UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

ÉTUDE DES FACTEURS AFFECTANT LA DÉTECTION ET RÔLE DE LA QUANTITÉ D'HABITAT SUR LES PETITS MAMMIFÈRES À FAIBLE CAPACITÉ DE DISPERSION EN PAYSAGE PERTURBÉ DU QUÉBEC

THÈSE

PRÉSENTÉE

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PAR
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"*Le bonheur pour une abeille ou un dauphin est d'exister. Pour l'homme, c'est de le savoir et de s'en émerveiller*"

(Capitaine Jacques Cousteau)

À mes parents,

pour m'avoir accompagnée

dans mes premiers émerveillements.

AVANT-PROPOS

L'aménagement écosystémique est une grande thématique de recherche, dont l'un des objectifs est de comprendre le rôle joué par les îlots résiduels post-feu dans le maintien de la biodiversité et de la dynamique forestière boréale. Les travaux présentés dans ce mémoire et rédigés dans le cadre du programme de doctorat en sciences de l'environnement, s'inscrivent dans ce contexte avec pour principale cible les petits mammifères à faible capacité de dispersion qui vivent en pessière noire à mousses de l'ouest du Québec. L'étude s'est penchée sur l'occurrence (occupation de site, colonisation et extinction) de ces espèces au sein d'îlots de rétention laissés dans des parterres de coupe totale et l'a comparée à l'occurrence de ces mêmes espèces dans des îlots résiduels post-feu. Cet axe de recherche, jamais exploré auparavant, a été jugé pertinent car l'étude s'est appliquée à inclure des variables de différentes échelles spatiales, y compris des échelles de paysage en adéquation avec l'étendue de pertubation qu'occasionnent les feux de forêt et les travaux sylvicoles. Ces travaux de recherche ont principalement permis de mettre en évidence la résilience comparable des populations de petits mammifères face aux perturbations naturelles et anthropiques, résultat des plus encourageant pour combiner un aménagement forestier bio-garant et une exploitation durable de la forêt boréale. Toutefois, les résultats démontrent également l'importance de la quantité d'habitat présente dans le paysage pour maintenir les procédés écologiques régulant les populations de petits mammifères, offrant ainsi de nouvelles pistes de recherche.

Cette thèse est composée de trois chapitres principaux et d'une annexe, rédigés sous forme d'article scientifique, ainsi que d'une introduction et conclusion générale. Une revue critique de littérature ainsi qu'un chapitre décrivant les méthodes utilisées tout au long de l'étude complètent ce mémoire. L'ordre des chapitres correspondant aux trois axes d'études de cette thèse réfère à l'ordre chronologique dans lequel ils ont été rédigés et soumis à une révision par les pairs. Selon la revue visée, la forme des articles varie sensiblement. Nous n'avons pu éviter la redondance des informations fournies au niveau des méthodes de chaque article. L'unique base de données sur laquelle ces trois axes d'étude s'appuient, obtenue sur un seul et même territoire d'étude et selon une combinaison précise de méthodes d'échantillonnage, a été considérée en intégralité ou partitionnée selon les objectifs fixés par les chapitres. L'annexe, quant à elle, se rapporte à une étude réalisée en partenariat avec une thèse doctorale similaire dans ses objectifs, mais avec pour espèces focales les bryophytes de la pessière noire à mousses.

Chapitre III - Chavel E. E., M. J. Mazerolle, L. Imbeau & P. Drapeau (2017) *Comparative evaluation of three sampling methods to estimate detection probability of American red squirrels (*Tamiasciurus hudsonicus*)*. Article publié dans *Mammalian Biology* 83(-) : 1-9.

Chapitre IV - Chavel E. E., L. Imbeau, M. J. Mazerolle & P. Drapeau (2017) *Boreal small mammals show evidence of density-dependent patterns with area-sensitivity.* Article publié dans *Forest Ecology and Management* 400(-) : 485-501.

Chapitre V - Chavel E. E., M. J. Mazerolle , L. Imbeau & P. Drapeau. Do harvesting strategies influence small mammal co-occurrence? Article à soumettre à *Canadian Journal of Zoology*.

Annexe 1 - Barbé M., E. E. Chavel, N. J. Fenton, L. Imbeau, M. J. Mazerolle, P. Drapeau, and Y. Bergeron (2016) *Dipersal of bryophytes and ferns in facilitated* *by small mammals in the boreal forest*. Article publié dans *Ecoscience* 23(3-4) : 67-76.

Je suis la première auteure de chacun de ces articles, ayant participé à chaque étape de leur élaboration, depuis la collecte de données, jusqu'à leur rédaction. Louis Imbeau, directeur de recherche, et Pierre Drapeau, co-directeur, ont participé à la définition des objectifs ainsi que l'ancrage des études dans le contexte d'aménagement écosystémique de la forêt boréale. Marc Mazerolle, co-directeur et référant statistique, a quant à lui, fourni un travail conséquent sur la mise en œuvre des analyses, d'où sa place de second auteur sur le premier article (de nature plus méthodologique) et le troisième article. Tous trois ont pleinement contribué à la rédaction et l'aboutissement de ces trois chapitres principaux.

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Nous souhaitons ajouter que certaines illustrations associées aux méthodes nécessitaient d'être présentes à la publication de chaque chapitre. Nous nous excusons pour cette redondance au cours de la lecture du présent travail.

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Sites d'échantillonnage

CONTROL	sites de vieille forêt témoin, sites contrôle, sigle issu de terme anglais "Control"
CTRL	sites de vieille forêt témoin, sites contrôle, sigle issu de terme anglais "Control"
CPRS	Coupe avec Protection de la Régénération et des Sols
GREENTREE	îlots résiduels post-coupe, sigle issu du terme anglais "Green Tree Retention Stand"
GTRP	îlots résiduels post-coupe, sigle issu du terme anglais "Green Tree Retention Stand"
HARVEST	combinaison des sites GREENTREE et LINEARCUT, sigle issu du terme anglais "Post-Harvested Stand"
LCBS	séparateur de coupe, sigle issu du terme anglais "Linear Cut-Block Stand"
LINEARCUT	séparateur de coupe, sigle issu du terme anglais "Linear Cut-Block Stand"
POSTFIRE	îlots résiduels post-feu, sigle issu du terme anglais "Post-Fire Residual Patch"
PRFP	îlots résiduels post-feu, sigle issu du terme anglais "Post-Fire Residual Patch"

Espèces animales

GlaSab	*Glaucomys sabrinus*, grand polatouche
MicPen	*Microtus pennsylvanicus*, campagnol des champs
MyoGap	*Myodes gapperi*, campagnol à dos roux de Gapper
PerMan	*Peromyscus maniculatus*, souris sylvestre
TamHud	*Tamiasciurus hudsonicus*, écureuil roux d'Amérique
TamSpp	*Tamiasciurus species*, toutes espèces d'écureuils non volants confondues
SorCin	*Sorex cinereus*, musaraigne cendrée
SorSpp	*Sorex species*, toutes espèces de musaraignes confondues

Variables explicatives

Age	âge du peuplement, exprimé en années
Arthro	biomasse d'arthropodes présente sur site, exprimée en grammes (g)
Can	recouvrement de la canopée, exprimé en pourcentage (%)
Can20	recouvrement de la canopée à 20 cm du sol, exprimé en pourcentage (%)
Can150	recouvrement de la canopée à 150 cm du sol, exprimé en pourcentage (%)
CanCov	recouvrement de la canopée, exprimé en pourcentage (%), sigle issu du terme anglais "Canopy Cover"

CanCov20	recouvrement de la canopée à 20 cm du sol, exprimé en pourcentage (%), sigle issu du terme anglais "Canopy Cover"
CanCov150	recouvrement de la canopée à 150 cm du sol, exprimé en pourcentage (%), sigle issu du terme anglais "Canopy Cover"
Decid	présence d'arbres feuillus, valeur binaire, sigle issu du terme anglais "Deciduous Tree"
DWD	volume de bois mort, exprimé en mètre cube par mètre carré ($m^3.m^{-2}$), sigle issu du terme anglais "Down Woody Debris"
DWDtot	volume total de bois mort, quelque soit le niveau de décomposition, exprimé en mètre cube par mètre carré ($m^3.m^{-2}$), sigle issu du terme anglais "Down Woody Debris"
EarlyDWD	volume de jeune bois mort, exprimé en mètre cube par mètre carré ($m^3.m^{-2}$), sigle issu du terme anglais "Early-decayed Down Woody Debris"
LateDWD	volume de vieux bois mort, exprimé en mètre cube par mètre carré ($m^3.m^{-2}$), sigle issu du terme anglais "Late-decayed Down Woody Debris"
Method	méthode d'échantillonnage de l'écureuil roux d'Amérique, variable catégorique (capture vivante, point d'écoute ou repasse par pré-enregistrement de cris), sigle issu du terme anglais "Method"

METHOD$^+$	influence d'une capture vivante sur l'échantillonnage des écureuils roux d'Amérique par méthode auditive, variable catégorique (capture vivante, point d'écoute sans capture, point d'écoute après capture, repasse sans capture et repasse après capture), sigle issu du terme anglais "Method"
MOLLUSC	biomasse de mollusques terrestres présente sur site, exprimée en grammes (g), sigle issu du terme anglais "Mollusc"
MOON	illumination lunaire, exprimé en pourcentage (%)
NONCONNECT	variable différenciant les sites non connectés à la vieille forêt (îlots post-feu et de rétention) des sites soit connectés à la vieille forêt (séparateurs de coupe) soit inclus dans la vieille forêt continue (site contrôle de vieille forêt)
RAIN	pluviométrie quotidienne, exprimé en millilitres (ml)
SESSION	session de capture, variable catégorique (Août 2013, Juin 2014, Juillet 2014, Août 2014)
SNAGDENS	densité de chicots de plus de 10 cm de diamètre, exprimée en nombre d'individus à l'hectare, sigle issu du terme anglais "Snag Density"
TEMP	températures nocturnes moyennes, exprimé en degré Celsius (°C)
TREEDENS	densité d'arbres vivants de plus de 10 cm de diamètre, exprimée en nombre d'individus à l'hectare, sigle issu du terme anglais "Tree Density"

TREE DENSITY	densité d'arbres vivants de plus de 10 cm de diamètre, exprimée en nombre d'individus à l'hectare, sigle issu du terme anglais "Tree Density"
TYPE	origine des parcelles, variable catégorique (îlots résiduels post-feu, îlots résiduels post-coupe, séparateur de coupe, vieille forêt)
VISIT	jour de capture dans une session, variable catégorique (Jour1, Jour 2, Jour 3), sigle issu du terme anglais "Visit"

Modèles d'occupation

β	estimé de régression pour une variable donnée
Δ	différence d'AIC (d'AICc, de QAIC ou de QAICc) entre le meilleur modèle et un autre modèle donné
ε	paramètre d'extinction dans les modèles d'occupation dynamique à une espèce et plusieurs saisons d'échantillonnage
γ	paramètre de colonisation dans les modèles d'occupation dynamique à une espèce et plusieurs saisons d'échantillonnage
γ	Facteur d'intéraction entre deux espèces (SIF, issu du terme anglais "Species Interaction Factor")
ψ	paramètre d'occupation de site initiale dans les modèles d'occupation dynamique à une espèce
ψ^A	paramètre d'occupation de site initiale de l'espèce A (dominante) dans les modèles d'occupation dynamique à deux espèces

ψ^{BA}	paramètre d'occupation de site initiale de l'espèce B quand l'espèce A est présente dans les modèles d'occupation dynamique à deux espèces
ψ^{Ba}	paramètre d'occupation de site initiale de l'espèce B quand l'espèce A est absente dans les modèles d'occupation dynamique à deux espèces
ω_i	poids d'Akaike pour un modèle donné
AIC	critère d'information d'Akaike, acronyme issu du terme anglais "Akaike's Information Criterion"
AIC_c	critère d'information d'Akaike après ajustement des données à la modélisation
$\hat{c}$	paramètre qui informe de la dispersion des données, paramètre introduit pour l'ajustement des données à la modélisation
[CI]	intervale de confiance, généralement à 95%, acronyme issu du term anglais "Confidence Interval"
K modèle	nombre de paramètres estimés dans un statistique
$\text{modavgEffect}_{\text{logit}}$	fonction d'inférence multi-modèles qui infère la taille de l'effet entre deux catégories d'une variable catégorique ou deux extrêmes d'une variable continue en se basant sur tous les modèles candidats, exprimée sur l'échelle logit
$\text{modavgEffect}_{\text{response}}$	fonction d'inférence multi-modèles qui infère la taille de l'effet entre deux catégories d'une variable catégorique ou deux extrêmes d'une variable continue en se basant sur tous les modèles candidats, exprimée sur l'échelle réponse

p	paramètre de détection dans les modèles d'occupation dynamique à une espèce
p^{A}	paramètre de détection de l'espèce A (dominante) lorsque l'espèce B est absente, dans les modèles d'occupation dynamique à deux espèces
p^{B}	paramètre de détection de l'espèce B lorsque l'espèce A (dominante) est absente, dans les modèles d'occupation dynamique à deux espèces
QAIC	critère d'information d'Akaike corrigé pour les échantillons de petits tailles, acronyme issu du terme anglais "Quasi-likelihood Akaike’s Information Criterion"
QAIC_{c}	critère d'information d'Akaike corrigé pour les échantillons de petits tailles, acronyme issu du terme anglais "Quasi-likelihood Akaike’s Information Criterion" après ajustement des données à la modélisation
r^{A}	paramètre de détection de l'espèce A lorsque les deux espèces sont présentes, dans les modèles d'occupation dynamique à deux espèces
r^{BA}	paramètre de détection de l'espèce B lorsque les deux espèces sont présentes et détectées dans les modèles d'occupation dynamique à deux espèces
r^{Ba}	paramètre de détection de l'espèce B lorsque les deux espèces sont présentes mais que l'espèce A n'a pas été détectée dans les modèles d'occupation dynamique à deux espèces
SE	erreur type, acronyme issu du terme anglais "Standard Error"

SIF	facteur d'interaction entre deux espèces, acronyme issu du terme anglais "Species Interaction Factor"

Autres

AFE	aménagement forestier écosystémique
CENTRE	point fictif au centre des grilles et transects de capture
dbh	diamètre des arbres à hauteur de poitrine acronyme issu du terme anglais "Diameter at Breast Height"
Fig	figure
FRQNT	Fonds de Recherche du Quebec - Nature et Technologies
gls	modèle par méthode des moindres carrés généralisés, acronyme issu du terme anglais "Generalised Least Squares"
MDDELCC	Ministère du Développement durable, de l'Environnement et de la Lutte contre les changements climatiques
n	taille d'échantillon
N/A	non-applicable
No/100TN	nombre d'individus capturés par 100 nuits de capture
NSERC	conseil de recherche en sciences naturelles et en génie du Canada, acronyme issu du terme anglais "Natural Sciences and Engineering Research Council of Canada"
UQAT	Université du Québec en Abitibi-Téminscamingue
UTC	Temps Universel Coordonné

LIST OF ABBREVIATIONS AND ACRONYMS

Sampling sites

CONTROL	control site composed of old-growth forest
CTRL	control site composed of old-growth forest
CPRS	cut with Protection of Regeneration and Soils
GREENTREE	green tree retention stand
GTRP	green tree retention stand
HARVEST	post-harvest sites, i.e. GREENTREE and LINEARCUT combined
LCBS	linear cut-block stand
LINEARCUT	linear cut-block stand
POSTFIRE	post-fire residual patch
PRFP	post-fire residual patch

Species

GlaSab	*Glaucomys sabrinus*, northern flying squirrel
MicPen	*Microtus pennsylvanicus*, field vole
MyoGap	*Myodes gapperi*, southern red-backed vole
PerMan	*Peromyscus maniculatus*, deer mouse
TamHud	*Tamiasciurus hudsonicus*, American red squirrel

TamSpp	*Tamiasciurus species*, all species of non-flying squirrels
SorCin	*Sorex cinereus*, masked shrew
SorSpp	*Sorex species*, all species of shrews

