotis* à travers la partie méridionale du massif des Laurentides.

ABSTRACT

Until now, the ecology of bats in boreal forest was not studied in Quebec. Little brown bats (*Myotis lucifugus*) and northern long-eared bats (*Myotis septentrionalis*) roost in trees during summer and might be affected by logging in boreal forest. My first objective was to find in the literature the main variables implicated in roost selection by cavity-roosting bats in North America. My second objective was to find the variables implicated in roost selection by *Myotis* species in a managed boreal forest. My third objective was to determine the spatial distribution and proportion of potential roosting habitats over the southern part of the Laurentian Highlands. My quantitative synthesis was based on 34 studies performed in North America. Tree diameter appeared to be a key element to consider in roost selection by cavity-roosting bats in North America, especially in Nordic latitudes. I monitored by telemetry 22 male bats captured in various sectors of the Montmorency forest (Quebec, Canada). I compared trees and stands selected by bats to random points to evaluate roost selection. Snags with an intermediate decay stage were mainly selected. Tree diameter and tree height, canopy opening and snag density were the most important variables to consider in the eastern balsam fir (*Abies balsamea*)-paper birch (*Betula papyrifera*) forest of Quebec. I used these results to generate roosting habitat suitability maps of *Myotis* species over the southern part of the Laurentian Highlands. Summits seemed to have a low potential for *Myotis* species. The balsam fir-white birch forest appeared more suitable for the northern long-eared bat, compared to the little brown bat. Promoting or maintaining large diameter trees and vegetation clusters of 0.1 hectares containing a minimum of 10 snags should preserve roosts of *Myotis* species in the managed boreal forest of Quebec. Increase the proportion of residual patches of old-growth forest should preserve suitable roosting habitats for *Myotis* species over the southern part of the Laurentian Highlands.

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AVANT-PROPOS

Cette thèse de doctorat s'articule en trois chapitres qui visent, avant toute chose, à améliorer les connaissances sur l'écologie des chauves-souris au Québec. L'introduction générale présente les connaissances qui m'ont servi à orienter mes recherches. Chacun des chapitres est ensuite présenté sous la forme d'un article scientifique rédigé en anglais. Anouk Simard et André Desrochers ont contribué à l'élaboration du design expérimental et à la rédaction des trois chapitres. Etienne Bellemare Racine a effectué les analyses LiDAR du second chapitre. La description détaillée des méthodes et l'interprétation de nos résultats sont présentées indépendamment dans chacun des chapitres, puis résumées dans la conclusion générale. La discussion de nos résultats est orientée vers une perspective de conversation des chauves-souris, réalisée dans un contexte d'aménagement écosystémique de la forêt boréale.

La docteure Élizabeth Clare a analysé les restes de proies contenus dans les fèces des chauves-souris que j'ai capturées. Ces analyses, présentées en annexe, n'ont pas fait l'objet d'un chapitre supplémentaire à cause du nombre trop restreint d'échantillons. J'ai également réalisé une clé dichotomique illustrée, adaptée aux chauves-souris du Québec. J'ai validé les critères d'identification de cette clé avec des mesures réalisées sur des spécimens conservés au muséum national du Canada. J'ai complété ces mesures avec des spécimens que j'ai capturés durant le projet de recherche. Vu mon engagement dans la réalisation de chaque étape de ce projet, je suis le premier auteur de tous les chapitres de cette thèse. La collaboration du MFFP et la contribution financière du Fonds de Recherche Québécois pour la Recherche, Nature et Technologies (FRQNT) ont été essentielles à l'accomplissement de ce projet.

« Les convictions sont des ennemis de la vérité plus dangereuses que les mensonges. » Friedrich Nietzsche,
Humain, trop humain; I, Aph. 483.

INTRODUCTION GÉNÉRALE

À ce jour, plus de 1160 espèces de chauves-souris ont été recensées à travers le monde, ce qui représente près d'un quart des mammifères connus (Altringham 2011). Ces espèces sont retrouvées sur la presque totalité du globe à l'exception des régions circumpolaires (Findley 1993). Les chauves-souris font toute partie de l'ordre des chiroptères et ont émergé en tant que groupe phylogénétique distinct il y a environ 65 millions d'années (Altringham 2011). L'ordre des chiroptères aurait ensuite divergé en deux sous-ordres il y a environ 53 millions d'années (Springer *et al.* 2001).

Le sous-ordre des pteropodiformes (Hutcheon & Kirsch 2006) est principalement représenté par des chauves-souris nectarivores et frugivores de grande envergure, communément appelées roussettes et renards volants (Altringham 2011). La majorité des espèces qui composent ce groupe font partie de la famille des ptéropodidés (Altringham 2011). Les chauves-souris appartenant au sous-ordre des vespertilioniformes (Hutcheon & Kirsch 2006) utilisent principalement l'écholocation pour s'orienter et rechercher leur nourriture en pleine obscurité. Environ 25 % des espèces incluses dans ce groupe se nourrissent d'amphibiens, de poissons, de petits mammifères, de fruits, de nectar ou de pollen (Kunz & Fenton 2006; Altringham 2011), alors que la grande majorité d'entre elles (*i.e.*, les 75 % restant) sont insectivores. La famille des vespertilionidés est la plus diversifiée de ce groupe avec plus de 407 espèces recensées (Adams & Pedersen 2013).

État des connaissances sur les chauves-souris du Québec

Quelques généralités sur les chauves-souris

Les huit espèces recensées au Québec (Canada) font partie de la famille des vespertilionidés et ont un régime insectivore (Banfield 1974). La chauve-souris argentée (*Lasionycteris noctivagans*), la chauve-souris cendrée (*Lasiurus cinereus*) et la chauve-souris rousse (*L. borealis*) sont des espèces dites « migratrices » (Tableau 1), qui effectuent des mouvements saisonniers importants (> 1000 km) au printemps et à l'automne (Cryan 2003; Cryan *et al.* 2004). Les distances parcourues et les facteurs impliqués dans le choix des couloirs migratoires sont encore bien mal compris. McGuire *et al.* (2012) ont montré que la chauve-souris argentée continue à chasser activement en migrant, probablement pour compenser l'importante dépense énergétique associée aux vols de longue distance. Le bâti

(*i.e.*, habitations, granges) était fréquemment utilisé par cette espèce pour nicher en période de migration (McGuire *et al.* 2012), ce qui souligne l'importance de ce type de structures lorsque l'offre en arbres gîtes vient à manquer (Brittingham & Williams 2000).

La grande chauve-souris brune (*Eptesicus fuscus*), la petite chauve-souris brune (*Myotis lucifugus*), la chauve-souris nordique (*M. septentrionalis*), la chauve-souris pygmée de l'Est (*M. leibii*) et la pipistrelle de l'Est (*Perimyotis subflavus*) passent la majeure partie de l'hiver en état d'hibernation, regroupées au sein d'hibernacles (Kunz & Fenton 2006). L'essentiel d'une population de chauves-souris peut être regroupé dans le même hibernacle et plusieurs espèces peuvent y cohabiter (Kunz & Fenton 2006). Les mines désaffectées et les grottes naturelles sont les principales structures utilisées au Québec par les chauves-souris hibernantes (Kunz & Fenton 2006). La grande chauve-souris brune est probablement la seule espèce recensée capable d'hiberner dans le bâti (Neubaum *et al.* 2004).

Bien qu'elles soient considérées comme résidentes (Tableau 1), les espèces hibernantes effectuent des déplacements importants entre leurs hibernacles et leurs sites estivaux, durant les périodes de transit printanier et automnal. Les distances de déplacement reportées dans la littérature varient entre 1 km (Johnson & Gates 2008) et 647 km (Norquay *et al.* 2013), selon l'espèce et la localité. Cette distance a par exemple été évaluée à 56 km pour la chauve-souris nordique (Caceres & Barclay 2000), à 53 km pour la pipistrelle de l'Est (Fujita & Kunz 1984) et à plus de 500 km pour la grande chauve-souris brune (Kurta & Baker 1990) et la petite chauve-souris brune (Norquay *et al.* 2013). Les relevés isotopiques de Fraser *et al.* (2012), suggèrent que les distances parcourues par la pipistrelle de l'Est pourraient être largement sous-estimées.

La période de migration automnale coïncide également avec la période de copulation pour les chauves-souris du Québec (Kunz & Fenton 2006). Les chauves-souris résidentes se regroupent au sein et à proximité d'un hibernacle pour copuler avant d'entrer en hibernation. Les chauves-souris étant actives durant cette période de regroupement copulatoire - aussi appelée phase de « swarming » (*sensu* Fenton 1969) - l'habitat forestier à proximité de l'hibernacle doit fournir des arbres gîtes disponibles et un territoire de chasse adéquat (Randall 2011; Lowe 2012). Lowe (2012) a montré qu'en Nouvelle Écosse, le bâti et les chicots (*i.e.*, arbres morts sur pied) étaient utilisés par les chauves-souris du

genre *Myotis* en période de swarming. L'utilisation de l'habitat forestier durant cette période reste peu documentée et aucune information à ce sujet n'est encore disponible au Québec.

L'écologie diurne des chauves-souris en saison estivale

En saison estivale, sept des huit espèces de chauves-souris recensées dans la province sont susceptibles d'utiliser des arbres pour nicher, mettre bas et élever les nouveau-nés en période d'allaitement (Kunz & Fenton 2006; Lacki *et al.* 2007). La chauve-souris argentée, la grande chauve-souris brune, la petite chauve-souris brune et la chauve-souris nordique sont considérées comme des espèces « cavicoles » (Tableau 1), car elles nichent habituellement sous l'écorce exfoliante, au sein de cavités et de fissures dans les troncs d'arbres (Barclay & Kurta 2007). Ces espèces sont accessoirement reportées dans des crevasses et des abris sous roche en saison estivale (Lausen & Barclay 2003; Barclay & Kurta 2007). La chauve-souris cendrée et la chauve-souris rousse sont les seules espèces au Québec qui nichent presque exclusivement dans le feuillage (Kunz & Lumsden 2007). La pipistrelle de l'Est est plutôt considérée comme une espèce généraliste en matière de nichoirs (Fujita & Kunz 1984). Cette espèce a été reportée nichant au sein de cavités (Kurta *et al.* 1999; Veilleux *et al.* 2003), dans le feuillage (Perry & Thill 2007b) et particulièrement dans le lichen (*Usnea trichodea*) en forêt boréale (Quinn & Broders 2007; Poissant *et al.* 2010). Les études de Thomson (2013), Whitby *et al.* (2013), Johnson *et al.* (2011) et Johnson et Gates (2008) ont recensé la chauve-souris pygmée de l'Est nichant principalement dans des fissures et abris sous roche en saison estivale. L'écologie diurne de cette espèce est peu étudiée, mais elle pourrait bien être la seule, au Québec, à ne pas utiliser d'arbres pour nicher durant cette période de l'année (Best & Jennings 1997).

Le bâti offre également des emplacements de repos, de gestation et de maternage disponibles pour certaines espèces de chauves-souris (Williams & Brittingham 1997; Kunz & Reynolds 2003). La grande chauve-souris brune (Kurta & Baker 1990; Agosta 2002), la petite chauve-souris brune (Fenton & Barclay 1980) et la pipistrelle de l'Est (Cope *et al.* 1991; Whitaker 1998) sont susceptibles d'utiliser le bâti comme alternative aux arbres gîtes en saison estivale (Brittingham & Williams 2000; Kunz & Reynolds 2003). La chauve-souris nordique (Broders *et al.* 2013) et les espèces migratrices y sont rarement retrouvées

et sont, par conséquent, plus susceptibles d'être affectées négativement par une diminution de l'offre en arbres gîtes.

Grégarité, ségrégation et fidélité aux arbres gîtes

La structure sociale des femelles résidentes en période de reproduction (*i.e.*, femelles porteuses et en lactation) est de type fission-fusion (Willis & Brigham 2004; Kerth *et al.* 2011): les femelles reproductives s'assemblent en petits groupes temporaires (Garroway & Broders 2007) selon leurs affinités (Kilgour *et al.* 2013) et leur lien de parenté (Patriquin *et al.* 2013). Les femelles non reproductives, les mâles et les chauves-souris migratrices ont un comportement de nidification plus solitaire (Barclay & Kurta 2007; Kunz & Lumsden 2007). Une ségrégation sexuelle est habituellement observée chez les chauves-souris en saison estivale (Senior *et al.* 2005) et les peuplements forestiers d'altitude sont moins susceptibles d'être exploités par les femelles (Grindal *et al.* 1999; Cryan *et al.* 2000; Russo 2002).

Les chauves-souris utilisent généralement un réseau d'arbres gîtes (Broders *et al.* 2006; Reckardt & Kerth 2007; Patriquin *et al.* 2010; Martinez-Nunez *et al.* 2011; Johnson *et al.* 2012; Johnson *et al.* 2013), comprenant des arbres primaires et secondaires (Barclay & Kurta 2007). Bien que les changements d'arbres gîtes soient relativement fréquents - soit aux deux jours en moyenne (Mager & Nelson 2001; Barclay & Kurta 2007) - les arbres primaires sont plus souvent utilisés. Les arbres secondaires semblent être privilégiés lorsque les conditions (*e.g.*, mauvaises conditions climatiques, perturbation) aux arbres primaires deviennent défavorables (Kelley *et al.* 2011). Ce faisant, les femelles montrent une forte philopatrie (*i.e.*, fidélité interannuelle) pour leurs maternités estivales (Lewis 1995; Veilleux & Veilleux 2004; Perry 2011). Peu d'études font en revanche état de la fidélité interannuelle des chauves-souris mâles.

L'hypothèse du microclimat

Selon « l'hypothèse du microclimat » (*sensu* Boyles 2007), la qualité d'un nichoir naturel ou artificiel, devrait dépendre de son inertie thermique (*i.e.*, sa capacité à diffuser durablement la chaleur emmagasinée) et du niveau d'insolation auquel il est exposé (Boyles 2007). Selon Klug *et al.* (2012), les chauves-souris qui nichent directement dans le feuillage chercheraient à exploiter des microclimats permettant de limiter le refroidissement éolien. Les chauves-souris cavicoles et particulièrement les femelles reproductives (Willis &

Brigham 2007; Park & Broders 2012), privilégident les arbres de gros diamètres (Kalcounis-Rueppell *et al.* 2005), censés mieux emmagasiner la chaleur et minimiser les fluctuations de températures extérieures entre le jour et la nuit (Park & Broders 2012; Lacki *et al.* 2013; Johnson & Lacki 2014), comparativement aux arbres de plus petits diamètres. Les femelles reproductives ne peuvent rentrer en torpeur aussi longtemps et aussi souvent que les mâles et les femelles non reproductives (Grinevitch *et al.* 1995; Dzal & Brigham 2013) lorsque les conditions deviennent défavorables (*i.e.*, avec des températures froides et une faible abondance de proies), car cela nuirait au développement du fœtus et à la croissance des juvéniles (Dzal & Brigham 2013; Stawski *et al.* 2014). Il est donc probable que les femelles reproductives soient plus sélectives dans leurs choix des arbres gîtes (Broders & Forbes 2004; Garroway & Broders 2008).

Les arbres gîtes situés en hauteur (Jung *et al.* 2004; Baker & Lacki 2006; Lacki & Baker 2007), au-dessus de la canopée (Menzel *et al.* 1998) ou dans une ouverture de canopée (Psyllakis & Brigham 2006; Vonhof & Gwilliam 2007; Klug, Goldsmith & Barclay 2012), disposant d'une faible densité d'arbres alentour (Baker & Lacki 2006; Lacki & Baker 2007; Lacki *et al.* 2009b) et d'une pente importante (Rabe *et al.*; Lacki & Baker 2007; Boland *et al.* 2009), sont généralement favorisés par les chauves-souris. Plusieurs auteurs avancent que la sélection de ces variables a pour principal intérêt d'accroître le niveau d'insolation des arbres gîtes (Boyles 2007), sans vraiment avoir mesuré cet accroissement directement. Il n'est donc pas exclu que ces variables puissent aussi être associées à une meilleure accessibilité ou à une meilleure visibilité des arbres gîtes depuis la canopée, sans toutefois impliquer un accroissement du niveau d'insolation. Un autre indice indirect en faveur de l'hypothèse du microclimat est la préférence reportée pour les arbres gîtes ayant une orientation Sud (Britzke *et al.* 2006; Johnson *et al.* 2010), censés bénéficier d'une plus longue période d'ensoleillement estival (Klug, Goldsmith & Barclay 2012).

La disponibilité en arbres gîtes

Les arbres aux troncs creux, avec présence de cavités, d'écorce soulevée sur le tronc, de branches mortes, ou recouverts de lichen, sont susceptibles d'être utilisés par les chauves-souris cavicoles (Barclay & Kurta 2007). Bien que les arbres vivants avec présence de

cavités soient régulièrement mentionnés dans la littérature (Barclay & Kurta 2007), les chicots avec un stade de dégradation intermédiaire sont majoritairement sélectionnés dans les peuplements résineux (Parsons *et al.* 2003; Perry & Thill 2008; Arnett & Hayes 2009; Lacki *et al.* 2012). Ces arbres doivent être suffisamment représentés dans l'habitat forestier pour garantir une offre en arbres gîtes satisfaisante pour les chauves-souris. De plus, ces arbres gîtes disponibles ne doivent pas être répartis uniformément dans l'habitat forestier (Mager & Nelson 2001; Barclay & Kurta 2007; Garraway & Broders 2007), mais plutôt compris dans un domaine vital qui va varier entre 0.2 ha et ~1500 ha (Tableau 2). Ces variations vont dépendre de l'espèce (Broders *et al.* 2006), du sexe (Hutchinson & Lacki 1999), du statut reproducteur (Henry *et al.* 2002) et de la localité (Tableau 2). Plusieurs études font état d'une forte abondance de chicots à proximité (*i.e.*, < 30 m) des arbres gîtes utilisés par les chauves-souris cavicoles (Kalcounis-Ruepell, Psyllakis & Brigham 2005; Lacki *et al.* 2009a; Kroll *et al.* 2012). Ces chicots sont considérés comme des arbres gîtes alternatifs pour les chauves-souris (Barclay & Kurta 2007), mais cette hypothèse a rarement été vérifiée empiriquement.

La distance aux ressources

Les suivis télémétriques indiquent que les arbres gîtes sélectionnés sont pour la plupart situés à moins de 1 km de l'arbre gîte le plus proche, moins de 2 km d'une étendue d'eau et moins de 10 km des habitats d'alimentation ou du site de capture de l'individu (Tableau 2). Les chauves-souris sont reconnues pour nicheter à proximité des points d'eau et de leurs habitats d'alimentation (Henry *et al.* 2002; Elmore *et al.* 2004; Kalcounis-Ruepell, Psyllakis & Brigham 2005; Quinn & Broders 2007). Elles sont tributaires des points d'eau pour aller s'hydrater à la pénombre (Seibold *et al.* 2013), particulièrement les femelles en période de reproduction (Kurta *et al.* 1989; Adams & Hayes 2008).

La majorité des chauves-souris, incluant les espèces du genre *Myotis* et la pipistrelle de l'Est, s'alimentent à proximité des points d'eau (Fenton & Barclay 1980; Fabianek *et al.* 2008; Clare *et al.* 2011) et dans les habitats riverains (Grindal, Morissette & Brigham 1999; Syme *et al.* 2001), généralement plus productifs en insectes (Holloway & Barclay 2000; Whitaker *et al.* 2000; Fukui *et al.* 2006). À l'opposé, les chauves-souris sont moins actives dans les peuplements d'altitude (Grindal, Morissette & Brigham 1999; Ellis *et al.* 2002;

Erickson & Adams 2003), probablement à cause de conditions climatiques plus rigoureuses et d'une moindre disponibilité en insectes (Grindal & Brigham 1999). Les cours d'eau et les bandes riveraines sont également employés comme corridors de dispersion entre les arbres gîtes et les habitats d'alimentations ou durant la migration de plusieurs espèces de chauves-souris (Brigham 1991; Campbell *et al.* 1996; Holloway & Barclay 2000; Ellis, Patton & Castleberry 2002). Il n'est pas rare de retrouver des individus nichant à proximité de ces habitats (Elmore, Miller & Vilella 2004; Kalcounis-Ruepell, Psyllakis & Brigham 2005; Quinn & Broders 2007), sans doute pour réduire les coûts énergétiques liés aux déplacements (Barclay 1988; Wilkinson & Barclay 1997; Henry *et al.* 2002), ou le risque de préddation (Rydell *et al.* 1996; Vonhof & Barclay 1997; Baxter *et al.* 2006; Jung *et al.* 2011), voire les deux. Certaines essences non-commerciales retrouvées en milieu riverain, notamment les aulnaies, sont utilisées comme arbres gîtes par les chauves-souris qui se perchent directement dans le feuillage (Kunz & Lumsden 2007).

Bref survol de l'écologie d'alimentation

La capacité d'une chauve-souris à exploiter un habitat d'alimentation va dépendre de sa corpulence, la morphologie de ses ailes et du degré d'obstruction de l'habitat forestier (Aldridge & Rautenbach 1987; Norberg & Rayner 1987; Schnitzler & Kalko 2001; Fukui *et al.* 2011). Les espèces à vol rapide, avec une faible manœuvrabilité, s'alimentent de préférence dans des habitats ouverts (Erickson & West 1996; Ford *et al.* 2005; Bender *et al.* 2015), alors que les espèces à vol lent, plus agiles, sont plus sensibles à la stratification verticale de la végétation (Adams *et al.* 2009; Jung *et al.* 2012; Mueller *et al.* 2013). Ces espèces sont davantage retrouvées chassant sous le couvert forestier (Patriquin & Barclay 2003; Broders *et al.* 2006) ou à l'orée des boisés (Owen *et al.* 2003; Ford *et al.* 2005; Loeb & O'Keefe 2011).

Les chauves-souris présentes au Québec émettent des ultrasons de forte intensité (*i.e.*, entre 80 et 110 dB) pour s'orienter et traquer efficacement leur proie dans l'obscurité (Schnitzler & Kalko 2001). Elles vont être capables de moduler la bande fréquentielle, la durée et la période d'émission de leurs ultrasons à l'approche d'une proie (Murray *et al.* 2001; Wund 2006), selon le niveau d'encombrement de l'habitat dans lequel elles évoluent (Barclay & Brigham 2002; Broders *et al.* 2004; Bayefsky-Anand *et al.* 2008) et la présence

d'individus de la même espèce (Obrist 1995). Ces modulations vont toutefois être limitées par des contraintes physiologiques liées à la morphologie des espèces (Barclay *et al.* 1999; Bogdanowicz *et al.* 1999; Jacobs *et al.* 2007). Ces contraintes vont à leur tour conditionner les stratégies de chasse des chauves-souris et leurs besoins en habitats d'alimentation (Bogdanowicz, Fenton & Daleszczyk 1999; Schnitzler & Kalko 2001; Fenton & Bogdanowicz 2002).

La chauve-souris nordique est une espèce à vol lent (*i.e.*, avec une forte manœuvrabilité) qui émet des signaux dont la durée moyenne est de 2,5 ms et la bande fréquentielle habituellement comprise entre 40 et 90 kHz (Figure 1). Cette espèce est sans doute la seule au Québec à glaner ses proies sur la surface du feuillage (Faure *et al.* 1993) et elle est davantage retrouvée au sein d'habitats forestiers obstrués par les branchages, chassant généralement sous le couvert forestier (Hogberg *et al.* 2002; Patriquin & Barclay 2003). À l'opposé de ce spectre sonore se situe la chauve-souris cendrée (Figure 1). Cette espèce à vol rapide (*i.e.*, avec une faible manœuvrabilité) émet des signaux de 8 ms en moyenne et dont la bande fréquentielle se situe habituellement entre 18 et 25 kHz (Figure 1). La chauve-souris cendrée est certainement la mieux adaptée au Québec pour s'alimenter en milieu ouvert (Barclay 1986; Loeb & O'Keefe 2011) et exploiter les trouées laissées par d'importantes perturbations du couvert forestier (Loeb & O'Keefe 2011).

Problématique de recherche

Les principaux impacts des aménagements sylvicoles sur les communautés

La réponse des communautés animales et végétales aux perturbations des écosystèmes forestiers dépend de l'intensité et de la fréquence des perturbations (Niemelä 1999; Bergeron 2000; Franklin *et al.* 2002). Les perturbations anthropiques et naturelles entraînent une succession d'espèces le long d'une chrono-séquence depuis la perturbation (Fuller *et al.* 2004; Fisher & Wilkinson 2005; Sullivan *et al.* 2005). Certaines espèces vont être capables de recoloniser l'habitat dès les premiers stades de succession (Grindal & Brigham 1998; Grindal & Brigham 1999; Potvin *et al.* 1999; Loeb & O'Keefe 2011), alors que d'autres ne vont apparaître que durant les stades de succession les plus avancés (Hansson 1994). Ce sont ces dernières qui sont les plus susceptibles d'être affectées par les aménagements sylvicoles (Imbeau *et al.* 2001; Vanderwel *et al.* 2009).

Dans le cas des aménagements sylvicoles en forêt boréale, la capacité de nombreuses espèces à recoloniser l'habitat perturbé dépend de la fréquence, de l'étendue et de la configuration des parterres de coupe (Potvin, Courtois & Bélanger 1999; Vanderwel, Mills & Malcolm 2009; Le Blanc *et al.* 2010; Vanderwel *et al.* 2011). À court terme, les perturbations engendrées par les coupes forestières peuvent être profitables pour certaines espèces animales, capables d'exploiter ces habitats perturbés (Fortin *et al.* 2011; Vanderwel *et al.* 2011).

À l'opposé, des modifications majeures et durables de la structure¹, de la composition² et de la configuration³ des peuplements peuvent empêcher d'autres espèces de recoloniser l'habitat forestier perturbé (Bélisle *et al.* 2001; Vanderwel *et al.* 2011). C'est particulièrement le cas lorsque les assiettes de coupes sont supérieures aux domaines vitaux des espèces considérées (Potvin, Courtois & Bélanger 1999). Cette érosion progressive et durable de la biodiversité peut entraîner une perte de plusieurs fonctions essentielles à la résilience des écosystèmes forestiers (Gauthier *et al.* 2007). La résilience d'un écosystème se définit par sa capacité à retrouver son état initial après avoir subi une perturbation (Gauthier *et al.* 2007).

L'intervalle de temps trop court du régime de perturbations anthropiques (*i.e.*, principalement liées aux coupes forestières) ne permet pas l'établissement des derniers stades de successions végétales inhérents aux forêts non exploitées (Franklin *et al.* 2002; Gauthier *et al.* 2007). Ces stades sont caractérisés par des peuplements surannés également définis sous l'appellation de « vieilles forêts » (Vaillancourt *et al.* 2009a). Selon la définition donnée par Kneeshaw et Gauthier (2003), les vieilles forêts se caractérisent par un remplacement graduel des arbres s'étant établis sous couvert, après disparition de la première cohorte, initiée lors de la dernière grande perturbation. Les aménagements sylvicoles des dernières décennies sont en grande partie imputables de la diminution des vieilles forêts au Québec (Bergeron & Harper 2009; Boucher *et al.* 2009; Cyr *et al.* 2009;

¹ La structure du peuplement fait référence à la distribution verticale et horizontale des composantes d'un peuplement.

² Les composantes d'un peuplement font référence à la proportion des essences, des strates et classes d'âge qui le composent. Une composition en essences variées et la présence simultanée de plusieurs strates et de classes d'âge sont caractéristiques d'un peuplement diversifié ou « hétérogène », par opposition à un peuplement « homogène », dont la composition est peu diversifiée.

³ La configuration fait référence à la répartition spatiale des composantes d'un peuplement forestier.

Bergeron & Fenton 2012). Les seuils actuels de forêts matures et surannées sont en effet inférieurs aux proportions historiques maximales évaluées avant l'avènement des premières pratiques forestières intensives (Cyr *et al.* 2009; Bureau du forestier en chef 2010).

Les vieilles forêts se caractérisent par la présence de gros débris ligneux au sol et une importante proportion de chicots (Sturtevant *et al.* 1997; Lee 1998; Smith *et al.* 2008; Smith *et al.* 2009; Moroni & Harris 2010; Moroni & Ryan 2010). Ces peuplements sont davantage sujets aux chablis et présentent un degré d'ouverture important au niveau des strates inférieures de la canopée (Kneeshaw & Bergeron 1998; Franklin *et al.* 2002; Bergeron & Fenton 2012), facilitant ainsi le déplacement de nombreux animaux. Les chicots et débris ligneux au sol sont également des composantes de l'habitat essentielles au maintien des cycles biologiques de nombreuses espèces animales et végétales (Savignac *et al.* 2000; Imbeau & Desrochers 2002; Smith 2007; Drapeau *et al.* 2009).

La diminution de la variabilité naturelle des peuplements causée par un rajeunissement global des forêts entraîne une homogénéisation du paysage forestier (Bergeron 2000; Harvey & Brais 2002; Bergeron & Fenton 2012). Les phénomènes d'homogénéisation et de diminution de la biodiversité sont accentués par la sélection de peuplements équiens et par la plantation d'une faible diversité d'essences indigènes (Park & Wilson 2007; Paquette & Messier 2010).

L'impact des aménagements sylvicoles sur les chauves-souris

L'impact des aménagements sylvicoles sur les comportements d'alimentation et de repos des chauves-souris varie selon l'espèce et le type d'aménagement considérés. La littérature fait surtout état du changement d'activité nocturne - principalement un comportement d'évitement des chauves-souris – lié à divers aménagements sylvicoles. Les impacts à long terme de ces aménagements et en particulier les impacts sur le comportement de repos, sont peu évalués et nécessiteraient une plus grande attention en recherche (Kroll, Lacki & Arnett 2012).

La coupe totale sur de grands blocs réguliers a un impact négatif sur la majorité des chauves-souris (Hein *et al.* 2008; O'Keefe *et al.* 2009). Les espèces à vol rapide (*i.e.*, avec une faible manœuvrabilité) se déplacent et s'alimentent davantage au sein des ouvertures récentes occasionnées par la récolte des peuplements matures (Erickson & West 1996; Jung

et al. 1999; Clarke *et al.* 2005; Ford *et al.* 2005; Hein, Castleberry & Miller 2008; O'Keefe *et al.* 2009; Loeb & O'Keefe 2011; Dodd *et al.* 2012b; Bender *et al.* 2015). C'est par exemple le cas des Lasiurines (*i.e.*, la chauve-souris rousse et la chauve-souris cendrée), retrouvées lors des premiers stades de succession après une perturbation du couvert forestier (Hogberg, Patriquin & Barclay 2002; Patriquin & Barclay 2003; Loeb & O'Keefe 2011; Dodd *et al.* 2012b). Il est probable que la coupe totale diminue l'offre en arbres gîtes pour la majorité des chauves-souris recensées au Québec.

Les espèces à vol lent (*i.e.*, avec une forte manœuvrabilité) sont moindrement observées en train de s'alimenter dans les assiettes de coupes récentes (Hayes & Adam 1996), comparativement aux peuplements forestiers surannés (Crampton & Barclay 1998; Patriquin & Barclay 2003). C'est principalement le cas des espèces du genre *Myotis* (*i.e.*, la petite chauve-souris brune et la chauve-souris nordique) et de la pipistrelle de l'Est, davantage associées au couvert forestier et aux bordures de forêt (Hogberg, Patriquin & Barclay 2002; Patriquin & Barclay 2003; Ford *et al.* 2005; Henderson *et al.* 2008; Segers & Broders 2014). L'effet cumulatif des ouvertures du couvert forestier à l'échelle du paysage peut représenter une barrière de dispersion pour certaines espèces (Farrow & Broders 2011; Segers & Broders 2014). La chauve-souris nordique est par exemple davantage recensée dans les peuplements matures (Loeb & O'keefe 2006; Conley 2011) et moindrement représentée dans les habitats fragmentés (Henderson, Farrow & Broders 2008; Segers & Broders 2014).

Les chauves-souris qui persistent dans les habitats forestiers fragmentés se déplacent habituellement le long des lisières des boisés denses, constituées de rangées d'arbres matures (Brandt *et al.* 2007; Hein, Castleberry & Miller 2008; Hein *et al.* 2009; Bates 2010). L'effet brise-vent procuré par les rangées d'arbres profite à la fois aux chauves-souris (Verboom & Spoelstra 1999) et aux insectes qui sont consommés (Lewis 1969; Lewis 1970). Les routes forestières et les sentiers de débardage créés durant la récolte et le transport du bois peuvent par exemple être utilisés comme corridors de déplacement par les chauves-souris (O'Keefe *et al.* 2009), en particulier les espèces à vol rapide (Erickson & West 1996). Toutefois, lorsque les zones déboisées et les sentiers sont linéaires, le phénomène d'accélération éolien peut nuire aux insectes et aux déplacements des chauves-souris (Verboom & Spoelstra 1999).

Les chauves-souris semblent moins sensibles aux aménagements sylvicoles générant une perturbation inférieure à celle générée par une coupe totale sur de grands blocs réguliers (Erickson & West 1996; Perdue & Steventon 1996; Grindal & Brigham 1998; Lacki *et al.* 2009b; Fukui *et al.* 2011). Un haut degré d'obstruction de l'habitat lié à des peuplements denses affecte négativement l'activité de chasse des chauves-souris (Brigham *et al.* 1997a; Erickson & West 2003; Adams, Law & French 2009; Obrist *et al.* 2011; Titchenell *et al.* 2011). À court terme, les éclaircies générées par des aménagements sylvicoles de petites et moyennes intensités pourraient améliorer la qualité des habitats d'alimentation en diminuant le degré d'obstruction du peuplement (Perdue & Steventon 1996; Brigham *et al.* 1997a; Loeb & O'Keefe 2011). Les impacts à long terme sont en revanche rarement évalués (Kroll, Lacki & Arnett 2012).

L'effet de lisière provoqué par les coupes de petites et moyennes intensités semble par exemple profiter à de nombreuses chauves-souris (Morris *et al.* 2010) et aux insectes (Peltonen *et al.* 1997), abondants dans cet écotone forestier (Grindal & Brigham 1999). Les lisières de coupes sont utilisées comme corridor de dispersion et habitat d'alimentation par la majorité des chauves-souris (Grindal 1996; Morris, Miller & Kalcounis-Rueppell 2010; Pettit 2011; Jantzen & Fenton 2013). Comparativement à l'intérieur des parcelles résiduelles et au centre du bloc de coupe, une plus grande activité nocturne est observé le long des lisières de forêt (Grindal 1996; Morris, Miller & Kalcounis-Rueppell 2010; Loeb & O'Keefe 2011; Pettit 2011; Jantzen & Fenton 2013). Une plus grande disponibilité d'insectes y est également observée (Peltonen, Heliövaara & Väistö 1997; Deans *et al.* 2005; Morris, Miller & Kalcounis-Rueppell 2010) comparativement aux parcelles résiduelles.

Les coupes partielles réalisées sur de petites surfaces, la coupe progressive et la coupe sélective par arbre extraient une partie du peuplement mature. Ceci génère de petites ouvertures et maintient une plus grande surface de forêt résiduelle, comparativement à une coupe totale. Ces aménagements permettent sans doute de maintenir des habitats résiduels couvrant les besoins d'alimentation et de repos d'un plus grand nombre d'espèces de chauves-souris (Erickson & West 1996; Perdue & Steventon 1996; Humes *et al.* 1999; Loeb & O'Keefe 2011), car les espèces à vol lent (Humes, Hayes & Collopy 1999) et les espèces à vol rapide (Titchenell, Williams & Gehrt 2011) pourraient exploiter des assiettes de coupe plus restreintes. Une mosaïque diversifiée de peuplements génère également une

entomofaune plus diversifiée qui serait potentiellement exploitée par les chauves-souris (Peltonen, Heliövaara & Väistönen 1997; Dodd *et al.* 2012b). La rétention d'arbres dominants pourrait offrir un couvert mature résiduel jusqu'à leur prochaine récolte. L'offre en arbres gîtes pourrait ainsi être temporairement préservée pour les espèces arboricoles (Hutchinson & Lacki 2000). En revanche, l'abatage systématique des chicots par mesure de sécurité pourrait diminuer l'offre en arbres gîtes pour les espèces cavicoles (Lacki, Baker & Johnson 2012; Perry & Thill 2013; Fabianek *et al.* 2015).

Nous avons vu à travers cette revue de littérature que les impacts à court terme générés par les coupes et le transport de bois sont très contrastés. Bien évidemment, la préparation des peuplements génère également un impact sur les chauves-souris qu'il convient de considérer. Tout comme les coupes partielles, progressives et sélectives, l'alternance d'habitats forestiers matures et de peuplements plus jeunes générée par coupes de jardinage permet sans doute de créer une hétérogénéité structurale indispensable à la cohabitation de plusieurs espèces de chauves-souris (Krusic *et al.* 1996; Titchenell, Williams & Gehrt 2011). Supprimer les arbres les moins vigoureux lors d'un élagage ou d'une éclaircie pré-commerciale augmente l'apport de lumière afin de favoriser la croissance des arbres à valeur commerciale (Pothier 2002; Prévost & Gauthier 2012). Ces aménagements pourraient générer des sites d'alimentation pour les chauves-souris, à condition qu'ils soient réalisés dans les peuplements denses et que les chicots et autres arbres à valeurs fauniques (*e.g.*, gros arbres creux et remarquables) ne soient pas systématiquement abattus (Lacki, Baker & Johnson 2012). La coupe d'ensemencement devrait en principe générer les mêmes impacts à court terme. Cependant, les peuplements équiens favorisés à long terme par ce type d'aménagement, présentent un moindre intérêt pour les chauves-souris (Jung *et al.* 2012).

L'approche écosystémique des aménagements sylvicoles au Québec

Les trois dernières décennies de recherche en écologie forestière ont permis aux aménagements sylvicoles nord-américains de s'orienter vers une gestion « écosystémique » des forêts (Galindo-Leal & Brunnell 1995; Hansson & Larsson 1997; Gauthier *et al.* 2008). Selon Gauthier *et al.* (2008) « l'aménagement écosystémique vise à maintenir des écosystèmes résilients, en misant sur une diminution des écarts entre les paysages naturels et ceux qui sont aménagés ». L'idée sous-jacente part du principe que les écosystèmes

boréaux sont adaptés aux régimes de perturbations naturelles engendrés par les cycles de feux, les chablis et les épidémies d'insectes ravageurs (McCullough *et al.* 1998; Franklin *et al.* 2002; Bergeron & Fenton 2012). Développer des aménagements forestiers s'inspirant de la fréquence et de l'intensité des perturbations naturelles, permettrait de limiter l'impact des activités forestières en milieu boréal (Gauthier *et al.* 2007; Gauthier *et al.* 2008; Bergeron *et al.* 2009; Vaillancourt *et al.* 2009b; Gauthier *et al.* 2010). L'aménagement forestier écosystémique vient tout juste d'être intégré au nouveau régime forestier québécois en vigueur depuis 2013 (Provencher 2014) et fait encore l'objet d'expérimentations à travers la province du Québec (Bureau du forestier en chef 2010).

La mise en place d'une telle approche nécessite une connaissance du fonctionnement des écosystèmes forestiers boréaux et des conséquences des perturbations naturelles et anthropiques sur les communautés animales et végétales. Dans une optique de conservation de la biodiversité, il est également important de s'assurer que les perturbations engendrées par les traitements sylvicoles soient, dans l'ensemble, bien tolérées par les communautés animales et végétales (Drapeau *et al.* 2010). À l'heure actuelle, il n'existe aucun programme gouvernemental d'évaluation de l'état des écosystèmes boréaux québécois et des conséquences des perturbations anthropiques sur la biodiversité (Grimard 2009). Déterminer la réponse des espèces aux différents types d'aménagements forestiers est donc de première importance pour la définition de stratégies de conservation provinciales répondant à la notion complémentaire de filtre fin⁴ (Noss 1987). Ces stratégies de conservation devraient idéalement intégrer les habitats favorisant la persistance des espèces 1) à statut précaire, 2) sensibles aux perturbations d'origine anthropique, 3) qui détiennent un rôle clé au sein des écosystèmes forestiers ou 4) dont le rôle au sein des écosystèmes boréaux reste encore à déterminer. Les inventaires permettant de caractériser et localiser ces habitats restent largement incomplets au Québec (Bureau du forestier en chef 2010).

Le besoin en connaissances sur les chauves-souris dans la province du Québec

Les chauves-souris sont les seuls grands prédateurs d'insectes nocturnes (Patterson *et al.* 2003; Boyles *et al.* 2011) et jouent sans doute un rôle important au sein des écosystèmes

⁴ Notion complémentaire au filtre brut, qui englobe l'ensemble des aménagements visant la protection des espèces en péril, de grande importance commerciale écologique ou commerciale.

forestiers boréaux (Kunz *et al.* 2011). Avec huit espèces recensées, l'ordre des chiroptères représente près de 10 % des 79 mammifères terrestres recensés au Québec. La moitié des chauves-souris sont inscrites sur la liste des espèces susceptibles d'être désignées menacées ou vulnérables au Québec (Tableau 1). Dans les faits, certaines espèces ne peuvent recevoir une désignation spécifique vu le manque de connaissance sur leur écologie (Tremblay & Jutras 2010). La propagation rapide du *Pseudogymnoascus destructans* à travers l'Est du Canada et les taux de mortalité massifs des chauves-souris résidentes atteintes du Syndrome du Museau Blanc (SMB; Frick *et al.* 2010) ont fait placer en urgence la petite chauve-souris brune, la chauve-souris nordique et la pipistrelle de l'Est sur l'Annexe 1 de la Loi sur les Espèces Protégées (LEP) au Canada (Gouvernement du Canada 2014). Ces espèces sont considérées en voie de disparition au Canada depuis 2014 (Gouvernement du Canada 2014). En considérant le fait qu'il n'y ait aucune mesure permettant de mitiger l'impact du SMB sur ces espèces, une stratégie de conservation complémentaire serait de réduire l'impact négatif associé à d'autres perturbations majeures d'origines anthropiques.

En modifiant les taux de mortalité, la taille et la densité d'arbres ainsi que la composition en essence et l'âge des peuplements forestier, les aménagements sylvicoles sont susceptibles de diminuer l'offre et la qualité des arbres gîtes utilisés par les chauves-souris cavicoles (Guldin *et al.* 2007). Ces espèces pourraient être affectées par les coupes forestières en milieu boréal, s'il s'avère qu'elles concentrent leurs choix sur un type d'arbre en particulier et que cette ressource soit limitée spatialement et temporellement dans les peuplements forestiers aménagés. Ces impacts potentiels doivent être documentés dans la province du Québec, où la sylviculture est réalisée à grande échelle (Bureau du forestier en chef 2010) et où les chauves-souris n'ont reçu qu'une attention mineure, autant du point de vue des stratégies de conservation que de la recherche fondamentale en biologie (Tremblay & Jutras 2010). Caractériser les besoins en arbres gîtes des chauves-souris permettra certainement de mieux les intégrer aux stratégies de conservation déjà en vigueur. Peu de travaux de recherche sur l'écologie diurne des chauves-souris ont été menés en forêt boréale et aucune étude de ce type n'a encore été entreprise au Québec (Tremblay & Jutras 2010).