Explanatory variables

Age	stand age, expressed in years
Arthro	arthropod biomass, expressed in grams (g)
Can	canopy cover, expressed in percentage (%)
Can20	canopy cover 20 cm from the ground, expressed in percentage (%)
Can150	canopy cover 150 cm from the ground, expressed in percentage (%)
CanCov	canopy cover, expressed in percentage (%)
CanCov20	canopy cover 20 cm from the ground, expressed in percentage (%)
CanCov150	canopy cover 150 cm from the ground, expressed in percentage (%)
Decid	presence of deciduous trees, binary measure
DWD	volumes of down woody debris, expressed in cubic meter per square meter ($m^3.m^{-2}$)
DWDtot	total volmes of down woody debris (both early- and late decayed), expressed in cubic meter per square meter ($m^3.m^{-2}$)
EarlyDWD	volumes of early-decayed down woody debris, expressed in cubic meter per square meter ($m^3.m^{-2}$)
LateDWD	volumes of late-decayed down woody debris, expressed in cubic meter per square meter ($m^3.m^{-2}$)

METHOD	method to sample American red squirrel, categorial variable (live-trapping, point count or playback call)
METHOD^+	influence of a trapping or handling effect on the detection probability during auditory methods, categorial variable (live-trapping, point count without capture, point count with capture, playback call without capture or playback call with capture)
MOLLUSC	terrestrial mollusc biomass, expressed in grams (g)
MOON	moon illumination, expressed in percentage (%)
NonConnect	categorical variable to separate sites that are not connected to old-growth forest (green-tree retention and post-fire remnant patches) from sites that are either connected to old-growth forest (linear cutblock stands) or included in an old-growth forest (control sites)
RAIN	daily rainfall, expressed in millilitres (ml)
SESSION	trapping session, categorical variable (August 2013, June 2014, July 2014, August 2014)
SNAGDENS	density of snag larger than 10 cm in diametre, expressed in number of large snags per hectare
TEMP	average nocturnal temperatures, expressed in Celsius degree (°C)
TREEDENS	density of tree larger than 10 cm in diametre, expressed in number of stems per hectare

TREE DENSITY	density of tree larger than 10 cm in diametre, expressed in number of stems per hectare
TYPE	site origin, categorical variable (post-fire residual stand, green-tree retention stand, linear cut-block stand, control site)
VISIT	sampling day in a trapping session, categorical variable (Day 1, Day 2, Day 3)

Occupancy modeling

β	regression estimate for any given variable included in a model
Δ:	AIC (AICc, QAIC or QAICc) difference between the top-ranked model and any other given model difference d'AIC
ε	probability of extinction in single-species, multi-seasons dynamic occupancy models
γ	probability of colonisation in single-species, multi-seasons dynamic occupancy models
γ	Species Interaction Factor (SIF)
ψ	probability of initial occupation in single-species dynamic occupancy models
ψ^{A}	probability of initial occupation by species A (dominant species) in two species dynamic occupancy models
ψ^{BA}	probability of initial occupation by species B when species A (dominant species) is present, in two species dynamic occupancy models

ψ^{Ba}	probability of initial occupation by species B when species A (dominant species) is absent, in two species dynamic occupancy models
ω_i	Akaike weight
AIC	Akaike's Information Criterion
AIC_c	ajusted Akaike's Information Criterion
$\hat{c}$	overdispersion parameter used to adjust models
[CI]	confidence interval, usually 95% confidence interval
K	number of estimated parameters in a model
$\text{modavgEffect}_{\text{logit}}$	function that model-averages the effect size between two categories of a categorical variable or two extremes of a continuous variable, based on the entire model set, and expressed on the logit scale
$\text{modavgEffect}_{\text{response}}$	function that model-averages the effect size between two categories of a categorical variable or two extremes of a continuous variable, based on the entire model set, and expressed on the response scale
p	probability of detection in single-species dynamic occupancy models
p^A	probability of detection of species A (dominant) when species B is absent, in two species dynamic occupancy models
p^B	probability of detection of species B when species A (dominant) is absent, in two species dynamic occupancy models

QAIC	quasi-likelihood Akaike’s Information Criterion, i.e. Akaike’s Information Criterion corrected for small samples
QAIC_c	ajusted quasi-likelihood Akaike’s Information Criterion
r^{A}	probability of detection of species A (dominant) when both species A and B are present, in two species dynamic occupancy models
r^{BA}	probability of detection of species B when both species A and B are present and detected, in two species dynamic occupancy models
r^{Ba}	probability of detection of species B when both species A and B are present but species A remains undetected, in two species dynamic occupancy models
SE	standard error
SIF	Species Interaction Factor

Others abbreviations and acronyms

AFE	ecosystem-based forest management, acronym from the french name "Aménagement Forestier Écosystémique"
CENTRE	imaginary point in the centre of capture grids and transects
dbh	diameter at breast height
Fig	figure
FRQNT	Québec fellowship, acronym from the french name "Fonds de Recherche du Quebec - Nature et Technologies"
gls	generalised least squares models

MDDELCC	environment department, acronym from the french name "Ministère du Développement durable, de l'Environnement et de la Lutte contre les changements climatiques"
n	sample size
N/A	non-applicable
No/100TN	number of individuals caught per 100 trap nights
NSERC	Natural Sciences and Engineering Research Council of Canada
UQAT	University of Quebec in Abitibi-Teminscamingue
UTC	Coordinated Universal Time

RÉSUMÉ

Les stratégies d'aménagement écosystémiques doivent s'adapter à la complexité des relations entre la biodiversité et l'habitat. Au Canada, ces stratégies visent à s'inspirer des patrons de feux qui sont à la base de la dynamique fonctionnelle de la forêt boréale. Plusieurs études ont donc tenté de caractériser la dynamique des îlots créés par processus naturels ou anthropogéniques, comparée à celle observée en forêt continue. Très peu se sont pourtant attardées à la comparaison directe entre des îlots résiduels post-feu et des îlots de rétention post-coupes. Dans cette thèse, nous avons donc voulu pallier ce manque en évaluant la pertinence de la rétention d'arbres dans des chantiers de coupe avec protection et régénération des sols à maintenir une petite faune à faible capacité de dispersion, par rapport à des îlots post-feu. Pour ce faire, nous avons mené quatre sessions d'échantillonnage dans 60 sites répartis entre des îlots résiduels de vieille forêt dans des parterres de feu et de coupes forestières, avec pour témoins des massifs de vieilles forêts continues dans la pessière noire du nord-ouest du Québec, au cours des étés 2013 et 2014.

Dans un premier temps, nous avons voulu explorer l'impact des méthodes d'échantillonnage sur le paramètre de détection des modèles d'occupation, et évaluer la pertinence des méthodes auditives (point d'écoute et repasse) pour étudier l'occupation de sites de l'écureuil roux d'Amérique. Selon nos résultats, les méthodes auditives moins invasives engendrent des probabilités de détection comparables à celles obtenues par la capture vivante.

Nous avons poursuivi avec les réponses des petits mammifères à la quantité de forêt en termes d'occupation de site, de colonisation et d'extinction, afin de fournir des pistes robustes pour un aménagement écosystémique du territoire. L'objectif principal était de modéliser les relations entre la quantité de forêt boréale et l’occurrence de petits mammifères, après avoir contrôlé l'influence de variables locales telles que le bois mort, sur l'occurrence de ces espèces. La quantité d'habitat (exprimée en pourcentage de forêt) a été mesurée dans 100 périmètres circulaires et concentriques (rayon entre 50 et 5000m), centrés sur chacune des grilles de capture. A l'issue de ce chapitre, nous avons mis en évidence des relations négatives entre l'occupation de sites par les petits mammifères et la quantité de forêt, résultats peu courants dans la littérature et rarement discutés. Nous soupçonnons que la faible densité des populations échantillonnées, et donc la distribution clairsemée des individus, a pu influencer les patrons de sensibilité à la quantité d'habitat disponible.

Le dernier chapitre mise sur une approche similaire à celle du paragraphe ci-dessus, à l'exception que nous nous sommes penchés sur des paires d'espèces et non des espèces individuelles. Nous avons testé la sensibilité de la co-occurrence de deux espècesà la quantité d'habitat mesurée dans les 100 mêmes périmètres que précédemment décrits. Ici nous avons questionné la capacité de la rétention en CPRS à satisfaire les besoins des deux espèces associées aux vieilles forêts (grand polatouche et campagnol à dos roux de Gapper), en présence d'une espèce ubiquiste, plus généraliste et opportuniste (écureuil roux d'Amérique et musaraigne cendrée). Soutenant l'inefficacité des îlots post-coupe, en terme d'isolement des îlots rémanents et de quantité d'habitat avoisinante à maintenir les grands polatouches, ce chapitre offre donc plusieurs pistes de recherche quant à la configuration spatiale des îlots de rétention au sein de parterres de coupe.

Une annexe présente enfin un travail collaboratif entre deux équipes de recherche qui visait à savoir si les petits mammifères boréaux représentaient des disséminateurs de cryptogammes. Par le brossage du pelage de 99 individus, appartenant à 5 espèces différentes (*Glaucomys sabrinus*, *Myodes gapperi*, *Peromyscus maniculatus*, *Phenacomys ungava* et *Tamisciurus hudsonicus*) et attrapés sur site, nous avons fait germer 172 propagules/diaspores en laboratoire, appartenant à 7 espèces distinctes de cryptogammes. Ces résultats soulignent l’importance des petits mammifères et de leur dynamique de déplacement quant à la régénération de la matrice suite à une perturbation majeure.

Au terme de cette thèse, nous apportons notre contribution au méta-projet qui visait à mieux comprendre l’importance des îlots de rétention dans une dynamique post-perturbation. Nos travaux soulignent l'importance de considérer à la fois les échelles locales et du paysage, tout en maintenant une quantité de peuplements forestiers âgés, de préférence continus, pour maintenir une biodiversité certes à faible capacité de dispersion mais au cœur de la dynamique régénératrice des forêts boréales.

Mots clefs :

Aménagement écosystémique ; Coupe avec Protection et Régénération des Sols (CPRS) ; Îlots résiduels ; Perturbations naturelle et anthropique ; Pessière noire à mousse ; Petits mammifères ; Quantité d'habitat ; Rétention variable

ABSTRACT

Ecosystem-based management strategies have to be adapted to the complexity of relationships between biodiversity and its habitat. In Canada, these strategies aim at mimicking wildfires patterns that are the core of boreal forest functional dynamics. Several studies therefore described the dynamics of remnant patches created by either natural or anthropogenic disturbances, compared to the functional dynamics observed in continuous old-growth forest. Very few studies, however, have directly compared post-harvest remnant patches to post-fire ones. Here, we wanted to address this issue by evaluating how efficient green-tree retention was in maintaining small mammals with reduced dispersal capacities in CPRS (Cut with Protection of Regeneration and Soils) cutblocks, in comparison to post-fire remnant patches. In order to do so, we conducted four trapping sessions in 60 sites located in old forest remnant patches of old forests in both wildfires and aggregated clearcuts, and in continuous old forest blocks within the black spruce forest of northwestern Quebec, Canada, over the summers of 2013 and 2014.

First, we explored the influences sampling methods (live trapping, point count and playbac calls) on the detection parameter included in occupancy models, and we evaluated the suitability of auditory methods (point count and playback call) to study American red squirrel occupancy. According to our results, auditory methods yield similar detection probabilities to the more traditional and more invasive live-trapping method.

Next, we assessed small mammal responses to the amount of forest in surrounding areas, in terms of site occupancy, colonisation and extinction, while controlling for local habitat associations. This chapter hoped to provide robust guidelines for ecosystem-based management as the main objective was to model the relationship between habitat amount and small mammal occupancy. Forest amount (expressed in percentage of forest) was measured within 100 concentric buffers (radii from 50 to 5000 m) around each capture grid using digital forest cover maps. In this chapter, we highlighted negative relationships between site occupancy and forest amount, i.e. uncommon results and rarely explained. We suspected that the low density at which mammalian populations were sampled, and therefore the sparse distribution of individuals, could have influenced area-sensitivity patterns.

Last chapter relied on a similar approach to the one described in the previous paragraph, but instead of focusing on one species at a time, we analysed pairs of species. We tested whether interspecific competition was sensitive to habitat amount. We questioned the suitability of green-tree retention from CPRS cutblock in providing resources for old-growth specialists (northern flying squirrel and southern red-backed vole) in the presence of a more generalist and opportunistic, ubiquitous species (American red squirrel and masked shrew). According to our results, remnant patches can not maintain northern flying squirrels due to the greater isolation of retention patches within the diturbed matrix and the smaller amounts of habitat available in surrounding areas. This chapter offers several leads for studies on green-tree retention spatial configuration within CPRS cutblocks.

The work carried out by two research teams is presented in an appendix, with the objective to demonstrate whether boreal small mammals were cryptogam dispersers. By brushing propagules of the fur of 99 ground-dwelling small mammals live-trapped throughout the summers of 2013 and 2014, we succeeded in growing viable bryophytes and ferns in lab conditions. Our results demonstrate the importance of small mammal dispersal dynamics regarding matrix regeneration following major disturbances.

At the end of this thesis, we contributed to a better understanding of the role played by remnant patches following major disturbances. We highlighted the importance of preserving subsequent amounts of (continuous) old-growth forest in cutblocks. Moreover, both local and landscape scales are to be considered when dealing with this so-called biodiversity with reduced dispersal capacities, even more so as it plays a key role in boreal forest regenerating dynamics.

Key words:

Black spruce forest; Cut with the Protection of Regeneration and Soils (CPRS); Ecosystem-based management; Green-tree retention stands; Habitat amount; Natural and anthropogenic disturbances; Small mammals; Variable retention

CHAPITRE I

INTRODUCTION GÉNÉRALE ET REVUE CRITIQUE DE LITTÉRATURE

1.1 Situation de l'aménagement forestier au Québec

1.1.1 Changement de paradigme pour une exploitation durable

Les forêts représentent des écosystèmes clefs dans un paysage. En plus des services écologiques qu'elles rendent, elles se composent de multiples habitats qui abritent une biodiversité unique. Les forêts sont aussi au cœur des activités humaines. Perçues autrefois comme un frein au développement économique, agricole et pastoral, elles ont été gérées intensivement, principalement par des coupes à blanc (Keenan et Kimmins 1993 ; Jönsson et al. 2009 ; Gustafsson et al. 2010). Lorsque l'ère industrielle prit son essor et que certains pays connurent une pénurie de bois, la gestion forestière s'orienta vers des aménagements garantissant certaines provisions de biens et de services écologiques. Les stratégies alors adoptées durèrent jusqu'aux années 1970, durant lesquelles les mentalités changèrent d'avantage avec l'apparition d'un "droit international de l'environnement" et d'une "charte mondiale pour la nature" (Lanly 1995 ; Rist et Moen 2013). La conférence des Nations Unies de 1992 sur l'environnement et le développement durable marque alors un tournant social et politique dans l'aménagement et la conservation des forêts à travers le monde. Le concept de "gestion et développement durables" grâce auquel protection de l'environnement et développement économique devaient aller de pair, fût alors introduit.

Plusieurs stratégies d'aménagement ont été successivement adoptées par les pays ratificateurs, afin de s'inscrire dans le cadre juridique et répondre aux différents principes définis lors de ce sommet mondial (Dupuy et al. 1999 ; Hagner 1999 ; Rametsteiner et Simula 2003 ; Stupak et al. 2011). Au Canada, on parle aujourd'hui d'aménagement forestier écosystémique (AFE). Cette approche, qui s'appuie sur les multiples travaux de recherche menés en écologie forestière, reconnait l'importance de gérer les écosystèmes à des échelles spatio-temporelles multiples ainsi que d'intégrer les perturbations anthropiques dans la gamme de variabilité naturelle de la forêt aménagée (Bergeron et al. 2007 ; Gauthier et al. 2008 ; Rist et Moen 2013). Les répercussions de cet aménagement ne doivent donc pas aller au-delà des limites dans lesquelles s'inscrit le dynamisme naturel de la forêt. La conservation de la biodiversité, la protection des sols et des ressources hydriques, et le maintien de niveaux de récolte élevés sont aujourd'hui des objectifs clefs de l'AFE (Grenon et al. 2010).

1.1.2 Principe de l'aménagement forestier écosystémique au Québec

Face à un morcellement de l'habitat causé par les coupes totales, au rajeunissement d'une mosaïque forestière boréale dans laquelle se raréfient les peuplements surannés, et la simplification de la structure interne des peuplements (Cyr et al. 2009), le gouvernement canadien a mis en place une initiative conjointe avec la Malaisie (Processus de Montréal, 1994) qui insiste sur l'élaboration de critères et d'indicateurs d'exploitation durable. L'exploitation forestière fennoscandinave, précédant de plusieurs décennies celle du Québec, et les études en écologie forestière associées, démontrèrent que les critères d'aménagement durable des forêts devaient tenir compte de la nature dynamique des écosystèmes forestiers dans lesquels certaines perturbations jouent un rôle important et récurrent de structuration des processus écologiques et d'assemblage des espèces (Mönkkönen et Welsh 1994 ; Lindenmayer et Noss 2006).