Objectifs et structure de la thèse

Le but de cette recherche était de générer les connaissances de base permettant de mieux appréhender l'utilisation estivale des arbres gîtes par les chauves-souris en forêt boréale aménagée. J'ai concentré mes efforts sur les espèces cavicoles qui semblent, selon la littérature, plus sensibles aux aménagements sylvicoles. Mon objectif principal était de déterminer les variables impliquées dans la sélection des arbres gîtes par les chauves-souris cavicoles. Mon objectif secondaire était de déterminer si les arbres gîtes possédant les caractéristiques recherchées par les chauves-souris cavicoles pouvaient être limités spatialement en forêt boréale aménagée.

Pour atteindre ces objectifs j'ai développé trois chapitres, chaque chapitre permettant de répondre à un objectif spécifique. L'objectif du premier chapitre était de déterminer les principales variables impliquées dans la sélection des arbres gîtes par les chauves-souris cavicoles en Amérique du Nord. L'objectif du second chapitre était d'identifier les variables impliquées dans la sélection des arbres gîtes par les chauves-souris du genre *Myotis* en forêt boréale aménagée. L'objectif du troisième chapitre était d'évaluer, grâce aux résultats des deux chapitres précédents, la répartition spatiale et la proportion des habitats diurnes potentiels pour chaque espèce du genre *Myotis* à travers la partie méridionale du massif des Laurentides.

Dans le premier chapitre, j'ai testé l'hypothèse que les résultats de sélection des variables reportées dans la littérature étaient suffisamment marqués (*i.e.*, taille d'effet importante) et consistants d'une étude à l'autre (*i.e.*, peu hétérogènes) pour rejeter l'hypothèse nulle (*i.e.*, pas de différence d'effet). J'ai également vérifié si la sélection pour le diamètre des arbres pouvait être influencée par l'ajout de variables modératrices en lien avec l'hypothèse du microclimat. J'ai testé l'hypothèse principale que les différences de sélection des chauves-souris cavicoles pour le diamètre des arbres gîtes dépendaient de la température moyenne estivale des régions considérées. D'autres hypothèses alternatives à la température ont été proposées et certaines conditions d'application des modèles ont été vérifiées, incluant l'autocorrélation spatiale des métadonnées. Pour tester ces hypothèses, j'ai réalisé neuf méta-analyses portant sur 34 études réalisées à travers l'Amérique du Nord. J'ai sélectionné uniquement les études qui comparent des arbres aléatoires aux arbres

sélectionnés par les chauves-souris, afin de calculer la taille et la direction des effets. J'ai mesuré le niveau d'hétérogénéité (*i.e.*, inconsistance des résultats entre études) et regardé les tendances qui s'en dégageaient à l'aide de graphiques de l'Abbé. J'ai également ajouté des variables modératrices telles que la température moyenne estivale, le type d'habitat, l'altitude, le sexe et l'espèce, pour en vérifier l'influence sur le patron de sélection du diamètre des arbres. J'ai testé l'influence de ces variables candidates à l'aide de modèles de méta-régression et j'ai vérifié que les résidus du meilleur modèle explicatif n'étaient pas auto-corrélos spatialement.

Dans le second chapitre, j'ai testé plusieurs hypothèses alternatives pouvant expliquer la sélection des arbres gîtes des chauves-souris du genre *Myotis* dans la sapinière à bouleau blanc de l'Est du Québec. J'ai testé l'hypothèse générale que 1) les chauves-souris sélectionnent des arbres dans lesquels elles peuvent nicher et des peuplements dans lesquels elles trouvent plusieurs arbres gîtes disponibles. J'ai aussi testé l'hypothèse que 2) les arbres sélectionnés bénéficient d'une meilleure isolation et l'hypothèse alternative que 3) ces arbres sont plus accessibles, sans toutefois bénéficier d'une meilleure isolation. J'ai également testé l'hypothèse que la sélection dépend 4) à la fois de la disponibilité en arbres gîtes et de l'avantage thermique qu'ils procurent ou 5) de leur disponibilité et de leur accessibilité. J'ai réalisé des suivis télémétriques à la Forêt Montmorency afin de retrouver les arbres gîtes utilisés par la petite chauve-souris brune et la chauve-souris nordique durant la journée. J'ai comparé ces arbres gîtes à des points aléatoires pour déterminer les patrons de sélection. J'ai caractérisé les variables des arbres gîtes et des points aléatoires à partir de relevés-terrain. J'ai complété ces relevés avec des données issues des cartes écoforestières de la région et des relevés LiDAR (Light Detection and Ranging). J'ai également profité des captures d'individus pour décrire la diète des chauves-souris du genre *Myotis* à l'aide d'outils moléculaires. Les résultats de cette analyse réalisée par la docteure Elizabeth Clare sont présentés dans l'annexe générale (Annexe 4).

Dans le troisième chapitre, j'ai utilisé les résultats des deux chapitres précédents pour évaluer la répartition et la proportion d'habitats diurnes potentiels à travers la partie méridionale du massif des Laurentides. J'ai testé l'hypothèse qu'à cette échelle spatiale, la petite chauve-souris brune et la chauve-souris nordique utilisent des habitats diurnes potentiels différents. J'ai également testé l'hypothèse que ces habitats potentiels étaient

limités spatialement pour les deux espèces du genre *Myotis*. J'ai utilisé les données des placettes échantillons permanentes et des cartes écoforestières de la zone d'étude pour générer les cartes raster correspondantes à trois variables, soit: une estimation du diamètre moyen et de la hauteur des essences dominantes, ainsi qu'une estimation du nombre de chicots. J'ai intégré dans mes modèles les cartes raster de deux variables additionnelles, soit: la distance Euclidienne aux points d'eau $\geq 20\text{ m}^2$ et l'élévation du terrain. J'ai utilisé un algorithme de classification par Random Forest pour générer mes cartes d'habitats diurnes potentiels des espèces du genre *Myotis*.

Tableaux

Tableau 1. Synthèse des éléments de l'écologie et des statuts légaux des huit espèces de chauves-souris recensées au Québec.

Nom commun	Nom scientifique	Cavicole	Foliage	Bâti	Migratrice	Hibernante	Statut Provincial*	Statut Fédéral**
Petite chauve-souris brune	<i>Myotis lucifugus</i>	X		X		X		X
Chauve-souris nordique	<i>Myotis septentrionalis</i>	X				X		X
Chauve-souris pygmée	<i>Myotis leibii</i>	X				X	X	
Pipistrelle de l'Est	<i>Perimyotis subflavus</i>	X	X	X		X		X
Grande chauve-souris brune	<i>Eptesicus fuscus</i>	X		X		X		
Chauve-souris argentée	<i>Lasionycteris noctivagans</i>	X			X		X	
Chauve-souris rousse	<i>Lasiurus borealis</i>		X		X		X	
Chauve-souris cendrée	<i>Lasiurus cinereus</i>		X		X		X	

* Ministère des Forêts, de la Faune et des Parcs (2014). *Liste des espèces de la faune susceptibles d'être désignées menacées ou vulnérables au Québec*, [En ligne]. <http://www3.mffp.gouv.qc.ca/faune/especes/menacees/liste.asp> (Page consultée le 14 mars 2015)

** Gouvernement du Canada (2014). Registre public des espèces en péril. *Annexe 1 (paragraphes 2(1), 42(2) et 68(2)) liste des espèces en péril.*, [En ligne]. http://www.registrelep-sararegistry.gc.ca/species/schedules_f.cfm?id=1 (Page consultée le 14 mars 2015)

Tableau 2. Liste non exhaustive des études faisant état des domaines vitaux, des distances au site de capture, à l'arbre gîte le plus proche, au point d'eau le plus proche et à la distance maximale parcourue par les individus suivis par télémétrie durant l'alimentation. Les moyennes \pm écarts types sont données lorsque disponibles.

Auteurs (date)	Espèce ¹	n ²	Distance de capture (km)	Distance à l'eau (km)	Arbre gîte le plus proche (km)	Domaine vital ³ (ha)	Distance maximale (km)
Badin (2014)	MYSE	23				5,4 \pm 5,27	
Brigham (1991)	EPFU	163				180 \pm 70	4,4
Broders <i>et al.</i> (2006)	MYSE	17	1,0 \pm 0,69		0,46 \pm 0,33	46,2 \pm 44,4	
Broders <i>et al.</i> (2006)	MYLU	13	0,76 \pm 0,62		0,28 \pm 0,41	52,0 \pm 57,4	
Coleman <i>et al.</i> (2014)	MYLU	7				143 \pm 188	
Henderson et Broders (2008)	MYSE	17			0,23 \pm 0,16	6,1 \pm 5,8	1,1
Henry <i>et al.</i> (2002)	MYLU	28				17,6 \pm 9,1	
Henry <i>et al.</i> (2002)	MYLU	25				30,1 \pm 15	
Hutchinson et Lacki (1999)	LABO	10				295 \pm 264	5,5
Hutchinson et Lacki (1999)	LABO	9				450 \pm 714	7,4
Kniowski et Gehrt (2014)	MYSO	36				212 \pm 132	> 1,6
Menzel <i>et al.</i> (2001)	EPFU	3				290 \pm 113	5,0
Menzel <i>et al.</i> (2005)	MYSO	11				144,7 \pm 61	
Owen <i>et al.</i> (2003)	MYSE	9				65 \pm 15,6	
Sparks <i>et al.</i> (2005)	MYSO	11				335	3,0
Thomson (2013)	MYLE	20	1,4 \pm 0,50		0,72 \pm 0,46		8,5
Walters <i>et al.</i> (2007)	LABO	13				68 \pm 137	18
Randall <i>et al.</i> (2014)	MYLU	9	3,8 \pm 2,1			380 \pm 230	6,3
Arnett et Hayes (2009)	EPFU	29	1,87	0,97			
Arnett et Hayes (2009)	EPFU	29	1,63	1,58			
Badin (2014)	MYSE	23			0,22		2,65
Campbell, Hallett et O'Connell (1996)	LANO	15	3,5				
Cryan <i>et al.</i> (2001)	EPFU	3	1,1				
Cryan, Bogan et Yanega (2001)	MYSE	9	0,6				

Elmore, Miller et Vilella (2004)	LABO	9	0,18	
Henderson et Broders (2008)	MYSE	21		0,44
Hutchinson et Lacki (2000)	LABO	10	0,36 ± 0,34	
Johnson <i>et al.</i> (2011)	MYLE	5	0,42 ± 0,05	0,46 ± 0,17
Johnson <i>et al.</i> (2011)	MYLE	5	0,37 ± 0,02	0,23 ± 0,03
Jung, Thompson et Titman (2004)	MYSE	10	2,28	0,01
Lacki et Schwierjohann (2001)	MYSE	13	0,13	
O'Keefe <i>et al.</i> (2009)	LABO	8	0,26	
O'Keefe <i>et al.</i> (2009)	PESU	7	0,10	
Poissant, Broders et Quinn (2010)	PESU	32	0,12 ± 0,13	
Psyllakis et Brigham (2006)	MYSP	12	0,27	
Quinn et Broders (2007)	PESU	21	0,3 à 1,5	
Rabe <i>et al.</i> (1998)	MYSP	53	0,46	
Rabe <i>et al.</i> (1998)	MYSP	53	0,76	
McGuire <i>et al.</i> (2012)	LANO	14	3	0,7

¹ Espèces de chauves-souris. MYSP inclut plusieurs espèces du genre *Myotis*; MYSO = *M. sodalis* (chauve-souris de l'Indiana); MYLE = *M. leibii* (chauve-souris pygmée de l'Est); MYSE = *M. septentrionalis* (chauve-souris nordique); MYLU = *M. lucifugus* (petite chauve-souris brune); EPFU = *Eptesicus fuscus* (grande chauve-souris brune); LABO = *Lasiurus borealis* (chauve-souris rousse); PESU = *Perimyotis subflavus* (pipistrelle de l'Est); LANO = *Lasionycteris noctivagans* (chauve-souris argentée)

² *n* correspond ici au nombre d'individus suivis par télémétrie

³ Domaine vital moyen (± écart type) calculé par triangulation durant l'alimentation de l'individu suivi par télémétrie.

Figures

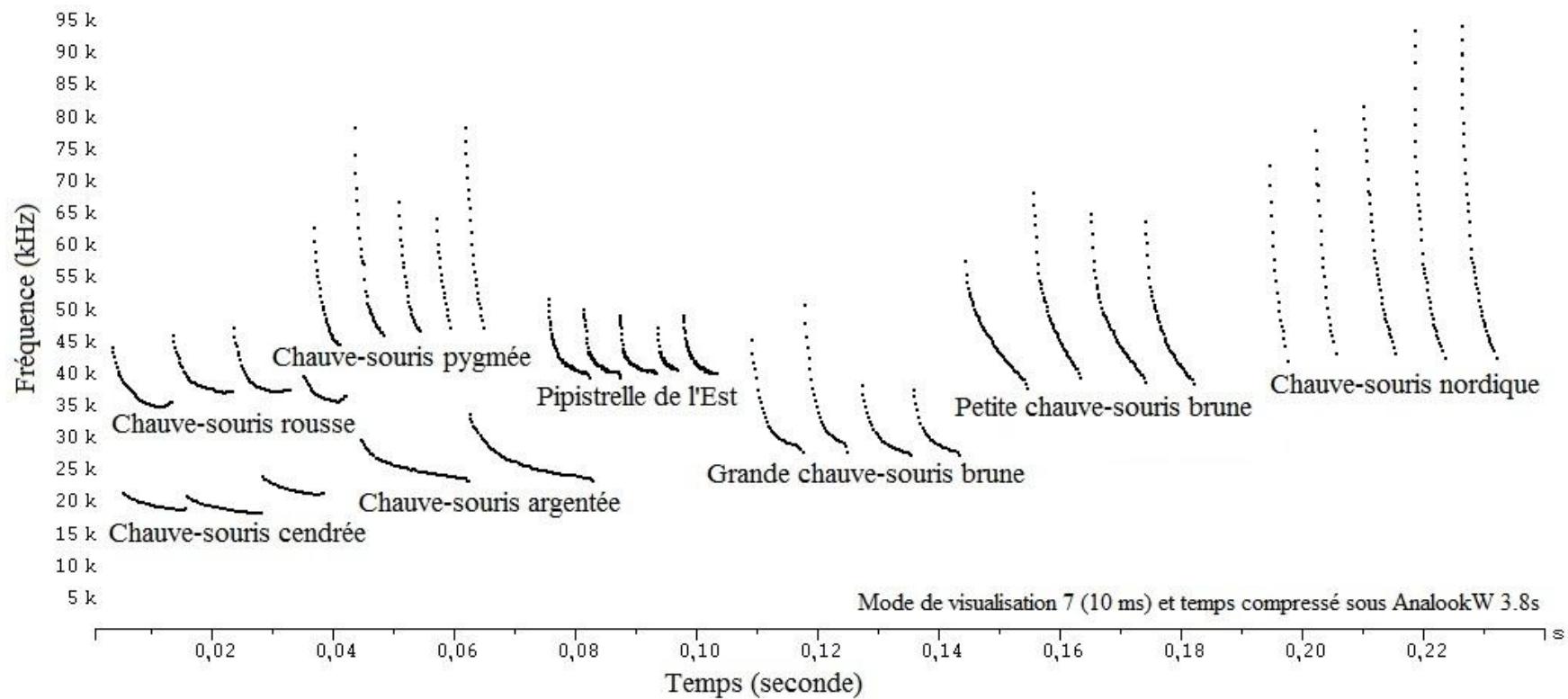


Figure 1. Signaux d'écholocation en phase de recherche des huit espèces de chauves-souris recensées au Québec (de gauche à droite): chauve-souris rousse (*Lasiurus borealis*), chauve-souris cendrée (*L. cinereus*), chauve-souris pygmée de l'Est (*Myotis leibii*), chauve-souris argentée (*Lasionycteris noctivagans*), pipistrelle de l'Est (*Perimyotis subflavus*), grande chauve-souris brune (*Eptesicus fuscus*), petite chauve-souris brune (*M. lucifugus*) et chauve-souris nordique (*M. septentrionalis*). Les chauves-souris modulent la bande de fréquences, l'intervalle de temps et la durée de leurs signaux en réponse à de nombreux facteurs (e.g., en phase d'approche, lors d'un cri d'alimentation ou de cris sociaux, en présence de conspécifiques, en sortie de gîte ou en cas de stress). Les signaux illustrés ci-dessus sont représentatifs des espèces susmentionnées, lorsqu'elles sont en phase de recherche de nourriture. Il s'agit ici d'observations comportementales enclines à énormément de plasticité.

CHAPITRE 1 – TREE SIZE AND TEMPERATURE INFLUENCE ROOST SELECTION BY BATS:
EVIDENCES FROM A META-ANALYSIS

François-Henri Fabianek, Centre d'Étude de la Forêt (CEF), and Faculté de Foresterie, de Géographie et de Géomatique, Université Laval, 2405, rue de la Terrasse, Québec, Québec G1V 0A6, Canada

Marie Anouk Simard, Ministère des Forêts, de la Faune et des Parcs (MFFP), 880, chemin Sainte Foy, Québec, Québec G1S 4X4, Canada

Centre de la Sciences de la Biodiversité du Québec (CSBQ), and Faculté de Foresterie, de Géographie et de Géomatique, Université Laval, 2405, rue de la Terrasse, Québec, Québec G1V 0A6, Canada

André Desrochers, CEF and Faculté de Foresterie, de Géographie et de Géomatique, Université Laval, 2405, rue de la Terrasse, Québec, Québec G1V 0A6, Canada

Ce chapitre est le fruit du travail de François-Henri Fabianek. Marie Anouk Simard et André Desrochers ont contribué à l'élaboration du design expérimental et à la rédaction de ce chapitre. Cet article a été soumis à la revue PLoS ONE

Résumé

Le diamètre, la hauteur des arbres et la fermeture de la canopée ont été décrits comme d'importantes variables pour la sélection des arbres gîtes des chauves-souris cavicoles. Cependant, il y a une variation substantielle de la taille d'effet de ces variables entre les études réalisées en Amérique du Nord. Nous avons déterminé la taille de l'effet et quantifié l'hétérogénéité entre-études des variables les plus couramment retrouvées dans la littérature. Nous avons également examiné si l'hétérogénéité pour le diamètre des arbres pouvait être expliquée par des variables modératrices telles que le sexe, l'espèce de chauve-souris, ainsi que des gradients géographiques et environnementaux. Nous avons réalisé neuf méta-analyses incluant 34 études (1988 - 2015) qui comparaient des arbres aléatoires aux arbres sélectionnés par les chauves-souris cavicoles. Nous avons déterminé le biais de publication potentiel avec des graphiques funnel et des tests d'asymétrie. Nous avons calculé les indices τ^2 et I^2 de Higgins pour quantifier l'hétérogénéité entre-études. Nous avons comparé 17 modèles de l'effet du diamètre des arbres en fonction de variables modératrices catégoriques et quantitatives. Nous avons confirmé que le diamètre de l'arbre, la hauteur de l'arbre, la densité de chicots, l'élévation de l'arbre et la fermeture de la canopée étaient des variables importantes pour la sélection des arbres gîtes des chauves-souris cavicoles. L'amplitude et la direction des effets entre les études variaient de manière importante concernant la distance à l'eau, la densité d'arbres, la pente et l'écorce restante sur les troncs. Nous n'avons pas détecté de biais de publication ni d'autocorrélation spatiale des métadonnées. Nous n'avons pas détecté un effet significatif du type d'habitat, de l'altitude et des espèces de chauves-souris sur la taille d'effet du diamètre des arbres. En revanche, le sexe, les températures moyennes estivales et la latitude expliquaient davantage d'hétérogénéité pour cette variable. Les chauves-souris cavicoles semblent plus sélectives envers les arbres de gros diamètres lorsque les températures moyennes estivales sont basses. Dans les régions nordiques, les arbres de gros diamètres doivent fournir une isolation thermique permettant d'aider les femelles reproductives à réduire le coût relié à la thermorégulation et favoriser la croissance des juvéniles. De nombreuses études ont évoqué la température comme facteur causal pour expliquer la sélection des arbres gîtes par les chauves-souris. Cette variable est en revanche rarement mesurée et devrait être incluse dans de futures recherches.

Abstract

Tree diameter, tree height and canopy closure have been described as important variables of roost selection by cavity-roosting bats. However, there is substantial variation in these variable effect sizes among studies in North America. We assessed the effect size and quantified between-studies heterogeneity of the most common variables in the available literature. We also examined if heterogeneity for tree diameter could be explained by moderator variables such as bat species, sex, as well as geographical and environmental gradients. We conducted nine meta-analyses including 34 studies (1988 - 2015) that compared random trees to selected trees by cavity-roosting bats. We assessed potential publication bias with funnel plots and asymmetry tests. We computed τ^2 and Higgins I^2 indices to quantify between-studies heterogeneity. We compared 11 candidate meta-regression models of the tree diameter effect size as a function of categorical and quantitative moderator variables. We confirmed that tree diameter, tree height, snag density, tree elevation, and canopy closure were significant variables of roost selection by cavity-roosting bats. Size and direction of effects varied greatly among studies with respect to distance to water, tree density, slope, and bark remaining on trunks. We did not detect significant publication bias or spatial autocorrelation in our metadata. We did not detect a significant effect of habitat type, altitude and bat species on tree diameter effect size. However, sex, mean summer temperature and latitude further explained heterogeneity for this variable. Cavity-roosting bats seem more selective towards large trees when the mean summer temperature is lower (with increasing latitude). In Northern regions, large trees should provide good thermal inertia to help reproductive females reducing thermoregulation cost and favoring juvenile growth. Several studies invoked temperature as a causal factor to explain roost selection by bats. This variable is however rarely measured and should be included in future research.

Introduction

Descriptions of roosts that are used by insectivorous bats in North American forests were mostly anecdotal prior to the mid-1990s. Technical developments in telemetry have been instrumental for our current understanding of habitat-species interactions with small mammals, such as bats (Kalcounis-Ruepell, Psyllakis & Brigham 2005). The large number of published radio-telemetry studies has led to three systematic reviews (Kunz & Lumsden 2003; Miller *et al.* 2003; Barclay & Kurta 2007) and three quantitative syntheses (Lacki & Baker 2003; Kalcounis-Ruepell, Psyllakis & Brigham 2005; Lacki, Cox & Dickinson 2009a) that summarize habitat use by bats in both unmanaged and managed forests. Miller, Arnett and Lacki (2003) observed that most studies had low sample sizes and suffered from pseudo-replication, but they did not account for these caveats quantitatively. Lacki and Baker (2003), and Kalcounis-Ruepell, Psyllakis and Brigham (2005) confirmed that tree diameter, tree height and canopy closure were important variables to explain roost selection by bats, despite notable differences in size and direction of effects among studies. In a more recent meta-analysis of two bat species, Lacki, Cox and Dickinson (2009a) found that the roosting requirements of the Indiana bat (*Myotis sodalis*) and the northern long-eared bat (*M. septentrionalis*) overlapped, except for tree diameter and the variability of roosts that were used. The authors concluded that the northern long-eared bat showed a greater plasticity than the Indiana bat in the choice of roosting sites.

None of these meta-analyses (*i.e.*, Lacki & Baker 2003; Kalcounis-Ruepell, Psyllakis & Brigham 2005; Lacki, Cox & Dickinson 2009a) have tried to explain differences in effect sizes and in direction of effects among studies, which is also referred to as between-studies heterogeneity (Borenstein *et al.* 2009). Another important aspect of quantitative syntheses that has not been previously exploited in this particular area of research is the inclusion of moderator variables that may help explain this heterogeneity (Borenstein *et al.* 2010), and which could reveal large-scale patterns in roost selection. Moderator variables are included in meta-analyses using meta-regression approaches to test if residual heterogeneity may be associated with differences in study methods (Borenstein *et al.* 2009), or in the present case, differences that could be related to sex (Broders & Forbes 2004), species (Lacki, Cox & Dickinson 2009a) or environmental factors (Johnson & Lacki 2014).

A decade of research has passed since the last meta-analysis on North American bats was conducted (Kalcounis-Rueppell, Psyllakis & Brigham 2005) and the number of studies on roost selection by bats has doubled (Appendix 1. Table 1). There are now enough studies to look for patterns using meta-regression approaches and test large-scale hypotheses based on previous knowledge on bat roosting ecology during the summer. Based on results from previous meta-analyses (Lacki & Baker 2003; Kalcounis-Rueppell, Psyllakis & Brigham 2005) and systematic reviews (Kunz & Lumsden 2003; Barclay & Kurta 2007), we identified three major hypotheses tested in the literature on cavity-roosting bats: roost availability, microclimate (*e.g.*, thermal inertia of roosts and level of solar radiation), and distance to resources (*e.g.*, water and insect availability).

Cavity-roosting bats rely upon both living and standing dead trees (*i.e.*, snags) in intermediate level of decay (Parsons, Lewis & Psyllakis 2003; Fabianek *et al.* 2015) for roosting (Barclay & Kurta 2007; Kunz & Lumsden 2007). They have been reported roosting under exfoliating bark, inside trunk crevices, and within the cavities of both living and dead trees during the summer (Barclay & Kurta 2007; Arnett & Hayes 2009; Lacki, Cox & Dickinson 2009a; Fabianek *et al.* 2015). The occurrence of several snags in a given stand is considered available roosts to bats (Johnson *et al.* 2010; Lacki *et al.* 2010). Bats are faithful to their roosting sites (Lewis 1995; Willis *et al.* 2003; Veilleux & Veilleux 2004) and switch regularly from primary roosts (*i.e.*, used more frequently) to alternate roosts (Willis & Brigham 2004; Lacki, Hayes & Kurta 2007). They therefore rely upon networks of clustered roost trees (Johnson, Ford & Edwards 2012) that share similar features, such as a large diameter and an intermediate stage of decay (Menzel *et al.* 2002b; Fabianek *et al.* 2015), perhaps to minimize predation risk, or to reduce commuting costs. Furthermore, snags are an ephemeral resource (Lee 1998; Angers *et al.* 2010; Lacki, Baker & Johnson 2012), which may explain - in addition to the aforementioned reasons - why bats favor a high density of potential roost trees (*i.e.*, snags) near roosts (Weller & Zabel 2001; Menzel *et al.* 2002b; Baker & Lacki 2006; Arnett & Hayes 2009; Fabianek *et al.* 2015).

Sexual differences in the choice of roots by bats are often reported (Hamilton & Barclay 1994; Broders & Forbes 2004; Perry & Thill 2007a; Hein, Castleberry & Miller 2008), with reproductive females (*i.e.*, pregnant and lactating females) selecting for trees with larger diameters (Broders & Forbes 2004; Park & Broders 2012) compared to males

and non-reproductive females. Large diameter trees seem to offer greater thermal inertia compared to trees with smaller diameters (Sedgeley 2001; Wiebe 2001; Park & Broders 2012). The thermoregulatory advantage of stable temperatures (Kerth *et al.* 2001; Ruczyński 2006; Lacki, Johnson & Baker 2013) is commonly accepted as a major driver of roost selection by cavity- and bark-roosting bats, especially in the case of reproductive females (Kunz & Lumsden 2003; Barclay & Kurta 2007; Boyles 2007; Johnson & Lacki 2014).

Like males and non-reproductive females, reproductive females may also use torpor (*i.e.*, state of reduced body temperature and metabolic rate) to reduce energy expenditures (Stawski, Willis & Geiser 2014), but this comes at the cost of reduced milk production (Wilde *et al.* 1999), and delayed fetal development and juvenile growth (Kunz & Lumsden 2003; Barclay & Kurta 2007). To counteract these costs, lactating females may enter torpor for shorter bouts (Dzial & Brigham 2013; Johnson & Lacki 2014) or adopt other behavioral strategies, such as social thermoregulation (Willis & Brigham 2007). Sticking together to stay warm requires large tree cavities (Willis *et al.* 2006; Randall, Jung & Barclay 2014), which underscores a central role that tree diameter plays in roost selection. Boland *et al.* (2009) suggested that in the northern range of Keen's myotis (*Myotis keenii*) distribution, reproductive females should select for trees with larger diameters, thus, providing warmer temperatures than smaller trees, due to a relatively cold and short summer in Alaska compared to southern regions. This large-scale hypothesis could be evaluated using a meta-analysis coupled with a meta-regression approach.

Like many birds and other small mammals, bats probably use passive rewarming to reduce energy expenditure during arousal (Geiser *et al.* 2004), which requires an external heat source in afternoon (Lacki, Johnson & Baker 2013). Several studies (Vonhof & Barclay 1996; Brigham *et al.* 1997b; Ormsbee & McComb 1998; Menzel *et al.* 2002b; Baker & Lacki 2006) proposed that treetops above the canopy and tall trees that are located in canopy openings or within stands of low tree density are more accessible to bats and also benefit from greater heat transfer by solar radiation (Clement & Castleberry 2013). Slope, slope aspect and elevation have also been associated to solar radiation (Lacki & Schwierjohann 2001; Lacki, Cox & Dickinson 2009a; Fleming *et al.* 2013). As has been suggested by Lacki, Cox and Dickinson (2009a), bats might favour trees that were located

in lower elevations to benefit from warmer microclimates relative to those located at higher elevations. Preference in elevation could also be related to variation in tree species composition (Broders 2003; Carter 2003; Fleming *et al.* 2013). Lacki, Baker and Johnson (2010) suggested that stands at lower elevations provide better roosting features to bats (*i.e.*, taller canopies, higher snag densities) than upper stands. Conversely, Lacki and Schwierjohann (2001) found that northern long-eared bats (*Myotis septentrionalis*) roosted mostly in stands located at higher elevations in Kentucky. In Missouri, Callahan *et al.* (1997) found that the Indiana bat roosted in both riparian and upland areas. Based on observation from Britzke *et al.* (2003) and Britzke *et al.* (2006), Lacki, Cox and Dickinson (2009a) suggested that Indiana bats (*Myotis sodalis*) avoided roosting in upland habitats in cooler climate and shorter growing season, near the northern end of the species distribution, with the reverse supposedly observed in southern populations (*sensu* Lacki, Cox and Dickinson 2009a).

Proximity (*i.e.*, < 10 km) to ponds and riparian habitat also appears to drive roost selection by bats (Grindal 1996; Krusic *et al.* 1996; Kalcounis-Rueppell, Psyllakis & Brigham 2005; Quinn & Broders 2007). Riparian habitats and ponds provide good foraging conditions for bats (Zahn & Maier 1997; Warren *et al.* 2000; Syme, Fenton & Zigouris 2001). Habitat complexity (*i.e.*, level of vegetation clutter) and acoustic interferences are reduced over calm water bodies (*i.e.*, ponds), increasing both prey detectability and capture success for bats (Mackey & Barclay 1989; Siemers *et al.* 2001). Moreover, the abundance and diversity of preys are generally greater over and near ponds (Holloway & Barclay 2000; Whitaker, Carroll & Montevercchi 2000; Fukui *et al.* 2006). Bats, especially lactating females (Kurta *et al.* 1989), also needs water to rehydrate at dusk after roosting (Kurta *et al.* 1989; Adams & Hayes 2008; Seibold *et al.* 2013).

Our first aim was to test whether selection by cavity-roosting bats for the most common variables in the literature were consistent enough among studies to reject the null hypothesis that trees selected by bats are not significantly different in their characteristics from randomly selected trees. In other words, we predicted that the size (or amplitude) of effects should be greater enough from zero and that the direction of effects should be consistent enough among studies (*i.e.*, homogeneous) to reject the null hypothesis (*i.e.*, no

significant difference in characteristics from random trees) for each variable we intended to test. After having identified the most consistent variables of roost selection by cavity-roosting bats, our second aim was to explain heterogeneity for the tree diameter size effect, according to the microclimate hypothesis (*sensu* Boyles 2007), by incorporating moderator variables such as habitat type, bat species, mean summer temperature, and elevation into a set of alternative meta-regression models. We predicted that reproductive females should select larger tree diameters (relative to random trees) in northern regions and in higher altitudes, because of lower mean summer temperatures, compared to southern regions and lower altitudes. We predicted that reproductive females (Broders & Forbes 2004; Park & Broders 2012) and larger species of bats (Arnett & Hayes 2009) should require trees with larger diameter, compared to non-reproductive females and males and to smaller species of bats. We also predicted that larger tree diameters should be found in unmanaged (*i.e.*, national parks) and riparian areas, compared to managed areas (*i.e.*, where logging activity still occur).

Material and methods

Selection of studies

We searched for published bat-roost selection studies available online in Google Scholar and the Web of Science. Those included journal articles, government reports, Ph.D. and M.Sc. theses, book chapters, and symposia. We included most of the studies that were presented in Miller, Arnett and Lacki (2003), Barclay and Kurta (2007), Kalcounis-Rueppell, Psyllakis and Brigham (2005), Lacki and Baker (2003), and Lacki, Cox and Dickinson (2009a). We retained only studies that reported comparisons between random and selected trees (*i.e.*, case / control design). Because of distinct roosting ecologies (Kunz & Lumsden 2007; Lacki, Hayes & Kurta 2007), we did not include studies on foliage-roosting bats, but retained those that dealt with bark- and cavity-roosting bats.

Dataset extraction and preparation

Studies that compared different treatments or sites, or differences in roost selection among bat species, and between sexes, had more than one dataset. We regarded each dataset as a sample unit for this meta-analysis (expressed as *n* unless otherwise mentioned).

We examined 20 candidate variables, but retained only nine for which we found a minimum of 10 studies (*i.e.*, 19 datasets): tree diameter (cm), tree height (m), bark remaining (%), distance to water (m), canopy closure (%), tree density (stems / 0.1 ha), snag density (stems / 0.1 ha), slope (%), and elevation (m). We extracted means, standard errors, standard deviations and sample sizes for each dataset. We converted standard errors to standard deviations by multiplying the standard error of the mean by the square root of the sample size, which is the number of trees. We converted all measurements of size, density and distance to the same units. For each of the nine variables, we calculated Hedges' g Standardized Mean Difference (SMD) as an estimate of the effect size between trees that had been selected by bats (*i.e.*, experimental group) and random trees (*i.e.*, control group) as suggested by Borenstein *et al.* (2010). We excluded studies with an effect size greater than 4 times the mean group standard deviation to meet criteria of effect size normality and variance homogeneity (Borenstein *et al.* 2010). We computed prediction intervals, fixed-effects and random-effects models (*meta* package, R Development Core Team 2015) for comparison purposes (Appendix 1. Tables 1 to 9), but used only random-effects models in our meta-analyses. Random-effects models assume that between-studies heterogeneity may not only depend upon sampling variance but also random population effect sizes (Borenstein *et al.* 2010), which is the case in our meta-analyses involving numerous bat species, together with potential variation between sexes and among habitat types.

Publication bias and heterogeneity

Testing for publication bias supposes that there is a tendency for publishing studies with significant findings. If such bias is present, studies should be unbalanced towards positive results with only a few published studies supporting the null hypothesis. Publication bias is considered null when studies are well balanced (*e.g.*, when about the same number of studies has reported significant findings and supported the null hypothesis). We used funnel plots (*i.e.*, effect size plotted against its standard error) to assess potential publication bias (Anzures-Cabrera & Higgins 2010) for each of the nine variables. We tested for funnel plot asymmetry using the conventional weighted linear regression method (Egger *et al.* 1997), which is provided in the package *meta* (Schwarzer 2014).

We used l'Abbé plots to display meta-data visually and investigate potential patterns of heterogeneity. In l'Abbé plots, the experimental group is plotted against the control group and the resulting regression line with 95 % CI is compared visually to the equality line (1:1), where the mean difference is null (Song 1999). We used the maximum likelihood approach (package *meta*, R Development Core Team 2015) to estimate heterogeneity (τ^2) in the population effect sizes. We further quantified heterogeneity using Higgins' I^2 index (expressed as percentage; Higgins *et al.* 2003) and used the classification given by the authors to interpret the severity of heterogeneity (see Higgins *et al.* 2003 for further details).

Moderator variables and meta-regression analyses

We geo-located study sampling sites by using GPS coordinates or from locations that were mentioned in the reviewed manuscripts. We integrated geo-locations into ArcGIS (version 10.1, Environmental Systems Research Institute, Redlands, CA, USA), around which we drew 1 km-radius buffer zones to compensate for imprecision. We integrated raster maps of mean summer temperature and elevation that were provided by the North American Environmental Atlas (INEGI, NR-Can, USGS, 2010) into ArcGIS. We averaged the raster pixel values that overlapped the 1 km-radius buffer zones for each of the aforementioned raster maps. We extracted additional moderator variables from the reviewed manuscripts, such as sex (male, female, and combined), habitat type (managed areas, protected areas such as national parks and riparian areas), and bat species. Given the limited number of datasets ($n = 63$), we grouped bat species with fewer than 5 datasets by their genus, resulting in only six classes of bat species. To interpret our meta-regression results properly, we also verified *a priori* that random-tree diameter was not correlated with latitude ($R^2 = 0.00$; $P < 0.9$). We verified that mean summer temperature was negatively correlated to elevation ($R^2 = 0.21$; $P < 0.001$) and negatively correlated with latitude ($R^2 = 0.77$; $P < 0.001$). We decided to exclude latitude from our set of moderator variables since it was strongly correlated (*i.e.*, Pearson $r \geq 0.7$; Dormann *et al.* 2013) to mean summer temperature.

Due to the apparent spatial proximity of several studies (Figure 2), we verified that our SMD estimates and our best meta-regression model residuals were not dependent on

the effect of spatial scale (*i.e.*, autocorrelated). We predicted that studies that are close to each other should not share similar SMD (and model residual) values and conversely for distant studies. In other words, we tested for the null hypothesis of spatial randomness, for which SMD (and model residual) values should not depend on values at neighboring locations (Dormann *et al.* 2007). We choose $K = 4$ nearest studies as a distance-based neighbors among studies. Once our neighborhood of studies was created, we assigned spatial weights for each pair of neighbors, which was the inverse Euclidian distance among studies (Dormann *et al.* 2007). We performed global Moran's I statistical test of spatial autocorrelation under randomisation on the resulting Inverse Distance Weight (IDW) matrices (Dormann *et al.* 2007). We also used Moran's I test for residual spatial autocorrelation provided in the package *spdep* (Bivand & Piras 2015).

We compared 17 candidate meta-regression models (package *metafor*, R Development Core Team 2015) to examine whether the heterogeneity for the tree diameter effect size was explained by the above mentioned moderator variables (Table 3). We constructed five subsets of candidate meta-regression models. The first set combined habitat type (*i.e.*, management level), microclimate (*i.e.*, mean summer temperature and elevation) and bat related (*i.e.*, bat species and sex) moderator variables. The second set combined both microclimate and bat related moderator variables. The third, fourth and fifth sets included respectively microclimate, bat related and habitat type moderator variables, respectively. We ranked the candidate set of models using the second-order Akaike's information criterion for small samples (AICc). We calculated Δ AICc values (Δi) and Akaike weights (ωi) to determine the importance of the candidate set of models relative to the best explanatory model ($\Delta i = 0$). Models were considered equivalent when they had a Δ AICc ≤ 2 (Burnham & Anderson 2002). In addition to Δ AICc, we used Higgins' I^2 index (%) of residual heterogeneity (*i.e.*, unaccounted variability) and pseudo- R^2 index (%) of heterogeneity accounted for by each candidate meta-regression model. Both indices were provided by the package *metafor* (Viechtbauer 2010).

Results

Selected studies

Of the 121 potential studies that we identified for roost selection by bats across North America, 74 studies compared roost trees that were selected by bats to random trees, and 40 of them studied rock-, lichen- or foliage-roosting bats (Figure 3). From this screening, we retained 34 studies on bark- and cavity-roosting bats for our meta-analysis, which corresponded to 66 datasets (Figure 3). We found 49 datasets in published manuscripts, 14 in unpublished Ph.D. theses, 2 in research symposia, and 1 in a governmental report. Datasets ranged from Prince of Wales Island in Alaska (northwest; Figure 1) to Baker County, on the Coastal Plain of Georgia (southeast; Figure 2). The datasets included 4 genera and 12 species of cavity-roosting bats: big brown bat (*Eptesicus fuscus*), silver-haired bat (*Lasionycteris noctivagans*), southeastern myotis (*M. austroriparius*), California bat (*M. californicus*), western long-eared bat (*M. evotis*), Keen's myotis, little brown bat (*M. lucifugus*), northern long-eared bat, Indiana bat, fringed myotis (*M. thysanodes*), long-legged myotis (*M. volans*), and evening bat (*Nycticeius humeralis*). Most studies were performed on females (62.1%, $n = 41$), while 18.2% ($n = 13$) were conducted on males, and 19.7% ($n = 12$) combined both sexes. Bats using both snags and living trees as roosts represented 47% ($n = 31$) of the datasets, while 47% ($n = 31$) reported only snags, and 6% ($n = 4$) reported only living trees. Studies were mostly performed in managed areas (50%, $n = 33$), followed by 30.4% ($n = 20$) in protected areas, and 13.6% ($n = 9$) in riparian areas; 6% of the remaining datasets ($n = 4$) considered other treatment effects, such as fire (3%, $n = 2$) or vegetation types (3%, $n = 2$).

Standardized mean differences

We found significant SMD for five of the nine variables (Table 2). Roost trees had significantly larger DBH ($n = 66$, SMD = 0.71, $P < 0.0001$) and were significantly taller ($n = 47$, SMD = 0.51, $P < 0.0001$) than random trees. Roost trees were mostly located in stands with a higher snag density ($n = 34$, SMD = 0.47, $P < 0.0001$), at a lower elevation ($n = 19$, SMD = -0.35, $P < 0.0001$), and with lower canopy closure ($n = 33$, SMD = -0.32, $P = 0.006$) compared to random stands. We found no significant difference between roost and random trees with respect to distance to water ($n = 22$, SMD = -0.16, $P = 0.05$), tree density

($n = 24$, SMD = 0.06, $P = 0.58$), slope ($n = 21$, SMD = 0.03, $P = 0.78$), and bark remaining on trunks ($n = 26$, SMD = 0.05, $P = 0.78$).

Publication bias and heterogeneity

Funnel plots were well balanced (Figure 4); thus, asymmetry tests did not reveal any significant publication bias (Table 2). Higgins' I^2 heterogeneity index indicated considerable levels of heterogeneity (*i.e.*, I^2 indices ranging from 50% to 100%) for each characteristic of roost selection by bats (Table 2; Figure 5).

Meta-regression models and spatial autocorrelation

SMD values and squared residuals of our best regression model (*i.e.*, tree diameter effect sizes vs. mean summer temperature) were not spatially autocorrelated. Moran's I test for spatial autocorrelation did not reject the null hypothesis of spatial randomness either for our SMD values (Moran I standard deviate = -0.29, $P = 0.62$) or for our best regression model residuals (Moran I standard deviate = -1.07, $P = 0.28$).