En forêt boréale, il y a des liens étroits de cause à effet entre la nature des perturbations naturelles, le régime (fréquence, sévérité et aire affectée) de cette perturbation et le maintien de la biodiversité et des fonctions écologiques essentielles de l'écosystème. Ces liens émanent principalement de l'évolution conjointe des écosystèmes forestiers et des espèces, qui démontrent alors une plus grande résilience suite à une perturbation naturelle. C'est précisément cette capacité à se régénérer qui autorise la récolte de bois à grande échelle, à condition que les conséquences écologiques d'une telle perturbation anthropique ne sortent pas l'écosystème de sa gamme de variabilité naturelle (Bergeron et al. 2007). Aménager de façon écosystémique la forêt boréale demande donc de réduire les écarts de structure et de composition entre les paysages naturellement perturbés et ceux aménagés par l'industrie forestière.

1.1.3 Pessière noire à mousses de l'ouest du Québec et coupe de protection et régénération des sols

La forêt boréale québécoise est façonnée par des perturbations naturelles telles les épidémies d'insectes, les chablis ou encore les trouées (Kneeshaw et Bergeron 1998 ; de Römer et al. 2007). La principale perturbation reste toutefois les grands feux de forêt qui laissent après leur passage une mosaïque d'habitats, dont les caractéristiques varient selon la topographie, les conditions climatiques et les espèces végétales présentes sur le terrain (Morneau et Payette 1989, Payette et al. 1989. Bergeron et al. 2004). Ainsi, selon les patrons spatio-temporels laissés par les grands feux de forêt et étudiés au cours des 20 dernières années, plusieurs stratégies d'aménagement ont été proposées (Bergeron et Harvey 1997 ; Cyr et al. 2009), notamment les coupes à rétention variable (Franklin et Forman 1987). Ces dernières conservent au sein même du parterre de coupe des éléments structuraux reportés comme essentiels pour le dynamisme de l'écosystème. Cette rétention prend la forme de legs biologiques tels que les débris ligneux au sol, les chicots, et surtout les arbres matures et sénescents qui maintiennent un pourcentage du couvert original du peuplement. La rétention d'arbres vivants se fait principalement par la délimitation de bouquets, d'îlots ou de séparateurs de coupes plus ou moins larges (bandes riveraines ou séparateurs de coupes), ce qui conserve aussi une plus grande proportion des éléments structuraux d'origine.

Dans le contexte de notre étude, nous avons focalisé sur des îlots dits "résiduels post-coupe", plus proche structuralement des îlots résiduels post-feu. Selon les directives opérationnelles dictées par le Ministère des Forêts, de la Faune et des Parcs, ces îlots post-coupe doivent se définir selon des critères (fiche technique communiquée par le Ministère - directive opérationelle # 7 CPRS_U-ILOT) :

- de composition et structure (legs biologiques, absence de terrain improductif en leur sein, protection de certaines essences),
- de représentativité de couvert du peuplement traité,
- d'intégrité (absence de perturbation anthropique en leur sein, par exemple des ornières),
- de localisation (distance à respecter par rapport à des chemins ou des bords de blocs de récolte),
- et de forme (forme compacte généralement préconisée).

Bien que ces critères soient basés sur un cortège d'études des îlots post-feu en comparaison avec la vieille forêt continue (ex : Côté et Ferron 2001 ; St-Laurent et al. 2007 ; Rosenvald et Lohmus 2008 ; Perhans et al. 2009), il est toutefois surprenant qu'aucune étude ne se soit attardée à comparer directement îlots résiduels post-feu et îlots de rétention dans des parterre de coupe. Notre approche vise donc à combler ce manque dans la littérature, et pour ce faire, nous avons ancré l'étude à la fois dans des sites d'îlots résiduels post-feu et post-coupe, tous deux comparés à la vieille forêt continue (âge du peuplement < 100 ans). Cet angle de recherche présente alors l’avantage de reporter à la fois la justesse de l’approche écosystémique et l’efficacité des structures résiduelles à maintenir dans le paysage.

1.2 Petits mammifères au coeur d'un paysage perturbé

1.2.1 Espèces bio-indicatrices, témoins de l'activité humaine

Les micro-mammifères témoignent des changements environnementaux occasionnés par l'activité humaine. Qu'il s'agisse de distinguer les effets d'un polluant (ex : Ma 1989 ; Hamers et al. 2006), de définir des zones de conservation (ex : Moore et al. 2003), ou d'optimiser les aménagements territoriaux (ex : Millán et al. 2003 ; Pearce et Venier 2005), les micro-mammifères permettent d'identifier les structures d'habitat et les procédés écologiques clefs pour le maintien d'un écosystème dynamique et biologiquement diversifié. Les micro-mammifères sont en conséquence souvent retenus comme étant d’efficaces bio-indicateurs. Plusieurs caractéristiques leur confèrent ce statut, à commencer par leurs rôles fonctionnels dans l'écosystème. Ils participent à l'équilibre du sol (Martin 2003). Ils disséminent graines, spores, propagules (Maser et al. 1978 ; Terwilliger et Pastor 1999 ; Barbé et al. 2016). Ils sont au centre de la chaîne alimentaire, en contrôlant les populations des plantes et insectes qu'ils consomment, et en étant la proie de nombreux prédateurs (Hanski et Parviainen 1985 ; Hanski et al. 1991 ; Bagchi et al. 2006). Les micro-mammifères sont également dépendants de plusieurs structures dont le maintien profite à d'autres espèces vertébrées et invertébrées. Ceci est particulièrement reconnu dans les milieux forestiers où le bois mort, la litière et les trouées aident au maintien d'une communauté faunique diversifiée (Gauthier et al. 2008). Être bio-indicateur nécessite aussi un temps de génération court pour rapidement adapter ses réponses physiologiques et comportementales aux perturbations du milieu. Les micro-mammifères répondent à ce critère, spécialement les micro-rongeurs terrestres, avec un temps de gestation moyen de 20 jours, donnant naissance en moyenne à quatre petits, deux fois par an (Merritt 1981 ; Reich 1981 ; Lackey et al. 1985). Enfin, d'un point de vue logistique non-négligeable, l'entière communauté de micro-mammifères est facilement échantillonnée, à des coûts raisonnables. Rappelons que certaines études ont recommandé l'emploi de multiples espèces indicatrices, taxonomiquement différentes, ainsi que de considérer la composition des assemblages d'espèces au lieu de se baser sur des bio-indicateurs uniques (Howard et al. 1998 ; Caro and O'Doherty 1999 ; Moore et al. 2003). Échantillonner une communauté entière de bio-indicateurs permettrait potentiellement de nuancer certaines de ces critiques. La communauté pourrait d'ailleurs être considérée elle-même comme bio-indicatrice, puisque sa composition s'adapte rapidement aux changements structurels et fonctionnels de l'écosystème.

1.2.2 Succession de communautés et aménagement écosystémique

Plusieurs études se sont penchées sur la succession des communautés fauniques suite à une perturbation naturelle de type grand feu ou des perturbations anthropiques telles que les aménagements agricoles et forestiers (Crête et al. 1995 ; Schweiger et al. 2000 ; Dunn 2004 ; Venier et Pearce 2005). Dans cette optique, les communautés micro-mammaliennes ont reçu une attention particulière. Certaines espèces généralistes recolonisent rapidement un milieu perturbé en régénération, pour laisser peu à peu la place à des espèces spécialisées à la végétation caractéristique des stades avancés de la succession secondaire végétale (Fox 1990). Les patrons de successions de communautés micro-mammaliennes sont constatés dans de nombreux biomes tels que la région forestière Mallee en Australie (Monamy 1998), la savane boisée du Cerrado au Brésil (Briani et al. 2004), ou le maquis méditerranéen (Torre et Díaz 2004). En forêt boréale nord-américaine, les premières espèces occupant un site récemment perturbé sont généralement des granivores qui peuvent s'affranchir de la présence de bois mort et de fort couvert végétal, telles que les souris sylvestres (*Peromyscus maniculatus*) (Kirkland 1990 ; Zwolak et Foresman 2008 - **Figure 1.1**). L'apparition d'un tapis herbacé entraîne la colonisation du milieu par des espèces folivores comme le campagnol des champs (*Microtus pennsylvanicus*) (Simon et al.

1998, 2002). Selon la quantité de débris de bois présente sur site perturbé, la recolonisation de ce dernier s'accélère (Sullivan et al. 2011), en raison du bois mort qui contribue à la présence de nombreux insectes dont tout un cortège de musaraignes est friand. Cependant, la présence seule du bois mort ne suffit pas: les musaraignes ont également besoin de micro-habitats hydriques et mésiques induits par la couverture buissonnante et la litière forestière (MacCracken et al. 1985 ; Craig, 1995). Avec une densité croissante d'arbres matures arrivent les sciuridés, à commencer par les tamias (*Tamias spp.*) qui s'associent aux premiers arbres feuillus (Snyder 1982). Avec la pousse des conifères apparaissent les écureuils roux d'Amérique (*Tamiasciurus hudsonicus*) qui trouvent alors les ressources nécessaires pour se nourrir et nicher (Crête et al. 1995 ; Allard-Duchêne et al. 2014). Finalement les forêts matures (80 ans) et vieilles forêts (> 100 ans) accueillent des espèces spécialistes telles que le grand polatouche (*Glaucomys sabrinus*) qui se nourrit quasi exclusivement de champignons forestiers. Cette espèce requiert également des arbres matures et sénescents pour nicher et/ou se déplacer (Carey 1995 ; Weigl 2007 ; Smith 2012a). Le campagnol à dos roux de Gapper (*Myodes gapperi*, anciennement *Clethrionomys gapperi* - Merritt 1981) se rencontre aussi surtout dans les derniers stades de la succession secondaire, puisque ce dernier s'associe fortement au bois mort des vieilles forêts pour se déplacer, nicher et se nourrir des champignons xylophages (Craig et al. 2014). L'espèce bénéficie également des micro-conditions mésiques et de la couverture forestière dense rencontrée dans les stades les plus avancés de la succession secondaire forestière (Nordyke et Buskirk 1991).

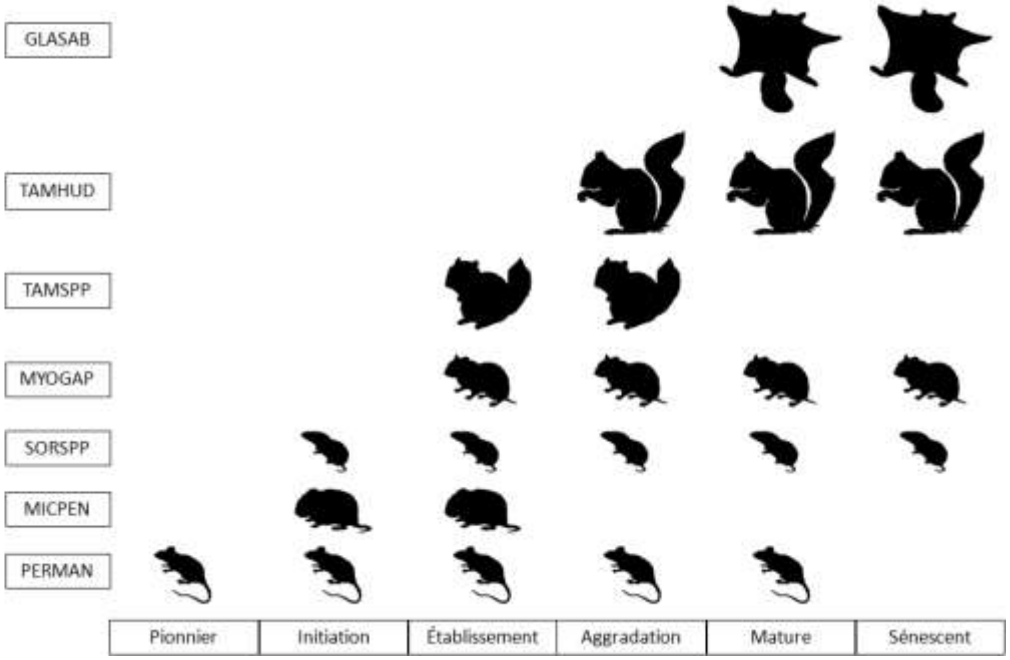

Figure 1.1 Représentation schématique des communautés de micro-mammifères se succédant au cours de la régénération de la pessière noire à mousses post-perturbation. Six stades se succèdent avec une végétation caractéristique: Stade pionnier, couche de matière organique mince ou inexistante, végétation dominée par les premières herbes ; Initiation, forte densité des espèces herbacées et présence des premières espèces buissonnantes ; Établissement, présence des premières espèces de feuillus; Aggradation, premières espèces de conifères apparaissent; Stade mature, espèces de conifères tolérantes à l'ombre pleinement établie (stade de récolte); stade sénescent, création de trouées suite à la mort d'arbres individuels et pousse des plantes associées aux premiers stades de succession dans ces trouées (Chen et Popadiouk 2002; Fisher et Wilkinson 2005). Acronymes : GLASAB, grand polatouche *Glaucomys sabrinus*; MICPEN, campagnol des champs *Microtus pennsylvanicus*; MYOGAP, campagnol à dos roux de Gapper *Myodes gapperi*; PERMAN, souris sylvestre *Peromyscus maniculatus*; SORSPP, musaraignes toutes espèces de genre *Sorex* confondues ainsi que la grande musaraigne *Blarina brevicauda*; TAMHUD, écureuil roux d'Amérique *Tamiasciurus hudsonicus*; TAMSPP, tamias toutes espèces de genre *Tamias* confondues.

Bien que cette succession de communautés micro-mammalienne s'observe sur sites brûlés (perturbation naturelle) et sur sites récoltés (perturbation anthropique), elle n'est comparable que dans ses grandes lignes. L'origine de la perturbation induit certaines différences subtiles. Une de ces différences est la rapidité à laquelle certaines espèces reviennent au site. Par exemple, l'écureuil roux d'Amérique recolonise les sites récoltés 20 ans plus tôt que les sites brûlés (Allard-Duchêne et al. 2014). L'amplitude de réponse semble également différer avec des populations toujours plus abondantes dans les sites récoltés que dans les sites brûlés (Fisher et Wilkinson 2005 ; Zwolak 2009). Ceci est notamment le cas du campagnol à dos roux de Gapper. Après feu, cette dernière espèce peut utiliser les parcelles brûlées, principalement pour le bois mort qui s'y retrouve. L'espèce recolonise peu à peu les sites sous trois ans malgré l'absence d'arbres matures et donc de couvert arborescent important (Kirkland 1990; Simon et al. 1998, 2002). En revanche, sur des parcelles aménagées, l'abondance du campagnol à dos roux de Gapper explose immédiatement après coupe, pour décroître drastiquement et rapidement, laissant les souris sylvestres dominer la communauté micro-mammalienne jusqu'à ce que le couvert forestier soit a nouveau présent (Martell 1985 ; Monthey et Soutière 1985 ; Hayward et al. 1999; Potvin et al. 1999 ; Sullivan et al. 1999). Aménager écosystémiquement la pessière noire à mousses reviendrait alors à corriger ces subtilités d'abondance et de composition de communautés qui pourraient être lourdes de conséquence pour la fonctionnalité de l'écosystème, notamment au niveau de direction et de l'échelle temporelle de la régénération matricielle.

1.2.3 Cyclicité des populations

Que l'on se place au niveau d'une espèce ou d'une communauté, le caractère bio-indicateur implique également une certaine stabilité temporelle de sorte à distinguer rapidement des patrons. Plusieurs populations de micro-mammifères sont toutefois caractérisées par de fortes fluctuations d'abondance annuelles, selon une périodicité fixe (Krebs 2013, Cheveau et al. 2004, Fauteux et al. 2015). Cette cyclicité s'est constatée chez le campagnol à dos roux de Gapper, bien qu'elle soit moins documentée que celle d'autres espèces du genre *Microtus* ou *Lemmus* (Elias et al. 2006 ; Fauteux et al. 2015). Il semblerait également que la cyclicité de ce campagnol dépende de la localisation de la population analysée. Dans la région du Maine et de la Pennsylvanie, les populations suivent un cycle de 3 à 5 ans, dont les abondances estivales sont toujours 3 à 9 fois supérieures aux abondances hivernales (Boonstra et Krebs 2012). En revanche, aucun cycle n'est confirmé pour les régions du Manitoba et de l'Ontario (Boonstra et Krebs 2012). En pessière noire à mousses de l'Ouest du Québec, Cheveau et al. (2004) suspectaient la cyclicité du campagnol à dos roux de Gapper et un suivi mené sur neuf années a permis alors de confirmer un cycle d'abondance de 4 ans (Fauteux et al. 2015).

Bien que les fluctuations d'abondances soient confirmées pour le campagnol à dos roux de Gapper, elles ne sont en revanche que suspectées pour d'autres espèces d'après des observations personnelles ou des analogies avec des espèces similaires. C'est le cas par exemple de la musaraigne cendrée, *Sorex cinereus* en Amérique, si on la rapproche de sa cousine européenne la musaraigne commune, *S. araneus* qui s'inscrit dans un cycle en Europe du Nord (Korpimäki et al. 2005).

Malgré ces fluctuations d'abondances confirmées ou suspectées et qui contraignent à des suivis à plus long terme, les cycles de populations permettent la mise en lumière de facteurs critiques au maintien des espèces pendant la phase sensible de faible abondance. Plus encore, les cycles de populations, inhérents au fonctionnement de l'écosystème dans lequel ils s'inscrivent, permettent d'apprécier directement les changements fonctionnels causés par les perturbations environnementales. Aménager écosystémiquement la pessière noire à mousses reviendrait alors à ne pas altérer cette cyclicité qui participe au dynamisme de la forêt. Pour ce faire, il faut alors respecter la gamme de variabilité naturelle des facteurs environnementaux qui peuvent influencer cette cyclicité (Gauthier et al. 2008 ; Krebs 2013).

1.3 Justification de l'étude

1.3.1 Choix des sites d'échantillonnage et espèces focales

Le but de l'étude était de comparer directement les îlots résiduels post-coupe et post-feu, en nous basant sur les populations d'espèces clefs trouvées en plus grandes abondances dans nos sites. Nous cherchions à savoir si ces îlots, quelque soit leur origine permettaient le maintien des espèces indicatrices de vieilles forêts, soit le campagnol à dos roux de Gapper et le grand polatouche, qui présentent également une distribution de faible étendue (Bowman et al. 2002; D'Eon et al. 2002; Weigl 2007). L'originalité de l'étude a donc été d'articuler les analyses autour de la comparaison directe d'îlots post-feu et post-coupe, pour définir certains critères de l'aménagement écosystémique des pessières noires à mousse.

L'intérêt de comparer les intérieurs des peuplements résiduels a aussi été de comprendre si ces peuplements constituaient des refuges d'espèces bio-indicatrices (soit des habitats caractérisés par des conditions environnementales capable de supporter une communauté micro-mammalienne retrouvée en forêt mature ou forêt vieille de plus de 100 ans) et si les populations maintenues pouvaient par la suite recoloniser le milieu perturbé lorsque ce dernier réunirait les conditions nécessaires pour accueillir ces bio-indicateurs (Robinson et al. 2013). Nous avons donc effectué l'échantillonnage au sein même des îlots composés de forêts matures et/ou vieilles (Moussaoui 2017). Par conséquent, nous nous attendions à échantillonner principalement les deux espèces bio-indicatrices mentionnées ci-dessus, une espèce de sciuridés supplémentaire, à savoir l'écureuil roux d'Amérique et deux espèces de soricidés, soit la grande musaraigne et la musaraigne cendrée (**Figure 1.1** - Carey 1995 ; Crête et al. 1995 ; Fuller et al. 2004).

Selon les critères de coupe totale avec protection et régénération des sols, certains îlots résiduels peuvent ne couvrir qu'une très faible surface (1-5 ha - fiche technique communiquée par le Ministère - 01-MRN-2014-2015 CPRS_U_îlot). Des bouquets de rétention d'une surface allant de 150 à 300 m^2 sont également préconisés dans certains parterres de coupe (Leblanc et Pouliot 2011 ; fiche technique communiquée par le Ministère - 01-MRN-2014-2015 CPRS_U_Bouq). Au sein de cette faible rétention d'arbres matures, nous n'avons pas exclu la possibilité de rencontrer occasionnellement des espèces associées aux jeunes forêts perturbées telles que la souris sylvestre, le campagnol des champs et le phénacomys commun (*Phenacomys ungava*) (Sullivan et Sullivan 2001). Nous espérions réaliser des études de co-occurrence entre espèces de milieux fermés et espèces de milieux ouverts au sein de des îlots résiduels. Cependant, leur rencontre a été suffisamment rare pour ne pouvoir satisfaire les pré-requis de fréquence d'occurrence des modèles employés (MacKenzie et al. 2003, 2006).

1.3.2 Quantité d'habitat et "area-sensitivity"

La perte et la fragmentation de l'habitat ont été identifiées comme des causes principales expliquant la perte de la biodiversité à travers le monde (Czech et Krausman 1997 ; Lawler et al. 2002 ; Kerr et Cihlar 2004). Calculer des tailles minimales de parcelles d'habitat à conserver pour maintenir des populations animales viables est devenu une opération récurrente (ex : Beier 1993 ; Howells et Edwards-Jones 1997 ; Brito and Grelle 2006). Pourtant, un dimensionnement de parcelle seul ne suffit pas à garantir la persistence d'espèces. En se basant entre autres, sur la théorie de la biogéographie insulaire (MacArthur et Wilson 1967) qui anticipe la richesse spécifique insulaire en terme de taille et d'isolement de parcelles, le contexte des parcelles d'habitat préservées prit alors toute son importance. Les études qui se cantonnaient à identifier les caractéristiques d'habitat et les mécanismes critiques au maintien des populations à échelle locale (ex. Dueser et Shugart 1978 ; Pough et al. 1987 ; Dupuis et al. 1995), élargirent leurs horizons. Les patrons d'occurrence d'espèces s'expliquèrent alors par l'hétérogénéité spatiale mesurée à plus grande échelle et par les procédés biotiques qui s'y rattachent, tels que les dynamiques source-puits ou encore l'aggrégation spatiale d'espèces compétitrices et prédatrices (Pickett et Cadenasso 1995 ; Mazerolle et Villard 1999 ; Jones 2011).

Le contexte paysager ou l'hétérogénéité spatiale se décrit en terme de composition (quantités et types d'éléments du paysage) et de configuration (arrangement spatial de ces éléments). La plupart des études à large échelle prennent en considération des variables de taille et d'isolement des parcelles, soit des variables de configuration. Cependant, les populations animales sont bien impactées par à la fois la configuration et la composition du paysage, avec plusieurs preuves empiriques qui suggèrent même une plus grande importance des effets de la configuration du paysage lorsque les quantités d'habitat (composition) se réduisent (Jansson et Angelstam 1999 ; Radford et al. 2005 ; Betts et al. 2007). D'autres études contrôlant les effets de la composition du paysage avant d'évaluer les conséquences d'un changement de configuration, démontrent aussi que certaines espèces animales répondent systématiquement à le composition du paysage avant de répondre à la configuration du paysage (Trzcinski et al. 1999 ; Heikkinen et al. 2004). Des taxons aussi variés que les arthropodes (Margules et al. 1994), les reptiles et amphibiens (Kolozsvary et Swihart 1999 ; Diaz et al. 2000), les oiseaux (Robbins et al. 1989 ; Villard et al. 1999), ou encore les mammifères (Lynch et Whigham 1984 ; Michalski et Peres 2007), répondent donc positivement à une augmentation des quantités d'habitat dont ils ont besoin pour compléter leur cycle biologique, réponse qui se mesure en terme de taille de population, d'occurrence et de biodiversité (Fahrig, 2003, 2013).

L'incidence de la composition du paysage pourrait donc dans ces cas, prédominer celle de la configuration. Riche de ces conclusions, Fahrig (2013) développa alors "l'hypothèse de la quantité d'habitat", nouvelle hypothèse de travail, sur laquelle nous nous sommes appuyés dans ce mémoire. Cette hypothèse suggère que la richesse spécifique d'un paysage "local" (soit à une échelle dans laquelle évolue la biodiversité spécifique étudiée), la quantité d'habitat de ce paysage, représenterait une variable alternative aux variables d'isolement et de taille de parcelles. La variable de quantité d'habitat est d'ailleurs centrale dans la théorie "d'area-sensitivity" (Robbins 1979), théorie qui tente de représenter la sensibilité de certaines espèces animales aux quantités d'habitat disponibles en termes de taux de reproduction et d'abondance des populations, et selon l'échelle à laquelle l'étude s'effectue. Principalement étudiée chez les oiseaux (Trzcinski et al. 1999 ; Walk et Warner 1999; Desrochers et al. 2010), l'area-sensitivity pourrait cependant permettre d'analyser les patrons d'occurrence de petits mammifères, surtout si ces derniers répondent en priorité à la composition du paysage et non à sa configuration (ex : le grand polatouche - Ritchie et al 2009), ou lorsque certaines espèces sont inféodées à des milieux spécifiques, telle que la vieille forêt boréale dans laquelle évolue le campagnol à dos roux de Gapper (Merritt 1981). L'area-sensitivity peut être une réponse à des mécanismes tels que la prédation et le paratisisme (Brittingham et Temple 1983 ; Robinson et al. 1995), un appauvrissement des ressources alimentaires (Burke et Nol 1998 ; Zanette et al. 2000), une réduction des opportunités de reproduction (Villard et al. 1993 ; Burke and Nol 2000 ; Ribic et al. 2009), ou encore des changements dans les statégies de dispersion (Lynch et Whigham 1984 ; Schtickzelle et al. 2006). Ainsi, dans un contexte de restructuration du paysage naturel et d'aménagement du territoire (tel qu'en forêt boréale canadienne), qui agit sur les quantités globales d'habitat à disposition, des études empiriques doivent mettre en évidence des seuils de quantités minimales d'habitat (et non des tailles de parcelles) à ne pas dépasser. Elles doivent également interpréter les relations d'area-sensitivity d'espèces bioindicatrices, pour comprendre les mécanismes sous-jacents qui permettent le maintien des populations, dans l'optique d'élaborer des stratégies d'aménagement réellement écosystémiques (Linehan et al. 1995 ; Boutin et Hebert 2002 ; Wiens 2009).

1.3.3 Approche statistique

Nous avons abordé les différents aspects de l'étude en employant des modèles d'occupation dynamique, à une ou deux espèces, selon les besoins des chapitres (MacKenzie et al. 2006). Contrairement aux modèles d'abondance ou de recrutement, les modèles d'occupation permettent d'étudier des populations d'espèces individuelles en fonction de leur occurrence, c'est-à-dire de leur présence dans une proportion d'habitat définie. Cette modélisation est donc particulièrement adaptée pour étudier la distribution d'espèces, la sélection d'habitat et les dynamiques de métapopulations dans lesquelles l'occupation de sites est en lien avec les caractéristiques de ceux-ci (Hanski 1998 ; Scott et al. 2002). Alternativement, les modèles d'occupation permettent l'étude d'espèces rares, cycliques sur de courtes périodes ou dont les populations sont de faible densité lorsque la pertinence et l'efficacité des modèles d'abondance seraient questionnés (Green 1997). L'utilisation de modèles d'occupation dans cette thèse s'est alors imposée pour deux raisons. Premièrement, nous avons échantillonné des espèces dont les populations présentaient des faibles densités. De plus, bien que nous n'ayons pas étudié des dynamiques de métapopulations, cette thèse visait à caractériser les sites permettant le maintien des populations de petits mammifères.

Les modèles d'occupation, récemment développés et qui reposent sur des données binaires de présence/absence de l'espèce focale, nous informent sur la probabilité d'occupation (symbolisée par la lettre grecque psi ψ) d'un site par cette espèce selon les caractéristiques environnementales du site. Or, selon les spécificités du protocole d'échantillonnage (méthode employée, période) et certaines variables environnementales (ex : densité d'arbres, nuisance sonore, météorologie), la présence de l'espèce sur un site peut passer inaperçue et le site peut être rapporté comme inoccupé. Ce paramètre de détectabilité (symbolisé par la lettre p) d'espèce, s'il n'est pas pris en compte, biaise les analyses car la mesure de l'occurrence est tributaire de la bonne détection des espèces focales. Ceci est confirmé par l'étude de MacKenzie (2006) sur la sélection d'habitat des antilopes d'Amérique (*Antilocapra americana*). Dans sa publication, l'auteur démontre la divergence des résultats d'occupation de site entre simple régression logistique et modèle intégrant la probabilité de détection de l'espèce. Dans cette étude en particulier, il rapporte également que la variable environnementale d'occupation soulignée par la régression logistique est en fait une variable de détection et non d'occupation. Les modèles d'occupation dynamiques ont donc permis d'intégrer certaines données environnementales critiques pour la détection des micro-mammifères. Parmi les plus fréquentes dans la littérature, se retrouvent les températures nocturnes, la pluviométrie et l'illumination lunaire (Getz 1961 ;Vickery et Bider 1981 ; Clarke 1983 ; Orrock et al. 2004).

Pour estimer la détection, les études d'occurrence s'appuient sur la réplication spatiale qui implique le choix de multiple sites d'études, ainsi que la réplication temporelle, soit une répétiton d'échantillonnage dans les sites d'études. On réfère alors à des périodes primaires et secondaires pour caractériser respectivement les sessions d'échantillonnage et les visites au sein même d'une session d'échantillonnage. Dans notre cas précis, nous avions donc quatre périodes primaires (*i.e.* les sessions d'échantillonnage de Juin 2013, Juin 2014, Juillet 2014 et Août 2014) et trois périodes secondaires au sein des périodes primaires (*i.e.* les trois jours de capture successifs à chaque session de capture).

Finalement, tous les modèles d'occupation ont en commun des conditions d'application :

1) L'état d'occupation doit être fermé. L'occupation de site ne change pas au cours d'une période primaire (*i.e.* session d'échantillonnage).

2) Les sites sont indépendants.

3) Il n'y a pas d'hétérogénéité d'occurrence inexpliquée. L'hétérogénéité est expliquée par des caractéristiques de sites (covariables) qui ont été intégrées dans les modèles.

4) Il n'y a pas d'hétérogénéité de détection inexpliquée. De même, l'hétérogénéité est expliquée par des covariables mesurées.

1.3.4 Échelle temporelle et spatiale

Nous avons échantillonné pendant le creux du cycle de population des campagnol à dos roux de Gapper et pendant la phase ascendante (Fauteux et al. 2015). La littérature consacrée aux creux de cycle est maigre étant donné la complexité et multitudes des processus écologiques potentiellement impliqués (Kreb 1996, 2013; Boonstra et al. 1998). Cette approche, novatrice et audacieuse, nous a permis de comprendre certains besoins critiques pour le maintien de l'espèce en zone perturbée pendant une phase sensible de son cycle (Fahrig 2013 ; Craig et al. 2014). Ceci nous a permis en plus de formuler de nouvelles hypothèses à tester quant à la valeur bio-indicatrice de cette espèce (Chavel et al. 2017).

Finalement, nous avons abordé des questions d'aménagement du territoire à l'échelle du paysage. À notre connaissance, la plupart des études consacrées aux micro-mammifères sont réalisées à l'échelle du peuplement. Pourtant, comprendre l'influence du paysage sur la présence locale d'une espèce micro-mammalienne semble être une approche de plus en plus envisagée (Nupp et Swihart 200 ; Umetsu et Pardini 2007 ; Ritchie et al. 2009 ; Mortelliti et al. 2011). Trois facteurs principaux expliquent l'arrivée de ces nouvelles études :

> 1) bien que la fragmentation de l'habitat s'est souvent documentée selon la taille des parcelles d'habitat et leur isolement, la quantité d'habitat présente dans un paysage et la perte de cet habitat expliquent avant toute autre variable le déclin des populations (Drapeau et al. 2000, Schmiegelow et Mönkkönen 2002 ; Fahrig 2013 ; voir Villard et al. 1999 pour une perspective différente),
>
> 2) cette théorie de "quantité d'habitat" est intimement liée aux études d' "area-sensitivity" qui démontrent que plusieurs espèces animales (principalement aviaires) répondent positivement à la quantité d'habitat présente dans le paysage (Robbins 1979 ; Desrochers et al. 2010, voir également Drapeau et al. 2016),
>
> et 3) malgré la faible capacité de dispersion des micro-mammifères, certains auteurs suggèrent que ces espèces pourraient répondre à des variables de paysages mesurées au-delà de leur distance de déplacement (Schweiger et al. 1999 ; Manning et Edge 2004 ; Fauteux et al. 2012).