According to Δ AICc (Table 3), the two meta-regression models that best explained heterogeneity in tree diameter effect sizes, included (i) mean summer temperature (pseudo- $R^2 = 13.26\%$; AICc $\omega = 0.42$) and (ii) mean summer temperature + sex (pseudo- $R^2 = 17.40\%$; AICc $\omega = 0.19$) as moderator variables. Tree diameter effect sizes for female bats increased significantly with decreasing mean summer temperature and increasing latitude. However, elevation (pseudo- $R^2 = 1.94\%$; AICc $\omega = 0.02$), sex (pseudo- $R^2 = 2.58\%$; AICc $\omega = 0.02$) and habitat type (pseudo- $R^2 = 4.34\%$; AICc $\omega = 0$), alone had little effect on heterogeneity in tree diameter effect sizes. These single predictor models were ranked among the poorest AICc models (Table 3).

The model that explained the most heterogeneity in tree diameter effect sizes (pseudo- $R^2 = 29.19\%$) included mean summer temperature, elevation, bat species and sex as moderator variables. This model had a high Δ AICc (Δ AICc = 10; AICc $\omega = 0$), compared to the two best AICc models (*i.e.*, with Δ AICc = 0 and = 1.58), which included only mean summer temperature and sex as moderator variables.

Discussion

Meta-analyses and heterogeneity

This meta-analysis included a larger number of variables, and increased the scope to a wider range of bat species and forest habitats thorough North America than previous quantitative reviews (Lacki & Baker 2003; Kalcounis-Rueppell, Psyllakis & Brigham 2005; Lacki, Cox & Dickinson 2009a). Despite an overall high level of heterogeneity among studies, five variables showed strong general trends in roost selection by bats. Cavity-roosting bats selected larger and taller roosts compared to random trees. They also roosted in stands with a larger number of surrounding snags, at lower elevations, and with less canopy closure compared to random stands. These results are consistent with those found by Lacki and Baker (2003), and by Kalcounis-Rueppell, Psyllakis and Brigham (2005). Other variables, such as distance to water, slope, and bark remaining on trunks, did not significantly differ from random trees because of strong differences in size and direction of effects among studies. With respect to the distance to water, our results slightly differed from those of Kalcounis-Rueppell, Psyllakis and Brigham (2005), since we included a larger set of studies (Jung, Thompson & Titman 2004; Boland *et al.* 2009; Clement & Castleberry 2013) with a positive effect size (*i.e.*, random trees that were closer to water). Water is an important resource for bats (Kurta *et al.* 1989; Adams & Hayes 2008; Seibold *et al.* 2013), especially in arid regions (Adams & Hayes 2008; Seibold *et al.* 2013). It would be interesting to investigate if studies located in more arid areas show distance to water being shorter than studies where the availability of water to bats and precipitations are important.

Variables commonly related to solar radiation

We found considerable heterogeneity in slope effect sizes and it was difficult to identify a general trend from the literature, since this variable seems to be strongly related to the topographical context of the study. Unlike slope, we found a moderate level of heterogeneity for elevation, indicating greater consistency between results from different studies. Heterogeneity for this variable was the lowest compared to other variables that we tested. Studies are conducted at a specific elevation (*i.e.*, roosts and random trees are in the same elevational zone), and short distances between roosts and matching random trees are

taken in the field (Miller, Arnett & Lacki 2003), which likely minimize the effect size for this variable. Despite the fact that studies are conducted at a specific elevation, we revealed that elevational difference between selected and random trees is a consistant pattern among studies. Bats might select trees located at lower elevations to benefit from warmer microclimate and greater insect availability near roosts, relative to trees located at higher elevations. Several studies found a sexual segregation in bats with reproductive females less likely to occur in stands at higher elevation (Senior, Butlin & Altringham 2005). Russo (2002) and Arnold (2007) obtained similar results with *Myotis daubentonii* (Kuhl, 1819) and *M. septentrionalis*, respectively. Cryan, Bogan and Altenbach (2000) showed an inverse relationship between habitat elevation and the presence of reproductive females in South Dakota, presumably because of lower ambient temperature and lower insect availability at higher elevations (Grindal, Morissette & Brigham 1999).

Tree decay and bark remaining on snags

Most bat species that we included in meta-analyses seek shelter inside trunk cavities (Boland *et al.* 2009; Lacki, Cox & Dickinson 2009a) and under the exfoliating bark of snags with an intermediate stage of decay (Vonhof & Barclay 1996; Brigham *et al.* 1997b; Menzel *et al.* 2002b; Baker & Lacki 2006). Only 3 studies have reported the exclusive use of cavities within living trees (Parsons, Lewis & Psyllakis 2003; Clement & Castleberry 2013; Fleming *et al.* 2013) and two of them were associated to the southeastern myotis (*Myotis austroriparius*; Clement & Castleberry 2013; Fleming *et al.* 2013). Although this variable was the most heterogeneous, we found a clear preference for bats towards snags with approximately 70 % of bark remaining on trunks (Figure 4). An intermediate stage of decay seems to offer the best compromise between an appropriate tree height and enough bark remaining on the trunk to provide a roost (Parsons, Lewis & Psyllakis 2003; Fabianek *et al.* 2015). Another interesting aspect of snags is that they seem to offer less buffering capacity against external temperature variations, compared to living trees (Wiebe 2001; Paclík & Weidinger 2007). However, they provide more available cavities (Fan *et al.* 2003) compared to living trees. This suggests that the selection of roosts might be driven by a trade-off between the availability of potential roost trees in a given stand (Clement & Castleberry 2013), their related benefits in terms of warm microclimates, and their relatively short distances to feeding sites (Kurta 2001). More studies are clearly needed to

better understand the thermal capacity of trees and its implication to bat behaviour (Sedgeley 2001; Johnson & Lacki 2014).

Moderator variables and tree diameter effect size

Tree diameter was the strongest variable explaining roost selection by cavity-roosting bats, since positive effect sizes (*i.e.*, selected trees with a larger diameter than random trees) were a common finding in several studies (Baker & Lacki 2006; Arnett & Hayes 2009; Boland *et al.* 2009; Clement & Castleberry 2013). The main hypothesis invoked by these studies was that trees with a larger diameter offered better thermal inertia against external temperature variations (Sedgeley 2001; Wiebe 2001; Paclík & Weidinger 2007; Coombs *et al.* 2010), compared to trees with a smaller diameter. The importance of stable temperatures for reproductive female bats have been discussed by Barclay and Kurta (2007). Reproductive females, are thought to benefit from warm and stable microclimates that minimize thermoregulation costs and maximize their fitness (Kunz & Lumsden 2003; Barclay & Kurta 2007). However, these assumptions have rarely been tested empirically in North America (Johnson & Lacki 2014). Most studies that measured temperature variations in roosts of bats and other mammals have been conducted in Europe (Kerth, Weissmann & König 2001; Ruczyński 2006; Grüebler *et al.* 2013) and in New Zealand (Sedgeley 2003; Sedgeley & O'Donnell 2004). To our knowledge, only Park and Broders (2012), showed that reductions in temperature fluctuations within roosts that were used by lactating northern long-eared bats in Newfoundland. Lacki, Johnson and Baker (2013) also showed reductions in temperature fluctuations within roosts used by long-legged myotis (*Myotis volans*) and located beneath the exfoliating bark of trees, in Idaho and Oregon.

Surprisingly, elevation, bat species, and habitat types were not included in our best model explaining residual heterogeneity for tree diameter effect size. When sex was combined with mean summer temperature, they further explained residual heterogeneity. Otherwise, this variable performed poorly. Further tests for subgroup differences indicated that intra-studies heterogeneity for female bats was greater than inter-studies heterogeneity, when considering all groups (males, females and combined). The variability that was attributed to sex, although present (Broders & Forbes 2004; Park & Broders 2012), was masked by other moderator variables having a greater influence on tree diameter effect size.

It was interesting to note that the model which explained the most residual model heterogeneity included mean summer temperature, elevation, bat species, and sex as moderator variables. This model had a lower AICc ranking since it was less parsimonious (*i.e.*, $K = 11$ parameters to estimate) compared to the two best models (Arnold 2010; Burnham *et al.* 2011), including only mean summer temperature ($K = 3$) and mean summer temperature + sex ($K = 5$) as moderator variables.

Mean summer temperature and sex were the two best moderator variables explaining residual heterogeneity for tree diameter effect size. Moreover, mean summer temperature significantly decreased with latitude and significantly increased with elevation. In northern regions with lower mean summer temperatures, cavity-roosting bats were more selective towards large trees, compared to southern regions, which benefit from higher mean summer temperatures. Our study is the first to establish a link between the selective behavior of bats towards three diameters and mean temperature variation across a large spatial scale. The majority of the studies we included in our analyses were from the Pacific Northwest, the southeastern US, and southeastern Canada / northeastern US. Although the studies within these tree regions appeared clustered (Figure 1), the SMD estimates from these studies were not spatially dependent. In light of these results, the challenge of retaining trees with large diameters seems critical to ensuring the survival of bats, particularly in regions with low mean summer temperatures and short growing seasons (Boland *et al.* 2009; Fabianek *et al.* 2015).

Limitations and research perspective

We expected a high degree of heterogeneity because the studies that we included in meta-analyses were conducted in various habitats, had included numerous bat species, and attempted to answer to different questions. Despite the inclusion of moderating variables, most of the tree diameter heterogeneity remained unexplained. We are aware that we have used a relatively coarse measure of summer temperature that likely underscored regional differences as opposed to what the various species of bats were actually cueing in on within these regions. More accurate moderator variables could likely capture more residual heterogeneity. It is likely that the differences in results among studies were also influenced by measurement methods (Miller, Arnett & Lacki 2003). We agree with Miller, Arnett and

Lacki (2003) that random sites that are located in close proximity to selected roosts by bats might increase the lack of independence, and therefore, minimize the true effect size. We were not able to estimate this potential bias since the authors rarely mentioned distances between trees that were selected by bats and random trees. Including this information in future research should greatly improve the interpretation of the results.

Ambient temperature, exposure to solar radiation, and thermal properties of trees appeared to play a central role in roost selection by bats. These aspects of the roost microclimate hypothesis, as described by Boyles (2007), have been rarely investigated in North America and should be included in future research. Driven by a forest management perspective, the majority of studies have focused their research on tree and stand features (*e.g.*, tree diameter, tree height, density of trees and canopy closure) that provided only indirect links to microclimate. Studies that we reviewed also rarely mentioned stand age, although this variable may be correlated with the most important variables of roost selection, such as tree diameter and tree height (Leak 1985; Vanclay 2009), canopy closure (McCarthy 2001), tree density (Tyrrell & Crow 1994), snag density (Lee 1998; Moroni & Harris 2010), and the number of available cavities (Rudolph & Conner 1991). The lack of published studies and available reports in northern Canada, in the desert southwest and the Midwest-West prairies in the US, and Mexico has also limited our analyses to the southeastern US, the Pacific Northwest and the southeastern Canada / northeastern US regions. It would be interesting to include studies on roost selection by bats that were done in arid and tropical regions to challenge our hypothesis.

Acknowledgements

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Tables

Table 2. Summary of the random effects meta-analyses of roost selection by North American bats, with heterogeneity indices and publication biases for each variable. K = number of datasets and SMD = standardized mean difference; τ^2 and I^2 indices indicate the severity of between-studies heterogeneity; t -tests are for funnel-plot asymmetry, with associated degrees-of-freedom and P -values. All values are rounded upward to two decimal places.

Variable	K	SMD	95 % CI	Z	P	τ^2 *	I^2 (%)	95 % CI (%)	t	df	P
Tree diameter	63	0.71	0.57 - 0.86	9.87	<0.0001	0.24	0.76	0.70 - 0.81	1.84	61	0.07
Tree height	47	0.51	0.34 - 0.69	5.67	<0.0001	0.30	0.85	0.81 - 0.88	-0.84	45	0.40
Number of snags	34	0.47	0.33 - 0.62	6.49	<0.0001	0.11	0.69	0.55 - 0.78	-0.25	32	0.80
Tree elevation	19	-0.35	-0.51 - 0.18	-4.11	<0.0001	0.07	0.58	0.31 - 0.75	-0.51	17	0.61
Canopy closure	33	-0.32	-0.54 - 0.09	-2.77	0.006	0.36	0.83	0.77 - 0.87	-1.70	31	0.10
Distance to water	22	-0.16	-0.33 - 0.00	-1.95	0.05	0.10	0.68	0.50 - 0.79	1.61	20	0.12
Tree density	24	0.06	-0.15 - 0.27	0.55	0.58	0.20	0.76	0.64 - 0.84	2.13	22	0.05
Slope	21	0.03	-0.16 - 0.21	0.30	0.78	0.12	0.72	0.56 - 0.82	-0.50	19	0.62
Remaining bark on trunk	26	0.05	-0.31 - 0.41	0.28	0.78	0.80	0.96	0.95 - 0.97	-0.17	24	0.86

* Estimated by maximum likelihood

Table 3. Meta-regression model number, number of estimated parameters (K), Higgins' I^2 heterogeneity index of residual heterogeneity (%), pseudo- R^2 of heterogeneity accounted for by each model (%), differences between model AICc and those of the best model (Δ_i), and Akaike weights (ω_i), for 17 meta-regression models. All values are rounded upward to two decimal places.

#	Meta-regression model	K	I²	R²	Δi	ωi
13	Temperature	3	76.74	13.26	0	0.43
10	Temperature + sex	5	75.66	17.40	1.58	0.20
12	Temperature + elevation	4	76.58	13.31	2.24	0.14
7	Temperature + elevation + sex	6	75.49	17.46	3.96	0.06
11	Temperature + elevation + temperature x elevation	5	76.30	13.93	4.24	0.05
16	Bat species	7	74.45	20.08	5.87	0.02
9	Temperature + bat species	8	73.62	23.11	5.97	0.02
14	Elevation	3	78.88	1.94	6.16	0.02
15	Bat species + sex	9	72.78	26.28	6.30	0.02
17	Sex	4	78.66	2.58	6.67	0.02
8	Temperature + bat species + sex	10	71.91	29.09	7.15	0.01
6	Temperature + bat species + elevation	9	73.46	23.11	8.69	0.01
5	Temperature + elevation + bat species + sex	11	71.69	29.19	10.00	0
1	Habitat type + Temperature + elevation + sex	11	74.01	23.32	13.31	0
4	Habitat type	7	78.60	4.34	14.86	0
3	Habitat type + elevation	8	78.01	6.75	16.12	0
2	Habitat type + elevation + sex	10	76.92	11.09	17.41	0

Figures

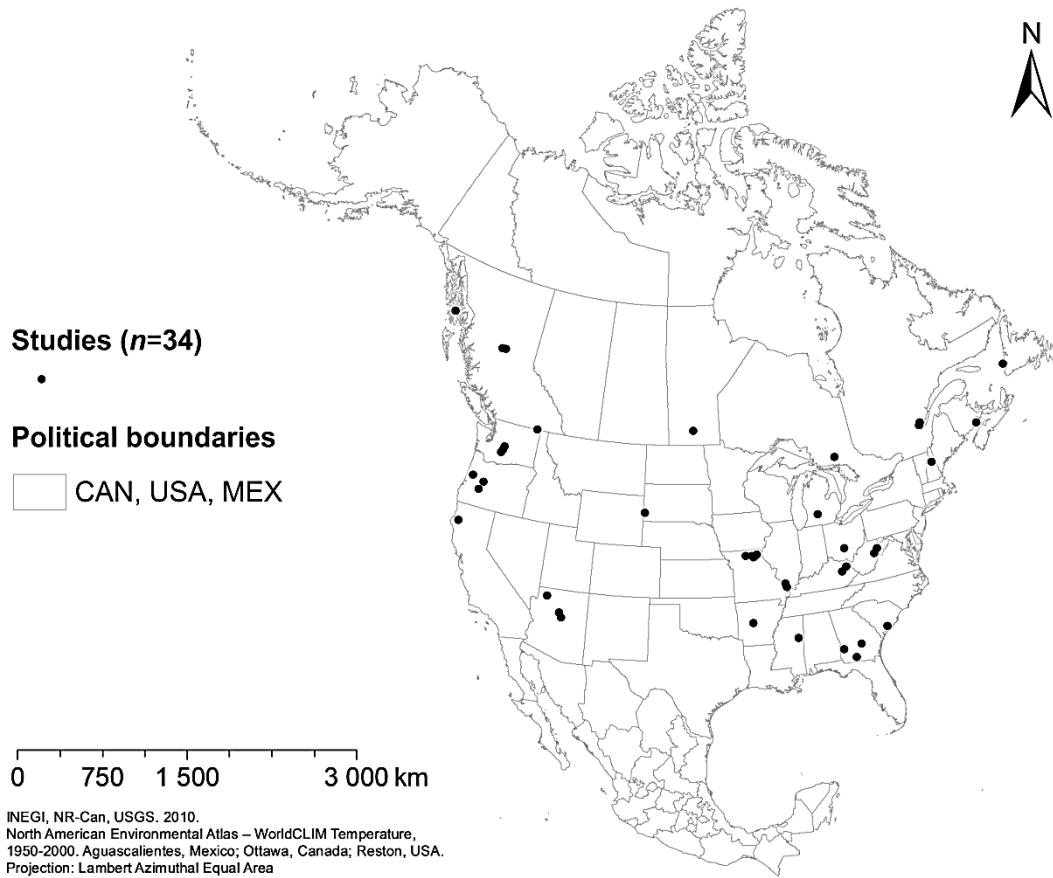


Figure 2. Locations of the 34 studies (66 datasets) that were included in quantitative meta-analyses of roost selection by North American bats. Map source: North American Environmental Atlas (INEGI, NR-Can, USGS, 2010).

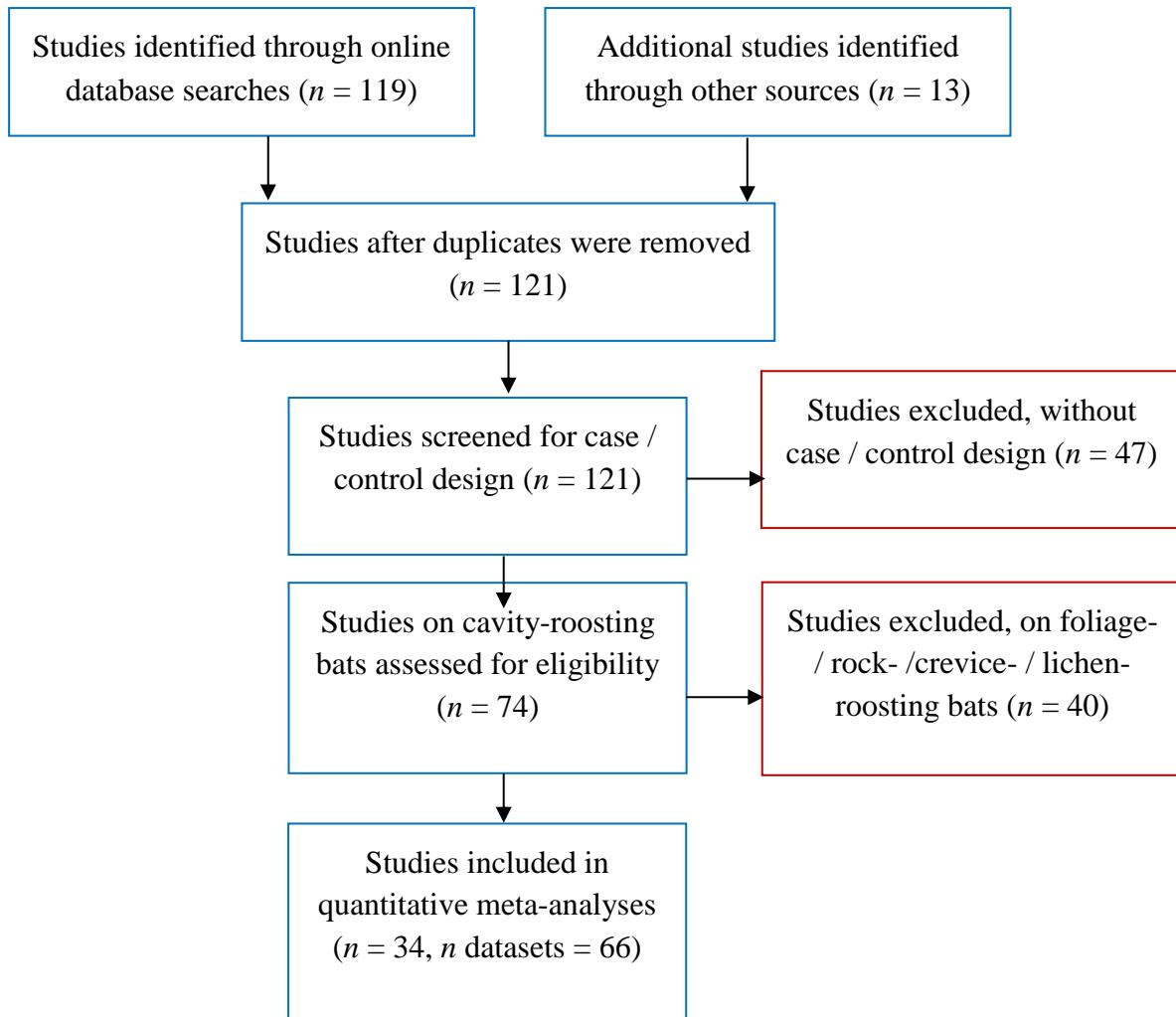


Figure 3. Flow diagram for identification and selection of studies of roost selection by North American bats for quantitative meta-analyses.

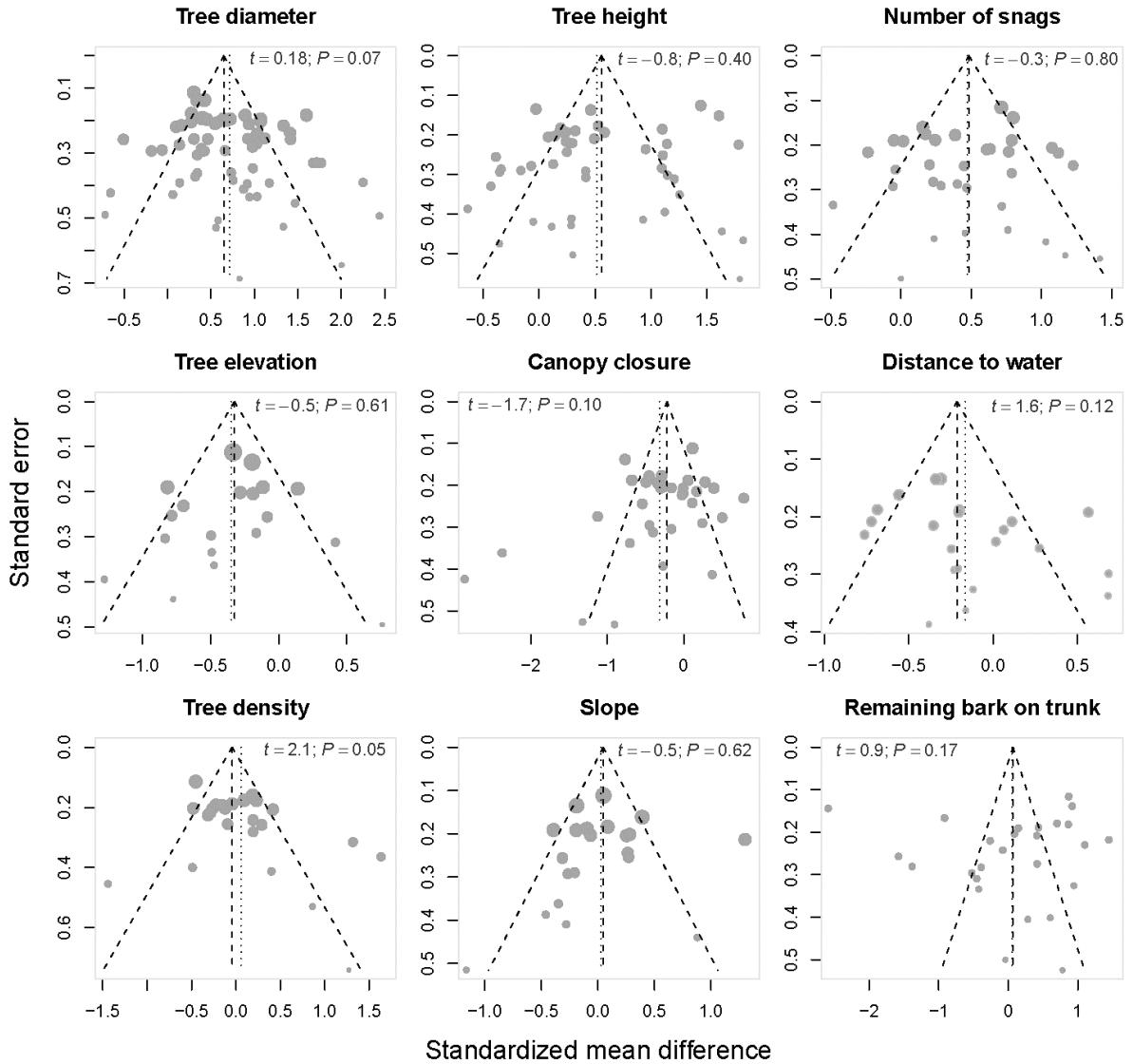


Figure 4. Funnel plots showing publication bias for each of the nine variables that were included in quantitative meta-analyses. For each dataset, the size effect measure on the horizontal axis (standardized mean difference) is plotted against its standard error on the vertical axis. Dotted lines define the 95 % CI limits around the mean size effect (vertical dotted line). The size of the circle varies according to the assigned random weight (inverse variance of the standardized mean differences) of each dataset. Funnel plot asymmetry t -test results and associated P -values are shown in each plot. In the absence of publication bias, studies should follow a symmetric funnel shape. Deviation from this shape may indicate publication bias.

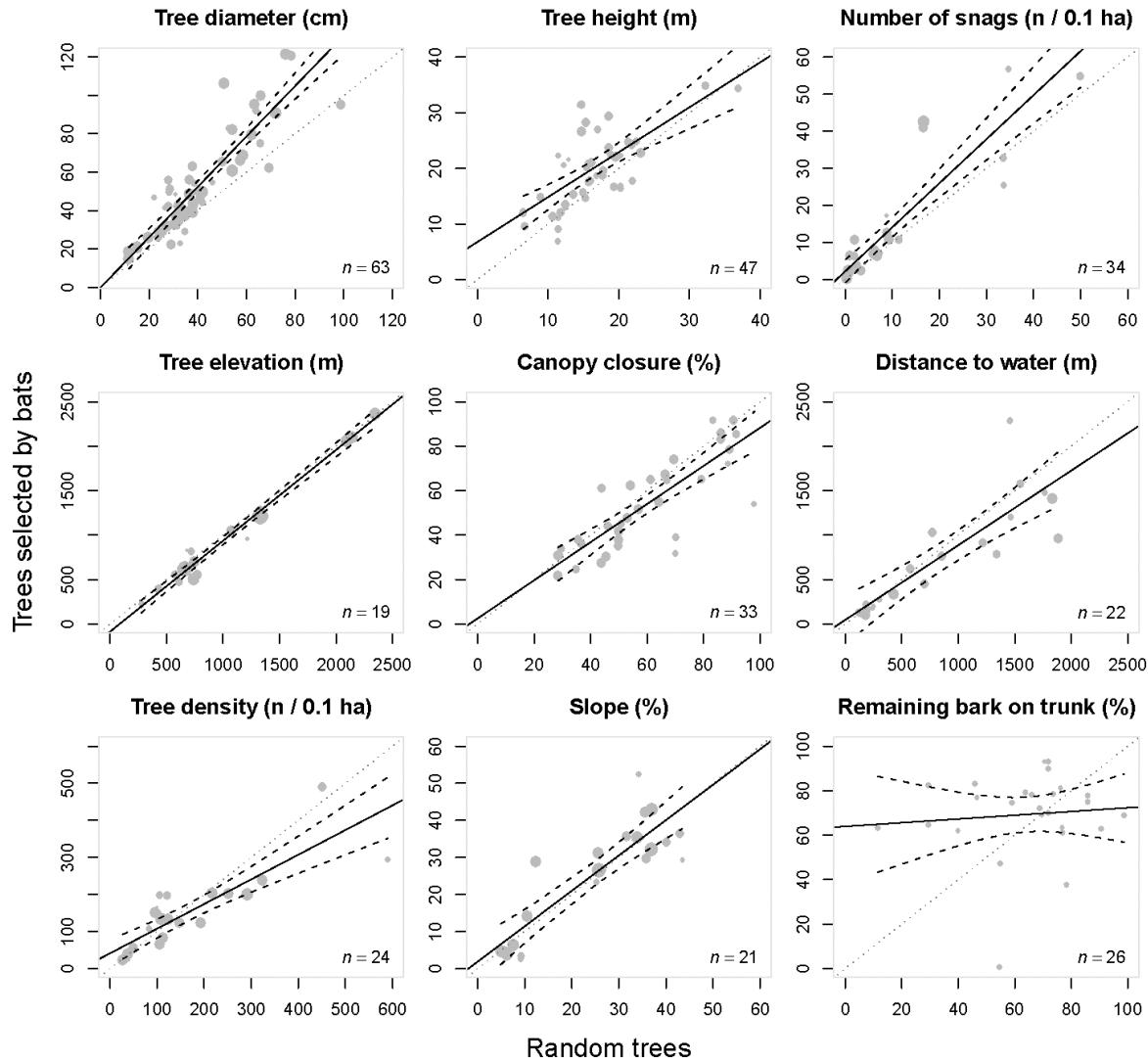


Figure 5. L'Abbé plots of the selected tree characteristics by bats (experimental groups) against the random tree characteristics (control group) with the 95 % CI (black dashed lines) for each dataset, and for each variable (tree diameter, tree height, snag density, bark remaining on trunks, distance to water, canopy closure, elevation, slope, and stand density). The size of the circle varies according to the assigned random weight (inverse variance of the standardized mean differences) of each dataset. The diagonal ($x = y$) grey dotted line is the equality line (1:1) between both means (*i.e.*, the zero effect line, where the mean difference = 0). Above the $x = y$ line, the selected tree mean is higher than the random tree mean. Below the $x = y$ line, the selected tree mean is lower than the random tree mean. Tau-squared (τ^2) and Higgins' I^2 heterogeneity indices are shown in each plot. Higgins' I^2 index is expressed in percentage and is used to interpret the severity of heterogeneity.

Appendix 1

Appendix 1. Table 1. Meta-analysis on diameter at breast height (cm). Number of selected and random trees is provided for each dataset with corresponding mean, standard deviation (SD), standardized mean difference (SMD) with 95 % CI, fixed weight (W), and random weight. Fixed effect and random effects SMD with 95 % CI, and prediction intervals are provided at the end of the table. All values are rounded upward to two decimal places.

Study	Selected trees			Random trees			SMD	95 % CI	W(fixed)	W(random)
	N	Mean	SD	N	Mean	SD				
(Arnett & Hayes 2009)	42	121.6	42.8	104	76.1	41.8	1.08	0.70; 1.46	2.6 %	1.9 %
(Arnett & Hayes 2009)	35	138.7	47.9	33	96.8	41.4	0.92	0.42; 1.43	1.5 %	1.7 %
(Arnett & Hayes 2009)	24	62.4	37.2	23	69.2	35.5	-0.18	-0.76; 0.39	1.1 %	1.6 %
(Arnett & Hayes 2009)	105	91.1	49.2	119	72.1	39.3	0.43	0.16; 0.69	5.3 %	2.0 %
(Arnett & Hayes 2009)	22	95.5	50.7	26	98.7	54.6	-0.06	-0.63; 0.51	1.2 %	1.6 %
(Baker & Lacki 2006)	164	60.9	24.3	160	54.0	21.5	0.30	0.08; 0.52	7.8 %	2.1 %
(Baker & Lacki 2006)	28	82.3	19.1	160	54.0	21.5	1.33	0.91; 1.76	2.1 %	1.8 %
(Brigham <i>et al.</i> 1997b)	19	56.0	16.8	38	28.0	15.0	1.77	1.12; 2.42	0.9 %	1.5 %
(Broders & Forbes 2004)	48	32.9	10.4	48	30.0	11.1	0.27	-0.13; 0.67	2.3 %	1.9 %
(Broders & Forbes 2004)	55	43.8	13.4	55	38.3	14.1	0.40	0.02; 0.78	2.6 %	1.9 %
(Broders & Forbes 2004)	57	32.0	12.1	57	27.2	11.3	0.41	0.04; 0.78	2.7 %	1.9 %
(Callahan, Drobney & Clawson)	7	49.3	16.4	8	40.0	15.0	0.56	-0.48; 1.60	0.3 %	1.0 %
(Callahan, Drobney & Clawson)	11	54.5	15.6	14	38.5	14.6	1.03	0.18; 1.88	0.5 %	1.2 %
(Callahan, Drobney & Clawson)	20	54.6	13.9	5	46.2	14.0	0.59	-0.41; 1.58	0.4 %	1.1 %
(Carter 2003)	19	37.3	20.6	46	34.9	15.0	0.14	-0.39; 0.68	1.3 %	1.7 %
(Carter 2003)	47	39.0	14.0	37	37.7	13.6	0.09	-0.34; 0.53	2.0 %	1.8 %
(Clement & Castleberry 2013)	25	95.5	30.0	314	63.3	34.7	0.93	0.52; 1.35	2.2 %	1.9 %
(Cryan, Bogan & Yanega 2001)	8	42.1	7.4	30	31.7	12.4	0.88	0.07; 1.69	0.6 %	1.3 %
(Cryan, Bogan & Yanega 2001)	21	39.0	8.2	30	31.7	12.4	0.66	0.09; 1.23	1.1 %	1.6 %
(Cryan, Bogan & Yanega 2001)	9	43.3	12.1	30	31.7	12.4	0.92	0.15; 1.70	0.6 %	1.3 %

(Cryan, Bogan & Yanega 2001)	7	42.6	3.2	30	31.7	12.4	0.94	0.09; 1.79	0.5 %	1.2 %
(Fabianek <i>et al.</i> 2015)	8	48.4	8.7	8	31.0	7.6	2.01	0.74; 3.27	0.2 %	0.8 %
(Fabianek <i>et al.</i> 2015)	40	20.7	4.5	40	15.5	5.4	1.03	0.57; 1.50	1.7 %	1.8 %
(Fleming <i>et al.</i> 2013)	8	74.9	28.9	157	65.7	26.3	0.35	-0.36; 1.06	0.7 %	1.4 %
(Fleming <i>et al.</i> 2013)	7	92.0	42.9	147	63.7	23.0	1.17	0.40; 1.94	0.6 %	1.3 %
(Foster & Kurta 1999)	29	63.0	32.3	46	37.7	12.8	1.12	0.62; 1.62	1.5 %	1.7 %
(Foster & Kurta 1999)	23	41.0	4.8	46	37.7	12.8	0.30	-0.20; 0.80	1.5 %	1.7 %
(Grindal)	8	29.1	7.4	241	23.6	7.5	0.74	0.03; 1.44	0.7 %	1.4 %
(Grindal)	8	29.1	7.4	84	25.9	10.1	0.32	-0.41; 1.05	0.7 %	1.4 %
(Herder & Jackson 2000)	52	79.9	21.6	61	62.2	31.2	0.65	0.27; 1.02	2.6 %	1.9 %
(Johnson <i>et al.</i> 2010)	16	41.4	10.2	6	26.6	11.9	1.34	0.30; 2.37	0.3 %	1.0 %
(Jung, Thompson & Titman 2004)	15	42.6	14.7	52	28.1	5.8	1.68	1.03; 2.32	0.9 %	1.5 %
(Jung, Thompson & Titman 2004)	11	49.5	19.2	52	28.1	5.8	2.25	1.48; 3.01	0.6 %	1.3 %
(Kniowski & Gehrt 2011)	56	47.3	16.7	16	41.0	12.5	0.39	-0.17; 0.95	1.2 %	1.6 %
(Lacki & Baker 2007)	6	82.6	26.2	50	52.8	19.2	1.47	0.58; 2.36	0.5 %	1.2 %
(Menzel <i>et al.</i> 2002b)	12	29.2	5.5	12	34.7	10.1	-0.65	-1.48; 0.17	0.5 %	1.3 %
(Miles <i>et al.</i> 2006)	111	50.0	19.0	111	42.1	26.3	0.34	0.08; 0.61	5.3 %	2.0 %
(Miles <i>et al.</i> 2006)	57	26.3	9.8	57	19.9	7.6	0.73	0.35; 1.11	2.6 %	1.9 %
(Ormsbee & McComb 1998)	33	100.0	34.5	66	66.0	16.3	1.41	0.95; 1.88	1.7 %	1.8 %
(Parsons, Lewis & Psyllakis 2003)	6	49.6	12.7	4	39.3	8.0	0.83	-0.52; 2.18	0.2 %	0.7 %
(Perry & Thill 2007a)	40	15.0	8.2	82	11.8	6.3	0.45	0.07; 0.84	2.5 %	1.9 %
(Perry & Thill 2007a)	42	18.7	6.5	82	11.8	6.3	1.07	0.68; 1.47	2.4 %	1.9 %
(Psyllakis & Brigham 2006)	19	26.1	7.2	25	23.6	7.3	0.34	-0.26; 0.94	1.0 %	1.6 %
(Psyllakis & Brigham 2006)	17	48.2	10.5	21	37.0	11.7	0.98	0.30; 1.66	0.8 %	1.5 %
(Rabe <i>et al.</i>)	43	66.0	11.8	58	57.4	16.8	0.57	0.17; 0.98	2.3 %	1.9 %
(Rabe <i>et al.</i>)	54	69.0	14.7	54	58.6	15.4	0.69	0.30; 1.07	2.5 %	1.9 %
(Sasse & Pekins)	47	40.9	19.2	47	33.0	6.9	0.54	0.13; 0.96	2.2 %	1.9 %
(Vonhof & Gwilliam 2007)	46	49.0	15.6	112	36.3	13.6	0.89	0.53; 1.25	2.9 %	1.9 %

(Vonhof & Gwilliam 2007)	46	40.0	13.4	112	36.3	13.6	0.27	-0.07; 0.62	3.1 %	2.0 %
(Vonhof & Gwilliam 2007)	20	55.8	14.2	112	36.3	13.6	1.41	0.91; 1.92	1.5 %	1.7 %
(Weller & Zabel 2001)	23	120.8	25.4	46	78.5	46.1	1.03	0.50; 1.56	1.3 %	1.7 %
(Perry & Thill 2008)	9	20.6	6.6	34	15.3	7.0	0.75	0.00; 1.50	0.7 %	1.4 %
(Perry & Thill 2008)	25	21.5	5.0	34	15.3	7.0	0.98	0.43; 1.53	1.2 %	1.7 %
(Boland <i>et al.</i> 2009)	60	106.5	34.1	114	50.7	35.2	1.59	1.24; 1.95	2.9 %	1.9 %
(Boland <i>et al.</i> 2009)	24	65.6	34.8	44	49.9	33.2	0.46	-0.04; 0.96	1.5 %	1.7 %
(Hein 2009)	31	22.3	13.4	31	28.8	11.7	-0.51	-1.02; 0.00	1.4 %	1.7 %
(Hein 2009)	24	36.6	14.2	24	31.2	10.8	0.42	-0.15; 0.99	1.1 %	1.6 %
(Hein 2009)	11	32.4	9.0	11	31.7	12.3	0.06	-0.77; 0.90	0.5 %	1.2 %
(Hein 2009)	9	23.0	13.8	9	32.5	11.1	-0.72	-1.68; 0.24	0.4 %	1.1 %
(Lacki <i>et al.</i> 2009b)	16	44.2	16.0	11	41.6	21.9	0.14	-0.63; 0.90	0.6 %	1.3 %
(Lacki <i>et al.</i> 2009b)	35	34.6	20.1	57	32.0	13.6	0.16	-0.26; 0.58	2.1 %	1.8 %
(Barclay <i>et al.</i> 1988)	27	51.6	16.5	25	28.7	8.0	1.72	1.08; 2.36	0.9 %	1.5 %
(Barclay, Faure & Farr 1988)	6	46.8	17.2	50	22.0	9.0	2.44	1.48; 3.41	0.4 %	1.1 %
Fixed effect							0.65	0.59; 0.71	100 %	-
Random effects							0.71	0.57; 0.86	-	100 %
Prediction range							-	-0.27; 1.70		

Appendix 1. Table 2. Meta-analysis on tree height (m). Number of selected and random trees is provided for each dataset with corresponding mean, standard deviation (SD), standardized mean difference (SMD) with 95 % CI, fixed weight (W), and random weight. Fixed effect and random effects SMD with 95 % CI, and prediction intervals are provided at the end of the table. All values are rounded upward to two decimal places.

Study	Selected trees			Random trees					W(fixed)	W(random)
	N	Mean	SD	N	Mean	SD	SMD	95 % CI		
(Arnett & Hayes 2009)	105	22.8	9.2	119	23.1	13.1	-0.03	-0.29; 0.24	6.5 %	2.6 %
(Arnett & Hayes 2009)	24	17.7	10.8	23	21.9	12.5	-0.35	-0.93; 0.22	1.3 %	2.1 %
(Arnett & Hayes 2009)	42	24.3	9.1	104	21.9	13.3	0.20	-0.16; 0.55	3.5 %	2.4 %
(Arnett & Hayes 2009)	35	34.9	8.9	33	32.3	11.5	0.25	-0.23; 0.73	2.0 %	2.3 %
(Arnett & Hayes 2009)	22	34.3	11.3	26	36.8	17.3	-0.17	-0.73; 0.40	1.4 %	2.1 %
(Baker & Lacki 2006)	164	26.7	7.7	160	14.7	8.9	1.45	1.20; 1.69	7.4 %	2.6 %
(Baker & Lacki 2006)	28	31.5	12.2	160	14.7	8.9	1.78	1.34; 2.22	2.3 %	2.3 %
(Brigham <i>et al.</i> 1997b)	19	27.0	7.9	38	17.0	8.9	1.15	0.56; 1.74	1.3 %	2.1 %
(Broders & Forbes 2004)	55	13.5	3.7	55	12.4	5.2	0.24	-0.13; 0.62	3.2 %	2.4 %
(Broders & Forbes 2004)	57	11.5	3.8	57	10.7	4.5	0.19	-0.18; 0.56	3.3 %	2.4 %
(Broders & Forbes 2004)	48	12.2	4.9	48	11.8	4.9	0.08	-0.32; 0.48	2.8 %	2.4 %
(Carter 2003)	47	17.5	6.5	37	15.7	6.1	0.29	-0.14; 0.73	2.4 %	2.3 %
(Carter 2003)	19	15.8	8.5	46	14.9	5.8	0.13	-0.41; 0.66	1.6 %	2.2 %
(Clement & Castleberry 2013)	25	24.8	4.3	314	21.4	7.0	0.50	0.09; 0.90	2.7 %	2.4 %
(Cryan, Bogan & Yanega 2001)	21	9.1	5.9	30	11.4	7.1	-0.34	-0.90; 0.22	1.4 %	2.1 %
(Cryan, Bogan & Yanega 2001)	8	22.2	2.5	30	11.4	7.1	1.63	0.76; 2.51	0.6 %	1.6 %
(Cryan, Bogan & Yanega 2001)	9	6.9	6.3	30	11.4	7.1	-0.64	-1.40; 0.12	0.8 %	1.8 %

(Cryan, Bogan & Yanega 2001)	7	11.0	7.1	30	11.4	7.1	-0.06	-0.88; 0.77	0.7 %	1.7 %
(Fabianek <i>et al.</i> 2015)	8	15.8	3.0	8	14.8	3.0	0.30	-0.68; 1.29	0.5 %	1.5 %
(Fabianek <i>et al.</i> 2015)	40	9.6	3.1	40	6.6	3.0	0.95	0.48; 1.41	2.1 %	2.3 %
(Herder & Jackson 2000)	52	21.1	7.2	61	16.1	9.4	0.59	0.21; 0.97	3.1 %	2.4 %
(Johnson <i>et al.</i> 2010)	16	21.7	4.4	6	12.9	5.3	1.80	0.69; 2.90	0.4 %	1.3 %
(Jung, Thompson & Titman 2004)	15	20.1	4.3	52	15.5	3.6	1.21	0.60; 1.82	1.2 %	2.1 %
(Jung, Thompson & Titman 2004)	11	21.0	7.0	52	15.5	3.6	1.25	0.56; 1.94	0.9 %	1.9 %
(Lacki & Baker 2007)	6	31.3	9.3	50	14.4	9.1	1.82	0.91; 2.74	0.5 %	1.6 %
(Lacki, Baker & Johnson 2010)	134	28.3	7.4	100	15.3	8.9	1.60	1.31; 1.90	5.0 %	2.5 %
(Menzel <i>et al.</i> 2002b)	12	18.7	5.2	12	16.8	7.3	0.29	-0.51; 1.10	0.7 %	1.7 %
(Miles <i>et al.</i> 2006)	111	22.2	5.3	111	19.5	6.3	0.46	0.20; 0.73	6.3 %	2.6 %
(Miles <i>et al.</i> 2006)	57	15.4	6.8	57	13.6	3.8	0.33	-0.04; 0.70	3.3 %	2.4 %
(Psyllakis & Brigham 2006)	19	22.6	8.2	25	18.8	9.2	0.42	-0.18; 1.02	1.2 %	2.1 %
(Psyllakis & Brigham 2006)	17	16.4	9.1	21	20.2	8.5	-0.43	-1.08; 0.22	1.1 %	2.0 %
(Rabe <i>et al.</i>)	43	18.8	6.6	58	17.7	8.4	0.14	-0.25; 0.54	2.9 %	2.4 %
(Rabe <i>et al.</i>)	54	17.8	8.1	54	15.9	8.8	0.22	-0.16; 0.60	3.1 %	2.4 %
(Sasse & Pekins)	47	14.8	6.9	47	8.8	2.7	1.14	0.70; 1.58	2.3 %	2.3 %
(Vonhof & Gwilliam 2007)	46	23.7	8.4	112	18.6	10.0	0.53	0.18; 0.88	3.7 %	2.5 %
(Vonhof & Gwilliam 2007)	46	29.4	9.0	112	18.6	10.0	1.10	0.74; 1.47	3.4 %	2.4 %
(Vonhof & Gwilliam 2007)	20	29.3	6.7	112	18.6	10.0	1.11	0.61; 1.60	1.8 %	2.2 %
(Perry & Thill 2008)	9	12.3	4.2	34	6.5	5.3	1.12	0.35; 1.90	0.7 %	1.8 %
(Perry & Thill 2008)	25	12.0	4.5	34	6.5	5.3	1.10	0.54; 1.65	1.4 %	2.1 %

(Hein 2009)	31	16.6	7.2	31	19.3	6.7	-0.38	-0.89; 0.12	1.8 %	2.2 %
(Hein 2009)	24	24.9	4.9	24	22.4	6.9	0.41	-0.16; 0.98	1.4 %	2.1 %
(Hein 2009)	11	22.3	5.0	11	20.3	8.0	0.29	-0.55; 1.13	0.6 %	1.7 %
(Hein 2009)	9	16.9	9.6	9	20.2	8.1	-0.35	-1.29; 0.58	0.5 %	1.6 %
(Lacki <i>et al.</i> 2009b)	16	20.6	10.0	11	12.1	7.0	0.93	0.11; 1.74	0.7 %	1.7 %
(Lacki <i>et al.</i> 2009b)	35	19.7	8.3	57	17.8	7.6	0.24	-0.18; 0.66	2.5 %	2.4 %
(Barclay, Faure & Farr 1988)	27	14.8	8.1	25	15.3	3.0	-0.07	-0.61; 0.48	1.5 %	2.2 %
(Barclay, Faure & Farr 1988)	6	12.9	5.0	50	12.5	3.1	0.12	-0.73; 0.96	0.6 %	1.7 %
Fixed effect							0.56	0.49; 0.62	100 %	-
Random effects							0.51	0.34; 0.69	-	100 %
Prediction range							-	-0.61; 1.64		

Appendix 1. Table 3. Meta-analysis on snag density (stems / 0.1 ha). Number of selected and random trees is provided for each dataset with corresponding mean, standard deviation (SD), standardized mean difference (SMD) with 95 % CI, fixed weight (W), and random weight. Fixed effect and random effects SMD with 95 % CI, and prediction intervals are provided at the end of the table. All values are rounded upward to two decimal places.

Study	Selected trees			Random trees						
	N	Mean	SD	N	Mean	SD	SMD	95 % CI	W(fixed)	W(random)
(Arnett & Hayes 2009)	105	2.3	3.1	119	0.5	1.1	0.80	0.53; 1.07	7.7 %	4.0 %
(Arnett & Hayes 2009)	24	1.5	2.5	23	0.6	1.0	0.47	-0.11; 1.05	1.7 %	2.7 %
(Arnett & Hayes 2009)	42	2.3	1.9	104	0.7	2.0	0.79	0.42; 1.16	4.2 %	3.6 %
(Arnett & Hayes 2009)	35	1.8	1.8	33	1.0	1.7	0.45	-0.03; 0.93	2.5 %	3.1 %
(Arnett & Hayes 2009)	22	1.4	1.9	26	0.9	1.5	0.29	-0.28; 0.86	1.8 %	2.7 %
(Baker & Lacki 2006)	164	42.7	46.1	160	16.6	22.8	0.71	0.49; 0.94	11.3 %	4.2 %
(Baker & Lacki 2006)	28	41.2	84.1	160	16.6	22.8	0.64	0.23; 1.05	3.4 %	3.4 %
(Brigham <i>et al.</i> 1997b)	19	55.0	37.0	38	50.0	3.0	0.23	-0.32; 0.78	1.9 %	2.8 %
(Broders & Forbes 2004)	55	7.0	5.2	55	6.9	5.9	0.02	-0.36; 0.39	4.1 %	3.6 %
(Broders & Forbes 2004)	57	11.0	7.6	57	9.3	6.0	0.25	-0.12; 0.62	4.2 %	3.6 %
(Broders & Forbes 2004)	48	12.7	6.9	48	9.0	4.9	0.61	0.20; 1.02	3.4 %	3.4 %
(Cryan, Bogan & Yanega 2001)	21	0.3	0.6	30	0.1	0.4	0.40	-0.16; 0.96	1.8 %	2.7 %
(Cryan, Bogan & Yanega 2001)	8	0.6	0.7	30	0.1	0.4	1.03	0.22; 1.85	0.9 %	1.9 %
(Cryan, Bogan & Yanega 2001)	9	0.5	0.8	30	0.1	0.4	0.76	0.00; 1.53	1.0 %	2.0 %
(Cryan, Bogan & Yanega 2001)	7	0.9	1.0	30	0.1	0.4	1.42	0.53; 2.31	0.7 %	1.7 %
(Fabianek <i>et al.</i> 2015)	8	1.0	1.8	8	1.0	1.1	0.00	-0.98; 0.98	0.6 %	1.5 %
(Fabianek <i>et al.</i> 2015)	40	6.4	4.4	40	1.9	2.6	1.23	0.75; 1.71	2.5 %	3.1 %

(Herder & Jackson 2000)	52	6.4	9.1	61	6.8	7.7	-0.05	-0.42; 0.32	4.2 %	3.6 %
(Jung, Thompson & Titman 2004)	15	32.7	22.5	52	33.7	17.3	-0.05	-0.63; 0.52	1.7 %	2.7 %
(Jung, Thompson & Titman 2004)	11	25.5	14.3	52	33.7	17.3	-0.48	-1.14; 0.18	1.3 %	2.4 %
(Lacki & Baker 2007)	6	17.2	9.3	50	8.8	6.8	1.17	0.30; 2.05	0.7 %	1.7 %
(Menzel <i>et al.</i> 2002b)	12	1.4	0.9	12	1.1	1.0	0.24	-0.56; 1.04	0.9 %	1.9 %
(Psyllakis & Brigham 2006)	17	56.7	38.2	21	34.8	20.9	0.72	0.06; 1.38	1.3 %	2.3 %
(Rabe <i>et al.</i>)	43	6.5	6.6	58	1.0	3.1	1.12	0.70; 1.55	3.2 %	3.3 %
(Rabe <i>et al.</i>)	54	10.6	10.3	54	2.0	4.4	1.08	0.67; 1.48	3.5 %	3.4 %
(Sasse & Pekins)	47	3.9	2.1	47	2.3	2.1	0.77	0.35; 1.19	3.2 %	3.4 %
(Vonhof & Gwilliam 2007)	46	7.0	7.4	112	6.0	5.0	0.17	-0.17; 0.52	4.8 %	3.7 %
(Vonhof & Gwilliam 2007)	46	8.0	5.6	112	6.0	5.0	0.38	0.04; 0.73	4.8 %	3.7 %
(Vonhof & Gwilliam 2007)	20	7.0	3.7	112	6.0	5.0	0.21	-0.27; 0.68	2.5 %	3.1 %
(Weller & Zabel 2001)	23	10.8	4.3	46	11.3	14.9	-0.04	-0.54; 0.46	2.3 %	3.0 %
(Boland <i>et al.</i> 2009)	60	0.4	0.2	114	0.4	0.1	0.16	-0.15; 0.47	5.8 %	3.8 %
(Boland <i>et al.</i> 2009)	24	0.5	0.2	44	0.4	0.1	0.79	0.28; 1.31	2.1 %	2.9 %
(Lacki <i>et al.</i> 2009b)	16	4.1	2.7	11	2.8	2.9	0.46	-0.32; 1.23	0.9 %	2.0 %
(Lacki <i>et al.</i> 2009b)	35	2.5	1.8	57	3.3	3.9	-0.23	-0.65; 0.19	3.2 %	3.3 %
Fixed effect						0.48	0.41; 0.56	100 %	-	
Random effects						0.47	0.33; 0.62	-	100 %	
Prediction range						-	-0.23; 1.17			

Appendix 1. Table 4. Meta-analysis on elevation (m). Number of selected and random trees is provided for each dataset with corresponding mean, standard deviation (SD), standardized mean difference (SMD) with 95 % CI, fixed weight (W), and random weight. Fixed effect and random effects SMD with 95 % CI, and prediction intervals are provided at the end of the table. All values are rounded upward to two decimal places.

Study	Selected trees			Random trees						W(fixed)	W(random)
	N	Mean	SD	N	Mean	SD	SMD	95 % CI			
(Arnett & Hayes 2009)	105	624	195	119	665	229	-0.19	-0.45; 0.07	14.1 %	8.2 %	
(Arnett & Hayes 2009)	24	554	152	23	578	139	-0.16	-0.73; 0.41	3.0 %	4.6 %	
(Arnett & Hayes 2009)	42	508	194	104	737	306	-0.82	-1.19; -0.45	7.1 %	6.8 %	
(Arnett & Hayes 2009)	35	562	166	33	771	339	-0.78	-1.28; -0.29	4.0 %	5.4 %	
(Arnett & Hayes 2009)	22	480	150	26	613	163	-0.83	-1.43; -0.24	2.8 %	4.4 %	
(Baker & Lacki 2006)	164	1217	323	160	1325	320	-0.34	-0.55; -0.12	20.3 %	8.8 %	
(Baker & Lacki 2006)	28	1263	361	160	1325	320	-0.19	-0.59; 0.21	6.1 %	6.4 %	
(Fabianek <i>et al.</i> 2015)	40	710	48	40	752	69	-0.69	-1.15; -0.24	4.8 %	5.8 %	
(Fleming <i>et al.</i> 2013)	8	230	64	157	276	97	-0.48	-1.19; 0.24	1.9 %	3.5 %	
(Fleming <i>et al.</i> 2013)	7	218	9	147	275	45	-1.28	-2.05; -0.50	1.6 %	3.2 %	
(Herder & Jackson 2000)	52	2068	264	61	2093	152	-0.12	-0.49; 0.25	7.1 %	6.8 %	
(Johnson <i>et al.</i> 2010)	16	834	130	6	680	315	0.76	-0.21; 1.73	1.0 %	2.3 %	
(Johnson <i>et al.</i> 2010)	34	813	200	15	721	247	0.42	-0.20; 1.03	2.6 %	4.3 %	
(Jung, Thompson & Titman 2004)	15	400	60	52	430	60	-0.49	-1.08; 0.09	2.9 %	4.5 %	
(Jung, Thompson & Titman 2004)	11	400	60	52	430	60	-0.49	-1.15; 0.16	2.3 %	3.9 %	
(Lacki & Baker 2007)	6	957	637	50	1218	286	-0.77	-1.63; 0.09	1.3 %	2.7 %	
(Rabe <i>et al.</i>)	43	2099	144	58	2142	156	-0.28	-0.68; 0.11	6.2 %	6.5 %	

(Rabe <i>et al.</i>)	54	2366	192	54	2341	168	0.14	-0.24; 0.52	6.9 %	6.7 %
(Weller & Zabel 2001)	23	1058	218	46	1072	139	-0.08	-0.58; 0.42	3.9 %	5.3 %
Fixed effect							-0.32	-0.42; -0.23	100 %	-
Random effects							-0.35	-0.51; -0.18	-	100 %
Prediction range							-	-0.92; 0.23		

Appendix 1. Table 5. Meta-analysis on canopy closure (%). Number of selected and random trees is provided for each dataset with corresponding mean, standard deviation (SD), standardized mean difference (SMD) with 95 % CI, fixed weight (W), and random weight. Fixed effect and random effects SMD with 95 % CI, and prediction intervals are provided at the end of the table. All values are rounded upward to two decimal places.

	Selected trees			Control trees						W(fixed)	W(random)
	N	Mean	SD	N	Mean	SD	SMD	95 % CI			
(Arnett & Hayes 2009)	105	27.5	16.4	119	43.6	24.0	-0.8	-1.04; -0.50	7.6 %	3.4 %	
(Arnett & Hayes 2009)	24	24.8	17.6	23	34.6	24.5	-0.5	-1.03; 0.13	1.7 %	2.9 %	
(Arnett & Hayes 2009)	42	30.7	16.2	104	45.4	23.5	-0.7	-1.04; -0.31	4.2 %	3.3 %	
(Arnett & Hayes 2009)	35	37.9	17.2	33	35.6	21.8	0.12	-0.36; 0.59	2.5 %	3.1 %	
(Arnett & Hayes 2009)	22	33.9	11.3	26	29.4	23.0	0.24	-0.33; 0.81	1.7 %	2.9 %	
(Baker & Lacki 2006)	164	31.2	24.3	160	28.5	21.5	0.12	-0.10; 0.34	11.9 %	3.5 %	
(Baker & Lacki 2006)	28	22.1	20.6	160	28.5	21.5	-0.3	-0.70; 0.10	3.5 %	3.3 %	
(Broders & Forbes 2004)	55	74.2	14.1	55	69.4	19.3	0.28	-0.09; 0.66	4.0 %	3.3 %	
(Broders & Forbes 2004)	57	67.4	16.6	57	66.4	16.6	0.06	-0.31; 0.43	4.2 %	3.3 %	
(Broders & Forbes 2004)	48	62.4	19.4	48	54.2	21.5	0.4	-0.01; 0.80	3.5 %	3.2 %	
(Carter 2003)	47	36.3	28.1	37	36.6	35.0	-0	-0.44; 0.42	3.0 %	3.2 %	
(Carter 2003)	19	61.3	28.3	46	44.0	35.7	0.51	-0.04; 1.05	1.9 %	3.0 %	
(Clement & Castleberry 2013)	25	85.9	12.3	314	86.0	7.6	-0	-0.42; 0.39	3.4 %	3.2 %	
(Fabianek <i>et al.</i> 2015)	8	54.0	65.0	8	98.0	3.0	-0.9	-1.95; 0.14	0.5 %	2.0 %	
(Fabianek <i>et al.</i> 2015)	40	44.0	75.0	40	46.0	74.0	-0	-0.46; 0.41	2.9 %	3.2 %	
(Herder & Jackson 2000)	52	55.2	19.5	61	64.2	17.2	-0.5	-0.86; -0.11	4.0 %	3.3 %	
(Johnson <i>et al.</i> 2010)	16	72.0	13.9	6	88.6	1.7	-1.3	-2.36; -0.29	0.5 %	2.1 %	

(Johnson <i>et al.</i> 2010)	34	85.4	18.1	15	91.5	1.7	-0.4	-1.01; 0.22	1.5 %	2.9 %
(Jung, Thompson & Titman 2004)	15	39.1	16.7	52	70.0	11.5	-2.4	-3.09; -1.67	1.1 %	2.7 %
(Jung, Thompson & Titman 2004)	11	31.6	19.6	52	70.0	11.5	-2.9	-3.71; -2.04	0.8 %	2.4 %
(Lacki & Schwierjohann 2001)	57	91.4	1.0	31	90.5	1.4	0.78	0.33; 1.24	2.8 %	3.2 %
(Menzel <i>et al.</i> 2002b)	12	91.7	8.3	12	83.4	29.1	0.37	-0.43; 1.18	0.9 %	2.5 %
(Psyllakis & Brigham 2006)	19	64.9	13.8	25	67.2	15.0	-0.2	-0.75; 0.44	1.6 %	2.9 %
(Psyllakis & Brigham 2006)	17	65.5	26.4	21	79.4	11.0	-0.7	-1.36; -0.04	1.3 %	2.8 %
(Rabe <i>et al.</i>)	43	48.0	13.1	58	53.0	22.9	-0.3	-0.65; 0.14	3.6 %	3.3 %
(Rabe <i>et al.</i>)	54	52.0	14.7	54	57.0	14.7	-0.3	-0.72; 0.04	3.9 %	3.3 %
(Sasse & Pekins)	47	83.0	9.6	47	86.0	24.0	-0.2	-0.57; 0.24	3.4 %	3.2 %
(Vonhof & Gwilliam 2007)	46	42.0	28.1	112	50.0	27.8	-0.3	-0.63; 0.06	4.8 %	3.3 %
(Vonhof & Gwilliam 2007)	46	38.0	23.2	112	50.0	27.8	-0.5	-0.80; -0.10	4.7 %	3.3 %
(Vonhof & Gwilliam 2007)	20	35.0	26.9	112	50.0	27.8	-0.5	-1.02; -0.06	2.4 %	3.1 %
(Weller & Zabel 2001)	23	78.5	12.5	46	89.2	7.5	-1.1	-1.66; -0.59	2.0 %	3.0 %
(Lacki <i>et al.</i> 2009b)	16	45.0	20.0	11	51.0	23.9	-0.3	-1.04; 0.50	0.9 %	2.5 %
(Lacki <i>et al.</i> 2009b)	35	65.0	26.0	57	61.0	22.7	0.17	-0.26; 0.59	3.2 %	3.2 %
Fixed effect						-0.2	-0.29; -0.14	100 %	-	
Random effects						-0.3	-0.54; -0.09	-	100 %	
Prediction range						-	-1.56; 0.93			

Appendix 1. Table 6. Meta-analysis on distance to water (m). Number of selected and random trees is provided for each dataset with corresponding mean, standard deviation (SD), standardized mean difference (SMD) with 95 % CI, fixed weight (W), and random weight. Fixed effect and random effects SMD with 95 % CI, and prediction intervals are provided at the end of the table. All values are rounded upward to two decimal places.

Study	Selected trees			Random trees						W(fixed)	W(random)
	N	Mean	SD	N	Mean	SD	SMD	95 % CI			
(Arnett & Hayes 2009)	105	1407	1332	119	1829	1385	-0.30	-0.57; -0.05	11.50 %	6.00 %	
(Arnett & Hayes 2009)	24	1205	926	23	1470	1352	-0.20	-0.80; 0.35	2.40 %	3.80 %	
(Arnett & Hayes 2009)	42	967	1056	104	1883	1428	-0.70	-1.05; -0.32	5.90 %	5.30 %	
(Arnett & Hayes 2009)	35	1582	1935	33	1551	1338	0.02	-0.46; 0.49	3.50 %	4.50 %	
(Arnett & Hayes 2009)	22	1480	1599	26	1766	1127	-0.20	-0.78; 0.36	2.50 %	3.90 %	
(Clement & Castleberry 2013)	25	627	469	314	580	400	0.11	-0.29; 0.52	4.80 %	5.00 %	
(Fabianek <i>et al.</i> 2015)	40	779	799	40	1342	663	-0.80	-1.21; -0.30	3.90 %	4.60 %	
(Fleming <i>et al.</i> 2013)	8	197	476	157	256	365	-0.20	-0.87; 0.55	1.60 %	3.10 %	
(Fleming <i>et al.</i> 2013)	7	177	229	147	244	174	-0.40	-1.14; 0.38	1.40 %	2.80 %	
(Herder & Jackson 2000)	52	1032	413	61	770	500	0.56	0.19; 0.94	5.60 %	5.20 %	
(Jung, Thompson & Titman 2004)	15	2283	871	52	1458	1262	0.69	0.10; 1.27	2.30 %	3.70 %	
(Jung, Thompson & Titman 2004)	11	2283	746	52	1458	1262	0.68	0.02; 1.35	1.80 %	3.30 %	
(Lacki & Schwierjohann 2001)	57	127	100	31	121	89.1	0.06	-0.38; 0.50	4.20 %	4.80 %	
(Miles <i>et al.</i> 2006)	111	333	247	111	429	312	-0.30	-0.60; -0.07	11.40 %	6.00 %	
(Miles <i>et al.</i> 2006)	57	164	139	57	192	146	-0.20	-0.57; 0.17	5.90 %	5.30 %	
(Ormsbee & McComb 1998)	33	923	925	66	1217	780	-0.40	-0.77; 0.07	4.50 %	4.90 %	
(Psyllakis & Brigham 2006)	17	272	288	21	301	206	-0.10	-0.76; 0.52	2.00 %	3.40 %	

(Rabe <i>et al.</i>)	43	458	315	58	701	350	-0.70	-1.13; -0.31	4.80 %	5.00 %
(Rabe <i>et al.</i>)	54	759	353	54	855	558	-0.20	-0.58; 0.17	5.60 %	5.20 %
(Weller & Zabel 2001)	23	117	131	46	150	130	-0.20	-0.75; 0.26	3.20 %	4.30 %
(Boland <i>et al.</i> 2009)	60	101	139	114	179	139	-0.60	-0.88; -0.24	7.90 %	5.60 %
(Boland <i>et al.</i> 2009)	24	219	137	44	182	133	0.27	-0.23; 0.77	3.20 %	4.30 %
Fixed effect							-0.20	-0.30; -0.12	100 %	-
Random effects							-0.20	-0.33; 0.00	-	100 %
Prediction range							-	-0.84; 0.52		

Appendix 1. Table 7. Meta-analysis tree density (%). Number of selected and random trees is provided for each dataset with corresponding mean, standard deviation (SD), standardized mean difference (SMD) with 95 % CI, fixed weight (W), and random weight. Fixed effect and random effects SMD with 95 % CI, and prediction intervals are provided at the end of the table. All values are rounded upward to two decimal places.

Study	Selected trees			Control trees						W(fixed)	W(random)
	N	Mean	SD	N	Mean	SD	SMD	95 % CI			
(Baker & Lacki 2006)	160	202	161.9	164	291.7	224.1	-0.46	-0.68; -0.23	15.7 %	5.4 %	
(Baker & Lacki 2006)	160	202	161.9	28	249.7	245.5	-0.27	-0.67; 0.13	4.7 %	4.7 %	
(Brigham <i>et al.</i> 1997b)	38	490	227.0	19	450.0	158.0	0.19	-0.36; 0.74	2.5 %	4.1 %	
(Broders & Forbes 2004)	55	123	61.6	55	192.3	423.5	-0.23	-0.60; 0.15	5.4 %	4.8 %	
(Broders & Forbes 2004)	57	205	248.4	57	217.6	373.0	-0.04	-0.41; 0.33	5.7 %	4.9 %	
(Broders & Forbes 2004)	48	239	474.6	48	322.5	805.1	-0.13	-0.53; 0.27	4.8 %	4.7 %	
(Clement & Castleberry 2013)	314	150	140.9	25	94.0	49.3	0.41	0.00; 0.82	4.6 %	4.7 %	
(Fabianek <i>et al.</i> 2015)	8	150	36.3	8	105.0	59.3	0.87	-0.17; 1.91	0.7 %	2.4 %	
(Fabianek <i>et al.</i> 2015)	40	124	81.9	40	147.8	68.7	-0.31	-0.75; 0.13	3.9 %	4.6 %	
(Jung, Thompson & Titman 2004)	52	198	53.4	15	120.0	75.1	1.31	0.70; 1.93	2.0 %	3.8 %	
(Jung, Thompson & Titman 2004)	52	198	53.4	11	104.6	69.7	1.64	0.92; 2.35	1.5 %	3.4 %	
(Lacki & Baker 2007)	50	294	193.8	6	590.0	279.2	-1.44	-2.33; -0.55	1.0 %	2.8 %	
(Menzel <i>et al.</i> 2002b)	12	108	69.3	12	83.0	48.5	0.40	-0.41; 1.21	1.2 %	3.1 %	
(Parsons, Lewis & Psyllakis 2003)	4	165	34.2	6	100.0	52.2	1.27	-0.18; 2.72	0.4 %	1.5 %	
(Rabe <i>et al.</i>)	58	82	48.7	43	111.4	73.6	-0.48	-0.88; -0.08	4.8 %	4.7 %	
(Rabe <i>et al.</i>)	54	66.6	323.0	54	104.7	74.2	-0.16	-0.54; 0.22	5.4 %	4.8 %	
(Vonhof & Gwilliam 2007)	112	134	116.5	46	123.4	100.2	0.10	-0.25; 0.44	6.5 %	5.0 %	

(Vonhof & Gwilliam 2007)	112	134	116.5	46	108.9	82.8	0.23	-0.11; 0.58	6.5 %	4.9 %
(Vonhof & Gwilliam 2007)	112	134	116.5	20	112.5	98.7	0.19	-0.29; 0.67	3.4 %	4.4 %
(Weller & Zabel 2001)	46	57.7	26.5	23	50.6	17.3	0.29	-0.21; 0.80	3.0 %	4.3 %
(Boland <i>et al.</i> 2009)	114	38.8	15.0	60	36.1	13.9	0.18	-0.13; 0.50	7.8 %	5.1 %
(Boland <i>et al.</i> 2009)	44	32.7	14.6	24	34.0	13.7	-0.09	-0.59; 0.41	3.1 %	4.3 %
(Lacki <i>et al.</i> 2009b)	11	28	9.0	16	36.3	20.0	-0.49	-1.27; 0.29	1.3 %	3.2 %
(Lacki <i>et al.</i> 2009b)	57	25.2	7.6	35	27.2	5.9	-0.28	-0.71; 0.14	4.3 %	4.6 %
Fixed effect							-0.04	-0.13; 0.04	100 %	-
Random effects							0.06	-0.15; 0.27	-	100 %
Prediction range							-	-0.88; 1.00		

Appendix 1. Table 8. Meta-analysis on slope (%). Number of selected and random trees is provided for each dataset with corresponding mean, standard deviation (SD), standardized mean difference (SMD) with 95 % CI, fixed weight (W), and random weight. Fixed effect and random effects SMD with 95 % CI, and prediction intervals are provided at the end of the table. All values are rounded upward to two decimal places.

Study	Selected trees			Random trees						
	N	Mean	SD	N	Mean	SD	SMD	95 % CI	W(fixed)	W(random)
(Arnett & Hayes 2009)	105	32.4	20.5	119	36.8	25.1	-0.19	-0.45; 0.07	11.5 %	6.3 %
(Arnett & Hayes 2009)	24	36.4	23.5	23	42.8	23.5	-0.27	-0.84; 0.31	2.4 %	4.2 %
(Arnett & Hayes 2009)	42	35.6	22.7	104	33.8	20.4	0.08	-0.27; 0.44	6.2 %	5.7 %
(Arnett & Hayes 2009)	35	42.3	28.4	33	35.6	20.1	0.27	-0.21; 0.75	3.5 %	4.8 %
(Arnett & Hayes 2009)	22	34.1	18.8	26	40.0	33.7	-0.21	-0.78; 0.36	2.5 %	4.3 %
(Baker & Lacki 2006)	164	26.7	25.6	160	25.6	21.5	0.05	-0.17; 0.26	16.8 %	6.5 %
(Baker & Lacki 2006)	28	31.2	25.9	160	25.6	21.5	0.25	-0.15; 0.65	4.9 %	5.4 %
(Broders & Forbes 2004)	55	6.6	3.7	55	7.4	4.5	-0.19	-0.57; 0.18	5.7 %	5.5 %
(Broders & Forbes 2004)	57	4.6	4.5	57	5.4	10.6	-0.10	-0.47; 0.27	5.9 %	5.6 %
(Broders & Forbes 2004)	48	4.6	4.2	48	4.9	4.9	-0.07	-0.47; 0.33	5.0 %	5.4 %
(Fleming <i>et al.</i> 2013)	8	3.3	2.5	157	9.3	17.5	-0.35	-1.06; 0.37	1.6 %	3.5 %
(Fleming <i>et al.</i> 2013)	7	2.6	1.9	147	9.3	14.8	-0.46	-1.22; 0.30	1.4 %	3.2 %
(Herder & Jackson 2000)	52	4.0	5.1	61	6.1	5.5	-0.39	-0.77; -0.02	5.7 %	5.6 %
(Johnson <i>et al.</i> 2010)	16	29.1	11.7	6	43.5	12.5	-1.16	-2.17; -0.15	0.8 %	2.3 %
(Lacki & Baker 2007)	6	52.3	15.3	50	34.3	20.6	0.88	0.02; 1.74	1.1 %	2.8 %
(Menzel <i>et al.</i> 2002b)	12	23.3	7.9	12	25.3	6.1	-0.28	-1.08; 0.53	1.2 %	3.0 %
(Rabe <i>et al.</i>)	43	14.1	11.5	58	10.5	13.3	0.28	-0.12; 0.68	5.1 %	5.4 %

(Rabe <i>et al.</i>)	54	29.1	12.9	54	12.3	12.9	1.30	0.88; 1.71	4.6 %	5.3 %
(Weller & Zabel 2001)	23	29.7	24.9	46	35.7	14.9	-0.32	-0.82; 0.19	3.1 %	4.7 %
(Boland <i>et al.</i> 2009)	60	43.0	14.7	114	36.9	16.0	0.39	0.07; 0.70	8.0 %	5.9 %
(Boland <i>et al.</i> 2009)	24	35.6	14.7	44	31.5	15.3	0.27	-0.23; 0.77	3.2 %	4.7 %
Fixed effect						0.05	-0.04; 0.14	100 %	-	
Random effects						0.03	-0.16; 0.21	-		100 %
Prediction range						-	-0.73; 0.79			

Appendix 1. Table 9. Meta-analysis on bark remaining on trunks (%). Number of selected and random trees is provided for each dataset with corresponding mean, standard deviation (SD), standardized mean difference (SMD) with 95 % CI, fixed weight (W), and random weight. Fixed effect and random effects SMD with 95 % CI, and prediction intervals are provided at the end of the table. All values are rounded upward to two decimal places.

Study	Selected trees			Random trees						
	N	Mean	SD	N	Mean	SD	SMD	95 % CI	W(fixed)	W(random)
(Baker & Lacki 2006)	164	64.6	44.8	160	29.6	34.2	0.87	0.65; 1.10	13.1 %	4.1 %
(Baker & Lacki 2006)	28	82.5	47.1	160	29.6	34.2	1.45	1.02; 1.88	3.7 %	4.0 %
(Brigham <i>et al.</i> 1997b)	19	75.0	29.6	38	86.0	27.3	-0.39	-0.94; 0.17	2.2 %	3.8 %
(Broders & Forbes 2004)	55	78.5	30.4	55	73.7	33.4	0.15	-0.22; 0.52	4.9 %	4.0 %
(Broders & Forbes 2004)	57	74.4	31.7	57	59.0	37.8	0.44	0.07; 0.81	4.9 %	4.0 %
(Broders & Forbes 2004)	48	72.1	31.2	48	69.0	34.6	0.09	-0.31; 0.49	4.3 %	4.0 %
(Callahan, Drobney & Clawson)	11	81.1	16.9	14	76.2	16.5	0.28	-0.51; 1.08	1.1 %	3.5 %
(Callahan, Drobney & Clawson)	20	69.1	18.3	5	69.8	23.0	-0.04	-1.02; 0.94	0.7 %	3.2 %
(Carter 2003)	47	47.0	26.7	37	55.0	35.3	-0.26	-0.69; 0.18	3.6 %	4.0 %
(Carter 2003)	19	79.2	30.9	46	63.8	38.4	0.42	-0.12; 0.96	2.3 %	3.8 %
(Fabianek <i>et al.</i> 2015)	8	93.1	15.8	8	70.6	34.9	0.79	-0.24; 1.81	0.6 %	3.1 %
(Fabianek <i>et al.</i> 2015)	40	0.7	26.7	40	54.5	39.7	-1.57	-2.08; -1.07	2.7 %	3.9 %
(Johnson <i>et al.</i> 2010)	34	76.8	31.0	15	46.7	31.8	0.95	0.31; 1.59	1.7 %	3.7 %
(Jung, Thompson & Titman 2004)	15	61.0	19.8	52	77.0	32.5	-0.52	-1.11; 0.06	2.0 %	3.8 %
(Jung, Thompson & Titman 2004)	11	63.6	27.2	52	77.0	32.5	-0.42	-1.07; 0.24	1.6 %	3.7 %
(Kniowski & Gehrt 2011)	56	68.8	33.1	1438	98.7	9.9	-2.58	-2.86; -2.30	8.5 %	4.1 %
(Lacki, Baker & Johnson 2010)	134	63.3	70.3	100	11.6	26.3	0.92	0.65; 1.20	9.2 %	4.1 %

(Psyllakis & Brigham 2006)	19	78.1	17.5	25	85.8	16.0	-0.45	-1.06; 0.15	1.9 %	3.8 %
(Sasse & Pekins)	47	78.0	38.4	47	66.0	13.0	0.42	0.01; 0.82	4.1 %	4.0 %
(Vonhof & Gwilliam 2007)	46	93.0	17.6	112	72.0	26.2	0.87	0.51; 1.23	5.4 %	4.0 %
(Vonhof & Gwilliam 2007)	46	90.0	23.3	112	72.0	26.2	0.71	0.35; 1.06	5.5 %	4.0 %
(Vonhof & Gwilliam 2007)	20	70.0	28.0	112	72.0	26.2	-0.08	-0.55; 0.40	3.0 %	3.9 %
(Boland <i>et al.</i> 2009)	60	63.0	28.7	114	90.6	31.0	-0.91	-1.24; -0.58	6.4 %	4.1 %
(Boland <i>et al.</i> 2009)	24	37.4	29.4	44	78.2	29.2	-1.38	-1.93; -0.83	2.2 %	3.8 %
(Lacki <i>et al.</i> 2009b)	16	62.0	36.0	11	40.0	33.8	0.61	-0.18; 1.39	1.1 %	3.5 %
(Lacki <i>et al.</i> 2009b)	35	83.0	26.0	57	46.0	37.0	1.10	0.65; 1.55	3.3 %	3.9 %
Fixed effect						0.07	-0.01; 0.15	100 %	-	
Random effects						0.05	-0.31; 0.41	-	100 %	
Prediction range						-	-1.83; 1.93			

CHAPITRE 2 – SELECTION OF ROOSTING HABITAT BY MALE *MYOTIS* BATS IN A BOREAL FOREST

François-Henri Fabianek, Centre d’Étude de la Forêt (CEF), and Faculté de Foresterie, de Géographie et de Géomatique, Université Laval, 2405, rue de la Terrasse, Québec, Québec G1V 0A6, Canada

Marie Anouk Simard, Ministère des Forêts, de la Faune et des Parcs (MFFP), 880, chemin Sainte Foy, Québec, Québec G1S 4X4, Canada

Centre de la Sciences de la Biodiversité du Québec (CSBQ), and Faculté de Foresterie, de Géographie et de Géomatique, Université Laval, 2405, rue de la Terrasse, Québec, Québec G1V 0A6, Canada

Etienne Bellemare Racine, CEF and Faculté de Foresterie, de Géographie et de Géomatique, Université Laval, 2405, rue de la Terrasse, Québec, Québec G1V 0A6, Canada

André Desrochers, CEF and Faculté de Foresterie, de Géographie et de Géomatique, Université Laval, 2405, rue de la Terrasse, Québec, Québec G1V 0A6, Canada

Ce chapitre est le fruit du travail de François-Henri Fabianek. Marie-Anouk Simard et André Desrochers ont contribué à l’élaboration du design expérimental. Etienne Bellemare Racine a effectué les analyses LiDAR. Marie-Anouk Simard, André Desrochers et Etienne Bellemare Racine ont contribué à la rédaction de ce chapitre. Cet article a été publié dans le Canadian Journal of Zoology

Résumé

La petite chauve-souris brune (*Myotis lucifugus* (Le Conte, 1831)) et la chauve-souris nordique (*Myotis septentrionalis* (Trouessart, 1897)), se perchent souvent sous l'écorce exfoliante, à l'intérieur des troncs et des cavités d'arbres durant l'été. Le manque actuel de connaissances sur l'écologie de perchage de ces espèces dans la forêt boréale limite notre compréhension sur la façon dont elles peuvent être affectées par l'exploitation forestière. L'objectif principal était d'identifier les caractéristiques des arbres et des peuplements forestiers qui étaient sélectionnés par les chauves-souris pour se percher au sein de la sapinière (*Abies balsamea* [L.] Miller) à boulot blanc (*Betula papyrifera* Marshall) du Québec (Canada). Durant trois ans, nous avons capturé et équipé 22 chauves-souris de radio-émetteurs pour localiser leurs arbres-gîtes durant sept à 14 jours après relâche. Nous avons mesuré les caractéristiques des arbres et du peuplement sur le terrain et en utilisant la technologie LiDAR (Light Detection and Ranging). Les arbres-gîtes ont été comparés à des arbres aléatoires en utilisant des modèles mixtes linéaires généralisés. Les chauves-souris mâles du genre *Myotis* ont choisi des chicots plus larges et plus hauts au sein de peuplements contenant une plus grande proportion de trouées et un plus grand nombre de chicots, comparativement aux arbres aléatoires. Des parcelles de végétation de 0,1 ha comprenant un minimum de 10 chicots avec un diamètre à hauteur de poitrine (DHP) ≥ 10 cm devraient être maintenues afin de préserver les sites de perchages des chauves-souris mâles du genre *Myotis* au sein des sapinières à bouleau blanc.

Abstract

Male little brown bat (*Myotis lucifugus* (Le Conte, 1831)) and northern long-eared bat (*Myotis septentrionalis* (Trouessart, 1897)), often roost under exfoliating bark, within the trunks and cavities of trees during summer. Current lack of knowledge about the roosting ecology of these species in boreal forest limits our understanding of how they may be affected by logging. The main objective was to identify tree and forest stand features that were selected by bats for roosting within a balsam fir (*Abies balsamea* [L.] Miller)-paper birch (*Betula papyrifera* Marshall) forest of Quebec (Canada). Over three years, we captured and fitted radio-transmitters to 22 individual bats to locate their roost trees for seven to 14 days following release. We measured tree and forest stand features in the field and using Light Detection and Ranging (LiDAR) technology. Roost trees were compared to random trees using generalized linear mixed models. Male *Myotis* bats selected larger and taller snags, within stands containing a higher proportion of canopy gaps and a larger number of snags compared to random trees. Vegetation clumps of 0.1 ha containing a minimum of 10 snags with a Diameter at Breast Height (DBH) ≥ 10 cm should be maintained to preserve roosting habitat that is used by male *Myotis* bats in balsam fir-paper birch forests.

Introduction

Nearly half of known bat species worldwide use trees as roosts for at least part of the year (Kunz & Lumsden 2007). Bats use trees as shelters, protection against predators, for social interactions (O'Shea & Bogan 2003) and likely, as a means of reducing thermoregulation costs (Smith & Racey 2005; Boyles 2007). Roosting habitat is thus an important component of bat ecology that is sometimes limiting (O'Donnell & Sedgeley 1999; Kunz & Lumsden 2007), especially under the effects of anthropogenic disturbances, such as logging (Campbell, Hallett & O'Connell 1996; Loeb & O'Keefe 2011). Indeed, logging has been recognized as a major threat to bats worldwide (Hutson *et al.* 2001). Forest management influences tree size and tree mortality rates, as well as stand species composition, stand density and stand age, such that management prescriptions are likely to affect both the availability of trees that are used as roosts by bats, as well as their surrounding environment (Guldin *et al.* 2007).

The increasing attention that bat roosting ecology has received over the last three decades indicates that roost selection depends upon a broad range of requirements (Kalcounis-Ruepell, Psyllakis & Brigham 2005) at various habitat scales (Miles *et al.* 2006; Boland *et al.* 2009; Fleming *et al.* 2013). Features such as tree decay (Parsons, Lewis & Psyllakis 2003; Baker & Lacki 2006), tree height and tree diameter (Lacki & Baker 2003) can influence selection by bats. At the stand scale, proportion of canopy gaps (Loeb & O'Keefe 2011) and the availability of nearby snags are also important features of bat habitat selection (Arnett & Hayes 2009). Recent research also suggests that bats use a network of roost trees (Johnson, Ford & Edwards 2012), although advantages associated with these networks remain unclear (Broders *et al.* 2006; Reckardt & Kerth 2007).