Dans cette thèse, nous avons cherché à comprendre l'importance de la quantité d'habitat présente dans un paysage perturbé quant à l'occupation de site, la colonisation et l'extinction locale des espèces micro-mammaliennes en forêts matures et surannées. Pour ce faire, nous avons initialement contrôlés les facteurs environnementaux locaux qui auraient une incidence sur ces paramètres ainsi que sur la détection des espèces.

1.3.5 Détails des objectifs

Cette thèse se divise en deux volets : 1) un volet méthodologique par rapport à l'échantillonnage de l'écureuil roux d'Amérique, qui permettra, dans le cadre de notre étude, de bonifier les données de détection de cette espèce, et 2) un volet à l'échelle du paysage, pour introduire de nouvelles considérations d'aménagement écosystémique et de gestion forestière.

Le volet méthodologique, présenté dans le chapitre IV, s'articule autour de deux objectifs :

> a) comparer les probabilités de détection associées à l'échantillonnage indépendant de l'écureuil roux d'Amérique par capture vivante, par points d'écoute passifs et par appels à partir d'enregistrements de cris territoriaux et d'alarmes. Bien que la capture vivante soit une méthode d'échantillonnage répandue pour l'étude de plusieurs paramètres biologiques de cette espèce (ex : abondance de population, taux de reproduction), les deux méthodes auditives présentées sont associées aux études comportementales de cette espèce vocale (Bayne et Hobson 2000 ; Dantzer et al. 2012 ; Wilson et al. 2015). Les méthodes auditives étant moins intrusives, logistiquement plus simples (rapides, souples, moins coûteuses, réalisables sur des aires plus extensives) et utilisées pour comprendre l'occupation de site de nombreuses espèces aviaires (Ralph et al. 1995), nous avons cherché à comprendre si elles permettaient une détection d'écureuils comparable à celle de la capture pour des études d'occupation de sites par l'espèce.

b) comparer les probabilité de détection associées à l'échantillonnage indépendant de l'écureuil roux d'Amérique par capture vivante et les deux méthodes auditives combinées. Les détections par capture vivante et par méthodes auditives diffèrent de par la nature du comportement animal qui entraîne l'échantillonnage. La capture vivante se réalise sur une période de temps extensive et échantillonne toute cohorte d'individus. Ce n'est pas le cas des méthodes auditives, ponctuelles, réalisées à des heures d'activité précises, et échantillonnant principalement des individus adultes, avec un territoire à défendre. En combinant les méthodes auditives, nous avons cherché à évaluer si la détection de l'espèce s'en trouvait améliorée.

Le volet aménagement écosystémique est scindé quant à lui, en deux chapitres (Chapitre V et Chapitre VI), avec des objectifs similaires mais des approches différentes. Dans le chapitre V, nous avons abordé la question d'area-sensitivity pour des espèces individuelles et en relation avec l'occupation, la colonisation et l'extinction de sites. Deux objectifs se dégagent :

c) comparer l'occurrence des micro-mammifères sur les parcelles rémanentes de forêt mature ou vieille dans les parterres de coupes et d'incendie, en s'appuyant sur des variables locales de structures et ainsi évaluer l'importance de ces structures à l'échelle du peuplement (ex : Ritchie et al. 2009 ; Fauteux et al. 2012 ; Craig et al. 2014). L'aspect novateur de cet objectif réside dans la comparaison directe entre les îlots de rétention post-feu et post-récolte et participe à la compréhension du rôle de refuge des îlots de rétention pour ces espèces micro-mammaliennes de fin de succession secondaire (Robinson et al. 2013).

d) mesurer la relation entre l'occurrence des micro-mammifères et l'aire totale de forêt quantifiée à plusieurs échelles (locale à régionale). Pourrions-nous qualifier les micro-mammifères d'espèces sensibles à cette quantité d'habitat dans le paysage au même titre que plusieurs espèces aviaires (Robbins 1979 ; Walk et Warner 1999 ; Desrochers et al. 2010) ? Quelle est la nature de cette relation ? Comment intégrer cette relation dans une optique d'aménagement écosystémique ?

Dans le chapitre VI, nous ne focalisons plus sur l'occurrence d'une espèce seule, mais sur la co-occurrence de deux espèces qui interfèrent. Nous ciblons donc les interactions et l'impact de variables locales et du paysage sur ces interactions pouvant expliquer l'occupation de site par chaque espèce .. Les objectifs associés sont :

e) comparer la co-occurrence de paires de micro-mammifères sur les îlots de rétention post-coupe et post-feu, en s'appuyant sur les quantités de bois mort présentes et ainsi évaluer l'importance de ces structures à l'échelle du peuplement (Fauteux et al. 2013).

f) mesurer la relation entre la co-occurrence de paires de micro-mammifères et l'aire totale de forêt quantifiée à plusieurs échelles (locale à régionale). Notre postulat de départ est que de la quantité d'habitat découle directement la richesse et la quantité de ressources disponibles, et que donc l'intensité de compétition entre deux espèces, qui varie avec la disponibilité des ressources, entraînera des patrons de co-occurrence différents selon cette quantité d'habitat.

Un dernier objectif, en annexe à cette thèse et n'appartenant à aucun des deux volets mentionnés ci-dessus, découle d'une volonté de collaboration entre deux projets de doctorat conjointement réalisés sur le même territoire (Annexe A) :

> g) confirmer le rôle des micro-mammifères en tant qu'agents biotiques de dispersion des bryophytes. Ce rôle, souvent suspecté et confirmé pour plusieurs espèces aviaires, d'insectes et de méga-faune (Heinken et al. 2001 ; Parsons et al. 2007 ; Rudolphi 2009 ; Lewis et al. 2014), participe au dynamisme forestier par la dispersion d'espèces floristiques à la base de la régénération d'une matrice perturbée.

CHAPITRE II

MÉTHODOLOGIE ET CADRE SCIENTIFIQUE

2.1 Aire d'étude

L’étude a été réalisée en forêt boréale canadienne, dans le domaine bioclimatique de la pessière noire à mousses. Avec une étendue allant jusqu’au 52^{e} parallèle (Saucier et al. 2011), ce domaine a été échantillonné sur 8325 km^2 au nord de l’Abitibi-Témiscamingue et dans la partie sud des territoires de la Baie James, Québec (79˚29’ W, 49˚00’ N - 75˚39’ W, 50˚22’ N - **Figure 2.1**). La topographie de cette région est relativement plane pour une altitude de moins de 250 m (Blouin et Berger 2002 ; Hardy 1977). Le climat y est subpolaire continental, soit des températures mensuelles moyennes variant de 20°C à -16°C et des précipitations annuelles moyennes de 850 mm (Blouin et Berger 2002 ; Environment Canada 2015).

La canopée forestière est dominée par l'épinette noire (*Picea mariana*), cette dernière essence pouvant être accompagnée par le pin gris (*Pinus banksiana*) et le sapin baumier (*Abies balsamea*). Le bouleau à papier (*Betula papyrifera*) ainsi que le peuplier faux-tremble (*Populus tremuloides*) figurent parmi les espèces de feuillus communément rencontrées en pessière noire. Le sous-bois est principalement arbustif, composé d'éricacées telles que le thé du Labrador (*Rhododendron groenlandicum*) et plusieurs espèces de baie (*Vaccinium angustifolium*; *Vaccinium oxycoccos*).

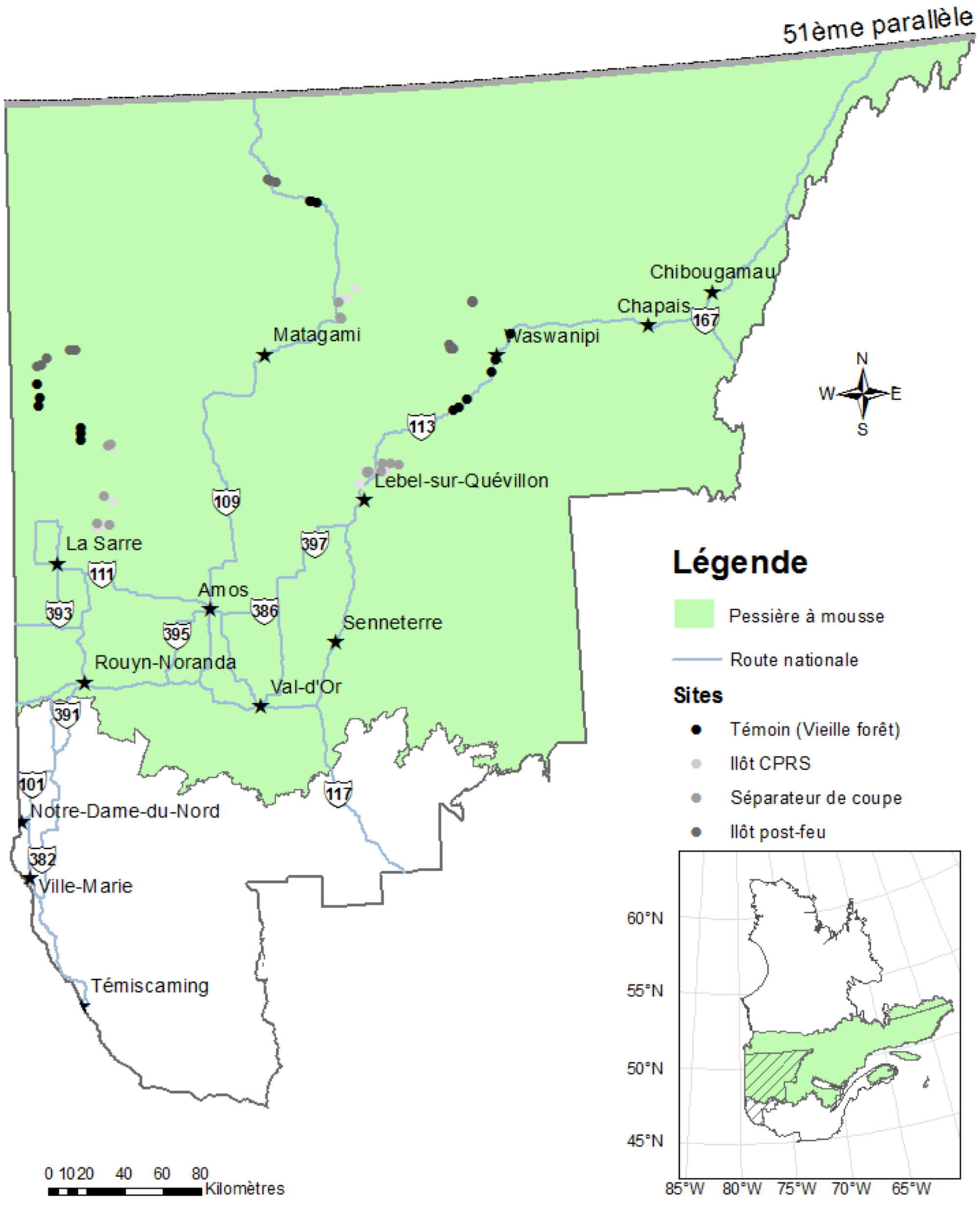

Figure 2.1 Localisation des sites d'études en pessière noire à mousses de l'Ouest du Québec, Canada.

Le parterre forestier, quant à lui, est formé d'un épais tapis de diverses espèces de mousses hypnacées (ex : *Pleurozium schreberi* et *Hylocomium splendens*), peu à peu remplacées par des sphaignes au cours de la paludification des sols, soit lorsque les conditions de drainage se détériorent (Fenton et Bergeron 2006).

La région est également caractérisée par des grands feux de forêt récurrents (cycle courts de l'ordre de 100 à 200 ans - Boucher et al. 2003 ; Potvin et al. 2006), sévères et de grande ampleur, brûlant en moyenne 8000 km^2 (Payette 1992 ; Bergeron et al. 2004 ; Le Goff et al. 2008). Néanmoins, cette perturbation naturelle est peu à peu remplacée par diverses stratégies de récoltes et d'aménagement forestiers (Imbeau et al., 2015) qui tentent de recréer dans les limites de variabilité naturelles, les mosaïques d'habitats laissées typiquement après le passage d'un feu (Morneau et Payette 1989, Payette et al. 1989).

Selon un plan d'échantillonnage stratifié, nous avons sélectionné un total de 60 sites, répartis équitablement en quatre origines. Un total de 15 sites a été définis au coeur d'îlots résiduels post-feu (POSTFIRE - aire moyenne de 3.1 ha [0.2 – 11.1 ha]) laissés intacts par des grands feux de forêt datant d'un minimum de 20 ans (aire moyenne de 16816 ha [1932 - 40713] ; **Figure 2.2**).

Figure 2.2 Aperçu extérieur des trois types de sites d'étude perturbés, séléctionnés en pessière noire à mousse. a) séparateur de coupe (LINEARCUT) ; b et c) îlots résiduels post-feu (POSTFIRE) ; d, e, et f) îlots/bouquets résiduels post-coupe (GREENTREE).

Quinze bouquets de rétention appartenant à 15 parterres de coupe CPRS de moins de 10 ans (aire moyenne de 6.3 ha [0.5 - 41.0]) ont été retenus (GREENTREE – aire moyenne de 0.8 ha [0.09 – 1.6 ha] - **Figure 2.2**). Quinze séparateurs de coupe (LINEARCUT) de 60 à 100 m de large et de 250 à 900 m de long et connectés à la vieille forêt ont également été selectionnés (**Figure 2.2**) ainsi que 15 sites de vieilles forêts de plus de 100 ans (CONTROL), ces derniers 15 sites servant de sites témoins et étant inclus dans des massifs forestiers de plusieurs milliers d'hectares. Les caractéristiques de structure et de composition des différents types de sites sont détaillées dans la première annexe du chapitre IV de ce manuscrit (**Figure 2.3**).

Figure 2.3 Intérieur des quatre types de site d'étude, sélectionnés en pessière noire à mousses. a, b, et c) vieille forêt (CONTROL) ; d, e et f) îlots résiduels post-feu (POSTFIRE) ; g, h, et i) îlots/bouquets résiduels post-coupe (GREENTREE) ; j, k et l) séparateur de coupe (LINEARCUT).

2.2 Échantillonnage de petits mammifères

L'échantillonnage a été réalisé par capture vivante du 23 juillet 2013 au 15 août 2013 ainsi que du premier juin 2014 au 21 août 2014. Au cours des étés 2013 et 2014, chaque site a été échantillonné une et trois fois respectivement. Chacune de ces sessions de capture représentant trois nuits et trois jours consécutifs au cours desquels des pièges à capture vivante étaient disposés en forêt. Le contenu de ces pièges était vérifié quotidiennement tôt le matin et en fin d'après-midi pour reporter les captures diurnes (principalement des écureuils roux d'Amérique) et nocturnes (tous autres petits mammifères) (Merritt 1981 ; Wells-Gosling et Heaney 1984 ; Steele 1998 ; Whitaker 2004). Les trois sessions de capture de l'été 2014 étaient séparés par 27 jours.

Les sciuridés ont été capturés à l'aide de pièges Tomahawk (Tomahawk Live Trap llc ®), disposés selon une ligne de transect de 50 m de long et apâtés avec du beurre d'arachide (source de lipides) et un morceau de pomme (source d'eau). Afin de limiter les mortalités face aux températures nocturnes, nous avons également ajouté une boule de coton non-compactée de 10 cm de diamètre dans laquelle pouvaient se nicher les captifs. Les écureuils roux ont également été échantillonnés en journée par méthodes auditives au cours de l'été 2014. Suite à la vérification du contenu des pièges Tomahawk et le relâché des éventuels captifs, une période de 10 min était observée en silence. Un point d'écoute était ensuite réalisé pendant 10 autres minutes suivi d'une troisième période au cours de laquelle nous émettions des cris pré-enregistrés d'écureuils roux, encourageant ainsi les individus présents sur site à vocaliser (Chavel et al. 2017a). Les cris, extraits du livre audio "Le son de nos forêts" (Elliot et Mack 1994), ont été émis à l'aide de dictaphones portables branchés à des amplificateurs et joués trois fois au cours d'une période de 10 min. Alors que les points d'écoute n'ont été réalisés qu'au cours de deux matins sur trois en 2014[1], l'émission de cris pré-enregistrés a été réalisée au cours des trois matins consécutifs de chacune des sessions de capture de 2014. Lorsque pour des raisons météorologiques nous ne pouvions réaliser un point d'écoute ou une émission de cris à un jour donné, nous avons considéré ce jour comme une donnée manquante. Contrairement à la capture vivante d'individus qui a permis d'obtenir des données d'abondance et de conditions physiques, les deux méthodes auditives n'ont permis que de reporter la présence d'écureuils (données binaires).