The little brown bat (*Myotis lucifugus* (Le Conte, 1831)) and the northern long-eared bat (*Myotis septentrionalis* (Trouessart, 1897)) are two cavity-roosting bats that were common throughout the north-eastern boreal forests of Canada prior to the appearance of White Nose Syndrome (WNS; Blehert *et al.* 2009b). Since its discovery in 2006 in New York State, WNS has caused mass mortality of hibernating bats throughout eastern North America (Dzial *et al.* 2010; Moosman *et al.* 2013) and is predicted to lead to regional extinctions of the little brown bat (Frick *et al.* 2010). Both *Myotis* bats are known to roost

under exfoliating bark, inside crevices, or within the cavities of large trees during summer (Parsons, Lewis & Psyllakis 2003; Jung, Thompson & Titman 2004; Garroway & Broders 2008). Roost selection by these species has been well documented for females and in temperate forests (Barclay & Kurta 2007), but few studies have investigated roost selection by males and within the Boreal Shield ecozone (Broders & Forbes 2004; Jung, Thompson & Titman 2004). Moreover, no study to date has investigated the habitat requirements of cavity-roosting bats, such as *Myotis* bats, in the province of Quebec (Canada). This lack of knowledge prevents the adaptation of forest management practices that favour habitat conservation of *Myotis* bats. Considering that direct WNS-associated mortality cannot yet be mitigated in North America, an appropriate strategy would be to reduce the influence of other anthropogenic disturbances to preserve the natural habitat of the bats. This requires greater knowledge of *Myotis* roosting habitats, particularly in the case of males, which remain largely underrepresented in habitat selection studies.

Based on a review of 34 published manuscripts on roost selection by bats, we predicted that *Myotis* bats select roosts in taller and larger trees with advanced decay stages and that these possess a higher percentage of remaining bark compared to trees selected at random (Parsons, Lewis & Psyllakis 2003; Kalcounis-Rueppell, Psyllakis & Brigham 2005; Perry & Thill 2007a). We also predict that roost trees that are selected by *Myotis* bats are surrounded by lower vegetation cover, a higher proportion of canopy gaps, and a larger number of snags compared to random trees (Broders & Forbes 2004; Arnett & Hayes 2009; Loeb & O'Keefe 2011). As suggested by Brigham *et al.* (1997b), a higher proportion of canopy gaps should also provide greater exposure to sunlight and limit daily thermoregulation costs (Lacki, Johnson & Baker 2013; Johnson & Lacki 2014).

Material and methods

Study area

We studied roosting behavior of bats at the Montmorency Research Forest ($47^{\circ}19'N$, $71^{\circ}07'W$; Figure 6), which is located 70 km north of Quebec City, within the balsam fir (*Abies balsamea* [L.] Miller)-paper birch (*Betula papyrifera* Marshall) bioclimatic domain. With an average elevation of 850 m asl, climatic conditions in the region are considered cold and wet, with an average summer (May to September) temperature of $11.4^{\circ}C \pm 3.3^{\circ}C$

(mean \pm SD; range: 4.0 to 16.4 °C) and precipitation of 128.0 mm \pm 49.2 mm (range: 44.5 to 267 mm). The boreal forest alternates between mixed and coniferous stands, which rarely exceed 90 years of age. The forest is actively managed with clear cuts, partial cuts and shelter wood cutting. Natural disturbances are mainly caused by outbreaks of spruce budworm (*Choristoneura fumiferana* Clemens) and tree decay, thereby creating a patchy mosaic of forest structures.

Capture and tracking

We captured bats from mid-June to mid-August 2011, 2012 and 2013, using 10 mist nets (Avinet Inc., Dryden, NY, USA) by night. We placed mist nets from 2100 to 0100 along trails, close to ponds and forest stands, and changed their locations after two consecutive nights to increase capture success. We weighed each captured individual and identified it to species (Appendix 3). We visually determined reproductive status (reproductive or not reproductive) and age classes (adult or juvenile), following the methodology described in Kunz and Parsons (2009). We collected fecal samples found in holding bags from captured individuals. We placed the samples in a 70° ethanol solution prior to store them at -20°C. Genotypic analyzes on fecal samples have been performed by Dr. Elizabeth Clare to evaluate the diet of each captured individual (results are provided in Clare *et al.* (2013) and in Appendix 4). We glued radio transmitters (Model LB-2X, Holohil Systems Limited, Carp, ON, Canada) onto the trimmed interscapular fur of adult bats that weighed more than 6 g, using non-toxic surgical adhesive (Skin-Bond, Smith and Nephew United, Memphis, TN, USA). We tracked released individuals on a daily basis, using a three-element Yagi antenna and receiver system (ATSR4500S model, Advanced Telemetry Systems, Isanti, MN, USA). We located their roost trees by homing in until the transmitter fell off. Because of the risk of WNS transmission, we decontaminated every item that was used during manipulations with a fungicide (Clinicide®, Biomed-MTC Animal Health Inc., Cambridge, ON), following the National White-Nose Syndrome Decontamination Protocol that was provided by the United States Fish and Wildlife Service (USFWS). We followed ASM guidelines for research on live mammals and the Animal Committee Care of Laval University approved all of the above described procedures and manipulations (License number # 2011064).

Habitat variables

We georeferenced roost trees with a Trimble GeoXM Global Positioning System (GPS) receiver (Trimble Navigation, Sunnyvale, CA). For comparative purposes, we selected a random location for each roost tree. We determined each random location by taking a random distance (from 32 to 250 m) and a random bearing (from 0 to 360°) from each roost tree. Comparisons at the stand scale were done between roosts and random locations. For comparisons at the tree scale, we took the closest living or closest dead tree from each random location, matching the corresponding roost tree (*i.e.*, alive or dead).

We determined tree species, percent of remaining bark on trunks, and tree decay classes (Imbeau & Desrochers 2002). In class (1) trees are alive with ≥ 95 % of foliage, showing no sign of deterioration; (2) senescent trees where remaining foliage is between ≥ 20 % and < 95 %; (3) senescent trees with < 20 % foliage remaining; (4) recently dead trees with firm bark cover, 0 % green foliage and small twigs still remaining; (5) no dead foliage present, no small twigs; (6) loose bark cover, broken top, height still more than 50 % of what is observed on trees with same DBH (Diameter at Breast Height, 1.3 m); (7) broken top with height less than 50 % of what is observed on trees with same DBH. Illustrations of decay classes (from 1 to 7) from Imbeau and Desrochers (2002) are provided in Figure 7. We measured tree height using a clinometer and tree DBH using a DBH tape.

At the stand scale, we estimated lateral vegetation cover in each cardinal direction, using a vegetation profile board at 2 m and 16 m distances from each (roost and random) tree (Table 4). The maximum distance of 16 m around each tree corresponds to a 0.1 ha plot. We performed angle count sampling (plotless point-sampling) of the surrounding trees using a wedge prism (with a basal area factor of 2). For each tree selected by the wedge prism, we recorded tree species, decay class and tree DBH. We determined dominant tree species, stand type (coniferous, mixed, or deciduous), stand basal area, the number of snags with DBH ≥ 10 cm, and the number of snags with DBH ≥ 20 cm from these counts. We performed all habitat measurements at roost sites after September to minimize disturbance to the bats. We also imported our selected bat roost and random tree locations into ArcGIS (version 10.1, Environmental Systems Research Institute, Redlands, CA) to extract mean distance among roosts, the origin of stand disturbance, and stand age at each location from

digitized eco-forest maps of the Montmorency Research Forest (4th forest inventory program, 2003-2013), which were provided by the Government of Québec's Ministère des Forêts, de la Faune et des Parcs (MFFP).

Light detection and ranging imagery

We have used airborne LiDAR (Light Detection and Ranging) to improve estimates of stand scale variables such as mean canopy height, proportion of canopy gaps, and insolation levels. Airborne LiDAR uses a laser beam to scan a complete scene from a fixed-wing aircraft (Suárez *et al.* 2005). It provides a three-dimensional point cloud that can be processed to extract landscape features such as elevation, slope, canopy height, tree density or light penetration. LiDAR has many applications in forestry (Dubayah & Drake 2000; Suárez *et al.* 2005) and has recently been used for detailed characterization of bat habitats (Jung *et al.* 2012; Yang *et al.* 2013).

Airborne LiDAR survey was performed in August 2011 using an Optech ALTM 3100 sensor that was flown at 1000 m above the terrain with a 100 kHz pulse rate, wavelength of 1046 nm, a divergence of 0.25 mrad, and with a maximal scan angle of 17° from the Nadir. Flight line overlap was 50 %, and final median density was about five points per square meter. The point cloud that we obtained was then converted to a surface model representing ground and vegetation, which we refer to as the Digital Surface Model (DSM). Identification of ground returns was carried out by the provider and triangulated to create a Digital Terrain Model (DTM). Subtraction of DTM from DSM yielded a Canopy Height Model (CHM), which we used as a representation of the canopy (Vazirabad & Karslioglu 2010). We derived mean stand height, proportion of canopy gaps (Figure 8), and mean insolation levels within 2 m and 16 m radius buffers around each tree from the LiDAR (Table 4). We defined canopy gaps as being greater than 2 m², with a tree height that was two-thirds lower than the surrounding mean canopy height. Insolation level refers here to the theoretical amount of solar radiation energy (expressed in megajoule) received by each roost tree or random location during a day (MJ / m² / day). We simulated DSM mean insolation for June and July 2011, from 0600 to 2000, at 47°17'60"N, using SAGA (System for Automated Geoscientific Analyses) GIS (Kumar *et al.* 1997).

Statistical analyses

We considered trees rather than individual bats as our sampling units and pooled the data from both species of bats to examine roost selection at the genus level, to overcome issues of limited sample sizes ($n = 14$ roosts for the little brown bat, $n = 26$ roosts for the northern long-eared bat; Table 4). We examined differences between roost trees and random trees using Generalized Linear Mixed Models (GLMM, *lme4* package, R Development Core Team 2015) with a binomial distribution and a logit link function. We based maximum likelihood estimation of our parameters on an Adaptive Gaussian Quadrature approximation. We assumed that a potential source of variation in roost selection could be attributed to individual bats. We therefore included individual bat IDs as a random effect in our GLMMs (Bolker *et al.* 2009). The “random effect” term here refers to a latent variable from which we wanted to estimate the potential variance component. If the variance that was associated with individuals does not vary consistently across treatments, (i) the random effect term should approach 0, (ii) its inclusion should not improve the model fit (and subsequently lower the AICc), and (iii) the model residual variance should stay unchanged, compared to a GLM including only fixed effects. To overcome the problem of combining two bat species with potential differences in roost selection into the same model, we included species codes (“MYLU” for little brown bat, “MYSE” for northern long-eared bat) as a fixed factor in our GLMMs. This categorical variable allows model building with an intercept for each species and a common slope for our variables of interest, which we believe, would be the best compromise between a model by species with a limited number of samples and a model that pools both species of bats.

We verified the presence of outliers and potential leverage effects, over-dispersion (coeff. > 1), and multicollinearity before interpreting our GLMM results. We decided to exclude from our analyses the number of snags that had DBH ≥ 20 cm, together with stand basal area and mean stand canopy height variables, to avoid strong correlations (Pearson $r \geq 0.7$; (Dormann *et al.* 2013) between variables (*i.e.*, stand basal area vs tree DBH; proportion of canopy gaps vs mean canopy height; snags with DBH ≥ 10 cm vs snags with DBH ≥ 20 cm). We also decided not to include decay classes (1 to 7) in our statistical analyses to avoid model over fitting, given the limited number of samples (n roost trees = 40; n random trees = 40).

We used the second-order Akaike's information criterion for small samples (AICc) to rank the candidate set of models according to our predictions (*AICcmodavg* package, R Development Core Team 2015). All of the variables that were included in the candidate set of models had been selected *a priori* (Burnham & Anderson 2002). To represent roosting habitat selection by bats at various spatial scales, we constructed three subsets of candidate models for a total of 20 alternative models (Table 5). The first set combined only stand feature variables. The second set combined both stand and tree feature variables, while the third set combined only tree feature variables (Table 5). We calculated Δ AICc values (Δi) and Akaike weights (ω_i) to determine the relative importance of the candidate set of models from the best explanatory model ($\Delta i = 0$). Models were considered equivalent when they had a $\Delta i \leq 2$ (Burnham & Anderson 2002). For each variable that was included in the best models, we calculated the odds ratio (and 95 % CI) by applying an inverse logarithm transformation to the model estimates (β). We calculated the relative-importance weights of each variable appearing in the 95 % confidence set of models (Burnham & Anderson 2002). We calculated a prediction curve for each estimate from the GLMM with the lowest AICc (Figure 9) and used these predictions to make recommendations for forest management.

Results

Capture and telemetry

Because of extreme sex ratio or capture bias, we only captured male *Myotis* bats. Individuals were captured at a mean mist net height of $2.5 \text{ m} \pm 1.3 \text{ m}$ (mean \pm SD; range: 0.5 to 5.5 m) from the ground. From a total of 22 captured males, we found five individuals roosting alone or in small groups in human habitations and six individuals were not recovered. Of the 11 successfully tracked individuals, we had six little brown bats ($8.0 \text{ g} \pm 1.1 \text{ g}$; range: 6.8 to 9.4 g) and five northern long-eared bats ($7.0 \text{ g} \pm 0.5 \text{ g}$; range: 6.1 to 7.3 g) in 2011. For both species, we found 5 ± 2 roost trees (range: 3 to 7) per individual bat, during a mean tracking period of $9 \text{ days} \pm 2 \text{ days}$ (range: 7 to 14 days). Bats switched roost trees every $2 \text{ days} \pm 1 \text{ day}$ (range: 1 to 6 days). We found 40 roost trees and identified the exact position of the roost sites within trees for 18 trees. *Myotis* bats selected roosts at a mean height of $4.9 \text{ m} \pm 2 \text{ m}$ (range: 1.5 to 8 m) and with a mean direction of $226^\circ \pm 50^\circ$.

(range: 110 to 292°), indicating a preference for southwestern exposures ($n = 18$ roost trees).

Tree characteristics and stand composition

Among the 40 roost trees that were selected by male *Myotis* species, 32 (80 %) were balsam fir, five (12.5 %) were paper birch, and three (7.5 %) were white spruce (*Picea glauca* [Moench] Voss). Of these 40 roost trees, 36 (90 %) were snags and the remaining four (10 %) were living paper birches (Figure 7). The random trees included 35 (87.5 %) balsam fir, 4 (10 %) paper birch, and 1 (2.5 %) black spruce (*Picea mariana* Miller BSP). Regarding tree decay classes, we found that male *Myotis* bats roosted primarily on class 6 snags, with 25 (62.5 %) roosts. Class 6 snags were only represented by 14 (35 %) random trees (Figure 7).

At the stand scale, roost trees were primarily located in mixed stands that were dominated by conifers (57.5 %, $n = 23$) or in conifer stands (40 %, $n = 16$), but rarely in deciduous stands (2.5 %, $n = 1$). Random locations were also located in mixed stands that were dominated by conifers (50 %, $n = 20$), in conifer stands (42.5 %, $n = 17$), and in deciduous stands (7.5 %, $n = 3$). The main source of disturbance was clear-cutting in bat-selected stands (78 %, $n = 21$) and random locations (68 %, $n = 21$). With respect to stand composition, we found that balsam fir dominated bat-selected stands (76.8 %, $n = 456$) and random locations (76 %, $n = 377$), followed by black and white spruce (bat-selected: 13.1 %, $n = 78$; random: 13.1 %, $n = 65$), paper birch (bat-selected: 9.8 %, $n = 58$; random: 9.1 %, $n = 45$), and trembling aspen (*Populus tremuloides* Michaux; bat-selected: 0.3 %, $n = 2$; random: 1.8 %, $n = 9$). When we considered tree decay classes (Figure 7), male *Myotis* bats selected roost trees in stands that contained a high proportion of snags in classes 6 (bat-selected: 14.2 %, $n = 14$; random: 5.6 %, $n = 45$) and 7 (bat-selected: 13.4 %, $n = 133$; random: 4 %, $n = 32$), together with a few living trees of class 3 (bat-selected: 38.8 %, $n = 386$; random: 64.2 %, $n = 519$).

Generalized linear mixed model ranking

The best model (AICc weight = 0.66) that explained differences between random trees and selected trees by male *Myotis* bats included five variables (Table 5): number of snags with DBH ≥ 10 cm (relative importance weight = 1.00), tree height (0.98), tree DBH

(0.97), proportion of canopy gaps at 2 m (0.95), and bat species (0.26). The random effect variance was 1.05×10^{-16} , with a standard deviation of 1.02×10^{-8} . At the tree scale, the odds of selecting larger and taller trees were respectively 1.28 (95 % CI: $1.08 \leq \beta \leq 1.50$) and 1.50 (95 % CI: $1.12 \leq \beta \leq 2.00$) times more likely than random (Table 6). At the stand scale, the odds of selecting a tree with a higher percentage of canopy gaps was 1.04 (95% CI: $1.01 \leq \beta \leq 1.07$) times more likely than random (Table 6). Every additional snag with a DBH ≥ 10 cm that was found near a roost tree increased the odds that male *Myotis* bats would select this habitat by 1.51 (95 % CI: $1.21 \leq \beta \leq 1.88$; Table 6). Means and standard errors for all of the aforementioned variables are shown in Table 4.

Discussion

Since bat species was of low relative importance weight in the 95 % confidence set of models, we suggest that males of both species showed overlap in roosting habitat requirements, at least for the variables that we tested. Similar results including *Myotis* bats were reported by Cryan, Bogan and Yanega (2001), and Jung, Thompson and Titman (2004), but contradict those found by Broders and Forbes (2004) in temperate Nordic forest. In light of these results, we are confident that the benefits of pooling the two species to increase our sample size outweighed the subsequent loss of information. The variance explained by the random effect was close to 0 (with a standard deviation of 1.02×10^{-8}), indicating that variation among individuals was not greater than would be expected according to random variation. Including this random effect only penalized our best model AICc, suggesting that this parameter was not ecologically meaningful (Arnold 2010).

Selection of roosting habitat requirements by male *Myotis* bat species operated at both tree and stand scales. Similar results were reported by Miles *et al.* (2006). Male little brown bats and male northern long-eared bats selected larger and taller snags compared to those selected at random. They preferred to roost in stands with a higher proportion of canopy gaps, and with a larger number of surrounding snags (with DBH ≥ 10 cm) nearby, when compared to random locations. These results are consistent with other studies in North America (Lacki & Baker 2003; Kalcounis-Ruepell, Psyllakis & Brigham 2005).

In conifer-dominated stands of the balsam fir-paper birch forest, solitary males of both bat species roosted under loose bark of balsam fir (*i.e.*, the dominant tree species) and

in white spruce snags. This behavior was also observed by Broders and Forbes (2004) and Jung, Thompson and Titman (2004). The only living trees that were used by male *Myotis* bats were senescent paper birches with less than 20 % remaining foliage (decay class 3; Figure 7) in which individuals found roosts under the exfoliating bark. Dead trees with broken tops, loose bark cover, and height less than 50 % of what is observed for adjacent trees with the same DBH (decay class 6; Figure 7) were mostly used by male *Myotis* bats. More advanced decay stages lead to smaller trees with less remaining bark (Imbeau & Desrochers 2002), which makes them less suitable for cavity-roosting bats such as *Myotis* species (Barclay & Mark Brigham 2001; Vonhof & Gwilliam 2007). At decay class 6, trees were probably tall enough to be both visible and accessible for bats (Kalcounis-Rueppell, Psyllakis & Brigham 2005; Barclay & Kurta 2007; Garoway & Broders 2008) and possessed sufficient remaining bark to provide available shelter (Parsons, Lewis & Psyllakis 2003; Perry & Thill 2007a).

Although the percentage of remaining bark was included in the second best model, it was of low relative importance. We believe that measuring the percentage of exfoliating bark rather than the percentage of remaining bark would lead to better results. Living paper birches provide a good example of this assertion: although 100 % of the bark remained on the trunks, this species differed from other living tree species (such as balsam fir and spruces) by the presence of exfoliating bark, which made them suitable for male *Myotis* bats.

Male *Myotis* bats selected slightly larger trees compared to random trees. Male bats are usually solitary roosters, so that they do not necessarily require large cavities in which to rest compared to lactating females (Psyllakis & Brigham 2006; Willis, Voss & Brigham 2006; Park & Broders 2012). Lacki and Schwierjohann (2001), and Perry and Thill (2007a) found that male bats used small diameter trees (mean DBH < 15 cm) to roost. Similarly, Broders and Forbes (2004) found that the DBH of trees that were selected by male *Myotis* bats in conifer-dominated stands were less than 20 cm. Within the managed balsam fir-paper birch stands of the Montmorency Research Forest, trees with DBH \geq 30 cm were rare since they represented only 2.5 % of our counts ($n = 1810$). This low proportion of large trees in the forest landscape might also force male *Myotis* bats to roost in trees with a small DBH. In a sugar maple (*Acer saccharum* Marshall)-yellow birch (*Betula alleghaniensis*

Britten) forest that was located 23 km south of our study area (Jacques-Cartier National Park), male *Myotis* bats had access to bigger trees (52 % of trees with DBH ≥ 30 ; $n = 227$). Male *Myotis* bats selected larger diameter roost trees ($40.3 \text{ cm} \pm 17.6 \text{ cm}$; $n = 8$) compared to random ones ($27.6 \text{ cm} \pm 12.6 \text{ cm}$; $n = 8$) in this unmanaged area (Fabianek *et al.* 2011, unpublished data).

At the stand scale, another feature that slightly increased roost selectivity by male *Myotis* bats was a high proportion of canopy gaps at 2 m around roosts. Although we predicted that trees with a higher proportion of canopy gaps would lead to greater exposure to sunlight, we failed to find differences between bat-selected stands and random locations with respect to mean insolation levels. These results suggest that a higher proportion of canopy gap does not necessarily imply greater exposure to sunlight (Canham *et al.* 1990) and might be linked to roost accessibility (e.g., from foraging sites) instead (Loeb & O'Keefe 2011). Solar radiation through forest canopy is a highly variable and complex phenomenon, which varies with size and location of canopy gaps, and according to stand species composition, slope and the angle of solar incidence, among other factors (Ni *et al.* 1997; Hardy *et al.* 2004). Furthermore, male *Myotis* bats might be less limited by thermoregulation costs and might thus seek for cooler roosts, since they undergo torpor more frequently and for a longer duration than do reproductive females (Hamilton & Barclay 1994; Grinevitch, Holroyd & Barclay 1995; Cryan & Wolf 2003; Johnson & Lacki 2014).

Among all of the roosting habitat features that we considered, the number of snags ($\geq 10 \text{ cm DBH}$) was the most important criterion for predicting roost selection by male *Myotis* bats. We found that bats used a network of roost trees and switched roosts regularly. This tendency of bats to switch roosts frequently is mentioned by several studies (Barclay & Kurta 2007; Reckhardt & Kerth 2007). The benefits of roosting in clumps of high density snags might be driven by predator avoidance in the case of frequent roost-switching behavior or disturbance to roosts (Sparks *et al.* 2003; Barclay & Kurta 2007), or perhaps simply due to the transient nature of the roost trees that are used (Lee 1998; Angers, Drapeau & Bergeron 2010). Of course, this hypothesis is plausible only if snags around roost trees share features similar to those of the occupied trees. Indeed, our stand sampling results showed respectively 3.1 times more class 6 snags and 3.8 times more snags with

DBH \geq 20 cm within stands selected by male *Myotis* bats, compared to random locations (Table 4).

At the landscape scale, several studies found a sexual segregation in bats with females less likely to occur in stands at higher elevation (Senior, Butlin & Altringham 2005). Cryan, Bogan and Altenbach (2000) showed an inverse relationship between habitat elevation and the presence of reproductive female bats in South Dakota, presumably because of lower ambient temperature and lower insect availability at higher elevations (Grindal, Morissette & Brigham 1999). Russo (2002) and Arnold (2007) obtained similar results with *Myotis daubentonii* (Kuhl, 1819) and *M. septentrionalis*, respectively. Because our study area was located at high elevation and because female bats are likely to have different roosting habits than males (Hamilton & Barclay 1994; Broders & Forbes 2004; Perry & Thill 2007a), we believe that relatively cold average summer temperatures occurring at the Montmorency Research Forest were unsuitable for females, which might explain why we only captured male *Myotis* bats over three consecutive summers.

Light detection and ranging

We used LiDAR remote sensing to assess vegetation structure associated to roost selection by male *Myotis* bats. LiDAR provided exhaustive continuous landscape measurements of the canopy that allowed gap identification (*i.e.*, proportion of canopy gaps), insolation estimation, and canopy height measurement (*i.e.*, mean canopy height) in specific sampled sites, replacing time-consuming field measurements and revealing habitat associations that would have otherwise been missed. To fully benefit from LiDAR high precision level, we took special care while positioning the plots relative to the LiDAR scan by using a GPS with sub-meter accuracy and matching it to the canopy height model. A complete airborne LiDAR coverage allows extending forest structure measurements outside of the field-sampled areas to identify landscape-wide potential roosting habitats, something inconceivable with field sampling methods of vegetation. LiDAR also offers a snapshot in time that would allow monitoring vegetation structure dynamics (Meyer *et al.* 2013) around *Myotis* roosting habitats through repeated scans.

Recommendations for management

We argue that snag retention is a simple and effective way to preserve roosting habitat for forest-dwelling species such as *Myotis* bats. Although the implications of our results pertain only to the ecology of male bats, we confirmed the use of large snags with intermediary state of decay that were located in relatively open stands for *Myotis* bats. We conclude from our GLMM estimates (Figure 9) that vegetation clumps of 0.1 ha containing a minimum of 10 snags with a DBH \geq 10 cm should be preserved or created thought logging. We propose that partial logging with variable retention management systems, to retain a maximum of class 6 and class 7 snags with DBH \geq 20 cm, should be considered by forest managers who are interested in promoting roosting habitat for male *Myotis* bats in particular and for wildlife conservation in general.

Acknowledgements

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Tables

Table 4. Mean \pm standard errors (SE) for habitat features for random trees, trees selected by male little brown bat (MYLU; *Myotis lucifugus*, male northern long-eared bat (MYSE; *Myotis septentrionalis*), and combined species in the Montmorency Research Forest (47°19'N; 71°07'W), Québec (Canada). All values are rounded upward to two decimal places.

Habitat feature	Random (n = 40)	MYSE (n = 26)	MYLU (n = 14)	Combined (n = 40)
Tree DBH (cm)	15.53 \pm 0.85	20.17 \pm 0.84	21.64 \pm 1.29	20.69 \pm 0.71
Tree height (m)	6.63 \pm 0.47	9.34 \pm 0.64	10.01 \pm 3.01	9.57 \pm 0.50
Percent of remaining bark (%)	0.55 \pm 0.06	0.74 \pm 0.05	0.74 \pm 0.08	0.74 \pm 0.04
Number of snags \geq 10 cm DBH (n)	1.93 \pm 0.41	6.73 \pm 0.91	5.79 \pm 1.05	6.40 \pm 0.69
Number of snags \geq 20 cm DBH (n)	0.45 \pm 0.15	1.81 \pm 0.31	1.57 \pm 0.44	1.73 \pm 0.25
Number of 6 class snags (n)	1.13 \pm 0.31	4.68 \pm 0.68	3.17 \pm 0.80	3.44 \pm 0.54
Proportion of canopy gaps at 2 m (%)	0.54 \pm 0.07	0.76 \pm 0.07	0.77 \pm 0.08	0.76 \pm 0.05
Proportion of canopy gaps at 16 m (%)	0.67 \pm 0.04	0.71 \pm 0.04	0.66 \pm 0.04	0.69 \pm 0.03
Lateral vegetation cover at 2 m (%)	0.88 \pm 0.03	0.80 \pm 0.04	0.80 \pm 0.05	0.80 \pm 0.03
Lateral vegetation cover at 16 m (%)	0.31 \pm 0.04	0.27 \pm 0.06	0.27 \pm 0.06	0.29 \pm 0.04
Mean canopy height at 2 m (m)	13.04 \pm 0.57	10.12 \pm 0.97	8.05 \pm 1.11	9.40 \pm 0.75
Mean canopy height at 16 m (m)	13.85 \pm 0.42	13.20 \pm 0.54	13.81 \pm 0.58	13.41 \pm 0.40
Insolation level at 2 m (MJ/m ² /day) [*]	452.78 \pm 3.15	446.00 \pm 7.62	454.21 \pm 5.78	448.88 \pm 5.34
Insolation level at 16 m (MJ/m ² /day) [*]	453.10 \pm 2.71	449.38 \pm 5.08	457.36 \pm 3.43	452.18 \pm 3.54
Stand Basal area (m ² /ha)	24.80 \pm 2.59	31.77 \pm 2.76	25.43 \pm 3.36	29.55 \pm 2.17
Mean stand age (years)	47.80 \pm 3.66	62.23 \pm 2.86	45.93 \pm 5.44	56.52 \pm 2.90
Mean distance among roosts (m)	276.7 \pm 48.1	204.6 \pm 49.30	243.0 \pm 54.70	214.4 \pm 37.90

*Mean insolation level simulated every day of June and July 2011, from 0600 to 2000, at 47°17'60"N.

Table 5. Model number, number of estimated parameters (K), differences between model AICc and those of the best model (Δ_i) and Akaike weights (ω_i) for 20 Generalized Linear Mixed Models. All values are rounded upward to two decimal places.

# Model	K	Δ_i	ω_i
13 Bat sp + snags + gap 02 + height + DBH	7	0.00	0.66
14 Bat sp + snags + gap 02 + height + DBH + bark	8	2.47	0.19
10 Bat sp + snags + insolation 02 + gap 02 + height + DBH + bark	9	3.80	0.10
12 Bat sp + snags + cover 02 + height + DBH	7	6.84	0.02
9 Bat sp + snags + cover 02 + insolation 02 + height + DBH + bark	9	8.12	0.01
11 Bat sp + snags + height + DBH + insolation 02	7	9.04	0.01
16 Bat sp + snags + height + DBH	6	10.50	0.00
15 Bat sp + snags + height + DBH + bark	7	12.34	0.00
5 Bat sp + snags + cover 02 + insolation 02 + gap 02	7	13.55	0.00
6 Bat sp + snags + insolation 02 + gap 02	6	14.25	0.00
17 Bat sp + snags + DBH	5	17.49	0.00
7 Bat sp + snags + gap 02	5	19.01	0.00
2 Bat sp + snags + cover 16 + insolation 16 + gap 16	7	24.45	0.00
4 Bat sp + snags + gap 16	5	24.46	0.00
3 Bat sp + snags + insolation 16 + gap 16	6	25.13	0.00
8 Bat sp + snags	4	26.21	0.00
18 Bat sp + Height + DBH + bark	6	27.18	0.00
19 Bat sp + DBH + bark	5	34.17	0.00
20 Bat sp + DBH	4	34.94	0.00
1 Null	2	50.20	0.00

Table 6. List of variables, beta coefficients (β), standard errors (SE), odd ratios and 95 % confidence intervals (CI), Z-statistics and associated P -values from the best Generalized Linear Mixed Model ($\Delta_i = 0$). All values are rounded upward to two decimal places.

Variable	β	SE	Odds	95 % CI	Z	P-value
(Intercept)	-2.41	0.87				
MYSE*	0.69	0.84	1.98	0.38 - 10.23	0.82	0.41
Number of snags \geq 10 cm DBH (n)	0.41	0.11	1.51	1.21 - 1.88	3.62	<0.001
Proportion of canopy gaps at 2 m (%)	0.04	0.01	1.04	1.01 - 1.07	2.96	0.003
Tree height (m)	0.40	0.15	1.50	1.12 - 2.00	2.75	0.006
Tree DBH (cm)	0.24	0.08	1.28	1.08 - 1.50	2.90	0.004

*MYSE = *Myotis septentrionalis* (northern long-eared bat)

Figures

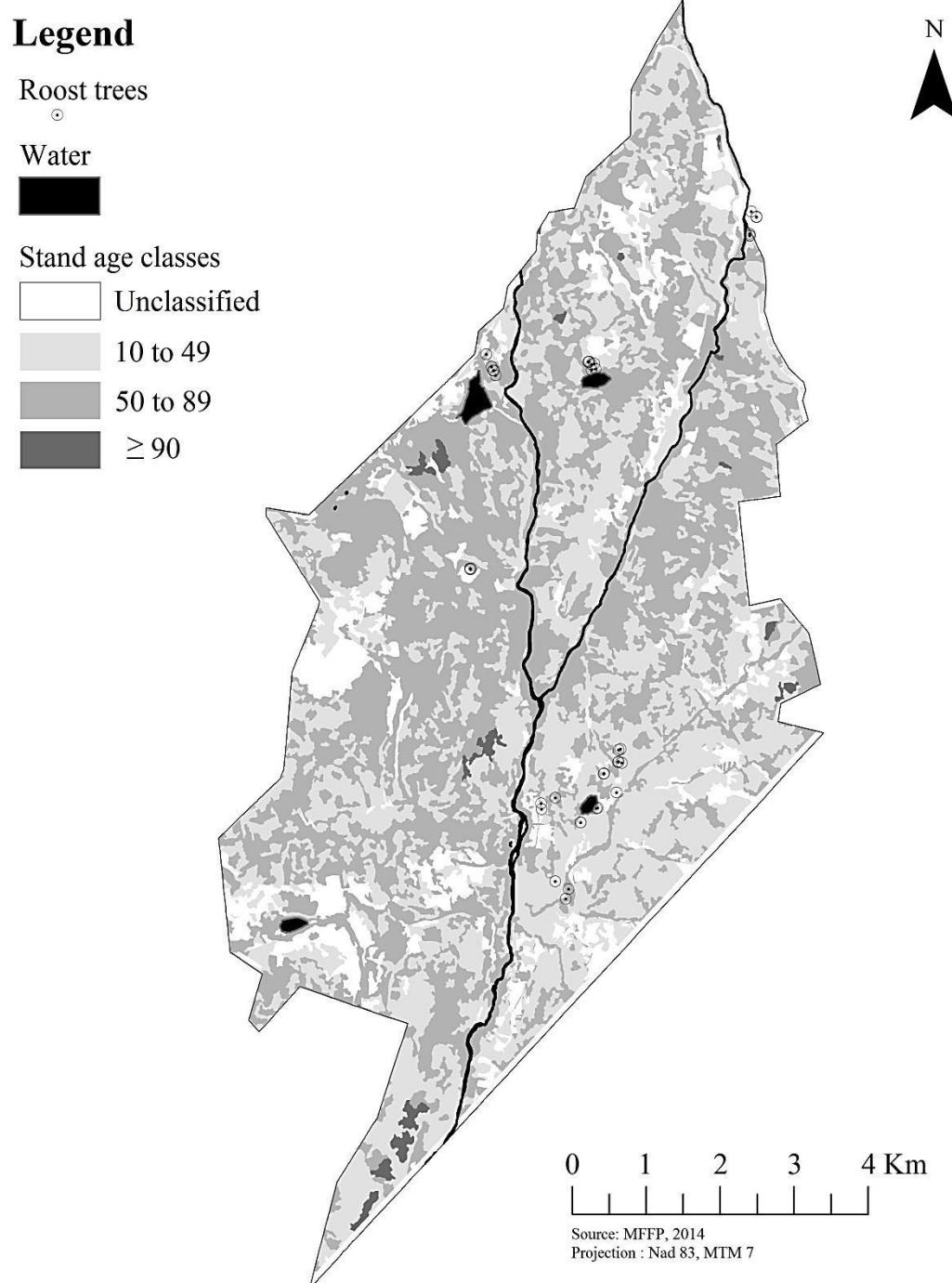


Figure 6. Location of the 40 roost trees across the Montmorency Research Forest ($47^{\circ}19'N$, $71^{\circ}07'W$) in Québec (Canada).

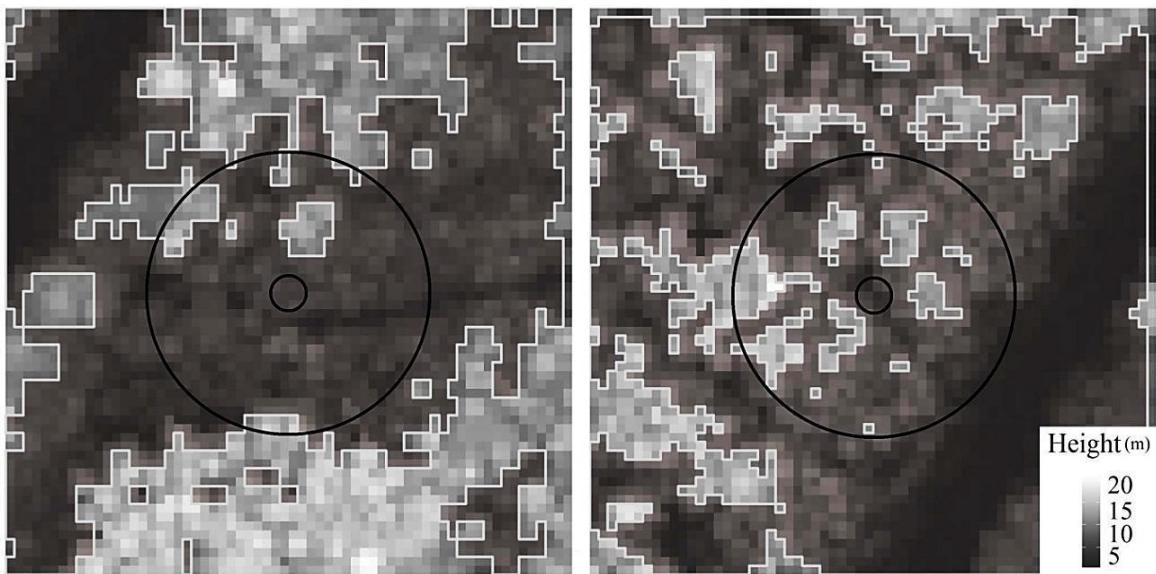


Figure 7. Proportion of trees recorded during plotless point-sampling in selected stands by male *Myotis* bats (996 trees), random locations (809 trees), selected roost trees by male *Myotis* bats ($n = 40$), and random trees ($n = 40$), distributed by decay class. Illustrations of decay classes (from 1 to 7) are modified from Imbeau and Desrochers (2002). In class (1) trees are alive with $\geq 95\%$ of foliage, showing no sign of deterioration; (2) senescent trees where remaining foliage is between $\geq 20\%$ and $< 95\%$; (3) senescent trees with $< 20\%$ foliage remaining; (4) recently dead trees with firm bark cover, 0 % green foliage and small twigs still remaining; (5) no dead foliage present, no small twigs; (6) loose bark cover, broken top, height still more than 50 % of what is observed on trees with same DBH; (7) broken top with height less than 50 % of what is observed on trees with same DBH.

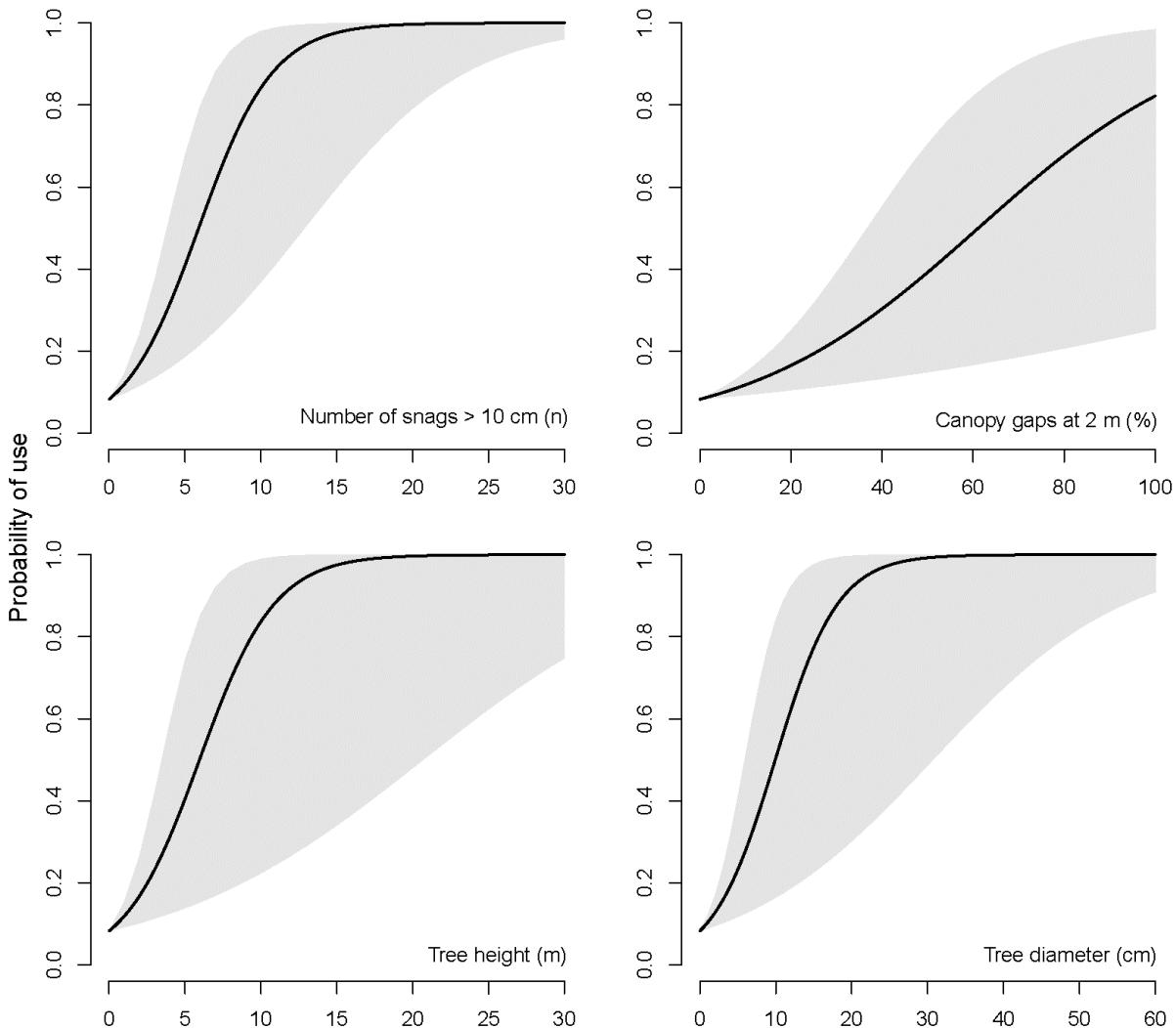


Figure 8. Mean stand height and canopy gap derivations at 2 and 16 m radius buffers around a roost (right) that was selected by a little brown bat (*Myotis lusifugus*) and its paired random tree (left), in the Montmorency Research Forest, Québec, Canada. Black circles show the radius buffers 2 m and 16 m around each tree. Highlighted white areas correspond to vegetation openness greater than 2 m^2 with tree height two-thirds lower than the surrounding mean stand height.

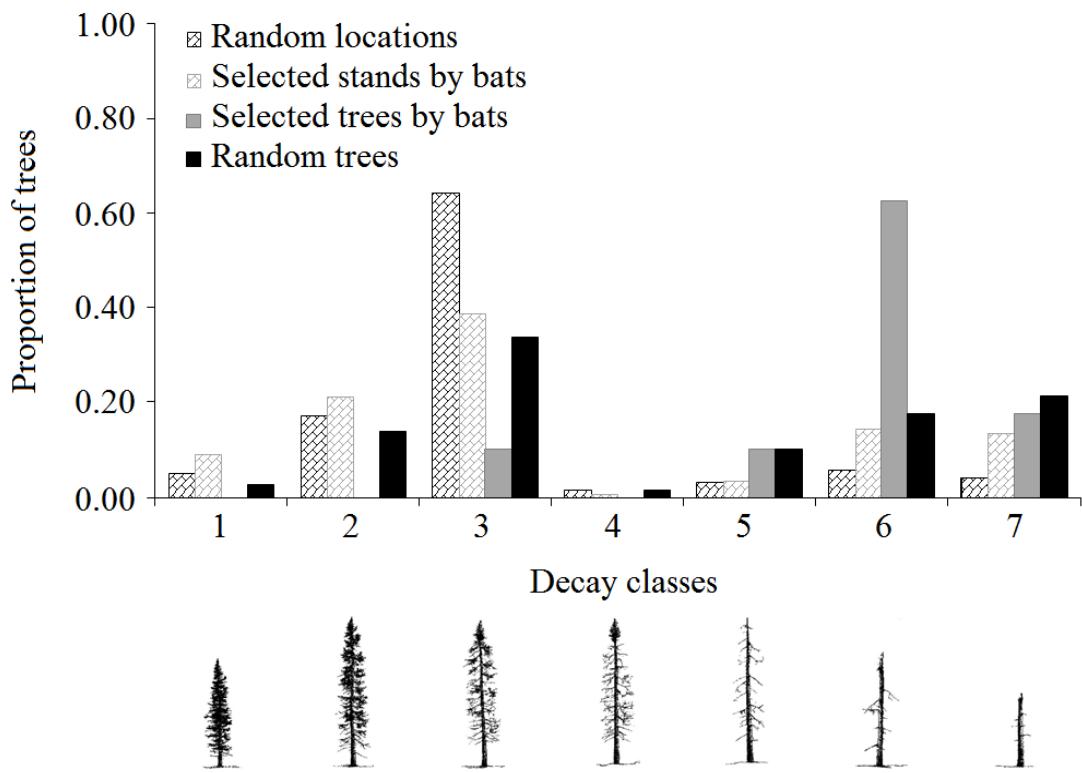


Figure 9. Estimated probability of use by male *Myotis* bats (black curve) with 95 % confidence intervals (grey area) as a function of the number of snags ≥ 10 cm DBH (n), proportion of canopy gaps (%), tree height (m) and tree DBH (cm). Prediction curves are derived from the General Linear Mixed Model estimates with the lowest AICc.

CHAPITRE 3 - ROOSTING HABITAT SUITABILITY FOR MALE *MYOTIS* BATS IN A BOREAL FOREST

François-Henri Fabianek, Centre d'Étude de la Forêt (CEF), and Faculté de Foresterie, de Géographie et de Géomatique, Université Laval, 2405, rue de la Terrasse, Québec, Québec G1V 0A6, Canada

Marie Anouk Simard, Ministère des Forêts, de la Faune et des Parcs (MFFP), 880, chemin Sainte Foy, Québec, Québec G1S 4X4, Canada

Centre de la Sciences de la Biodiversité du Québec (CSBQ), and Faculté de Foresterie, de Géographie et de Géomatique, Université Laval, 2405, rue de la Terrasse, Québec, Québec G1V 0A6, Canada

André Desrochers, CEF and Faculté de Foresterie, de Géographie et de Géomatique, Université Laval, 2405, rue de la Terrasse, Québec, Québec G1V 0A6, Canada

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Résumé

Les cartes de qualité d'habitat sont utiles pour localiser et conserver l'habitat faunique à l'échelle du paysage. Nous avons estimé la répartition spatiale et la proportion d'habitats diurnes potentiels à travers la sapinière (*Abies balsamea* [L.] Miller) à bouleau blanc (*Betula papyrifera* Marshall) de l'Est du Québec (Canada) pour les mâles de la petite chauve-souris brune (*Myotis lucifugus* (Le Conte, 1831)) et la chauve-souris nordique (*Myotis septentrionalis* (Trouessart, 1897)). Nous avons utilisé le diamètre moyen du peuplement, le décompte de chicots, la hauteur de chicot, la distance aux plans d'eau de superficie d'au moins 20 m^2 , l'âge du peuplement forestier et l'élévation pour construire des modèles d'habitat de perchage potentiels pour chaque espèce de chauves-souris et pour les deux espèces combinées au genre *Myotis*. Nous avons eu recours à plusieurs bases de données pour générer une carte raster correspondant à chacune des variables préalablement mentionnées. Nous avons extrait les classes d'âge et de hauteur des peuplements des cartes écoforestières du 4eme inventaire forestier du Québec. Nous avons calculé la distance Euclidienne des points d'eau $\geq 20 \text{ m}^2$ à partir d'une carte hydrographique et récupéré l'élévation à partir d'un Modèle d'Élévation de Terrain. Parce que les cartes raster de diamètre moyen du peuplement et de décompte de chicots n'étaient pas disponibles, nous avons d'abord extrait ces variables de 898 placettes échantillons permanentes localisées au sein de l'aire d'étude. Nous avons ensuite extrait les classes de pente, de drainage, d'âge, de hauteur, de type et de densité de peuplement des cartes écoforestières, que nous avons utilisés comme proxy pour prédire le diamètre moyen du peuplement et le décompte de chicots au sein de l'aire d'étude. Nous avons utilisé une procédure de classification par Random Forest pour dériver les cartes raster des modèles prédictifs de diamètre moyen du peuplement, de décompte de chicots et d'habitat de perchage potentiel pour les espèces combinées au genre. Nous avons majoritairement retrouvés les meilleurs habitats diurnes potentiels dans les peuplements de basse élévation. La distribution des habitats diurnes potentiels se chevauchait pour les deux espèces de chauves-souris. Toutefois la sapinière à bouleau blanc semble plus propice aux mâles de la chauve-souris nordique qu'à ceux de la petite chauve-souris brune.

Abstract

Habitat suitability maps are useful for locating and conserving wildlife habitat at the landscape scale. We estimated the spatial distribution and proportion of suitable roosting habitats across the eastern balsam fir (*Abies balsamea* [L.] Miller)-paper birch (*Betula papyrifera* Marshall) forest of Quebec (Canada) for male little brown bat (*Myotis lucifugus* (Le Conte, 1831)) and male northern long-eared bat (*Myotis septentrionalis* (Trouessart, 1897)). We used mean tree diameter, snag counts, snag height, distance to ponds of at least 20 m² area, forest stand age, and elevation to build roosting habitat suitability models for each bat species alone and in combination. We relied on several databases to build a raster map corresponding to each aforementioned explanatory variable. We extracted stand age and tree height classes from ecoforest maps of the 4th forest inventory program of Québec. We computed Euclidean distance to ponds ≥ 20 m² from a hydrographic map and retrieved elevation from a digitalized elevation model. Because raster maps of mean tree diameter and snag counts were not available, we extracted these variables from 898 permanent sample plots that were located across the study area. We also extracted slope gradient, water drainage, stand age, stand height, stand type, and stand density classes from forest inventory maps, to use them as proxies in predicting mean tree diameter and snag counts across the study area. We used a Random Forest classification procedure to derive raster maps from predictive models of mean tree diameter, snag counts, and roosting habitat suitability of *Myotis* bat species. The best suitable roosting habitats were predominantly found in stands at lower elevations. The distribution of suitable roosting habitats overlapped for both species of bats. Yet, the balsam fir-paper birch forest appeared to be more suitable for male northern long-eared bat compared to male little brown bat.

Introduction

Silvicultural practices are known to decrease the proportion of old-growth forest (Boucher *et al.* 2009; Cyr *et al.* 2009; Bergeron & Fenton 2012) and the availability of snags (Harper *et al.* 2007; Wisdom & Bate 2008; Smith, Moroni & Warkentin 2009) within the landscape. Snags and coarse woody debris are essential habitat components for numerous wildlife species (Drapeau *et al.* 2009) and their abundance can increase significantly for several years after the age at which logging normally occurs (Sturtevant *et al.* 1997; Franklin *et al.* 2002; Vanderwel *et al.* 2006; Smith, Warkentin & Moroni 2008; Moroni & Harris 2010). Several species of birds, such as woodpeckers (*Dryocopus pileatus*; Savignac, Desrochers & Huot 2000; Imbeau & Desrochers 2002), and small mammals, such as flying-squirrels (*Glaucomys* spp; Smith 2007), rely upon large snags in the boreal forest as food sources or shelters.

A fine-filter conservation strategy (Noss 1987) involves locating the types of areas that best promote the persistence of threatened or key species (Flather *et al.* 2009) and determining to what extent these areas are represented throughout the forested landscape. This requires decision-making tools that integrate complex interactions between species and key habitat features at multiple spatial scales (George & Zack 2001). Habitat suitability modelling is a GIS-based method that is appropriate, especially for raster data (Beck & Suring 2009; Thuiller & Münkemüller 2010). This modelling allows the capacity of a given habitat to be evaluated regarding its support for a given species, based on species-specific habitat requirements (Beck & Suring 2009). There is a wide range of available habitat suitability modeling techniques that rely upon abundance, presence-only, or presence-absence data to identify the explanatory variables that best explain habitat use of the targeted species (Larson *et al.* 2009; Thuiller & Münkemüller 2010). Random Forests® is an ensemble machine-learning technique (*e.g.*, regression, classification or unsupervised tasks) that produces multiple decision trees relying upon presence-absence data (Breiman 2001). It has been successfully employed in habitat suitability and species distribution modelling (Garzón *et al.* 2006; Cutler *et al.* 2007; Magness *et al.* 2008; Vezza *et al.* 2012).

Forest-dwelling bats are good candidates for performing habitat suitability models in an actively logged landscape because of their sensitivity to forest disturbances (Hogberg,

Patriquin & Barclay 2002; Patriquin & Barclay 2003; Jones *et al.* 2009), especially forest fragmentation (Henderson & Broders 2008; Segers & Broders 2014). The importance of canopy openings, tree height and tree diameter in roost selection by cavity-roosting bats (Kalcounis-Rueppell, Psyllakis & Brigham 2005) are generally associated with the microclimate hypothesis (Boyles 2007), for which individuals should find roosts that best minimize thermoregulation costs (Johnson & Lacki 2014). A roost that is located at the top of a tree and within a canopy opening should incur greater heat transfer through insolation. Similarly, a tree with large diameter should provide greater thermal inertia (Park & Broders 2012) compared to a smaller diameter individual (Sedgeley 2001; Wiebe 2001). Bats also appear to be sensitive to elevation. Bats are less active and fewer females are recovered at high elevation compared to lower elevations (Grindal, Morissette & Brigham 1999; Cryan, Bogan & Altenbach 2000; Russo 2002), probably because of harsher climatic conditions and lower insect availability in the former (Grindal, Morissette & Brigham 1999; Erickson & Adams 2003).

The little brown bat (*Myotis lucifugus* (Le Compte, 1831)) and northern long-eared bat (*Myotis septentrionalis* (Trouessart, 1897)) have been recently added to Schedule 1 of the Species at Risk Act (SARA) and are considered endangered species in Canada (Gouvernement du Canada 2014). Our aim was to build fine-scale roosting habitat suitability models (*i.e.*, 1 km x 1 km raster grid maps) for these two bat species, alone and in combination, throughout the eastern part of the Laurentian Highlands of Quebec (Canada). We were interested in (1) finding the most influent variables in our habitat suitability models, (2) to locate the most suitable roosting areas in the forested landscape, (3) estimating the proportion of these areas for each species, and (4) estimating to what extent these areas overlap between the two species of bats.

Both *Myotis* bat species rely upon snags for roosting (Kalcounis-Rueppell, Psyllakis & Brigham 2005; Fabianek *et al.* 2015), giving birth, and raising young during the summer (Barclay & Kurta 2007). Their home ranges during feeding rarely exceed 10 km from their roosting sites (Henry *et al.* 2002; Broders 2003; Owen *et al.* 2003; Broders *et al.* 2006; Henderson & Broders 2008; Randall, Jung & Barclay 2014), perhaps to reduce commuting costs (Henry *et al.* 2002), predation risk (Jung *et al.* 2011), or both. They seem, however, to differ in their habitat use for roosting (Broders & Forbes 2004) and feeding (Patriquin &

Barclay 2003; Broders *et al.* 2006). Compared to the northern long-eared bat, the little brown bat relies more upon human-made structures for roosting (Broders, Burns & McCarthy 2013). The little brown bat is mainly associated with ponds (Fenton & Barclay 1980) and forested areas less cluttered by vegetation (Owen *et al.* 2004; Broders *et al.* 2006), while the northern long-eared bat is considered an interior-forest obligate that is associated with cluttered forested areas (Owen *et al.* 2003; Ford *et al.* 2005; Loeb & O'Keefe 2011), mature stands (Loeb & O'Keefe 2006; Conley 2011), and less fragmented areas (Henderson, Farrow & Broders 2008; Segers & Broders 2014). Because of different habitat use related to their feeding behaviour, we expected *Myotis* species to use snags located in different areas (*i.e.*, closer to ponds for little brown bat, and closer to mature and old-growth stands for northern long-eared bat) across the landscape. If these differences are sufficiently pronounced at the landscape scale, we should find little overlap between suitable roosting habitats of the two species of bats.

Material and methods

Study area

We applied habitat suitability models over the eastern part of the Laurentian Highlands (47°34'N; 70°48'W; Figure 10). This mountainous forested area of 12380 km² is located in the southern part of the Canadian Shield, between Quebec City and the region of Saguenay-Lac-Saint-Jean (Figure 10). The area includes three national parks, *viz.*, the Parc National de la Jacques-Cartier (670 km²) the Parc National des Grands Jardins (310 km²), and the Parc National des Hautes-Gorges-de-la-Rivière-Malbaie (225 km²), which have been free of logging since the early 1980s. Other sectors, including a wildlife reserve (Réserve faunique des Laurentides, 7,861 km²) and the Montmorency Research Forest (412 km²), are being actively managed using clear cutting, partial cutting and shelter-wood cutting, following an ecosystem-based management program (Grenier 2009).

The bioclimatic domain is mainly represented by the eastern balsam fir (*Abies balsamea* [L.] Miller)-paper birch (*Betula papyrifera* Marshall) association. Here, the boreal forest alternates between mixed and coniferous stands, with marginal patches of deciduous stands. Balsam fir, white spruce (*Picea glauca* [Voss] Moench) and black spruce (*Picea mariana* Miller BSP) are the main softwood species. Paper birch, yellow birch

(*Betula alleghaniensis* Britton), and trembling aspen (*Populus tremuloides* Michx.) are the main hardwood species (Grenier 2009). Young stands (< 50 y) and commercially mature forests (50 to 70 y) cover 45.3 % and 38.3 % of the study area, respectively. The remaining 16.4 % is represented by old-growth stands (> 70 y), which rarely exceed 120 years of age. Mean elevation is 800 m asl (range: 26 - 1144 m), mean annual rainfall is 1400 mm (range: 1200 - 1600 mm), and mean summer temperature is of 11.4 °C (range: 4 - 16.4 °C). In this wet boreal forest, natural disturbances are mainly caused by outbreaks of spruce budworm (*Choristoneura fumiferana* Clemens) and windthrows (Grenier 2009; Waldron *et al.* 2013).

Explanatory variable selection and telemetry data

We based our habitat suitability models on six explanatory variables: mean tree diameter at breast height (DBH, 1.3 m), snag counts with DBH \geq 10 cm, snag height (m), stand age, distance to ponds \geq 20 m², and elevation (Table 7). We selected these explanatory variables *a priori*, based on a synthesis of 34 studies on roost selection by cavity-roosting bats in North America, and a study on roost selection by male *Myotis* bats performed at the Montmorency Research Forest (Fabianek *et al.* 2015). Although canopy openings play a role in roost selection by *Myotis* bats in this area (Fabianek *et al.* 2015), we could not include this explanatory variable in our habitat suitability models due to the lack of available raster maps.

We obtained radio-tracking data from (Fabianek *et al.* 2015), with tree use as a binary response variable. This dataset (Table 7) included tree DBH, snag counts with DBH \geq 10 cm, height, and degradation class (Imbeau & Desrochers 2002) from 40 random trees and 40 roost trees that had been selected by male little brown bats (n random trees = 14, n roost trees = 14) and male northern long-eared bats (n random trees = 26, n roost trees = 26). To account for additional landscape variables (*e.g.*, stand age, elevation and distance to ponds), we extracted stand age estimates from forest inventory maps of the 4th forest inventory program of Québec (2003-2013) and elevation from a digital elevation model. We performed a proximity analysis of trees to the closest pond \geq 20 m² using a hydrographic map in ArcGIS (version 10.1, Environmental Systems Research Institute, Redlands, CA, USA). All digitized maps were provided by the Government of Québec's Ministère des Forêts, de la Faune et des Parcs (MFFP).

Building a raster map for each explanatory variable

We relied upon several geo-databases to generate raster maps from explanatory variables that matched habitat variables that were used by Fabianek *et al.* (2015) (Table 7). We used ArcGIS to extract stand height and stand age from forest inventory maps, to retrieve elevations from a digital elevation model, and to calculate Euclidean distances to every pond $\geq 20 \text{ m}^2$ from a hydrographic map of the study area. *Myotis* bats at the Montmorency Research Forest mainly selected class 6 snags (Fabianek *et al.* 2015), *i.e.*, dead trees with a broken tip, with a height that was still more than 50 % of what was observed for trees with similar DBH (Imbeau & Desrochers 2002). We thus converted stand heights to class 6 snag heights by dividing stand height raster values by two (as a minimum height threshold value of 50 %).

We relied upon the network of permanent sample plots that had been established by the MFFP to estimate mean tree diameter and snag counts at the landscape scale. Permanent circular sample plots (400 m^2) assessed, in which every living and dead tree with a DBH $\geq 10 \text{ cm}$ was recorded. Permanent sample plots are sampled on average every 10 years, yielding between 1 to 4 inventories per sample plot. We used the most recent inventories for which the oldest sample plots were inventoried in 2003. We used only snags $\geq 10 \text{ cm}$, excluding all living trees and stumps, to estimate snag counts. We used only DBH measured on dominant balsam fir to estimate mean tree diameter. We extracted stand type (mixed or coniferous), stand density, stand height, stand age, water drainage (*i.e.*, the speed at which a surplus of water drains itself from the ground), and slope classes from forest inventory maps (Appendix 2. Figure 1) and used them as proxies (Bacaro *et al.* 2011) to generate raster maps of mean tree diameter and snag counts (Figure 11). We eliminated deciduous stands from our analysis (and subsequent raster maps) because of the lack of radio-tracking data for this habitat type.

A quick look into the Random Forest

To construct a training dataset, the Random Forest algorithm (Liaw & Wiener 2002; R Development Core Team 2015) builds a large ensemble of decision trees from bootstrapped samples of the original dataset. When each decision tree is growing, a random subset of explanatory variables is permuted at each node (Breiman 2001). The underlying

idea is that if a given explanatory variable is strongly associated with the response variable, random permutation should greatly increase classification error rates.

While the forest is growing, about one-third of the decision trees are excluded from the sample and referred as the “Out-Of-the-Bag” (OOB), which is a validation dataset (Breiman 2001). The OOB is used to estimate the Random Forest model classification error rate and to provide a relative measure of variable importance (Breiman 2001). The OOB error rate may also be used to find the optimal number of decision trees (*i.e.*, with the lowest OOB error rate) and the optimal number of explanatory variables to permute at each node (Breiman 2001). The OOB error rate is the mean proportion of classification error rates over all trees in the Random Forest.

Mean Decrease Accuracy (MDA) and Mean Decrease Gini (MDG) measure the relative importance of each explanatory variable that is included in the Random Forest. Classification error rates between predictions that are generated from the OOB and the original dataset are used to estimate MDA variable importance. MDA increases when the addition of an explanatory variable decreases the classification error rate. MDG is a measure of node impurity that is computed each time an explanatory variable is used to split a node. Impurity (or heterogeneity) of a given node depends upon the number of observations that belong to the same class within that node. MDG variable importance increases when decreases are observed in the Gini impurity index (Liaw & Wiener 2002). Gini impurity is a common measure of misclassification used in classification and regression trees. When Random Forest is used for regression, the importance of an explanatory variable is given by the Mean Squared Error (MSE) instead of MDA (Liaw & Wiener 2002). MSE is expressed as a percentage and, like MDA, measures the loss of predictive power when a given explanatory variable is randomly permuted. Higher values of MSE indicate the greater importance of an explanatory variable.

Our Random Forest procedures

Prior to our analyses, we assessed the presence of collinearity (*i.e.*, Pearson $r \leq 0.7$) between explanatory variables using median Pearson correlation coefficients (Dormann *et al.* 2013). We found the strongest correlation (Pearson $r = 0.59$) between stand height and stand age. We performed two Random Forest nonlinear regression models that predicted

mean tree diameter and snag counts (Appendix 2. Figure 2). Predictions from these models were used to generate raster maps of mean tree diameter and snag counts over the study area (Figure 11). We then performed three Random Forest classification procedures to predict roosting habitat suitability models for little brown bat, northern long-eared bat, and the combined species.

We constructed all of our Random Forest models with 5000 trees without replacement (Strobl *et al.* 2007) and used MDA, MSE and MDG that were provided by the randomForest package (Liaw & Wiener 2002) in R (R Development Core Team 2015) to assess the relative importance of each explanatory variable (Calle & Urrea 2011). We verified *a posteriori* that 5000 trees were sufficient to stabilize the OOB error rate for each Random Forest model. Stabilization of the OOB error rate occurred between 600 and 3100 trees in our analyses. We used a default random permutation value of 1 and tested *a posteriori* if increasing values decreased the OOB error rate. A random permutation value of 1 incurred the most decreases in OOB error rates, except when predicting mean tree diameter, where a value of 6 was required instead. We used partial dependence plots to visualize the marginal effect of each explanatory variable on mean tree diameter, snag counts (Appendix 2. Figure 3), and predicted probabilities of use by each species of bat and combined species (Figure 12).

Evaluating overlap and model performance

We extracted predictions from our Random Forest models to generate each habitat suitability model. We computed Schoener's D statistic (0 = no overlap; 1 = complete overlap), a measure of niche overlap (Schoener 1968) on the probability surfaces of each habitat suitability model (Warren *et al.* 2008) to quantify to what extent suitable roosting areas overlapped between the two species of bats.

We evaluated the performance of each Random Forest classification model with a Receiver Operating Characteristic (ROC) curve (Fielding & Bell 1997; Greiner *et al.* 2000; Boyce *et al.* 2002). The true positive rate of each classification is plotted against its false positive rate and the resulting Area Under the Curve (AUC) is calculated (Fawcett 2006). AUC values between 1 and 0.9 are considered excellent, while AUC values ≤ 0.5 have no predictive power (Greiner, Pfeiffer & Smith 2000). We evaluated the predictive power of

our Random Forest regression models by plotting observed values (*i.e.*, response variables) against predicted values from the OOB samples. We graphically determined intercept and slope deviations from the 1:1 line (Appendix 2. Figure 2), and relied upon r^2 to evaluate Random Forest regression model performance (Piñeiro *et al.* 2008).

Results

Evaluating Random Forest model performances

Random Forest classification models performed very well for the combined species (AUC = 0.95; OOB error rate = 10 %), for the northern long-eared bat (AUC = 0.90; OOB error rate = 6 %), and the little brown bat (AUC = 0.86; OOB error rate = 14 %). Random Forest regression models explained 40.5 % of the variance for mean tree diameter (r^2 = 0.40, $P < 0.00001$; mean of squared residuals = 4.9) and 37.8 % for snag counts (r^2 = 0.38, $P < 0.00001$; mean of squared residuals = 23.3). Mean tree diameter were slightly under-predicted when high mean tree diameter values are observed (Appendix 2. Figure 2). Conversely, snag counts were slightly over-predicted when low numbers of snags are observed (Appendix 2. Figure 2).

Partial dependence and variable importance plots

We present partial dependence plots illustrating the marginal effect of each variable that was included in our Random Forests (Figure 12 for classification; Appendix 2. Figure 3 for regression). We obtained similar responses to tree diameter, snag height, snag counts and distance to ponds by the two species of bats. Responses varied, however, for stand age and elevation (Figure 12).

We also present Mean Decrease Accuracy (MDA), Mean Decrease Gini (MDG), and Mean Squared Error (MSE) to illustrate the relative importance of each variable that was included in our Random Forests (Figure 13; Appendix 2). Roosting habitat suitability for northern long-eared bat was best described by distance to ponds (MDA = 67.3; MDG = 3.0), but was poorly predicted by snag height (MDA = 29.6; MDG = 2.3). Distance to ponds best predicted roosting habitat for the little brown bat (MDA = 62.1; MDG = 2.2), which was poorly predicted by stand age (MDA = 5.8; MDG = 0.9). Roosting habitat for combined species was best predicted by snag counts (MDA = 78.7; MDG = 4.5) and poorly predicted by snag heights (MDA = 42.8) and stand age (MDG = 3.4). Mean tree diameter

was best predicted by stand height ($\text{MSE} = 492.2$; $\text{MDG} = 636.9$) and poorly predicted by water drainage ($\text{MSE} = 301.5$) and stand type ($\text{MDG} = 217.4$). Snag counts was best predicted by stand age ($\text{MSE} = 130.9$; $\text{MDG} = 1207.6$), and poorly predicted by stand type ($\text{MSE} = 47.2$; $\text{MDG} = 179$).

Location, proportion and overlap of suitable roosting habitats

Roosting habitat suitability values ranging from 0.6 to 1 represented 19 % of the total habitat suitability model for northern long-eared bat, 1 % for little brown bat and 13% for the combined species (Figure 14). Schoener's D indicated that 80 % of roosting habitat suitability overlapped between northern long-eared bat and little brown bat (Schoener's D = 0.8).

Discussion

Random Forest model performance and bias

Random Forest models that were applied to define suitable roosting habitats had strong predictive power. Proxies from forest inventory maps were adequate for building predictive raster maps of mean tree diameter and snag counts across the study area. Random Forest regression models overestimated snag counts in stands with snag densities that were less than 3 snags per 0.01 ha (Appendix 2. Figure 3). Because such stands were rarely used as roosts by bats (*i.e.*, partial probability of use < 0.2), we are confident that this overestimate did not compromise our habitat suitability models. Underestimates of mean tree diameter increased gradually, but remained of low magnitude (Appendix 2. Figure 2), which again indicated a low incidence in modeling performance of our habitat suitability models.

The most influent variables explaining roosting habitat suitability

Consistent with other studies (Peng *et al.* 2001; Claveau *et al.* 2002; Kalliovirta & Tokola 2005; Sharma & Parton 2007), we found that stand height was a good predictor of mean tree diameter. According to McCarthy and Weetman (2006), and Moroni and Harris (2010), the proportion of balsam fir with large diameters increased considerably in old-growth forests that were > 120-years-old. The oldest stands in our study area rarely exceeded 90 years, which could partially explain why stand age had little influence on our

estimates of mean tree diameter, which contrasts with results that were obtained by Arseneau *et al.* (1997), Thompson *et al.* (2003), and Moroni and Harris (2010).

In our study, stand height was an important variable predicting the abundance of snags because it was correlated with stand age, a response that was also found by Kalliovirta and Tokola (2005), and McCarthy and Weetman (2006). Stand age best predicted the abundance of snags. Several studies in wet boreal forest have reported an increasing number of snags in old-growth stands compared to younger stands (McCarthy & Weetman 2006; Vanderwel, Caspersen & Woods 2006; Smith, Warkentin & Moroni 2008; Moroni & Harris 2010).

As discussed by Fabianek *et al.* (2015), tree diameter, tree height, and snag counts have all positive influence on habitat use by little brown bat and northern long-eared bat. Similarly, *Myotis* species are frequently found near ponds (Brooks & Ford 2005; Broders *et al.* 2006; Fabianek *et al.* 2011), especially the little brown bat (Owen *et al.* 2004; Broders *et al.* 2006; Segers & Broders 2014). Differences between *Myotis* species partly stem from their preferences for stand age and elevation. For the northern long-eared bat, stand age and snag counts best-determined suitable roosting habitats, together with distance to ponds. Conversely, stand age was the least important variable with respect to suitable habitat for little brown bat. Little brown bat used snags in young (*i.e.*, < 50-years-old) and in mature stands (*i.e.*, between 50- and 80-years-old), while northern long-eared bat only used snags in mature stands (Fabianek *et al.* 2015). Differences in preference with respect to stand age might be linked to different habitat needs for both roosting (Broders & Forbes 2004; Olson 2011) and feeding (Patriquin & Barclay 2003; Broders *et al.* 2006).

Localization of suitable roosting areas across the forested landscape

Summits in the eastern part of the Laurentian Highlands did not provide suitable roosting habitats for male *Myotis* bats, especially for little brown bat. Harsh climatic conditions are encountered at high elevations, both for bats (Cryan, Bogan & Altenbach 2000; Senior, Butlin & Altringham 2005; Bellamy *et al.* 2013; McGuire & Boyle 2013) and for trees (Cogbill & White 1991). Black spruce-balsam fir stands are more common at high (> 900 m) than on lower elevations (Cogbill & White 1991; Grenier 2009). Stands that are dominated by black spruce have reduced DBH (Vaillancourt *et al.* 2008; Moroni & Harris

2010) and possibly fewer snags compared to stands at low elevation, where balsam fir is dominant (Vaillancourt *et al.* 2008; Moroni & Harris 2010). Stand characteristics, when coupled with cool nights and potentially reduced insect availability (Grindal, Morissette & Brigham 1999), likely decrease the suitability of high elevation stands for *Myotis* bats.

Overlap and proportion of suitable roosting areas for each species of bat

Male little brown bat and male northern long-eared bat had 80 % overlap in their suitable roosting areas, suggesting that they are likely to use the same potential sites, especially the lowland balsam fir-paper birch stands that were located in the northwestern portion of the study area. This information may be crucial for designing protected areas that are shared by both *Myotis* species. Fabianek *et al.* (2015) did not detect sufficiently pronounced differences in the ecology of the two *Myotis* species for this to be reflected in roosting habitat suitability maps. Of course, the finding that both *Myotis* species are likely to exploit the same potential habitats does not exclude hypotheses that they might use different resources for roosting within these suitable roosting habitats (Broders & Forbes 2004; Lacki, Cox & Dickinson 2009a; Olson 2011), or that they might use different nearby feeding habitats (Patriquin & Barclay 2003).

Despite a substantial overlap for suitable roosting habitat between the two *Myotis* species, balsam fir-paper birch forest appeared to be more suitable for northern long-eared bat (*i.e.*, 19 % of suitable roosting habitat) compared to little brown bat (*i.e.*, 1 % of suitable roosting habitat; Figure 14). These results are supported by mist-netting data that were obtained by Fabianek *et al.* (2015), who had a greater capture success with northern long-eared bat in the Montmorency Research Forest. In Newfoundland, Park and Broders (2012) found that this species was more widely distributed than little brown bat across wet boreal forest that was dominated by balsam fir. Most little brown bats that were captured in the Montmorency Research Forest were found in human-made structures (Fabianek *et al.* 2015). Broders and Forbes (2004) in New Brunswick and Broders, Burns and McCarthy (2013) in Labrador similarly observed disparities in the use of human-made structures by these two *Myotis* species. It is possible that human-made structures facilitate the establishment of little brown bat beyond its natural range in the boreal forest. In doing so,

this species might be over-represented in habitats with low roosting habitat suitability in boreal forest.

Major limitations for building roosting habitat suitability models

We faced certain limitations that are associated with the use of permanent sample plots to generate raster maps of mean tree diameter and snag counts. The lack of data on tree degradation stages in permanent sample plots and the lack of permanent sample plots in national parks have limited both the accuracy and range of our predictive models. Not being able to obtain or generate raster maps that closely match explanatory variables that were collected in the field represents a major constraint when building habitat suitability models. Although canopy openings have been documented to influence roost selection by *Myotis* bats at the Montmorency forest (Fabianek *et al.* 2015), we were unable to include this variable in our habitat suitability models. Its inclusion would have required LiDAR coverage of the entire study area that is not yet available. Finally, our results should be interpreted by keeping in mind that they do not take into account gender-specific requirements. Several studies have shown sexual segregation in habitat use between males and females of various species of bats (Cryan, Bogan & Altenbach 2000; Russo 2002; Senior, Butlin & Altringham 2005; Arnold 2007; McGuire & Boyle 2013). Female bats are likely to have roosting habits that differ from males (Broders & Forbes 2004; Perry *et al.* 2007; Randall, Jung & Barclay 2014), suggesting that our habitat suitability models, which pertain only to males, cannot be applied to female bats.

Conclusion

Despite the lack of information on females, we found that boreal forest stands with high suitability for both *Myotis* species included 1 to 19 % of the study area. Several variables that explained roosting habitat suitability (*e.g.*, snag density, stand age and stand height) were associated with and mature and old-growth forests. These preliminary results are consistent with previous recommendations to increase the proportion of old-growth forest (Vaillancourt *et al.* 2009a; Rompré *et al.* 2010), which represents only 16.4 % of the study area. These residual patches should preferentially be connected to or located near ponds to provide suitable roosting habitat for bats. Maintaining a heterogeneous forested landscape that arises from a diverse mosaic of stand ages is a sustainable forest management practice

(Burton *et al.* 2010; Drapeau *et al.* 2010; Gauthier *et al.* 2010), which would certainly contribute to conserving suitable habitats for bats and other old boreal forest specialists, such as brown creeper (Poulin *et al.* 2008), marten (Thompson 1991), and black-backed woodpecker (Drapeau *et al.* 2009; Nappi & Drapeau 2011)

Acknowledgements

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Tables

Table 7. List of explanatory variables that were included in Random Forest models. Range of values are from radio-tracking data that were collected at the Montmorency Research Forest ($47^{\circ}19'N$; $71^{\circ}07'W$) by Fabianek *et al.* (2015) and from explanatory variables that were used to build roosting Habitat Suitability Model (HSM) raster maps. All values are rounded upward to one decimal place.

Code	Variable description	Telemetry range	HSM map range	Unit
DBH	Mean tree (balsam fir) diameter	8.9 – 31.1	9.0 – 19.0	cm
Snag	Snag counts with DBH ≥ 10 cm	0.0 – 17.0	1.0 – 7.0	<i>n</i>
Snag_ht	Snag height (stand height / 2)	2.1 – 17.4	1.0 – 12.5	m
Age	Stand age classes	10 – 90	10 – 120	Class
Pond	Distance to the closest pond ≥ 20 m ²	0.3 – 2.6	0.0 – 16.0	km
Elev	Elevation	0.6 – 0.9	0.0 – 1.1	km
Type	Mixed or coniferous stands	(M) or (C)	(M) or (C)	Class
Dens	Stand density class	-	30 – 90	%
Stand_ht	Stand height	-	2.0 – 25.0	m
Drain	Water drainage class	-	0 – 100	%
Slope	Slope gradient	-	1 – 42	%

Figures

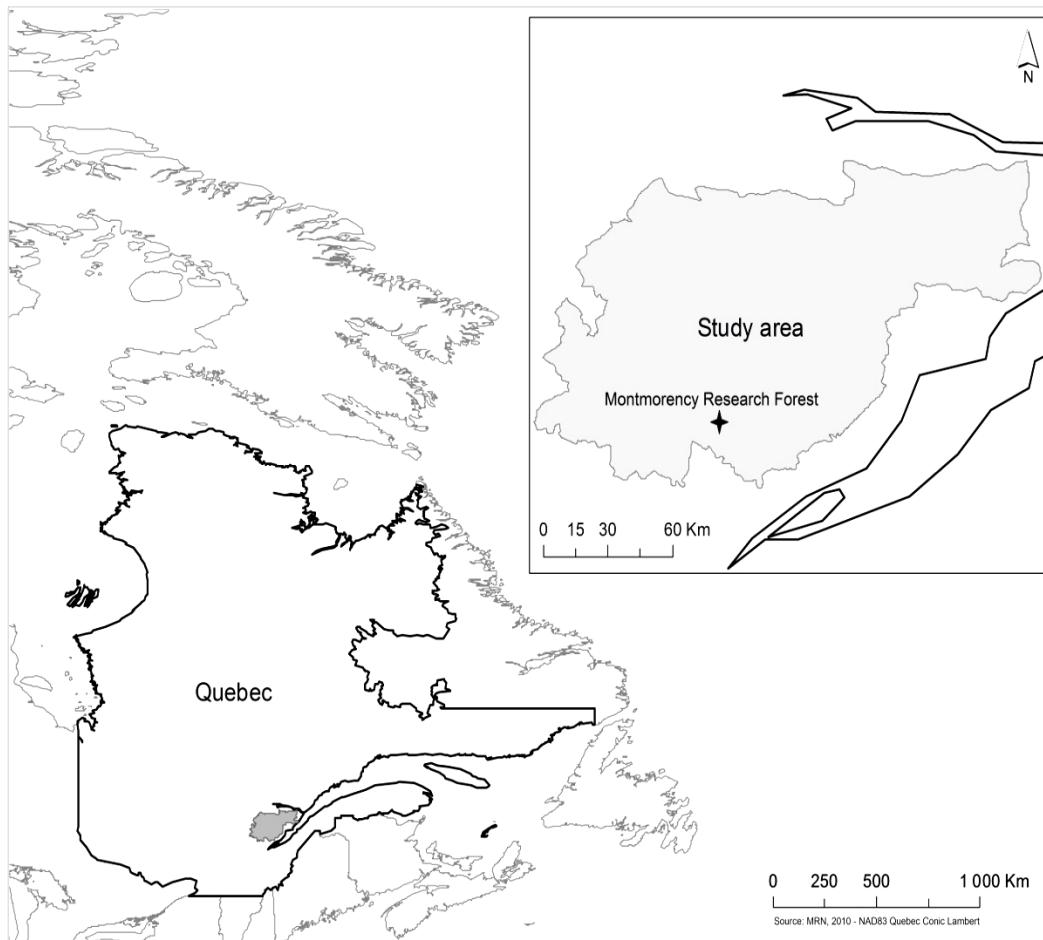


Figure 10. Location of the Montmorency Research Forest ($47^{\circ}19'N$; $71^{\circ}07'W$) and the study area ($47^{\circ}34'N$; $70^{\circ}48'W$) throughout the eastern part of the Laurentian Highlands of Quebec (Canada), which is covering a portion of the eastern balsam fir-paper birch bioclimatic domain of Quebec.

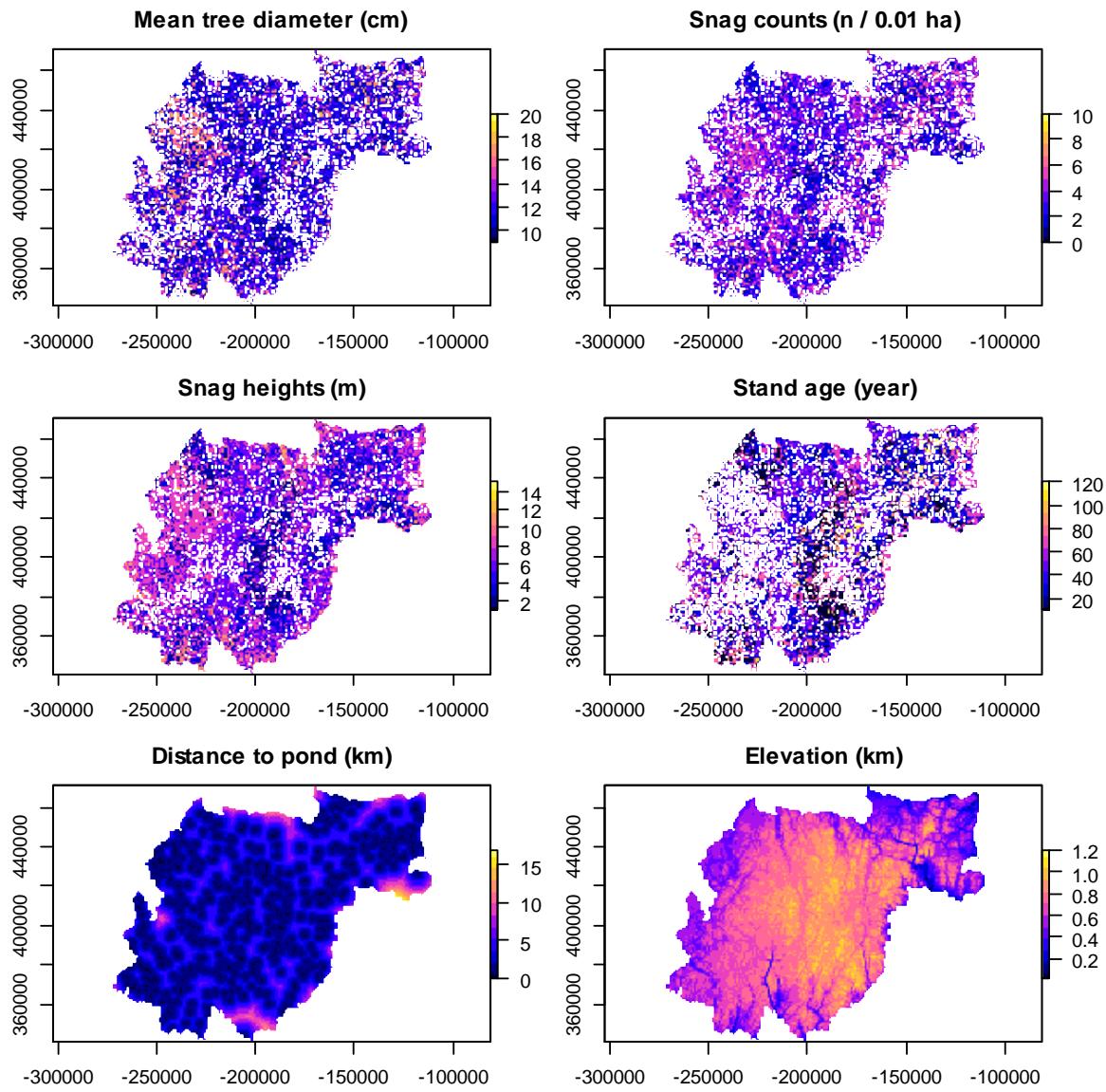


Figure 11. Raster maps of the study area ($47^{\circ}34'N$; $70^{\circ}48'W$) for each explanatory variable included in the Random Forest classification models. White pixels on raster maps indicate no data (for deciduous stands or missing data). Low values are in black pixels while high values are in yellow pixels. Horizontal and vertical axes represent Easting and Northing respectively, from a Modified Transverse Mercator projection.