Les cricétidés ont été capturés à l'aide de pièges Sherman (H.B. Sherman Traps, Inc. ®) appâtés et fournis en coton comme précédemment. Une grille de capture de 4 x 4 pièges a été dessinée à chaque site, avec un intervalle de 5 m entre chaque piège. Les données de soricidés, quant à elles, proviennent de captures accidentelles dans des pièges fosse de 26 cl, déployés au nombre de quatre par site selon un carré de 20 m de côté et ayant pour but d'échantillonner les arthropodes (données environnementales). Contrairement aux pièges à capture vivante qui étaient vérifiés quotidiennement selon la procédure décrite ci-dessus, les pièges fosse (pièges mortels) n'ont été vérifiés quotidiennement qu'à partir de la seconde session de capture (soit à partir de l'été 2014). Au cours de l'été 2013, les pièges fosse déployés à chaque site n'ont fait l'objet que d'une vérification qu'à la fin de la session de capture de 2013. Les grilles de captures et lignes de transect étaient centrées les unes par rapport aux autres en un point nommé CENTRE (**Figure 2.4**).

Les individus capturés ont été identifiés à l’espèce sur place dans le cas d'individus vivants et en laboratoire pour tous les individus trouvés morts, spécialement les musaraignes dont certaines espèces ne se différencient que par des caractéristiques craniales (Lupien 2001, 2002 ; Fauteux et al. 2014). Les individus capturés vivants

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[1] Des problèmes techniques rencontrés sur les amplificateurs au cours du mois de juin 2014, n'ont permis de reporter la présence / absence d'écureuils que dans 12 des 60 sites.

ont été marqués à l'aide d'un transpondeur passif sous-cutanné (Biomark ®), âgés, sexés et auscultés pour d'éventuelles blessures ou présence de parasites externes. Une fois la capture et le traitement réalisés, tous les individus vivants ont été relâchés au site de capture. Les individus trouvés morts ont été placés dans des sacs de congélation à glissière pour un traitement hors-site.

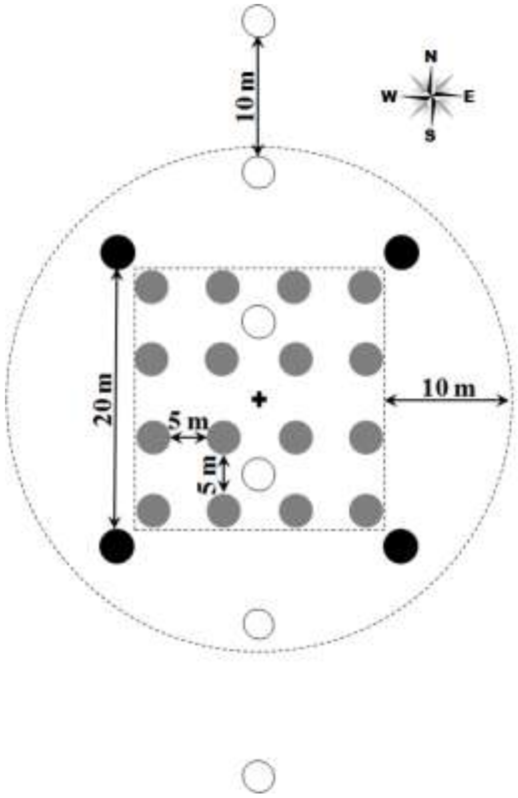

Figure 2.4 Représentation schématique d'un site d'échantillonnage. La croix noire (✚ - CENTRE) représente le centre des diverses parcelles d'échantillonnage ainsi que le point d'où toutes les données environnementales ont été prises. Les cercles blancs (○) représentent chacun un piège Tomahawk à capture vivante, les cercles gris (●) représentent chacun un piège Sherman à capture vivante, les cercles noirs (●) représentent chacun un piège fosse à capture mortelle, le cercle en pointillé représente le quadrat dans lequel les densités de gros arbres (dhp > 10 cm) et chicots ont été calculées, tout comme les volumes de bois mort, le cercle en pointillé représente la parcelle dans laquelle le pourcentage de la canopée à été mesuré et les carottes de tronc d'arbres ont été prélevées.

Les musaraignes capturées à l'aide des pièges Sherman ont été exclues des analyses pour deux raisons principales. Premièrement, la plupart des espèces de musaraignes potentiellement trouvées dans nos sites sont trop légères pour déclencher le mécanisme de fermeture des pièges Sherman. Seuls des individus lourds peuvent être capturés, et par conséquent seule une petite proportion de la population présente sur site pouvait effectivement être échantillonnée. De plus, comme nous l'avons mentionné précédemment, certaines espèces de soricidés telles que la musaraigne cendrée (*Sorex cinereus*) et la musaraigne pygmée (*Sorex hoyi*), ne se distinguent que par dissection. La capture par piège Sherman étant une capture vivante, les individus des ces deux espèces ne pouvaient être identifiés sur place.

Nous avons considéré que chaque piège Sherman et Tomahawk fournissait un effort d'une nuitée/nuit de capture, à l'exception des pièges qui ont été accidentellement déclenchés et par conséquent rapportés comme fournissant un effort d'une demi nuitée/nuit de capture (Nelson et Clark 1973). De même, chaque piège fosse fournissait un effort d'une nuitée/nuit de capture, à moins d'être déterré.

La capture et manipulation de petits mammifères ont respecté les règles établies par le comité d’éthique animale de l’Université du Québec en Abitibi-Témiscamingue en collaboration avec les vétérinaires de l’Université de Montréal (UQAT, permis no. 2013-04-02, renouvelé en 2014).

2.3 Données environnementales à l'échelle du peuplement/site/grille/microhabitat

Le microhabitat a été caractérisé à l'échelle des grilles de pièges Sherman (grilles de 15 x 15 m). Toutes les parcelles d'échantillonnage des données de micro-habitat ont été centrées sur un point fictif (CENTRE) symbolisé par la croix noire de la figure 2.4, et toutes les données météorologiques ont été prises en ce point.

L'âge du peuplement (AGE) a été obtenu en carottant à hauteur de poitrine le coeur du tronc de dix des plus gros arbres situés dans un rayon de 30 m autour de CENTRE, à l'aide d'une tarière de Pressler de 400 x 5,15 mm. L'âge de ces dix arbres a ensuite été déterminé par comptage des anneaux de croissance dans les échantillons de coeur sablés au préalable, en utilisant un microscope binoculaire Olympus SZX12 (grossissement 90 fois).

Le couvert de la canopée (CANCOV) a été mesuré sur des photographies hémisphériques prise à l'aide d'un Nikon CoolPix 990 et d'un objectif grand angle fisheye FC-E8, et lues sur Adobe Photoshop Element 2.0 (Adobe Systems 2002) grâce à son outil "Seuil de saturation". Neuf paires de photographies ont été prises par site, une au CENTRE, quatre à chaque coin de grille de pièges Sherman, et quatre à 10 m de chaque côté de cette grille de capture. Les photographies ont été prises à 20 et 150 cm du sol (CANCOV20 et CANCOV 150). CANCOV 20 et CANCOV 150 ont été exprimées en pourcentage (%).

Nous avons identifié toutes les espèces d'arbres (conifères et feuillus) du CENTRE ainsi qu'à quatre points situés à 15 m du CENTRE et faisant face à chaque point cardinal. Cette mesure a principalement été prise pour évaluer la présence de feuillus (DECID - variable binaire). Nous avons compté tous les gros arbres debout ainsi que tous les gros chicots dans un quadrat de 15 x 15 m. Nous avons défini comme gros arbre vivant ou gros chicot tout arbre avec un dhp (diamètre à hauteur de poitrine) égal ou supérieur à 10 cm (Déry et Leblanc 2005). Tout chicot plus petit que 1,2 m était exclu du décompte. Nous avons ainsi obtenu la densité des gros arbres vivants (TREEDENS) et celle des gros chicots (SNAGDENS). Toutes les valeurs ont été exprimées comme le nombre de tiges par hectare (tiges. ha^{-1}).

Le volume de bois mort au sol (DWD) a été inventorié dans un triangle équilatéral de 15 m de côté (Harvey et Brais 2007), selon les méthodes et classes de décomposition décrites dans Fauteux et al. (2012). Les volumes des troncs ont été calculés selon la formule canonique-paraboloïde (Fraver et al. 2007) et exprimés en mètre cube par hectare ($m^3.ha^{-1}$).

Les températures atmosphériques ont été enregistrées à chaque site grâce à des sondes enregistreuses (Hydrochron iButton®, Maxim Integrated, San Jose, CA, USA) placées à 1 m du sol, sous couvert et à l'abri du vent. Les sondes ont été programmées pour enregistrer la température ambiente (°C) aux 4 heures et ces enregistrements ont été réalisés à chaque session de capture, excepté celle de juin 2014 pour cause de problèmes techniques. Nous avons séparé les températures diurnes des températures nocturnes selon les heures de lever et de coucher du soleil (http://www.sunrise-and-sunset.com). Les températures moyennes nocturnes étaient ensuite calculées pour chaque nuit de capture. Seules les températures nocturnes ont été utilisées puisque la grande majorité des espèces focales étaient nocturnes. L'écureuil roux d'Amérique était la seule espèce d'exception, principalement active au lever et au coucher du soleil (Steele 1998). La pluviométrie quotidienne (mm) était mesurée grâce à des pluviomètres placés au CENTRE. L'illumination lunaire, exprimée en pourcentage de lune visible, a été déterminée grâce au calendrier lunaire (http://time.unitarium.com/moon/where.html).

Les biomasses d'arthropodes (ARTHRO) et des mollusques terrestres (MOLLUSC), exprimées en grammes, ont été déterminées par échantillonnage de la communauté d'invertébrés présente à chaque site et à chaque session de capture. L'échatillonnage s'est réalisé à l'aide des pièges fosse décrits ci-dessus, et dont le contenu était vidé quotidiennenent. Les invertébrés ainsi collectés étaient séchés sur du papier absorbant avant d'être pesés par ordre de la classification systématique.

2.4 Données environnementales à l'échelle du paysage

Les espèces rencontrées à nos sites d'études ont été reportées de par le passé dans différents types de forêt, même si certaines de ces espèces favorisent les vielles forêts de conifères (Merritt 1981 ; Wells-Gosling et Heaney 1984 ; Steele 1998 ; Whitaker 2004). Par conséquent nous nous sommes focalisés sur la quantité totale de forêt autour des sites de capture, quelque soit sa composition, sa densité d'arbres et son type de sol (entourbé ou non). La couverture forestière a été obtenue grâce aux couches ArcGIS datant de 2013 et produites par le Ministère du Développement durable, de l'Environnement et de la Lutte contre les changements climatiques (MDDELCC) (Bissonnette et Lavoie 2015).

Le pourcentage d'aire couverte par la forêt a été mesuré dans un total de 100 cercles concentriques, définis autour du CENTRE, selon des rayons allant de 50 m à 5 km, avec une augmentation de 50 m à chaque rayon. Nous avons choisi un rayon maximal de 5 km puisque les deux espèces les plus mobiles de nos sites, à savoir le grand polatouche - *Glaucomys sabrinus* - et l'écureuil roux d'Amérique, sont possiblement impactés par des perturbations dans le paysage dans un rayon qui dépasse celui de leur domaine vital (Larsen et Boutin 1994 ; Bowman et al. 2002 ; Ritchie et al. 2009). La résolution cartographique (30 x 30 m) a été conservée quelque soit le rayon considéré.

2.5 Modèles d'occupation utilisés

2.5.1 Modèles d'occupation dynamique multi-saisonniers à une espèce

Ces modèles s'appuient sur les changement d'occurrence au cours du temps, changements qui sont régis par la colonisation de site (*i.e.* site devenant occupé) et l'extinction (*i.e.* site devenant inoccupé). Les populations sont donc ouvertes, postulat de départ biologiquement adapté au contexte de l'étude., puisque les juvéniles de petits mammifères boréaux se dispersent au cours des mois d'été (Merritt 1981 ; Steele 1998). Cette approche nous semblait également cohérente avec les objectifs de l'aménagement écosystémique, qui visent à conserver le dynamisme de la forêt récoltée. Nous ne visions donc pas à comparer des sites à un instant *t* mais bien à observer une évolution de la réponse micro-mammalienne à une perturbation.

Ces modèles comportent initialement quatre paramètres, à savoir la probabilité d'occupation intiale (ψ), la probabilité de colonisation (γ), la probabilité d'extinction (ε) et la probabilité de détection (p) (MacKenzie et al. 2003). Le maximum de vraisemblance se calcule selon l'équation suivante :

$$L(\psi_{1},\gamma,\varepsilon,p|h_1,\ldots,h_s) = \prod_{i=1}^{s} \Pr(h_i)$$

avec h symbolisant les histoires de détection, s les périodes primaires d'échantillonnage, et i les sites d'échantillonnage.

2.5.2 Modèles d'occupation à une saison et deux espèces

Ces modèles tentent d'expliquer l'occurrence de deux espèces au cours d'une même période primaire. Les populations de ces deux espèces sont fermées.

Deux paramétrisations peuvent être considérées pour ces modèles à savoir une paramétrisation inconditionnelle, sans dominance de l'une ou l'autre espèce (MacKenzie et al. 2006) ou une paramétrisation conditionnelle dans laquelle une des deux espèces est considérée comme plus compétitive (Richmond et al. 2010). Dans le cadre de cette thèse, nous avons consiéré les espèces opportunistes et généralistes comme des meilleurs compétiteurs que les espèces spécialistes, inféodées aux vieilles forêts. En effet, nous assumons que les espèces généralistes peuvent s'accommoder d'une diversité de ressources et sont donc peu facilement exclues. En revanche, nous constatons l'inverse avec des espèces spécialistes, rapidement mises en concurrence en l'absence de certaines ressources qui leurs sont critiques.

Huit paramètres initiaux sont à considérer avec l'emploi d'une paramétrisation conditionnelle, limitant la convergence des algorithmes lorsqu'on multiplie le nombre de covariables ajoutées. On dénombre trois paramètres d'occupation initiale : ψ^A (probabilité d'occupation de l'espèce A, espèce la plus compétitive), ψ^{BA} (probabilité d'occupation de l'espèce B sachant que A est présente), and ψ^{Ba} (probabilité d'occupation de l'espèce B sachant que A est absente). Les modèles incluent cinq paramètres de détection : p^A (probabilité de détection de A lorsque B est absente), p^B (probabilité de détection de B lorsque A est absente), r^A (probabilité de détection de A lorsque les deux espèces sont présentes), r^{BA} (probabilité de détection de B lorsque les deux espèces sont présentes et détectées), and r^{Ba} (probabilité de détection de B lorsque les deux espèces sont présentes mais que A reste non-détectée). Le maximum de vraisemblance du modèle se calcule selon l'équation suivante :

$$L(\phi, p|h_1^A, h_1^B..., h_s^A, h_s^B) = \prod_{i=1}^{s} \Pr(h_i^A, h_i^B)$$

avec h symbolisant les histoires de détection, s les périodes primaires d'échantillonnage, i les sites d'échantillonnage, A l'espèce A (la plus compétitive), B l'espèce B et ϕ la matrice de transition de probabilités des huit paramètres mentionnés dans le paragraphe précédent.

2.5.3 Critère d'information d'Akaike (AIC) et inférence multimodèle

Le critère d'information d'Akaike est un critère estimant la quantité d'information perdue lors de la modélisation de la réalité (ex. l'occurrence d'une espèce). Un tel critère s'utilise lorsqu'on recherche un modèle qui s'ajuste convenablement aux données, avec le moins de variables explicatives possible. En conséquence, l'AIC se base sur le log-likelihood, soit la mesure d'ajustement du modèle, et K, le nombre de paramètres estimés :

$$\text{AIC} = -2(\text{Log-Likelihood}) + 2K$$

Toutefois, un AIC seul n'est pas informatif. C'est la différence d'AIC entre les modèles candidats qui permettent de distinguer des variables explicatives qui semblent s'accorder aux données brutes. Vient ensuite l'inférence multimodèle, qui à partir de tous les modèles candidats, calcule pour les variables d'intérêt, une moyenne pondérée des tous les estimés calculés. Cette approche robuste permet alors de comprendre si l'effet des variables d'intérêt est suffsament conséquent pour expliquer les données brutes.