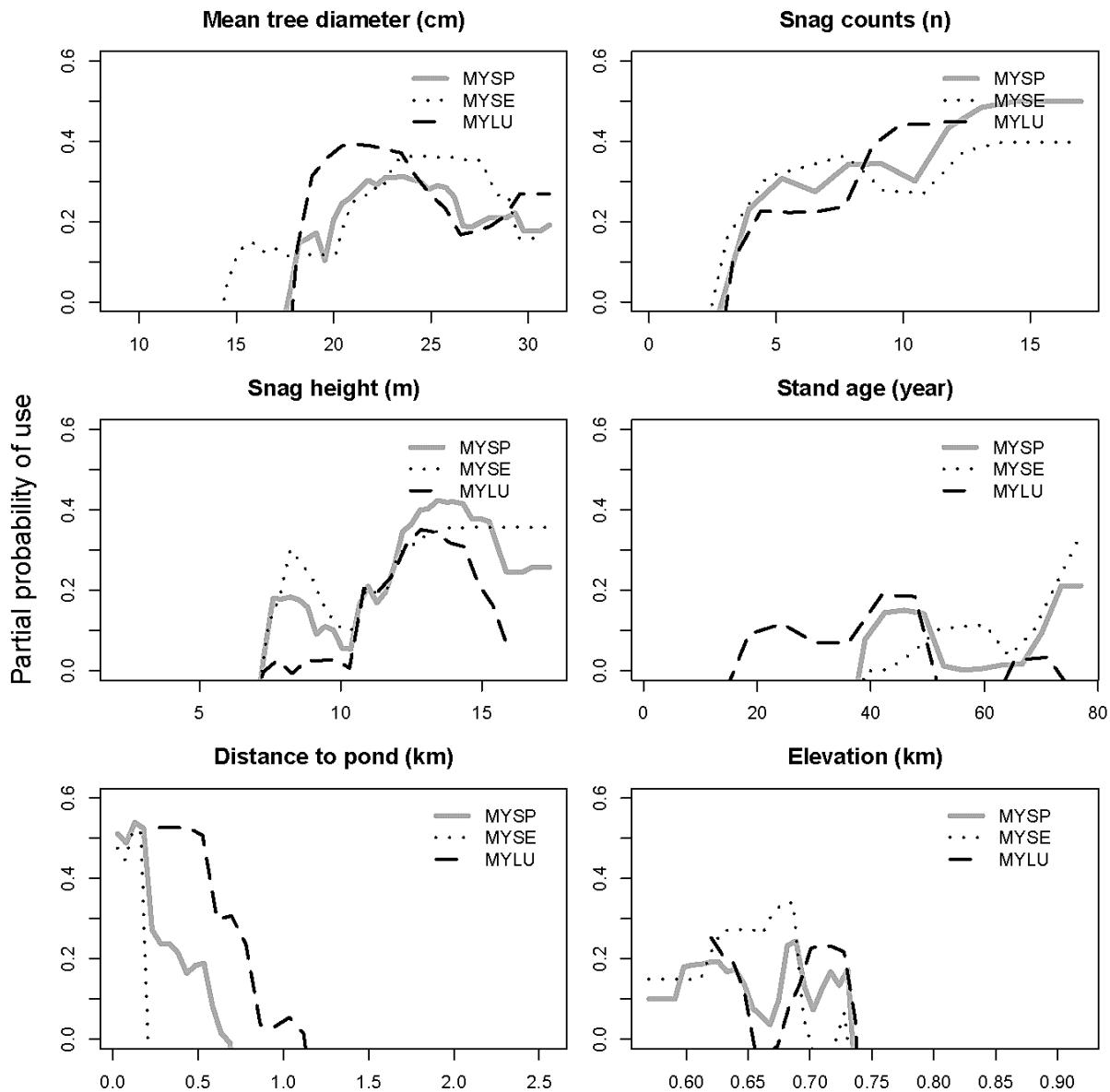


Figure 12. Partial dependence plots of explanatory variables for Random Forest predictions of two species of bats (*Myotis septentrionalis*, MYSE; *Myotis lucifugus*, MYLU) and combined species (MYSP). Each plot shows the marginal effect of an explanatory variable included in Random Forest classification models on the partial probability of use, while the effects of other explanatory variables are averaged.

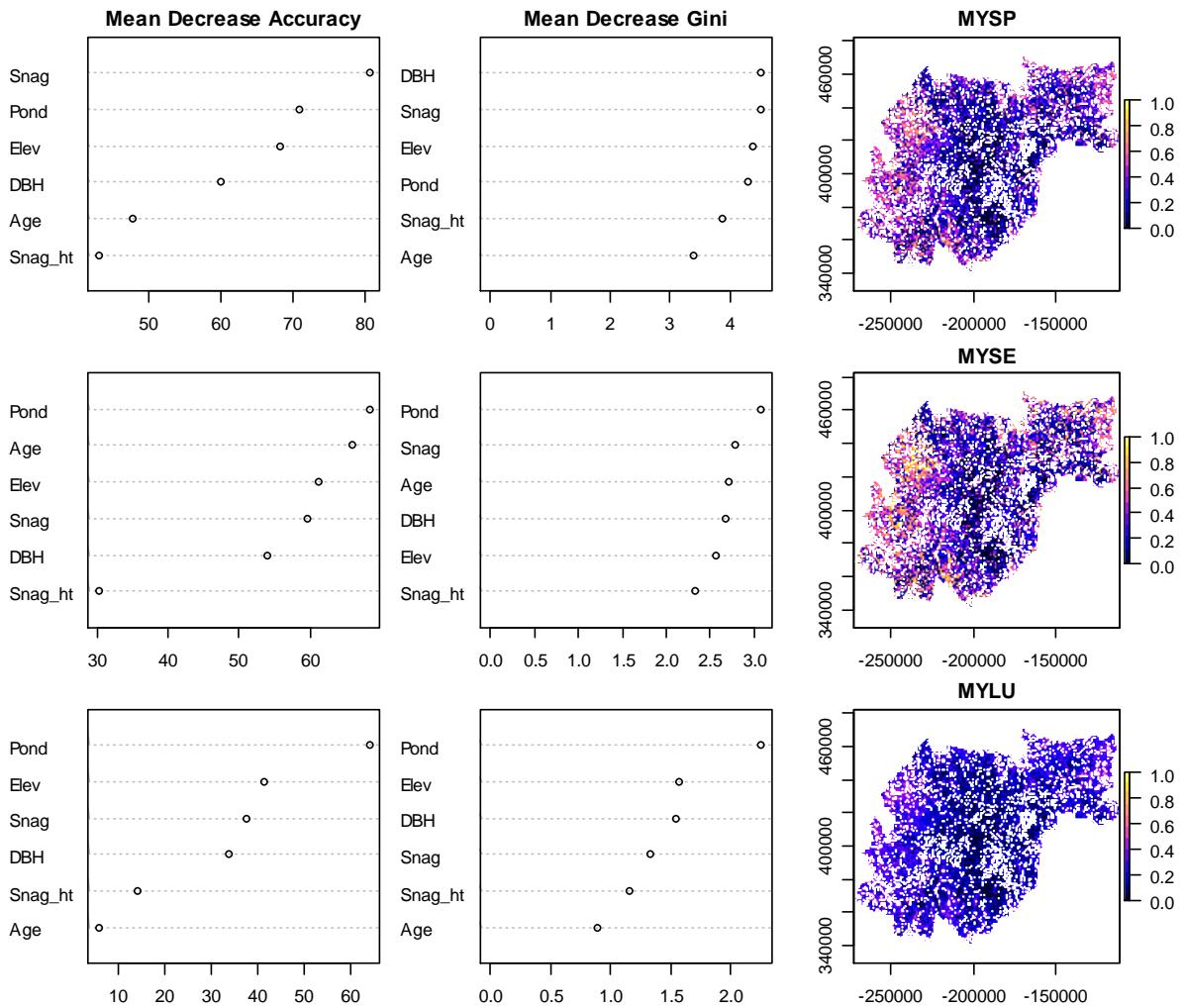


Figure 13. Mean decrease accuracy and mean decrease Gini variable importance plots, including habitat suitability models for combined species (*Myotis* spp.; MYSP), little brown bat (*Myotis lucifugus*; MYLU), and northern long-eared bat (*Myotis septentrionalis*; MYSE). Description of each variable code is given in Table 1. White pixels on habitat suitability models indicate no data (for deciduous stands or missing data). Low values are in black pixels while high values are in yellow pixels. Horizontal and vertical axes on habitat suitability models represent Easting and Northing respectively, from a Modified Transverse Mercator projection.

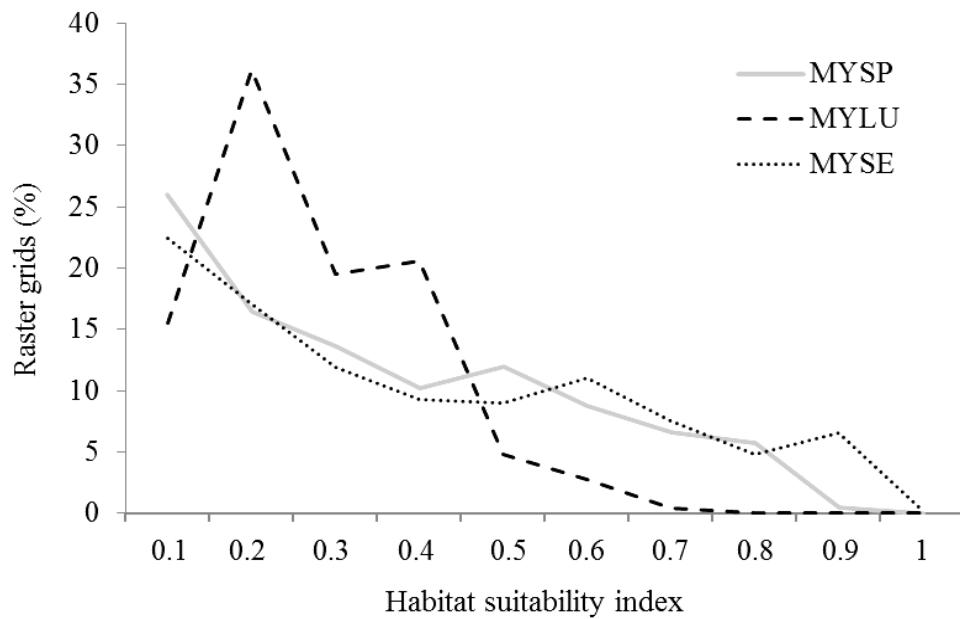
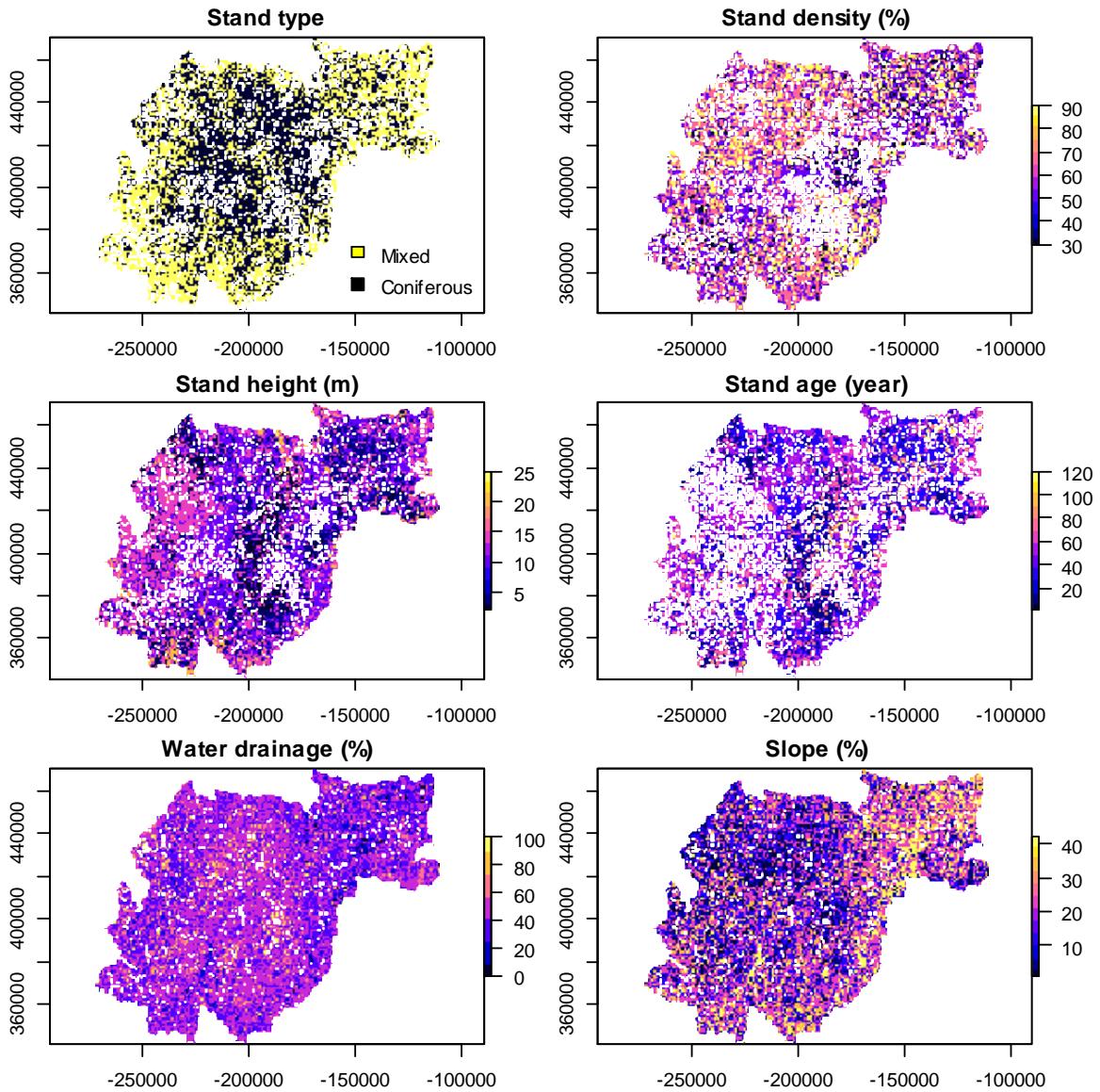
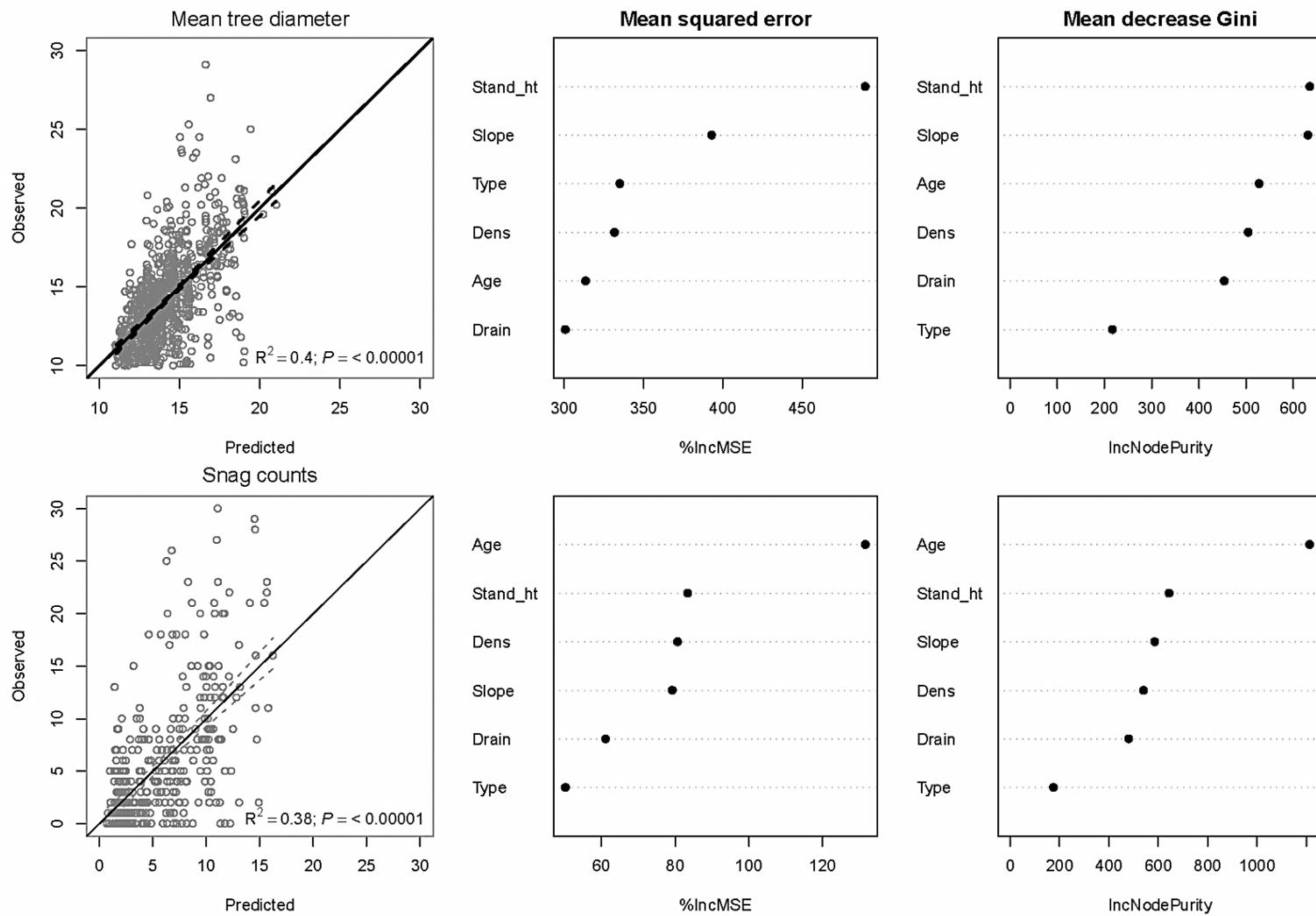


Figure 14. Percent of raster grids for each roosting habitat suitability index for combined species (MYSP), little brown bat (*Myotis lucifugus*; MYLU), and northern long-eared bat (*Myotis septentrionalis*; MYSE).

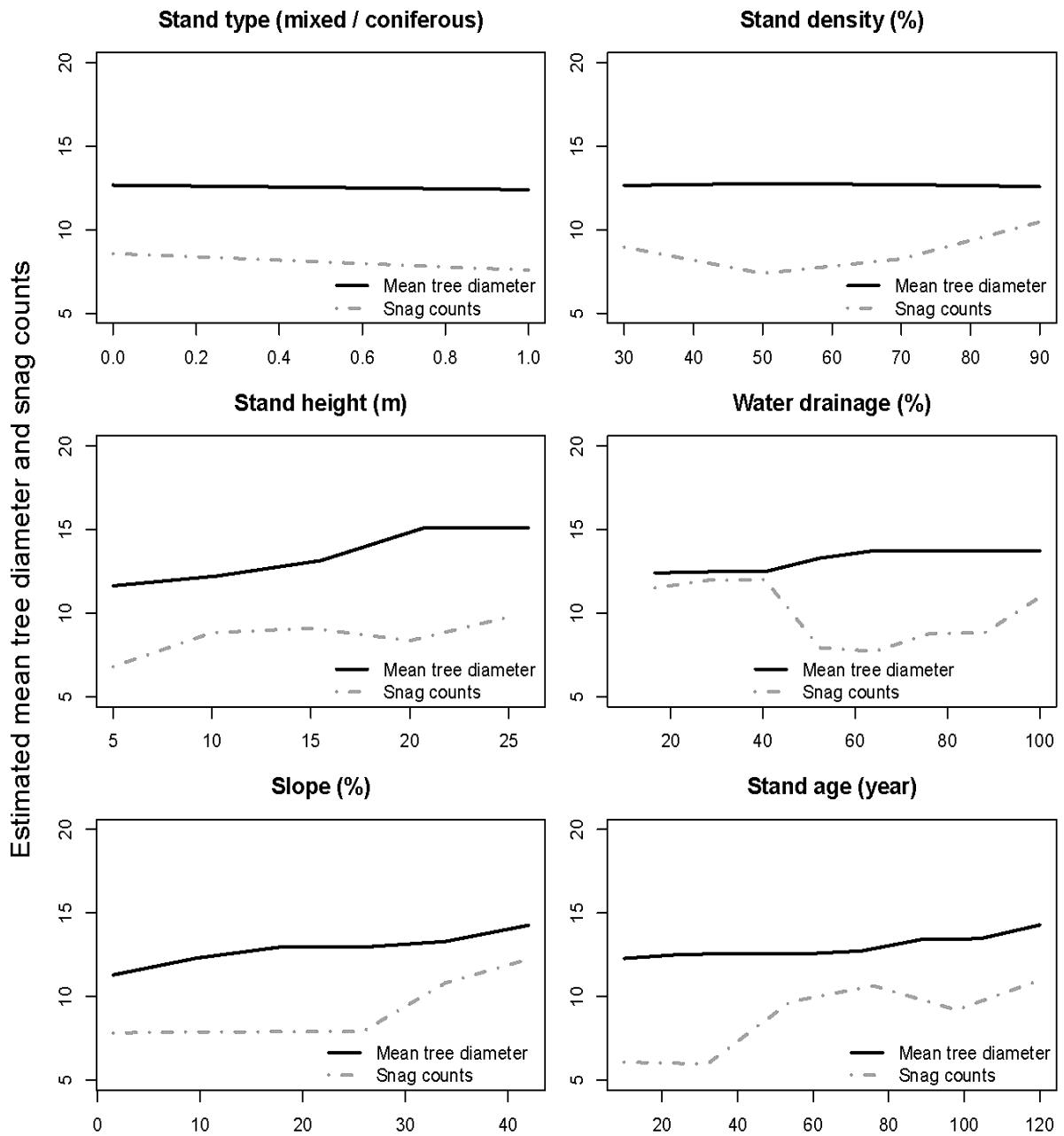
Appendix 2



Appendix 2. Figure 1. Raster map of the study area ($47^{\circ}34'N$; $70^{\circ}48'W$) for each explanatory variable included in the Random Forest regression models. White pixels on raster maps indicate no data (for deciduous stands or missing data). Low values are in black pixels while high values are in yellow pixels. Horizontal and vertical axes represent Easting and Northing respectively, from a Modified Transverse Mercator projection.



Appendix 2. Figure 2. Observed against predicted regression plots from Random Forest regression models on predicting mean tree diameter ($r^2 = 0.40$, $P < 0.00001$) and snag counts ($r^2 = 0.38$, $P < 0.00001$), including mean squared error and mean decrease Gini variable importance plots.



Appendix 2. Figure 3. Partial dependence plots of each explanatory variable used in Random Forest regression models to predict mean tree diameter and snag counts. Each plot shows the marginal effect of an explanatory variable included in Random Forest regression models on partial estimation of mean tree diameter and snag counts, while the effects of other explanatory variables are averaged.

DISCUSSION GÉNÉRALE

Cette thèse visait à répondre à deux objectifs principaux en lien avec le manque de connaissances sur l'écologie diurne des chauves-souris cavicoles en forêt boréale. Le premier objectif était de déterminer les variables impliquées dans la sélection des arbres gîtes des chauves-souris. Le second objectif était de déterminer si les peuplements boréaux présentant les arbres gîtes recherchés par les chauves-souris cavicoles étaient spatialement limités dans le paysage forestier aménagé. Dans les deux premiers chapitres, j'ai déterminé les principales variables sélectionnées par les chauves-souris cavicoles. Lors du troisième chapitre, j'ai modélisé un indice d'habitat diurne pour évaluer la répartition et la proportion de ces variables à l'échelle du paysage forestier.

Les variables impliquées dans la sélection des arbres gîtes des chauves-souris cavicoles

Dans le premier chapitre de thèse, j'ai réalisé une synthèse quantitative de la littérature qui portait sur la sélection des arbres gîtes des chauves-souris cavicoles en Amérique du Nord. Concernant le diamètre, la hauteur des arbres, la densité de chicots, la fermeture de la canopée et l'élévation, les résultats des études étaient suffisamment marqués (*i.e.*, taille d'effet importante) et consistants d'une étude à l'autre (*i.e.*, peu hétérogènes) pour rejeter l'hypothèse nulle (*i.e.*, pas de différence d'effet). La taille et la direction des effets variaient de manière trop importante entre les études pour ce qui a trait à la distance à l'eau, la densité d'arbres, la pente et l'écorce restante sur les troncs. J'ai déterminé que le diamètre des arbres était la variable la plus importante à considérer (*i.e.*, avec la plus forte taille d'effet) dans la sélection des arbres gîtes des chauves-souris cavicoles en Amérique du Nord.

Du fait de la proximité spatiale des études, je me suis assuré que les tailles d'effet pour le diamètre des arbres n'étaient pas auto-corrélatées spatialement avant d'interpréter mes résultats. J'ai montré que les différences de sélection observées entre études pour le diamètre des arbres pouvaient être corrélées au sexe et aux températures moyennes estivales. Il semblerait que les femelles reproductives choisissent des arbres de plus gros diamètre dans les régions nordiques, c'est-à-dire où la température moyenne estivale est relativement basse comparativement aux régions méridionales. Les arbres de gros diamètres sont supposés tamponner les fluctuations extérieures de température ce qui

permettrait aux femelles reproductives de réduire le coût énergétique relié à la thermorégulation et favoriser la croissance des juvéniles. Il s'avère que l'hypothèse du microclimat (Boyles 2007), est largement évoquée dans la littérature pour expliquer la sélection de plusieurs variables (*i.e.*, le diamètre et la hauteur des arbres, l'ouverture de canopée et l'élévation). Paradoxalement, les relevés de températures et d'insolation qui permettraient d'invalider cette hypothèse ont rarement été mesurés sur le terrain et n'ont fait l'objet que d'une attention récente (Park & Broders 2012; Lacki, Johnson & Baker 2013; Johnson & Lacki 2014). Je recommande que de tels relevés soient inclus dans les futures recherches.

Les études sur lesquelles je me suis basé ont été conduites dans des habitats variés, incluaient différentes espèces de chauves-souris et visaient à répondre à différents objectifs, ce qui a sans doute été vecteur d'une hétérogénéité importante. Malgré l'inclusion de variables modératrices pour tenter d'expliquer cette variabilité entre études, la majeure partie de l'hétérogénéité résiduelle pour la sélection du diamètre des arbres est restée inexpliquée. Il est possible qu'une partie de l'hétérogénéité non expliquée soit attribuable à des biais potentiels et à différentes méthodes d'estimations employées sur le terrain (Miller, Arnett & Lacki 2003). J'ai été limité dans mon estimation de ces biais par le manque de description des méthodes employées sur le terrain. Par exemple, les distances entre les arbres sélectionnés par les chauves-souris et les arbres aléatoires sont rarement mentionnées. Cette information permettrait pourtant d'estimer le degré d'autocorrélation spatiale entre ces deux types d'arbres. Une sélection des arbres aléatoire réalisée sur de courtes distances (*i.e.*, moins de 100 m) par rapport aux arbres sélectionnés pourrait sous-évaluer l'effet des variables d'élévation et d'autres caractéristiques des peuplements (telles que l'âge et la composition en essences notamment), surtout lorsque le relief de la zone d'étude est accentué. Générer des points aléatoires au sein de l'aire d'étude via un SIG permettrait de remédier facilement à ce biais.

Les études que j'ai examinées n'ont pas fourni de description suffisamment détaillée de l'habitat pour que je puisse extraire des variables modératrices additionnelles. L'âge des peuplements est, par exemple, rarement mentionné dans la littérature alors que cette variable est dépendante de plusieurs variables couramment examinées, telles que le diamètre et la hauteur des arbres (Vanclay 2009), le degré d'ouverture du couvert forestier

(McCarthy 2001; McCarthy & Weetman 2006), la densité d’arbres (Tyrrell & Crow 1994), la densité de chicots (Lee 1998; Moroni & Harris 2010), et le nombre d’arbres présentant des cavités disponibles pour la faune (Rudolph & Conner 1991; Fan *et al.* 2003; Smith, Warkentin & Moroni 2008).

Il ressort de ce chapitre que la recherche d’un microclimat favorable pourrait jouer un rôle central dans la sélection des arbres gîtes des chauves-souris cavicoles, en particulier dans le cas des femelles reproductives situées à la limite nordique de leur aire de distribution. Inclure de futures études situées dans le centre des États-Unis, dans le nord du Canada et en Amérique latine permettrait d’augmenter considérablement l’étendue spatiale de nos analyses. Dans une perspective de conservation, il semble primordial de maintenir des arbres à cavités ayant un diamètre important (Fan *et al.* 2003) pour garantir une offre en arbres gîtes satisfaisante pour les chauves-souris cavicoles en milieu boréal.

Les arbres gîtes sélectionnés par les chauves-souris du genre *Myotis* en forêt boréale aménagée

Lorsque j’ai entrepris cette étude à la forêt Montmorency, j’étais intéressé à comparer la sélection des arbres gîtes entre les deux espèces du genre *Myotis*. Plusieurs études ont en effet montré des différences spécifiques dans la sélection des arbres gîtes chez les espèces du genre *Myotis* (Broders & Forbes 2004; Lacki, Cox & Dickinson 2009a; Timpone *et al.* 2009). Toutefois, en raison d’une taille d’échantillon limitée (*i.e.*, 40 arbres sélectionnés à partir de 11 individus suivis avec succès), j’ai dû combiner les résultats des deux espèces. La taille d’échantillon a également limité l’inclusion de variables réponses additionnelles (*e.g.*, stades de détérioration des chicots) dans mes modèles de sélection alternatifs. Des tests de puissances calculés *a posteriori* ont toutefois confirmé qu’une taille d’échantillon de 40 arbres était suffisante (Lacki & Baker 2003) pour détecter des différences significatives avec les variables réponses incluses dans mes modèles de sélection.

Pour des raisons non élucidées, je n’ai pas capturé de femelles durant cette étude, ce qui limite la portée de mes résultats aux chauves-souris mâles uniquement. Je pense que les températures estivales relativement froides de la forêt Montmorency pourraient ne pas convenir aux femelles reproductives, ce qui expliquerait pourquoi je n’y ai capturé que des mâles. La province du Québec se trouve à la limite nordique de distribution des espèces du

genre *Myotis* (Banfield 1974). En outre, la forêt Montmorency est située à une altitude moyenne de 850 m et présente des conditions climatiques froides et humides, se rapprochant davantage de celles observées à des latitudes plus nordiques. L'hypothèse d'une ségrégation sexuelle chez les chauves-souris, avec les femelles reproductives moins susceptibles d'être retrouvées dans les peuplements d'altitude, est bien documentée dans la littérature (Grindal, Morissette & Brigham 1999; Cryan, Bogan & Altenbach 2000; Russo 2002; Arnold 2007; McGuire & Boyle 2013). Les raisons évoquées sont généralement des températures trop basses et une disparité en insectes ne permettant pas aux femelles de supporter les coûts énergétiques associés à la reproduction (Grindal, Morissette & Brigham 1999; McGuire & Boyle 2013). Mes résultats doivent être interprétés en gardant en tête le fait qu'ils ne tiennent pas compte des exigences en arbres gîtes des femelles reproductives, prouvées comme étant différentes de celles des mâles (Hamilton & Barclay 1994; Broders & Forbes 2004; Perry, Thill & Carter 2007; Randall, Jung & Barclay 2014).

Dans les forêts mixtes dominées par les sapins baumier, les chauves-souris mâles du genre *Myotis* privilégiavaient des gros chicots dont la cime était tombée au sol. Ces chicots avaient un stade de détérioration intermédiaire (Imbeau & Desrochers 2002) et présentaient des fissures dans le tronc ou suffisamment d'écorce soulevée sur le tronc pour permettre aux individus d'y trouver refuge. J'ai retrouvé des gîtes sous l'écorce exfoliante de bouleaux à papier et majoritairement de sapin baumiers. J'ai également retrouvé deux petites chauves-souris brunes nichant dans des fissures de roches et moins de la moitié des individus de cette espèce (*i.e.*, 46 %) nichaient dans des habitations. Ces résultats contrastent avec ceux trouvés pour la chauve-souris nordique, dont les individus étaient uniquement retrouvés perchés dans des arbres vivants ou morts. Les chicots sélectionnés par les chauves-souris étaient légèrement plus gros et plus hauts que les chicots sélectionnés aléatoirement. Les arbres gîtes étaient situés dans des peuplements moins denses, contenant une proportion légèrement plus importante de trouées et davantage de chicots, comparativement aux peuplements aléatoires. En dépit d'une plus grande proportion de trouées, je n'ai pas décelé que les arbres gîtes bénéficiaient d'une meilleure insolation journalière, lorsque comparés aux arbres pris aléatoirement. Cela pourrait signifier que le rôle des trouées était uniquement d'améliorer l'accessibilité aux arbres gîtes. Les chauves-souris du genre *Myotis* nichaient dans des peuplements de seconde

venue âgés entre 30 et 80 ans, ce qui concorde avec les observations de Menzel *et al.* (2002b). Toutefois, la chauve-souris nordique nichait dans des peuplements plus âgés de 15 ans en moyenne, comparés aux peuplements aléatoires. La majorité de ces peuplements (*i.e.*, 69.2 % des cas) avait atteint ou excédait le stade de maturité commerciale (*i.e.*, de 55 à 75 ans) à la forêt Montmorency. Il aurait été intéressant de vérifier la sélection des habitats diurnes de ces deux espèces au sein de sapinières primitives ou de peuplements surannés (*i.e.*, ≥ 90 ans), faiblement représentés (*i.e.*, 1 %) à la Forêt Montmorency.

Le meilleur prédicteur de l'habitat diurne des chauves-souris mâles du genre *Myotis* était le nombre de chicots retrouvés dans la parcelle forestière d'environ 0,1 ha jouxtant l'arbre sélectionné. Maintenir des îlots de sénescence de 0,1 ha comprenant un minimum de 10 chicots avec un DHP ≥ 10 cm devrait contribuer à préserver une offre en arbres gîtes, indispensable au maintien des habitats diurnes de ces espèces. Les aménagements sylvicoles permettant de maintenir ou de favoriser la présence de chicots ayant un DHP ≥ 20 cm et un stade de dégradation intermédiaire (classes 6 et 7) pourraient être considérés par les gestionnaires forestiers soucieux de préserver l'habitat diurne des chauves-souris du genre *Myotis* en forêt boréale. La capacité des nichoirs artificiels à supplémenter l'offre en arbres gîtes (Brittingham & Williams 2000) reste encore à être évaluée en milieu forestier. La mise en place de plusieurs nichoirs artificiels à proximité les uns des autres (White 2004) permettrait de couvrir les besoins en nichoirs primaires et secondaires des chauves-souris (Lewis 1995). Ces aménagements pourraient être considérés dans le cas où l'offre en arbres gîtes devenait limitée en forêt boréale pour les chauves-souris du genre *Myotis*, ce qui reste encore à évaluer.

Les habitats diurnes potentiels dans la partie méridionale du massif des Laurentides

Dans le troisième chapitre, j'ai modélisé un indice d'habitat diurne potentiel pour deux chauves-souris du genre *Myotis* (*M. lucifigus* et *M. septentrionalis*) à partir des éléments de réponses fournis par les deux chapitres précédents. Étendre la portée des résultats obtenus à la forêt de Montmorency sur une échelle beaucoup plus vaste a permis de vérifier la qualité des habitats diurnes potentiels pour chaque espèce de chauves-souris et pour les deux espèces combinées au genre. Mes modèles d'habitats diurnes potentiels sont

basés sur les données du second chapitre et les conclusions qui en découlent ne peuvent par conséquent s'appliquer qu'aux chauves-souris mâles du genre *Myotis*.

J'ai généré mes modèles en utilisant une approche par Random Forest (Cutler *et al.* 2007). Ces modèles sont basés sur des estimations du diamètre moyen des sapins baumiers dominants et du nombre de chicots, sur la hauteur des chicots de classe intermédiaire, la distance aux plans d'eau $\geq 20\text{ m}^2$, l'âge des peuplements forestiers et l'élévation. Un des enjeux majeurs de ce chapitre fut d'obtenir ou de générer des cartes raster qui correspondaient étroitement aux variables utilisées lors du second chapitre. Malgré l'influence de l'ouverture de la canopée sur la sélection des arbres gîtes à la forêt Montmorency (Fabianek *et al.* 2015) je n'ai pas inclus cette variable dans les modèles. Son inclusion aurait exigé une modélisation de la proportion d'ouverture de canopée à partir de relevés LiDAR. De tels relevés ne sont pas encore disponibles dans la zone d'étude. Puisque ce chapitre portait sur les habitats diurnes à l'échelle du paysage forestier, j'ai rajouté les variables d'âge des peuplements, d'élévation et de distance aux points d'eau qui n'étaient pas prises en compte dans les analyses du second chapitre.

J'ai majoritairement retrouvé les meilleurs habitats diurnes potentiels dans les peuplements mixtes de basse élévation (*i.e.*, $< 900\text{ m}$) ce qui implique que la pessière à mousse d'altitude incluant des sapins baumiers soit moins favorable à la nidification des chauves-souris. Il est probable que les peuplements principalement composés d'épinettes noires (Vaillancourt *et al.* 2008; Moroni & Harris 2010) couplés aux conditions climatiques rigoureuses présentes en altitude limitent la distribution des deux espèces du genre *Myotis*, particulièrement dans le cas des femelles reproductives (Grindal, Morissette & Brigham 1999; Senior, Butlin & Altringham 2005; Arnold 2007).

La répartition spatiale des habitats diurnes potentiels se chevauchait pour les deux espèces du genre *Myotis*. Je n'ai donc pas pu valider mon hypothèse de départ impliquant des différences spécifiques à ce niveau. La sapinière à bouleau blanc semblait plus propice pour la nidification de la chauve-souris nordique, ce qui concorde avec mes données de captures issues du second chapitre. J'ai en effet capturé davantage de chauves-souris nordiques à la forêt Montmorency comparativement à la petite chauve-souris brune. Hors, dans la vallée du parc national de la Jacques-Cartier située aux contreforts du massif des

Laurentides (*i.e.*, en aval de forêt Montmorency), j'ai uniquement capturé de la petite chauve-souris brune. Il se pourrait que la chauve-souris nordique ait une aire de distribution plus étendue que la petite chauve-souris brune en forêt boréale humide, ce qui fut également constaté par Park et Broders (2012) à Terre-Neuve.

Une forte proportion d'arbres à cavité et de chicots était une composante essentielle des habitats diurnes des chauves-souris du genre *Myotis*, pouvant être associée aux peuplements matures ainsi qu'aux vieilles forêts (Sturtevant *et al.* 1997; Franklin *et al.* 2002; Vanderwel, Caspersen & Woods 2006; Smith, Warkentin & Moroni 2008; Moroni & Harris 2010). Les données extraites du 4e inventaire forestier et des placettes échantillons permanentes indiquaient que la proportion estimée de chicots augmentait avec l'âge des peuplements, jusqu'à la limite d'âge supérieure de 120 ans disponible pour notre échantillon (*i.e.*, 898 placettes-échantillons permanentes). J'ai par ailleurs constaté à l'aide des cartes écoforestières que les vieilles forêts ne couvraient que 16,4 % de la zone d'étude, ce qui reste en deçà du seuil jugé acceptable pour le maintien de la biodiversité (Rompré *et al.* 2010).

Le manque de relevés ne me permet pas de déterminer l'influence des vieilles forêts sur la qualité des habitats diurnes des chauves-souris du genre *Myotis*. À ce stade de mes recherches, il est encore trop tôt pour aller dans le sens des recommandations antérieures, prônant une augmentation de la proportion des vieilles forêts au sein de l'aire d'étude (Vaillancourt *et al.* 2009a; Rompré *et al.* 2010). Dans le cas où de telles mesures soient entreprises pour garantir le maintien d'autres espèces cavicoles en forêt boréale aménagée, je recommande que les parcelles résiduelles de vieilles forêts soient situées à proximité des points d'eau (Grindal 1996) et de préférence, connectées entre elles par un réseau de corridors forestiers fonctionnels pour les chauves-souris (Estrada & Coates-Estrada 2002; Boughey *et al.* 2011; Farrow & Broders 2011; Fuentes-Montemayor *et al.* 2013). Il conviendrait surtout d'éviter les ruptures importantes du couvert forestier (Farrow & Broders 2011; Segers & Broders 2014) et d'éviter d'isoler les arbres gîtes potentiels, lors de leur rétention. Le maintien d'un paysage forestier hétérogène résultant d'une mosaïque diversifiée de peuplements est une pratique de gestion durable des forêts (Burton *et al.* 2010; Drapeau *et al.* 2010; Gauthier *et al.* 2010) qui contribuerait certainement à conserver

les habitats diurnes des chauves-souris et d'autres espèces cavicoles (Poulin *et al.* 2008; Drapeau *et al.* 2009; Nappi & Drapeau 2011) en forêt boréale aménagée.

Conclusion: ai-je atteint mes objectifs ?

À la lumière de mes résultats, je peux conclure que j'ai partiellement répondu à mon objectif de départ qui était de déterminer l'aspect limitant des variables impliquées dans la sélection des arbres gîtes par les chauves-souris cavicoles en forêt boréale. Plusieurs éléments importants de l'écologie diurne des chauves-souris cavicoles restent encore indéterminés, en particulier pour les femelles reproductives qui n'ont pas été retrouvées dans notre aire d'étude. Ces incertitudes ne me permettent pas de tirer de conclusions générales, à savoir si l'offre en arbres gîtes actuelle satisfait ou non les besoins en habitats diurnes des chauves-souris cavicoles en forêt boréale aménagée. Pour ce qui a trait aux chauves-souris mâles du genre *Myotis*, j'ai cependant montré que les chicots potentiels avec un stade de détérioration intermédiaire doivent être maintenus au sein d'îlots de sénescence d'environ 0,1 ha. J'ai également montré une sélection pour les peuplements qui présentent, entre autres, une plus faible densité d'arbres et une proportion légèrement plus importante de trouées dans la canopée. Ces caractéristiques structurales de l'habitat sont davantage retrouvées au sein des vieilles forêts. La proportion de chicots modélisée dans l'habitat forestier augmentait d'ailleurs avec l'âge des peuplements forestiers. J'ai également confirmé à l'aide des cartes écoforestières que la proportion de peuplements surannés restait marginale à la forêt Montmorency et dans la partie méridionale du massif des Laurentides. Toutefois, les résultats de cette thèse ne me permettent pas de statuer sur l'importance des peuplements surannés pour l'habitat diurne des chauves-souris.

Les données extraites des 898 placettes échantillons permanentes indiquaient que les peuplements avec une densité optimale de chicots (≥ 10 chicots par 0.1 ha) ne représentaient que 0.01 % des placettes. Ceci laisse supposer que les îlots de sénescences sont des phénomènes ponctués, sans me permettre d'inférer sur leur récurrence en forêt boréale aménagée. Malgré tout, la proportion d'habitats diurnes disponible pour la chauve-souris nordique – espèce considérée comme spécialiste des vieilles forêts - était supérieure à la proportion de peuplements surannés. La proportion d'habitats diurnes disponible pour

les deux espèces du genre *Myotis* était également bien supérieure à la proportion d'îlots de sénescence (*i.e.*, 0,01 %) estimée dans l'aire d'étude.

L'utilisation des chicots de sapin baumier dans les peuplements arrivés à maturité et de bouleaux à papier présents dans les peuplements plus jeunes (< à 50 ans) laisse penser que les chauves-souris mâles du genre *Myotis* peuvent persister au sein des aires de coupe, à condition qu'ils puissent y trouver un réseau d'arbres gîtes situés à proximité des points d'eau et des habitats de chasse. Les sapins baumiers - essence dominante à la forêt Montmorency - sont relativement abondants et leur sénescence arrive rapidement en comparaison avec d'autres essences boréales (Angers, Drapeau & Bergeron 2010), ce qui suggère que cette ressource était abondante dans le cas des chauves-souris mâles. Lacki, Baker et Johnson (2012) ont modélisé un taux de persistance des chicots utilisés par le vespertilion à longues pattes (*Myotis volans*) de seulement 4,3 % ($n = 339$ chicots) sur une période de 10 ans suivant leur découverte dans les états de Washington, d'Oregon et d'Idaho (USA). La demi-vie des chicots utilisés comme arbres gîtes était inférieure à trois ans dans les forêts de conifères du nord-ouest du pacifique (Lacki, Baker & Johnson 2012). Dans les sapinières de l'Est du Canada, la demi-vie des chicots de sapin baumiers excède rarement les 25 ans après mortalité (Lee 1998; Garber *et al.* 2005; Vanderwel, Caspersen & Woods 2006; Taylor & MacLean 2007; Angers, Drapeau & Bergeron 2010), ce qui est bien supérieur aux estimations données par Lacki, Baker et Johnson (2012). Cet écart vient en partie du fait que les chauves-souris utilisent des chicots avec un stade de dégradation intermédiaire (Parsons, Lewis & Psyllakis 2003; Arnett & Hayes 2009; Fabianek *et al.* 2015), qui sont déjà morts sur pieds depuis quelques années.

En suivant durant trois ans les chicots utilisés par les chauves-souris du genre *Myotis*, j'ai constaté un taux de persistance (*i.e.*, avant effondrement du chicot) de 78 % ($n = 28$ chicots). Ces données, contrastent également avec celles de Lacki, Baker et Johnson (2012), car elles comprennent une plus courte période d'observation suivant la découverte des arbres gîtes utilisés par les chauves-souris. Il serait intéressant d'évaluer la dynamique spatio-temporelle des chicots et particulièrement des îlots de sénescence utilisés par les chauves-souris cavicoles à la forêt Montmorency. Ces connaissances permettraient certainement de mieux apprécier l'aspect limitant de cette ressource pour les chauves-souris cavicoles en forêt boréale aménagée.

Avec la propagation du SMB dans l'Est du Canada, les chauves-souris du genre *Myotis* et la pipistrelle de l'Est ont subi un déclin sans précédent de leurs populations (Blehert *et al.* 2009a; Frick *et al.* 2010; Blehert 2012). Pour ces espèces, la densité actuelle d'individus rend l'utilisation des arbres gîtes (*i.e.*, chicots et arbres à cavités) relativement rare dans les secteurs les plus touchés par le SMB. De ce fait, il est important de se questionner sur la priorité de préserver les arbres gîtes dans ces secteurs qui restent d'ailleurs à localiser à travers la province du Québec. Avec un taux de fécondation de seulement un à deux juvéniles par femelle et par an, il faudra certainement attendre plus d'un demi-siècle avant de retrouver une densité d'individus équivalente à celle pré-SMB (Maslo & Fefferman 2015). Dans ce contexte, il paraît urgent de protéger en priorité les maternités estivales et les hibernacles pour garantir la pérennité des quelques individus rescapés qui constituent à présent l'essentiel des populations de chauves-souris atteintes par le SMB. Les chicots, les parcelles boisées et les plans d'eaux situés à proximité des hibernacles sont des habitats essentiels à maintenir pour les chauves-souris du genre *Myotis* et la pipistrelle de l'Est en période de swarming (Randall 2011; Lowe 2012). Les aménagements que je propose pour les espèces du genre *Myotis* pourraient s'appliquer pour la gestion et la conservation des boisés situés à proximité (~ 2 km) des maternités et des hibernacles recensés par le MFFP. De plus, d'autres espèces de chauves-souris cavicoles, telles que la grande chauve-souris brune et la chauve-souris argentée, sont peu ou pas encore affectées par le Syndrome du Museau Blanc (SMB). Ces espèces pourraient également bénéficier des aménagements que je propose pour le maintien des habitats diurnes des chauves-souris mâles du genre *Myotis* (*i.e.*, rétention d'îlots de végétation comprenant de gros chicots et autres arbres à cavités).

Principales limites

Mon succès de captures, déjà mitigé en 2011 (*i.e.*, 22 captures), a chuté radicalement les deux étés suivants (*i.e.*, 5 captures en 2012 et 1 seule capture en 2013), ce qui a grandement limité la portée de mon étude. Il est probable que cette chute soit reliée aux taux de mortalité importants imputés à l'avancée du SMB à la forêt Montmorency et ailleurs au Québec. D'autres tentatives de captures ont été entreprises à la Forêt d'Enseignement et de Recherche du Lac Duparquet en 2012, au parc national d'Aiguebelle (Fabianek & Provost 2013), au parc national de la Jacques-Cartier ainsi qu'au secteur du

Camp Mercier de la réserve faunique des Laurentides en 2012 et 2013, respectivement. Les captures dans ces secteurs étaient initialement destinées à comparer la réponse des chauves-souris du genre *Myotis* selon divers milieux forestiers boréaux et en fonction de plusieurs aménagements sylvicoles. Malgré quelques captures fructueuses au parc national de la Jacques Cartier en 2012 ($n = 5$), le nombre d'arbres gîtes découverts pour la petite chauve-souris brune était trop faible ($n = 8$) pour exploiter statistiquement ces données. J'ai par conséquent abandonné ma stratification des sites de captures dans divers types d'habitats forestiers et je n'ai pas pu déterminer les aménagements sylvicoles les plus favorables au maintien des habitats diurnes des chauves-souris du genre *Myotis*. J'ai redéfini mes objectifs secondaires, pour m'en tenir à l'étude des habitats diurnes des chauves-souris en forêt boréale aménagée.

Les peuplements forestiers disponibles à la forêt Montmorency atteignent rarement les 90 ans, ce qui a limité les comparaisons avec des forêts résiduelles plus anciennes. Les résultats obtenus dans le parc national de la Jacques-Cartier laissaient entrevoir une sélection pour les bouleaux jaunes avec un diamètre important (*i.e.*, > 40 cm DHP), lorsqu'ils étaient disponibles dans l'habitat forestier. Ces évènements ne m'ont pas empêché d'atteindre partiellement mes objectifs principaux et d'employer des méthodes pour le moins innovantes pour répondre aux questions que je m'étais posées initialement. Mes résultats soulèvent de nombreuses questions qui mériteraient d'être approfondies afin de mieux évaluer les effets des aménagements forestiers sur l'écologie diurne des chauves-souris cavicoles en milieu boréal.

Future recherche

Pour répondre de manière plus précise aux objectifs que je m'étais fixé, il serait nécessaire de poursuivre certains travaux déjà amorcés à la forêt Montmorency et d'entreprendre de nouvelles recherches dans divers domaines bioclimatiques du Québec. En 2012 et 2013, j'ai déposé des trappes à guano au pied des chicots utilisés par les chauves-souris et des chicots situés à proximité. Les objectifs étaient d'évaluer la fidélité interannuelle des chauves-souris mâles et de vérifier l'hypothèse que les chicots autour des arbres gîtes utilisés soient bien des arbres gîtes potentiels. Des trappes à guano pourraient être installées de nouveau afin de confirmer l'utilisation de ces arbres gîtes sur le long

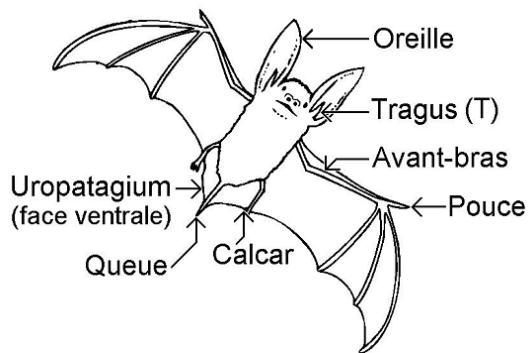
terme (*i.e.*, > 5 ans). Des analyses moléculaires des échantillons de guano récoltés permettraient par exemple de préciser qu'il s'agisse bien de la même espèce de chauve-souris (Zielinski *et al.* 2007) sans toutefois être en mesure de confirmer l'identité de l'individu. Je pourrais également profiter de ces visites pour évaluer la dynamique temporelle des chicots utilisés par les chauves-souris (Lacki, Baker & Johnson 2012) à la forêt Montmorency sur une période supérieure à cinq ans.

De nouveaux inventaires réalisés à l'aide de placettes-échantillons permettraient en effet de vérifier la proportion des chicots répertoriés en 2011 qui sont toujours sur pieds et d'évaluer le taux de recrutement de chicots alentour. Afin d'élargir le champ de recherches à d'autres espèces cavicoles, des micro-thermomètres pourraient être également installés dans des cavités et sous l'écorce d'un panel représentatif d'arbres à valeurs fauniques dans la forêt Montmorency. Les relevés de températures estivales couplées à des analyses LiDAR permettraient de préciser les capacités thermiques des arbres et les facteurs végétaux qui permettent l'émergence de microclimats favorables aux espèces cavicoles. La proportion d'arbres à valeur faunique pourrait ensuite être évaluée selon divers traitements sylvicoles et comparée à un site contrôle localisé au sein d'une sapinière primitive surannée ou de peuplements de seconde venue, exempts de coupes forestières depuis plus de 90 ans.

ANNEXES GÉNÉRALES

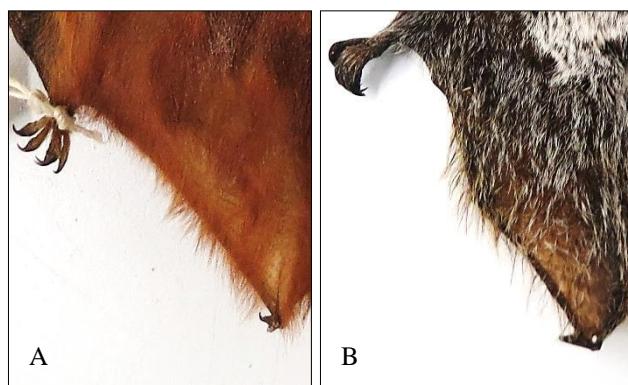
Annexe 3. Clé dichotomique d'identification des chauves-souris du Québec

J'ai adapté cette clé pour les chauves-souris du Québec à partir des publications de Menzel *et al.* (2002a) et du Ontario Ministry of Natural Resources (2006). J'ai pris les mensurations présentées dans cette clé sur 10 spécimens conservés au muséum national du Canada, incluant cinq mâles et cinq femelles pour chacune des huit espèces de chauves-souris recensées dans la province du Québec ($n = 80$ spécimens). J'ai complété ces données avec des mensurations prises sur 30 spécimens que j'ai capturé au Québec entre 2011 et 2013, incluant, 15 petites chauves-souris brunes (*Myotis lucifugus*), 10 chauves-souris nordiques (*M. septentrionalis*), deux grandes chauves-souris brunes (*Eptesicus fuscus*), deux chauves-souris cendrées (*Lasiurus cinereus*) et une chauve-souris rousse (*L. borealis*).



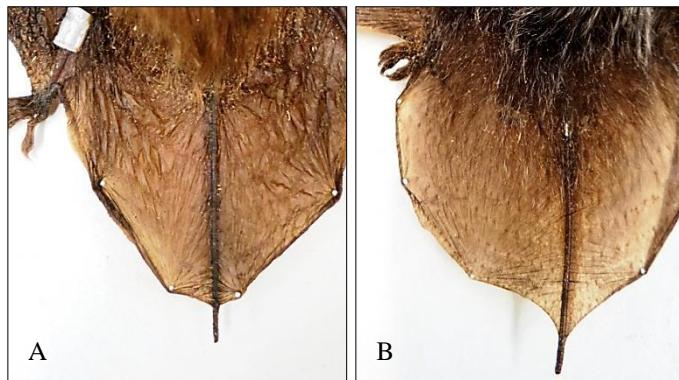
Annexe 3. Figure 1. Illustration d'une chauve-souris et des principaux critères morphologiques abordés dans cette clé.

- 1a.** Plus d'un tiers de la surface dorsale de l'*uropatagium* est recouvert d'une fourrure dense
(A. 3. Photographie 1) 2



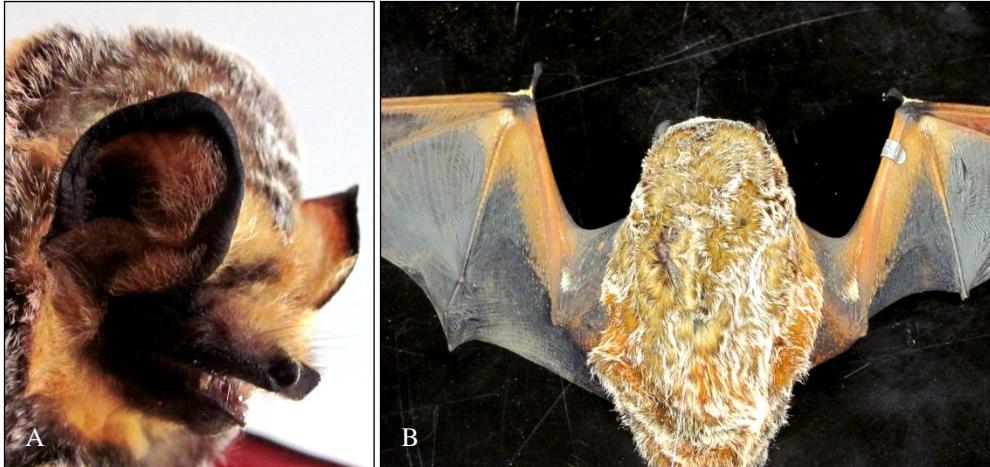
Annexe 3. Photographie 1. *Uropatagia* (A) d'une chauve-souris rousse (*Lasiurus borealis*) et (B) d'une chauve-souris cendrée (*L. cinereus*). La fourrure dorsale dépasse nettement le tiers supérieur de l'*uropatagium*.

1b. La surface dorsale de l'*uropatagium* est nue ou partiellement recouverte de poils épars, ou la fourrure ne dépasse pas le tiers supérieur (en partant de la jonction au corps) de l'*uropatagium* (A. 3. Photographie 2)3



Annexe 3. Photographie 2. *Uropatagia* d'une (A) petite chauve-souris brune (*Myotis lucifugus*) et (B) d'une chauve-souris argentée (*Lasionycteris noctivagans*). La fourrure ne dépasse pas le tiers supérieur de l'*uropatagium*.

2a. L'avant-bras est > à 50 mm; la fourrure est marron foncé avec des teintes jaunes; la surface des poils à un aspect givré ou cendré; un patch de fourrure jaunâtre entoure la tête; le contour de l'oreille est noir (A. 3. Photographie 3)
..... Chauve-souris cendrée (*Lasiurus cinereus*)



Annexe 3. Photographie 3. Vues de profil de la tête (A) et du pelage dorsal (B) d'une chauve-souris cendrée (*Lasiurus cinereus*). Le contour de l'oreille noir qui contraste avec la fourrure jaune est caractéristique de cette espèce. La membrane des ailes, plus claire sous les avant-bras, se distingue nettement chez les lasiurines lorsque les ailes sont déployées.

2b. L'avant-bras est \leq à 45 mm; la fourrure est soit rousse-orange (pour les mâles), soit jaune-marron (pour les femelles) et la surface des poils a parfois un aspect givré, surtout sur la face ventrale; l'oreille ne présente pas de contour noir

..... **Chauve-souris boréale (*Lasiurus borealis*)**



Annexe 3. Photographie 4. Vues dorsales d'un spécimen (A) mâle et un spécimen (B) femelle de chauves-souris rousses (*Lasiurus borealis*). La fourrure orangée est caractéristique chez cette espèce. La membrane des ailes, plus claire sous les avant-bras, se distingue nettement chez les Lasiurines lorsque les ailes sont déployées.

3a. Présence de fourrure sur le tiers supérieur de l'*uropatagium*; la fourrure est noire ou marron foncé à la racine des poils et l'extrémité présente souvent des reflets gris-argentés, abondants sur la partie dorsale

..... **Chauve-souris argentée (*Lasionycteris noctivagans*)**



Annexe 3. Photographie 5. Un spécimen femelle de chauve-souris argentée (*Lasionycteris noctivagans*) vue de dessus. Le bout des poils argentés contraste nettement avec la base de la fourrure noire dorsale.

3b. Pas de fourrure dense sur l'*uropatagium*; la fourrure dorsale est marron foncé ou marron clair à la racine des poils, sans présence de poils argentés.....4

4a. La chauve-souris est de grande envergure avec un avant-bras généralement \geq à 42,5 mm; le museau est noir et sans poil; le tragus (T) est court, recourbé et arrondi (A.3. Fig. 2.A).....

.....**Grande chauve-souris brune (*Eptesicus fuscus*)**

4(b). La chauve-souris est de petite envergure avec un avant-bras généralement \leq à 42,5 mm5

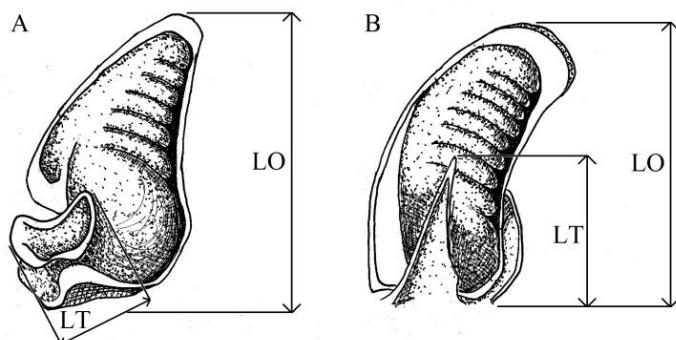
5(a). La fourrure ventrale ne contraste pas avec la fourrure dorsale qui comporte distinctement trois bandes de couleurs: sombre à la base, claire au milieu, avec la surface des poils assombrie; le tragus (T) est court et arrondi (A.3. Fig. 2.A)

.....**Pipistrelle de l'Est (*Perimyotis subflavus*)**

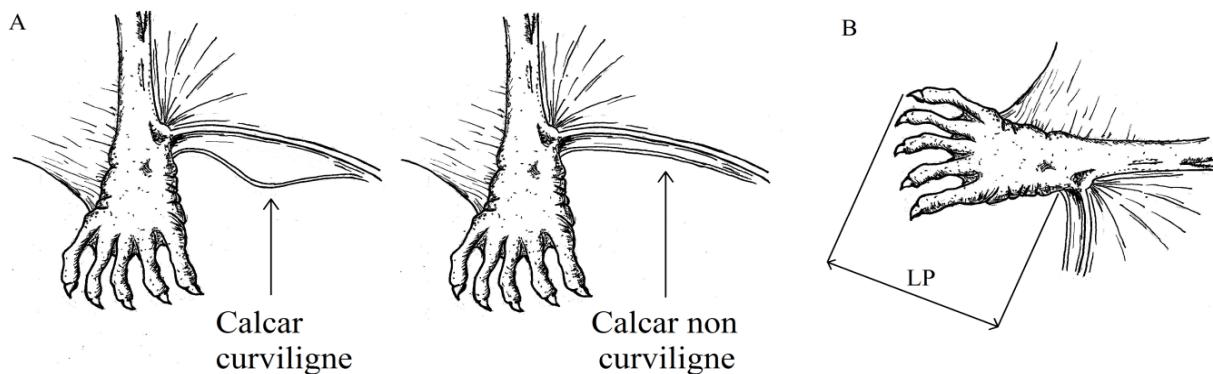


Annexe 3. Photographie 6. Pelage dorsal (A) d'une pipistrelle de l'Est (*Perimyotis subflavus*) et (B) d'une petite chauve-souris brune (*Myotis lucifugus*) montrant respectivement trois et deux bandes de couleurs. Les trois bandes de couleurs qui apparaissent lorsque l'on souffle sur la fourrure dorsale sont caractéristiques de la pipistrelle de l'Est.

5(b). La fourrure ventrale est plus claire ou contraste avec la fourrure dorsale; le tragus (T) est allongé et en forme de pointe (A.3. Fig. 2.B; Genre *Myotis*) 6



Annexe 3. Figure 2. Illustration des prises de mesures pour calculer la longueur de l'oreille (LO) et la longueur du tragus (LT) sur deux types morphologiques distincts: (A) une grande chauve-souris brune (*Eptesicus fuscus*) et (B) une chauve-souris nordique (*Myotis septentrionalis*).



Annexe 3. Figure 3. (A) Illustrations de la forme du calcar chez deux types morphologiques distincts et (B) de la prise de mesure pour calculer la longueur du pied (LP). Le calcar curviligne est caractéristique de la chauve-souris pygmée (*Myotis leibii*)

6(a). Le calcar est curviligne; le pied est < à 9 mm (LP) et l'avant-bras est < à 33 mm; la fourrure est habituellement claire avec un patch de poils noirs entourant les yeux.....
.....Chauve-souris pygmée de l'Est (*Myotis leibii*)

6(b). Le calcar n'est pas curviligne; le pied est > à 9 mm (LP); l'avant-bras est > à 33 mm...

7(a). La longueur des oreilles (LO) est généralement ≥ 15 mm, lorsque mises en avant celles-ci dépassent légèrement le museau.....

..... **Chauve-souris nordique (*Myotis septentrionalis*)**



Annexe 3. Photographie 7. Oreille d'une (A) chauve-souris nordique (*Myotis septentrionalis*) et (B) d'une petite chauve-souris brune (*M. lucifugus*). La forme recourbée et la longueur de l'oreille ainsi que le tragus long en forme d'éperon sont caractéristiques de (A) la chauve-souris nordique. Le tragus de (B) la petite chauve-souris brune est plus court et arrondi.

7(b). La longueur des oreilles (LO) est généralement ≤ 15 mm; au niveau des pieds, quelques longs poils s'étendent jusqu'au bout des griffes voir au-delà

..... **Petite chauve-souris brune (*Myotis lucifugus*)**

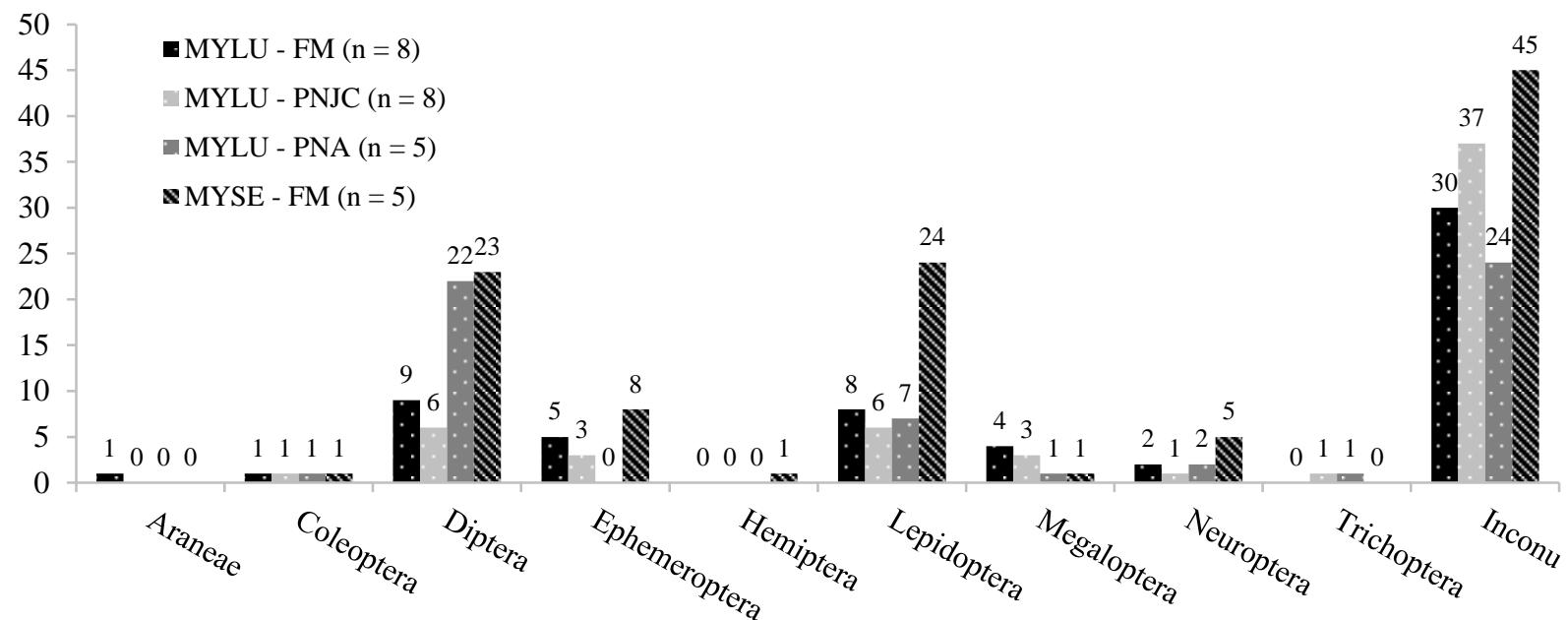
Annexe 3. Tableau 1. Mensurations moyennes \pm écarts-types des longueurs d'avant-bras, d'oreilles, de tragus et de pieds des huit espèces de chauves-souris recensées dans la province du Québec. Les mensurations ont été prises sur 80 spécimens mâles (M) et femelles (F) conservés au muséum national du Canada ainsi que sur 30 spécimens capturés au Québec entre 2011 et 2013.

Espèce*	n	Sexe	Avant-bras	Oreille	Tragus	Pied
EPFU	6	F	46,3 \pm 2,2	16,5 \pm 0,2	6,4 \pm 0,5	10,5 \pm 0,9
EPFU	6	M	46,0 \pm 2,0	14,9 \pm 0,4	6,4 \pm 0,8	10,1 \pm 0,5
EPFU	12	FM	46,2 \pm 1,9	15,7 \pm 0,9	6,4 \pm 0,6	10,3 \pm 0,7
LABO	5	F	42,9 \pm 0,7	12,4 \pm 0,3	5,3 \pm 0,1	8,9 \pm 0,4
LABO	6	M	39,2 \pm 0,8	11,3 \pm 1,1	4,9 \pm 0,3	8,3 \pm 0,4
LABO	11	FM	40,8 \pm 2,1	11,8 \pm 1,0	5,1 \pm 0,3	8,5 \pm 0,5
LACI	6	F	55,4 \pm 0,7	16,2 \pm 0,4	7,0 \pm 0,8	10,8 \pm 0,8
LACI	6	M	53,0 \pm 1,4	15,4 \pm 1,4	6,5 \pm 0,4	11,9 \pm 1,0
LACI	12	FM	54,2 \pm 1,6	15,8 \pm 0,6	6,7 \pm 0,6	11,3 \pm 1,0
LANO	5	F	41,9 \pm 0,7	13,3 \pm 0,3	5,5 \pm 0,6	8,8 \pm 0,7
LANO	5	M	42,0 \pm 0,7	13,0 \pm 0,6	5,5 \pm 0,3	9,1 \pm 0,2
LANO	10	FM	42,0 \pm 0,6	13,1 \pm 0,5	5,5 \pm 0,4	9,0 \pm 0,5
MYLE	5	F	31,6 \pm 0,2	12,3 \pm 0,6	6,4 \pm 0,1	6,7 \pm 0,5
MYLE	5	M	31,0 \pm 0,6	11,7 \pm 0,3	5,9 \pm 1,0	6,4 \pm 0,7
MYLE	10	FM	31,3 \pm 0,5	12,0 \pm 0,5	6,1 \pm 0,7	6,6 \pm 0,6
MYLU	6	F	39,6 \pm 0,5	13,0 \pm 0,5	6,3 \pm 0,7	9,3 \pm 0,5
MYLU	24	M	39,0 \pm 2,2	13,0 \pm 1,3	6,3 \pm 0,8	9,0 \pm 2,0
MYLU	30	FM	39,1 \pm 2,1	13,0 \pm 1,2	6,3 \pm 0,7	9,1 \pm 1,8
MYSE	5	F	36,5 \pm 0,6	16,1 \pm 1,1	8,7 \pm 1,2	7,8 \pm 0,1
MYSE	15	M	36,3 \pm 1,3	15,9 \pm 0,6	8,7 \pm 0,8	9,5 \pm 1,2
MYSE	20	FM	36,4 \pm 1,2	15,9 \pm 0,7	8,7 \pm 0,9	9,1 \pm 1,3
PESU	5	F	34,9 \pm 1,0	12,3 \pm 0,4	5,8 \pm 0,9	8,6 \pm 0,7
PESU	5	M	35,5 \pm 1,5	11,2 \pm 0,6	5,3 \pm 0,7	8,8 \pm 0,5
PESU	10	FM	35,2 \pm 1,2	11,8 \pm 0,8	5,5 \pm 0,8	8,7 \pm 0,5

*EPFU = *Eptesicus fuscus* (grande chauve-souris brune); LABO = *Lasiurus borealis* (chauve-souris rousse); LACI = *L. cinereus* (chauve-souris cendrée); LANO = *Lasionycteris noctivagans* (chauve-souris argentée); MYLE = *Myotis leibii* (chauve-souris pygmée de l'Est); MYLU = *M. lucifugus* (petite chauve-souris brune); MYSE = *M. septentrionalis* (chauve-souris nordique); PESU = *Perimyotis subflavus* (pististrelle de l'Est)

Annexe 4. Résultats d'analyses de la diète des chauves-souris du genre *Myotis*

Cette annexe présente les résultats de l'identification des fragments d'ADNm des proies retrouvés dans les excréments des chauves-souris mâles capturées entre 2011 et 2012. Les individus ont été capturés à la Forêt Montmorency en 2011, ainsi qu'aux parcs nationaux de la Jacques-Cartier et d'Aiguebelle, en 2012. Cette identification a confirmé la présence d'une grande diversité de proies, incluant de nombreuses espèces de diptères et de lépidoptères, conformément à la littérature (Patterson, Willig & Stevens 2003; Clare *et al.* 2009; Clare *et al.* 2011; Dodd *et al.* 2012a; Clare *et al.* 2013; Clare *et al.* 2014).



Annexe 4. Figure 1. Regroupement par ordre des proies identifiées au genre ou à l'espèce, consommées par la petite chauve-souris brune (MYLU = *Myotis lucifugus*; n = 21) et la chauve-souris nordique (MYSE = *M. septentrionalis*; n = 5), à la forêt Montmorency (FM; n = 12), au Parc national de la Jacques-Cartier (PNJC; n = 8) et au parc national d'Aiguebelle (PNA; n = 5).

Annexe 4. Tableau 1. Liste des proies identifiées au genre ou à l'espèce, consommées par les chauves-souris mâles du genre *Myotis* à la Forêt Montmorency (FM), ainsi qu'aux parcs nationaux d'Aiguebelle (PNA) et de la Jacques-Cartier (PNJC). Le nombre d'échantillons (*n*) correspond au nombre d'individus pour lesquelles les fèces ont été analysées selon le lieu (FM, PNA, PNJC) et l'espèce (MYLU, MYSE). La fréquence correspond aux nombres d'échantillons (*n*) dans le(s)quel(s) le genre ou l'espèce d'insecte a été retrouvé.

Lieu ¹	Espèce ²	<i>n</i>	Date ³	Classe	Ordre	Famille	Proie identifiée	Fréquence
FM	MYLU	8	2011	Arachnida	Araneae	Araneidae	<i>Larinoides patagiatus</i>	1
FM	MYLU	8	2011	Insecta	Coleoptera	Melandryidae	<i>Serropalpus substraitus</i>	1
FM	MYLU	8	2011	Insecta	Diptera	Chironomidae	<i>Chironomus sp</i>	1
FM	MYLU	8	2011	Insecta	Diptera	Chironomidae	<i>Dicrotendipes tritomus</i>	1
FM	MYLU	8	2011	Insecta	Diptera	Limoniidae	<i>Antocha sp</i>	1
FM	MYLU	8	2011	Insecta	Diptera	Limoniidae	<i>Rhipidia maculata</i>	1
FM	MYLU	8	2011	Insecta	Diptera	Muscidae	<i>Musca autumnalis</i>	1
FM	MYLU	8	2011	Insecta	Diptera	Muscidae	<i>Muscina pascuorum</i>	1
FM	MYLU	8	2011	Insecta	Diptera	Mycetophilidae	<i>Sciophila sp</i>	1
FM	MYLU	8	2011	Insecta	Diptera	Tipulidae	<i>Tipula subtenuicornis</i>	1
FM	MYLU	8	2011	Insecta	Ephemeroptera	Caenidae	<i>Caenis amica</i>	1
FM	MYLU	8	2011	Insecta	Ephemeroptera	Heptageniidae	<i>Heptagenia sp</i>	1
FM	MYLU	8	2011	Insecta	Ephemeroptera	Heptageniidae	<i>Maccaffertium mediopunctatum</i>	2
FM	MYLU	8	2011	Insecta	Ephemeroptera	Siphlonuridae	<i>Siphlonurus rapidus</i>	1
FM	MYLU	8	2011	Insecta	Lepidoptera	Gelechiidae	<i>Coleotechnites sp</i>	1
FM	MYLU	8	2011	Insecta	Lepidoptera	Hepialidae	<i>Korscheltellus gracilis</i>	3
FM	MYLU	8	2011	Insecta	Lepidoptera	Tortricidae	<i>Ancylis sp</i>	1
FM	MYLU	8	2011	Insecta	Lepidoptera	Tortricidae	<i>Eana sp</i>	1
FM	MYLU	8	2011	Insecta	Lepidoptera	Tortricidae	<i>Epinotia trigonella</i>	1
FM	MYLU	8	2011	Insecta	Lepidoptera	Tortricidae	<i>Olethreutes sp</i>	1
FM	MYLU	8	2011	Insecta	Megaloptera	Corydalidae	<i>Chauliodes sp</i>	4

FM	MYLU	8	2011	Insecta	Neuroptera	Hemerobiidae	<i>Hemerobius sp</i>	2
FM	MYLU	8	2011	Insecta	Diptera	Simuliidae	<i>Simulium murmanum</i>	1
FM	MYSE	8	2011	Insecta	Lepidoptera	Tortricidae	<i>Choristoneura fumiferana</i>	1
FM	MYSE	8	2011	Insecta	Lepidoptera	Argyresthiidae	<i>Argyresthia sp</i>	2
FM	MYSE	8	2011	Insecta	Lepidoptera	Geometridae	<i>Protoboarmia sp</i>	1
FM	MYSE	8	2011	Insecta	Neuroptera	Hemerobiidae	<i>Hemerobius sp</i>	4
FM	MYSE	8	2011	Insecta	Lepidoptera	Tortricidae	<i>Argyrotaenia sp</i>	2
FM	MYSE	8	2011	Insecta	Lepidoptera	Hepialidae	<i>Korscheltellus gracilis</i>	2
FM	MYSE	8	2011	Insecta	Ephemeroptera	Isonychiidae	<i>Isonychia bicolor</i>	2
FM	MYSE	8	2011	Insecta	Lepidoptera	Depressariidae	<i>Bibarrambla allenella</i>	3
FM	MYSE	8	2011	Insecta	Lepidoptera	Gelechiidae	<i>Carpatolechia belangerella</i>	1
FM	MYSE	8	2011	Insecta	Diptera	Tipulidae	<i>Tipula entomophthorae</i>	1
FM	MYSE	8	2011	Insecta	Ephemeroptera	Caenidae	<i>Caenis horaria</i>	1
FM	MYSE	8	2011	Insecta	Coleoptera	Tenebrionidae	<i>Tenebrio molitor</i>	1
FM	MYSE	8	2011	Insecta	Diptera	Ceratopogonidae	<i>Culicoides obsoletus</i>	1
FM	MYSE	8	2011	Insecta	Diptera	Limoniidae	<i>Helius flavus</i>	1
FM	MYSE	8	2011	Insecta	Lepidoptera	Nolidae	<i>Nycteola frigidana</i>	1
FM	MYSE	8	2011	Insecta	Diptera	Chironomidae	<i>Ablabesmyia</i>	1
FM	MYSE	8	2011	Insecta	Ephemeroptera	Caenidae	<i>Caenis sp</i>	4
FM	MYSE	8	2011	Insecta	Diptera	Pediciidae	<i>Ula bolitophila</i>	1
FM	MYSE	8	2011	Insecta	Diptera	Simuliidae	<i>Simulium sp</i>	1
FM	MYSE	8	2011	Insecta	Diptera	Geometridae	<i>Metarranthis refractaria</i>	1
FM	MYSE	8	2011	Insecta	Diptera	Psychodidae	<i>Psychoda sp</i>	1
FM	MYSE	8	2011	Insecta	Lepidoptera	Erebidae	<i>Mocis latipes</i>	1
FM	MYSE	8	2011	Insecta	Hemiptera	Miridae	<i>Phytocoris sp</i>	1
FM	MYSE	8	2011	Insecta	Diptera	Limoniidae	<i>Metalimoobia quadrimaculata</i>	1
FM	MYSE	8	2011	Insecta	Lepidoptera	Geometridae	<i>Hydriomena impluviata</i>	1
FM	MYSE	8	2011	Insecta	Ephemeroptera	Heptageniidae	<i>Maccaffertium mediopunctatum</i>	1

FM	MYSE	8	2011	Insecta	Neuroptera	Hemerobiidae	<i>Hemerobius sp</i>	1
FM	MYSE	8	2011	Insecta	Lepidoptera	Gelechiidae	<i>Coleotechnites picaella</i>	1
FM	MYSE	8	2011	Insecta	Lepidoptera	Tortricidae	<i>Pandermis lamprosana</i>	1
FM	MYSE	8	2011	Insecta	Lepidoptera	Tortricidae	<i>Ancylis subaequana</i>	1
FM	MYSE	8	2011	Insecta	Diptera	Chaoboridae	<i>Chaoborus sp</i>	1
FM	MYSE	8	2011	Insecta	Megaloptera	Sialidae	<i>Sialis sp</i>	1
FM	MYSE	8	2011	Insecta	Diptera	Tipulidae	<i>Tipula senega</i>	1
FM	MYSE	8	2011	Insecta	Diptera	Chironomidae	<i>Polypedilum sp</i>	1
FM	MYSE	8	2011	Insecta	Lepidoptera	Gracillariidae	<i>Caloptilia stigmatella</i>	1
PNA	MYLU	5	2012	Insecta	Coleoptera	Melandryidae	<i>Serropalpus substraitus</i>	1
PNA	MYLU	5	2012	Insecta	Diptera	Chironomidae	<i>Paracladopelma winnelli</i>	1
PNA	MYLU	5	2012	Insecta	Diptera	Pediciidae	<i>Ula bolitophila</i>	1
PNA	MYLU	5	2012	Insecta	Diptera	Psychodidae	<i>Psychoda sp</i>	1
PNA	MYLU	5	2012	Insecta	Lepidoptera	Gelechiidae	<i>Chionodes sp</i>	1
PNA	MYLU	5	2012	Insecta	Lepidoptera	Gelechiidae	<i>Coleotechnites piceaella</i>	1
PNA	MYLU	5	2012	Insecta	Lepidoptera	Gelechiidae	<i>Gelechia lynceella</i>	1
PNA	MYLU	5	2012	Insecta	Lepidoptera	Noctuidae	<i>Mythimna unipuncta</i>	1
PNA	MYLU	5	2012	Insecta	Lepidoptera	Tortricidae	<i>Epinotia trigonella</i>	2
PNA	MYLU	5	2012	Insecta	Megaloptera	Corydalidae	<i>Chauliodes sp</i>	1
PNA	MYLU	5	2012	Insecta	Neuroptera	Hemerobiidae	<i>Hemerobius sp</i>	1
PNA	MYLU	5	2012	Insecta	Neuroptera	Hemerobiidae	<i>Hemerobius stigma</i>	1
PNA	MYLU	5	2012	Insecta	Trichoptera	Polycentropodidae	<i>Polycentropus pentus</i>	1
PNJC	MYLU	5	2012	Insecta	Coleoptera	Melandryidae	<i>Serropalpus substraitus</i>	1
PNJC	MYLU	5	2012	Insecta	Diptera	Chironomidae	<i>Dicrotendipes tritomus</i>	1
PNJC	MYLU	5	2012	Insecta	Diptera	Chironomidae	<i>Tanytarsus mendax</i>	1
PNJC	MYLU	5	2012	Insecta	Diptera	Culicidae	<i>Aedes vexans</i>	1
PNJC	MYLU	5	2012	Insecta	Diptera	Limoniidae	<i>Helius flavus</i>	1
PNJC	MYLU	5	2012	Insecta	Diptera	Mycetophilidae	<i>Exechia sp</i>	1

PNJC	MYLU	5	2012	Insecta	Diptera	Simuliidae	<i>Simulium sp</i>	1
PNJC	MYLU	5	2012	Insecta	Ephemeroptera	Heptageniidae	<i>Heptagenia sp</i>	3
PNJC	MYLU	5	2012	Insecta	Lepidoptera	Geometridae	<i>Metarranthis sp</i>	1
PNJC	MYLU	5	2012	Insecta	Lepidoptera	Hepialidae	<i>Korscheltellus gracilis</i>	1
PNJC	MYLU	5	2012	Insecta	Lepidoptera	Tortricidae	<i>Archips argyrospila</i>	1
PNJC	MYLU	5	2012	Insecta	Lepidoptera	Tortricidae	<i>Epinotia misella</i>	1
PNJC	MYLU	5	2012	Insecta	Lepidoptera	Tortricidae	<i>Epinotia trigonella</i>	1
PNJC	MYLU	5	2012	Insecta	Lepidoptera	Tortricidae	<i>Metendothenia separatana</i>	1
PNJC	MYLU	5	2012	Insecta	Megaloptera	Corydalidae	<i>Chauliodes sp</i>	3
PNJC	MYLU	5	2012	Insecta	Neuroptera	Hemerobiidae	<i>Hemerobius sp</i>	1
PNJC	MYLU	5	2012	Insecta	Trichoptera	Helicopsychidae	<i>Helicopsyche borealis</i>	1

¹PNJC = Parc national de la Jacques-Cartier; PNA = Parc national d'Aiguebelle; FM = Forêt Montmorency

²MYLU = *Myotis lucifugus* (petite chauve-souris brune); MYSE = *M. septentrionalis* (chauve-souris nordique)

³Année de capture des chauves-souris

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