CHAPITRE III

COMPARATIVE EVALUATION OF THREE SAMPLING METHODS TO ESTIMATE DETECTION PROBABILITY OF AMERICAN RED SQUIRRELS (*TAMIASCIURUS HUDSONICUS*)

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3.1 Abstract

Measuring changes in species distribution and understanding factors influencing site occupancy are recurring goals in wildlife studies. Imperfect detection of species hinders such studies, resulting in the underestimation of the number of sites occupied by the species of interest. American red squirrels (*Tamiasciurus hudsonicus*) are sampled traditionally with live-traps that require substantial resources to deploy and monitor. Here, we assessed whether auditory methods yield similar detection probabilities. We compared the detection probability of American red squirrels in boreal forest using point counts, playback counts, and live-trapping. Over the summer of 2014, we conducted three trapping sessions in 60 sites within black spruce forests of northwestern Quebec, Canada. We also conducted 10 min point counts in the same sites, together with playback counts using recordings of American red squirrel alarm and territorial calls. Using dynamic occupancy models to analyse three primary periods, all composed of three secondary periods, we found that the detection probability of squirrels from point counts was as high as with live-trapping. Our results thus highlight the value of the point count method in measuring American red squirrel occupancy.

Keys words: detectability; live-trapping; playback count; point count; site occupancy; sciurids

3.2 Résumé

Un objectif récurrent des études fauniques consiste à mesurer à la fois les changements dans la répartition des espèces et à comprendre les facteurs qui influencent leur occupation des sites. Une détection imparfaite de la faune limite néanmoins de telles études, entraînant alors une sous-estimation du nombre de sites occupés par l'espèce d'intérêt. L'écureuil roux d'Amérique (*Tamiasciurus hudsonicus*) est traditionnellement échantillonné au moyen de pièges à capture vivante dont le déploiement et le suivi sous-tendent d'importants efforts sur le terrain. Dans cette étude, nous souhaitions déterminer si des méthodes non invasives, à savoir la méthode des points d'écoute et des appels, pouvaient engendrer des probabilités de détection comparables à celles obtenues par la capture vivante des individus. Pour ce faire, nous avons capturé des écureuils à trois reprises au cours de l'été 2014 dans 60 sites en pessière noire à mousses dans le nord-ouest du Québec. Nous avons aussi réalisé des points d'écoute de 10 min ainsi que des appels à partir d'enregistrements de cris d'alarme et de cris territoriaux d'écureuil roux dans les mêmes sites. En utilisant des modèles d'occupation dynamique, nous avons démontré que la probabilité de détection était aussi élevée au moyen des points d’écoute que de la capture vivante. Bien que les points d'écoute représentent une méthode souvent utilisée en ornithologie, nos résultats indiquent que cette méthode d'échantillonnage s'avère des plus efficaces pour mesurer l'occupation de site par les écureuils roux d'Amérique.

3.3 Introduction

Studies on wildlife populations are often designed to understand patterns of species distribution to inform management strategies. Site occupancy, i.e. the probability of a landscape unit to be occupied by a species of interest (MacKenzie et al. 2006), can help determine the factors that influence species presence at a given location (*e.g.,* habitat modelling – Scott et al. 2002; Pearce and Boyce 2006; Richmond et al. 2010), as well as understand metapopulation dynamics (Sjögren-Gulve and Hanski 2000). Over the last decade, occupancy models have been developed to cope with the underestimation of site occupancy due to the imperfect detectability of the species of interest (MacKenzie et al. 2002, 2006). Detection probability may vary with site characteristics (*e.g.,* lateral cover, tree density), sampling periods (*e.g.,* weather conditions), and sampling methods, which lead to heterogeneity in detection probabilities across sites and surveys (MacKenzie et al. 2006; Otto and Roloff 2011). When the variation in detection probability explained by covariates remains low, investigators should use sampling protocols with high detection probability (Pollock et al. 2002).

American red squirrels (*Tamiasciurus hudsonicus*) are widespread across North America and are often studied to understand population dynamics in relation to their territorial behaviour. Individuals are promiscuous, defend long-term territories, and adapt their territorial behaviour according to gender, reproductive status, and identity of squirrel competitors (Price et al. 1990; Larsen 1993). Territory size, covering on average 65 m^2 (Larsen and Boutin 1994), mainly depends on food availability and quality, which also influence density (Klenner and Krebs 1991; Larsen and Boutin 1995; Boutin et al 2006). Like most small mammals, red squirrels are usually sampled using live-trapping techniques. However, auditory surveys are commonly carried out as this species is highly vocal, marking and defending territories using loud and distinctive alarm calls (Smith 1978; Larsen and Boutin 1994; Green and Meagher 1998). Several studies have relied on this behaviour to either understand associations and competition among individuals (Price et al. 1990, Dantzer et al. 2012, Wilson et al. 2015) or to estimate the relative abundance of this species in an area (Buchanan et al. 1990; Sieving and Willson 1998; Bayne and Hobson 2000; Russell et al. 2010). Likewise, site occupancy could be studied using auditory methods. To our knowledge, the reliability of passive point counts and playback surveys in detecting individuals as compared to live-trapping has yet to be assessed for American red squirrels.

Our first objective was to compare the detection probability of squirrels with these two auditory methods relative to live-trapping. Live-trapping and auditory methods rely on different individual behaviours for detection. Whereas auditory methods depend on territorial or vocal animals during short observation periods, live-trapping detects animals moving in the vicinity of traps that have been captured. Because live-trapping targets individuals in the site over extended hours regardless of territorial behaviour and life stage, we hypothesised that live-trapping would yield the highest detection probability, followed by playback counts, and passive point counts.

For our second objective, we combined the two auditory methods (point and playback counts) to increase species detection, and compared the resulting detection probability against the detection probability of American red squirrels obtained from live-trapping. We hypothesised that we would observe an increase in detection probability when combining the two auditory methods compared to when used on their own. We also hypothesised that if these auditory methods were initially associated with lower detection probabilities than live-trapping, combined together, they would allow the detection of American red squirrel with similar probabilities to those of live-trapping.

3.4 Methods

3.4.1 Study area

The study area covered a total of 8325 km^2 (79˚29' W, 49˚00' N - 75˚39' W, 50˚22' N) and was located in black spruce forests of northwestern Quebec, Canada (**Figure 3.1**). This boreal region is characterised by a subpolar continental climate with mean monthly temperatures ranging from -16 °C to 20 °C and 850 mm of annual precipitation (Blouin and Berger 2002; Bergeron et al. 2004). The forest canopy is dominated by black spruce (*Picea mariana*, Mill.). Jack pine (*Pinus banksiana*, Lamb.) and balsam fir (*Abies balsamea*, Mill.) also occur, along with deciduous species such as paper birch (*Betula papyrifera*, Marshall) and trembling aspen (*Populus tremuloides*, Michx.). The understory is mainly composed of dwarf ericaceous shrubs. Feather mosses form a dense carpet, which is slowly replaced by *Sphagnum* species as drainage conditions deteriorate or in the absence of wildfire

(Fenton and Bergeron 2006). The region is characterised by recurrent and severe wildfires over vast areas (Bergeron et al. 2004), although this major disturbance is being increasingly replaced by forest management and harvesting strategies (Imbeau et al. 2015).

Using a stratified sampling design, we selected a total of 60 forested sites that were equally distributed among old undisturbed forest (CTRL - continuous forest over 100-years-old), post-fire remnant patches (PFRP - 3.1 ha [range: 0.2 - 11.1]) left after wildfires that occurred over 20 years ago, green tree retention patches (GTRP - 0.8 ha [range: 0.1 - 1.6]) left after recent clear-cutting (< 10 years), and linear cutblock separators (LCBS - 60-100 m large, connected to old-growth forests) that separate clearcut areas. Sites were at least 500 m apart. Based on the average movement distance of American red squirrels (Larsen and Boutin 1994), the distance between any two sites was sufficiently large to ensure independence among sites.

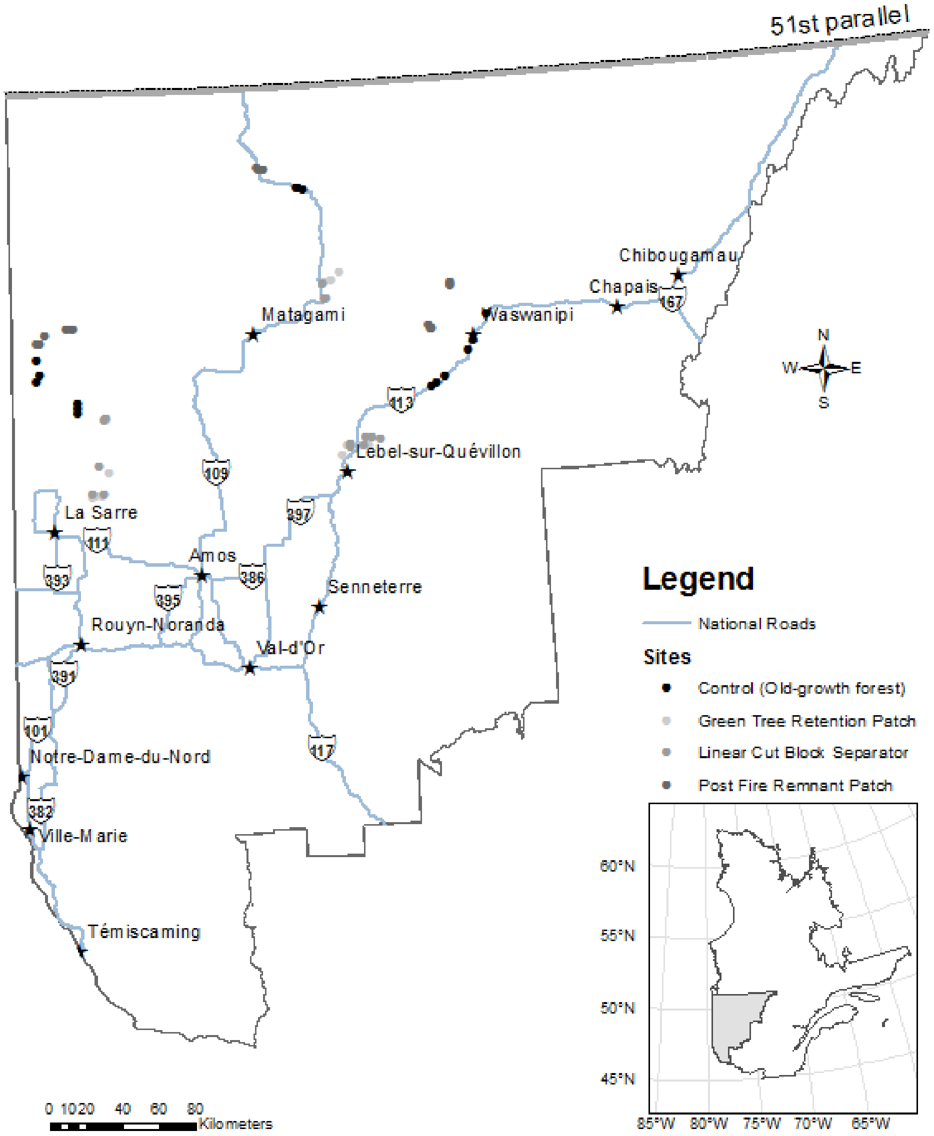

Figure 3.1 Location of the study sites in black spruce forest of northwestern Quebec, Canada.

Sites were characterised by a density of large trees ranging from 0 to 2444 trees.ha^{-1} (first quartile = 333 ha; median = 756 ha, third quartile = 1 400 ha). GTRP were mostly composed of small trees with a dbh less than 10 cm, with a resulting average density of large trees of 584 trees.ha^{-1} [range: 44 - 2 133]. The average density of large trees found in CTRL and PRFP was 839 trees.ha^{-1} [range: 0 - 2 089] and 827 trees.ha^{-1} [range: 0 - 1 644], respectively. LCBS were densely packed with large trees, with an average density of 1407 large trees.ha^{-1} [range: 311 - 2 444].

3.4.2 Squirrel survey

Live-trapping was conducted from 1 June 2014 to 21 August 2014, using Tomahawk (Tomahawk Live Trap llc ®) live-traps baited with peanut butter and apple pieces. No pre-baiting was carried out. Based on 17 recent studies that used live-trapping with various squirrel species and under different sampling regimes, only 53% of these used pre-baiting (see **Appendix 3.9.1**). We established one transect line of six live-traps per site with a distance of 10 m between traps. Transects were 50 m long to accommodate our smallest sites. Traps were set late in the afternoon and left on site for three consecutive days. Traps were checked twice a day (early morning and late afternoon). Each site was monitored with this trapping regime of three consecutive days during three sessions over the summer 2014 (three days in June, three days in July, and three days in August). Trapping sessions in a given site were separated by 27 days. Captured squirrels were pit-tagged, identified to sex and age, weighed, and assessed for health and reproductive conditions for a concurrent study. All individuals were subsequently released. All manipulations adhered to the Canadian Council on Animal Care Guidelines and were approved by the Institutional Animal Care Review Committee, Université du Québec en Abitibi-Témiscamingue (UQAT, permit no. 2013-04-02).

Point and playback counts were both conducted during the same period as live-trapping in a given site, from sunrise to mid-morning when squirrels are the most active. Once all traps on site were checked and potentially captured individuals were released, we waited 10 min before starting the auditory sampling. We listened for squirrels for 10 consecutive minutes and noted all detections within this period. Following the point count, we played squirrel calls using portable players plugged into amplifiers. Squirrel calls were extracted from the audio book "Le son de nos forêts" (Elliot and Mack 1994), and they were played back three times over a period of 10 minutes. For both playback and point counts, and for each site, we recorded whether individuals were detected or not. Point counts were carried out over two consecutive days, three times over the summer (two days in June, July, and August). We encountered technical problems in June that prevented us from using playback counts on more than 12 occasions over that month. However, playback was carried out over three consecutive days, on the two last trapping sessions at each site (three days in both July and August). When a playback or point count was not conducted on a given day due to unfavourable weather conditions or to technical problems, we considered it as a missing value in the analyses.

3.4.3 Environmental data

We did not expect understory strata to impede the hearing of listeners. Rather, we expected large live tree density to influence the listeners' ability to detect calling squirrels. Therefore, we characterised tree density by counting the number of trees that were equal to or larger than 10 cm in diameter at breast height (dbh), within a 15 x 15 m quadrat. All values were expressed as a number of stems per hectare.

3.4.4 Cost analysis of each methods

We calculated costs of each sampling method based on the effort required to survey 60 sites during one sampling session (i.e., 3 consecutive nights). We considered four types of expenditures: equipment, personnel, lodging and travel. Equipment costs were based on 2014 purchase prices. Personnel costs were calculated for a team of four people based on institutional salary for a research assistant in 2014 ($17.25/hour plus taxes). Travel costs included the rental of a vehicle of two King-cab 4 x 4 trucks, insurance, and fuel. Lodging costs were of $16 per night per person, based on the price paid to stay overnight in the institutional research station. As sites were sampled by groups of 12 at a time, a total of 20 days were required to sample 60 sites using live-trapping [5 groups of sites x (1 day for travelling towards a given group of sites and setting traps + 3 days of sampling)]. A total of 16 days were required to conduct playback counts [1 day for travelling towards the first group of sites + 5 groups of sites x (2 mornings of sampling + 1 day of sampling and travelling towards the next group of sites)]. A total of 11 days were required to conduct point counts [1 day for travelling towards the first group of sites + 5 groups of sites x (1 mornings of sampling + 1 day of sampling and travelling towards the next group of sites)].

3.4.5 Statistical analyses

Our data frame was composed of detections and non detections during three primary periods (i.e. sampling sessions) for each of the three sampling methods. Each primary period consisted of three secondary periods (i.e. sampling days). We used dynamic occupancy models to estimate the detection probability (p) of squirrels, as well as the probabilities of initial occupancy (ψ), extinction (ε), and colonisation (γ) (MacKenzie et al. 2003). The dynamic occupancy model allows potential changes in squirrel occupancy among trapping sessions. We opted for this approach because juveniles begin dispersing within the first month after leaving the family den (Larsen and Boutin 1994). Considering that American red squirrels defend territories of about 65 m^2 (Larsen and Boutin 1994), they probably never travel outside hearing distances of our sites using auditory methods, and seldom use areas not crossed by our trapping transects.

All analyses were conducted using the *unmarked* package (Fiske and Chandler 2010) in R (version 3.0.1, R Development Core Team 2015). All hypotheses and corresponding model structures are listed in **Table 3.1.**

Table 3.1 List of hypotheses tested with dynamic occupancy models to primarily assess the effects of covariates on detection probability of American red squirrels (*Tamiasciurus hudsonicus*) sampled in black spruce forest of northwestern Quebec with three different sampling methods, *viz.*, live-trapping, playback counts, and point counts. All following hypotheses were tested when analysing detection probabilities associated to each sampling method. We excluded the two hypotheses that proposed changes in site colonisation and local extinction over the summer of 2014 from the analyses of combined auditory methods, because the latter only included two primary sampling sessions. Note that models containing interactions also include main effects.

Model parameter	**Model structure**	**Hypotheses**
Detection (p)	p(.)	Detection probabilities are constant among visits and sites, regardless of sampling and environmental variables
Detection (p)	p(METHOD)	Detection probabilities associated with live-trapping are higher than auditory methods (hypothesis 1)
Detection (p)	p(METHOD$^+$)	Detection probabilities associated with auditory methods are negatively impacted by the prior successful trapping of squirrel individuals (hypothesis 2)
Detection (p)	p(SESSION)	Detection probabilities increase throughout the summer of 2014 (hypothesis 3)

(suite)

Model parameter	**Model structure**	**Hypotheses**
Detection (p)	p(Visit)	Detection probability in a given primary period is higher on later sampling visits than first sampling visits, regardless of the sampling method (hypothesis 4)
Detection (p)	p(Session + Method)	Hypotheses 1 + 3
Detection (p)	p(Session + Method$^+$)	Hypotheses 2 + 3
Detection (p)	p(Session + Visit)	Hypotheses 3 + 4
Detection (p)	p(Method : Tree Density)	Detection probabilities associated with auditory methods are negatively impacted by the density of large live trees due to sound obstruction.
Detection (p)	p(Visit : Method)	Detection probability in a given primary period from live-trapping is higher on later sampling visits than first sampling visit ("pre-baiting" effect for live-trapping only)
Occupancy (ψ)	ψ(Tree Density)	Probabilities of initial site occupancy increase with the density of large live trees

(suite)

Model parameter	**Model structure**	**Hypotheses**
Colonisation (γ)	γ(.)	Colonisation probabilities are constant throughout the study and independent of any environmental variable
Colonisation (γ)	γ(SESSION)	Colonisation probabilities increase from June to August 2014
Local extinction (ε)	ε(.)	Local extinction probabilities are constant throughout the study and independent of any environmental variable
Local extinction (ε)	ε(SESSION)	Local extinction probabilities decrease from June to August 2014

Note: Covariate acronyms: METHOD, sampling method (live-trapping, playback count, or point count); METHOD$^+$, sampling method that takes into account whether an individual squirrel was trapped before conducting the two auditory methods (live-trapping, playback count after at least one capture, playback count after no capture, point count after at least one capture, or point count after no capture); TREE DENSITY, number of live trees with a diameter larger than 10 cm; SESSION, sampling session (i.e. primary period - 3 in total); VISIT, sampling visits (i.e. secondary period - 3 in total) within a sampling session. Parameters followed by (.) indicate that they are constant.

3.4.5.1 Effect of sampling method

We compared the detection probability of different sampling methods by considering a categorical variable (METHOD) that consisted of three levels (live-trapping, playback counts, and point counts). We predicted that live-trapping would yield a higher detection probability than the auditory methods because live-trapping samples any individual (regardless of age or status) over a longer period of time than auditory methods.

3.4.5.2 Effect of live-trapping on auditory methods

Trap-induced stress may cause squirrels to change their behaviour, including vocalisation (Bosson et al. 2012). Because playback and point counts were always conducted after having checked traps, we quantified the influence of a trapping or handling effect on the detection probability during auditory methods with a second categorical variable (METHOD^{+}). The latter variable consisted of five levels: live-trapping, playback count following a capture, playback count following no capture, point count following a capture, and point count following no capture. METHOD and METHOD^{+} were never included together in the same candidate model. We predicted that live-trapping a squirrel would increase the detection probability of playback and point counts, given that territorial individuals would likely vocalise a few minutes after having been released at a site.

3.4.5.3 Primary period and pre-baiting effects

Two time categorical variables were considered in our candidate models, *viz.*, the primary sampling period (SESSION) with three levels and the sampling visit during a primary sampling period (VISIT) with three levels. We allowed the detection probability to vary with Session as we predicted that detection probability would increase over the summer due to changes in density following juvenile dispersal. We introduced the categorical variable VISIT to test for a possible "pre-baiting" effect, caused by individuals getting accustomed to traps. The VISIT x METHOD interaction formally tests the pre-baiting effect for live-trapping.

3.4.5.4 Effect of tree density

Finally, we introduced a variable reporting the density of live trees greater than 10 cm in dbh per hectare (TREE DENSITY- numerical variable standardised to zero mean and unit variance). We predicted that detection probability would decrease with TREE DENSITY when using point and playback counts due to hearing impediment.

We contrasted the different detection scenarios above to a null model with constant detection probability, for a total of 10 detection probability scenarios. Our study focused on detection probability, but we included a single variable on occupancy to account for potential heterogeneity in occupancy in all models. Specifically, we allowed occupancy to vary with TREE DENSITY as large trees provide good habitat for American red squirrels (Carey 2000). We predicted that more juveniles would disperse between the last two periods rather than between the first two. We considered three different scenarios involving colonisation probability (γ) and extinction probability (ε): 1) probabilities of extinction and colonisation constant across primary periods, 2) probability of extinction varying among primary periods (Session), but constant colonisation probability, 3) constant probability of extinction, but colonisation probability varying among primary periods. Thus, we considered a total of 30 a priori models (10 scenarios of detection probability x three scenarios of colonisation and extinction probabilities, **Appendix 3.9.2**).

We used an information-theoretic approach based on Akaike's Information Criterion for small samples (AIC_c) to compare candidate models (Burnham and Anderson 2002). We assessed the goodness-of-fit of the most complex model using an extension of the MacKenzie and Bailey (2004) goodness-of-fit test with 10 000 bootstraps implemented in the *AICcmodavg* package (Mazerolle 2015). The goodness-of-fit test did not suggest overdispersion ($\hat{c} < 1$). We identified variables appearing in the top-ranked models (delta AICc < 4) and computed model-averaged predictions and 95% unconditional confidence intervals using the entire set of candidate models.

3.4.5.5 Pooled auditory methods

The analyses described above were also conducted on a second data set consisting of pooled detections from point and playback counts at each visit. Here, we compared detection probabilities from combining two low-cost sampling methods relative to live-trapping. As previously mentioned, playback counts were not entirely conducted over the first sampling session due to technical problems. Thus, the models considered in the second analysis only included two sampling sessions (i.e. primary periods) of three consecutive days each (i.e. secondary periods) in July and August. In this analysis, METHOD became a two-level categorical variable (live-trapping vs combined auditory methods) and, METHOD^{+} became a three-level categorical variable (live-trapping, combined auditory methods following no capture, and combined auditory methods following a capture). A total of 10 a priori models were explored (**Appendix 3.9.3**). We expected a higher detection probability when combining playback and point counts together than when considering them on their own, because the complementary information on detection patterns among visits should result in a greater number of detections than either method alone. The most complex model did not suggest overdispersion ($\hat{c} < 1$).

3.5 Results

3.5.1 Squirrel survey

We live-trapped a total of 65 American red squirrels over the summer of 2014, with a total effort of 3 131 trap nights ($n_{live\text{-}trapping}$ = 1 061, 1 057,1 013 for sessions 1, 2 and 3, respectively). We recorded the presence of 22 individuals with a total effort of 372 playback calls ($n_{playback.count}$ = 12, 180, 180 for sessions 1, 2 and 3, respectively), whereas 36 individuals were detected with 360 point counts ($n_{point.count}$ = 120 for each session).

The number of sites where squirrels were detected varied with sampling methods and sampling sessions (**Table 3.2**). The total number of sites where squirrels were detected at least once over the summer of 2014 was higher when using point counts (22 sites) than with the two other methods (18 sites each). When combining point and playback counts, a total of 26 sites had at least one detection of American red squirrel over the summer of 2014. A total of 13 sites were apparently colonised between the first and second session, whereas 11 sites were colonised between the second and third session. Likewise, apparent local extinction was observed at four sites between the first and second session, and at 11 sites between the second and third session.

Table 3.2 Number of sites where American red squirrels (*Tamiasciurus hudsonicus*) were detected for each sampling session and each sampling method, with the corresponding percentage in brackets. A total of 60 sites were sampled each session in black spruce forests of northwestern Quebec.

	Number of sites where squirrels were detected			**Total number of sites where squirrels were detected (summer of 2014)**
Method	**Session 1**	**Session 2**	**Session 3**	
Live-trapping	2 (3)	9 (15)	15 (25)	18 (30)
Point count	12(20)	12 (20)	7 (12)	22 (37)
Playback count	NA	7 (12)	13 (22)	18 (30)
Combined auditory methods	NA	16 (27)	16 (27)	26 (43)
All methods	12 (20)	21 (35)	21 (35)	34 (57)

3.5.2 Comparison of sampling methods

All models converged. The top-ranked model consisted of the interactive term between METHOD and TREE DENSITY on the detection probability (**Table 3.3**). This model had 26% of the Akaike weight and was closely followed by the model allowing the detection probability to vary with the sampling method. Taken together, these two models accounted for 45% of the weight (**Table 3.3**). For the two covariates that had some support, multimodel inference indicated that live-trapping had the highest detection probability across all sampling sessions (model-averaged prediction ± unconditional SE: 0.269 ± 0.071), followed by point counts (0.231 ± 0.059), whereas playback counts had the lowest detection probability (0.139 ± 0.057, **Figure 3.2**). There was neither a difference between live-trapping and point counts (model-averaged effect size on logit scale, [95% CI], *i.e.* $\text{modavgEffect}_{\text{logit[CI]}}$: -0.19, [-1.10, 0.71]), nor between live-trapping and playback counts ($\text{modavgEffect}_{\text{logit[CI]}}$: -0.81, [-1.89, 0.28]). Increasing density of live large trees from 0 to 2444 trees.ha^{-1} had no effect on the detection probability of any sampling method, i.e. live-trapping ($\text{modavgEffect}_{\text{logit[CI]}}$: 1.14, [-1.63, 3.9]), point count ($\text{modavgEffect}_{\text{logit[CI]}}$: -0.48, [-2.02, 1.06]), and playback count ($\text{modavgEffect}_{\text{logit[CI]}}$: -0.68, [-2.57, 1.21]).

Table 3.3 Ranking of dynamic occupancy models comparing the three sampling methods used to detect American red squirrels (*Tamiasciurus hudsonicus*), based on their relative support (Akaike weight, ω_i). The top-ranked model scored an AICc of 535.36. Models with weights adding up to 0.95 are displayed.

Candidate model	**ΔAICc**	ω_i	**K**
ψ(TREE DENSITY)p(TREE DENSITY:METHOD)γ(.)ε(.)	0.00	0.26	10
ψ(TREE DENSITY)p(METHOD)γ(.)ε(.)	0.75	0.19	7
ψ(TREE DENSITY)p(TREE DENSITY:METHOD)γ(SESSION)ε(.)	1.51	0.12	11
ψ(TREE DENSITY)p(METHOD)γ(SESSION)ε(.)	2.57	0.07	8
ψ(TREE DENSITY)p(SESSION+METHOD)γ(.)ε(.)	2.89	0.06	9

(suite)

Candidate model	ΔAICc	ω_i	K
ψ(TREE DENSITY)p(TREE DENSITY:METHOD)γ(.)ε(SESSION)	3.00	0.06	11
ψ(TREE DENSITY)p(METHOD)γ(.)ε(SESSION)	3.27	0.05	8
ψ(TREE DENSITY)p(VISIT)γ(.)ε(.)	3.67	0.04	7
ψ(TREE DENSITY)p(VISIT)γ(SESSION)ε(.)	5.52	0.03	8
ψ(TREE DENSITY)p(SESSION+METHOD)γ(.)ε(SESSION)	5.62	0.02	10
ψ(TREE DENSITY)p(.)γ(.)ε(.)	5.77	0.02	5
ψ(TREE DENSITY)p(SESSION+METHOD)γ(SESSION)ε(.)	5.78	0.01	10
ψ(TREE DENSITY)p(METHOD$^+$)γ(.)ε(.)	5.80	0.01	9
ψ(TREE DENSITY)p(VISIT)γ(.)ε(SESSION)	6.17	0.01	8

Considering the other variables, there was no evidence of a trapping or handling effect on the detection probability of auditory methods, as the models including (METHOD$^+$) had no support (**Table 3.3**). Detection probability did not vary with the sampling session and we found no evidence for a pre-baiting effect, because models including this hypothesis on detection probability had no support relative to the other candidate models (sum of Akaike weights = 0.04, **Table 3.3**). Finally, there was no support for models allowing local extinction and colonisation probabilities to vary with primary sampling sessions (**Table 3.3**).

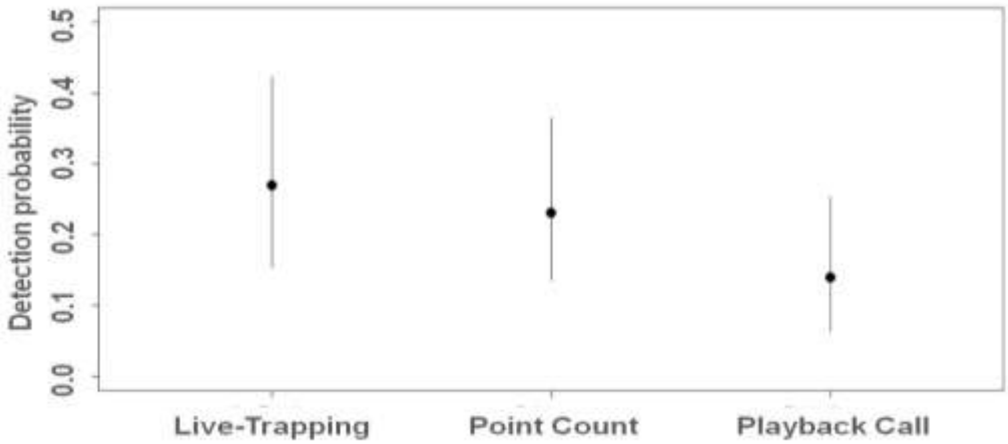

Figure 3.2 Predicted detection probabilities for three methods used to sample American red squirrel (*Tamiasciurus hudsonicus*). Error bars denote 95% unconditional confidence intervals.

For the analysis of the detection data pooled among auditory methods, all models also converged. The top-ranked model allowed the detection probability to vary with the interaction between the sampling visit (VISIT) and the sampling method (METHOD) (Akaike weight = 0.33, **Table 3.4**). This model was followed closely by the model allowing the detection probability to vary with the sampling session. Taken together, these two models accounted for 49% of the Akaike weight (**Table 3.4**).

Although combining the two auditory sampling methods (point and playback counts) increased detection probabilities of American red squirrels compared when using each separately, we found no difference between the combined auditory methods and live-trapping (**Figure 3.3**, modavgEffect$_{\text{logit[CI]}}$: 0.14 [-0.89, 1.17]). Moreover, there was no effect of the sampling day on the detection probability associated to either sampling method, as confidence intervals around model-averaged differences between visits largely included 0 for all methods. Similarly, detection probability did not vary with the sampling session (modavgEffect$_{\text{logit[CI]}}$: -0.24 [-1.25, 0.77]). There was no support for models that included the effect of tree density or a live-trapping effect on detection probability (**Table 3.4**).

Table 3.4 Ranking of dynamic occupancy models comparing live-trapping *vs* auditory methods combined (point and playback counts) in detecting American red squirrels (*Tamiasciurus hudsonicus*), based on their relative support (Akaike weight, ω_i). The top-ranked model scored an AICc of 470.94. Models with weights adding up to 0.95 are displayed.

Candidate model	ΔAICc	ω_i	K
ψ(Tree Density) p(Visit : Method) $\gamma(.)$ $\varepsilon(.)$	0.00	0.33	10
ψ(Tree Density) p(Session) $\gamma(.)$ $\varepsilon(.)$	1.47	0.16	6
ψ(Tree Density) p(Session + Visit) $\gamma(.)$ $\varepsilon(.)$	2.05	0.12	8
ψ(Tree Density) p(Obstruction : Method) $\gamma(.)$ $\varepsilon(.)$	2.44	0.10	8
ψ(Tree Density) $p(.)$ $\gamma(.)$ $\varepsilon(.)$	2.60	0.09	5
ψ(Tree Density) p(Visit) $\gamma(.)$ $\varepsilon(.)$	3.00	0.08	7
ψ(Tree Density) p(Session + Method) $\gamma(.)$ $\varepsilon(.)$	3.21	0.07	7

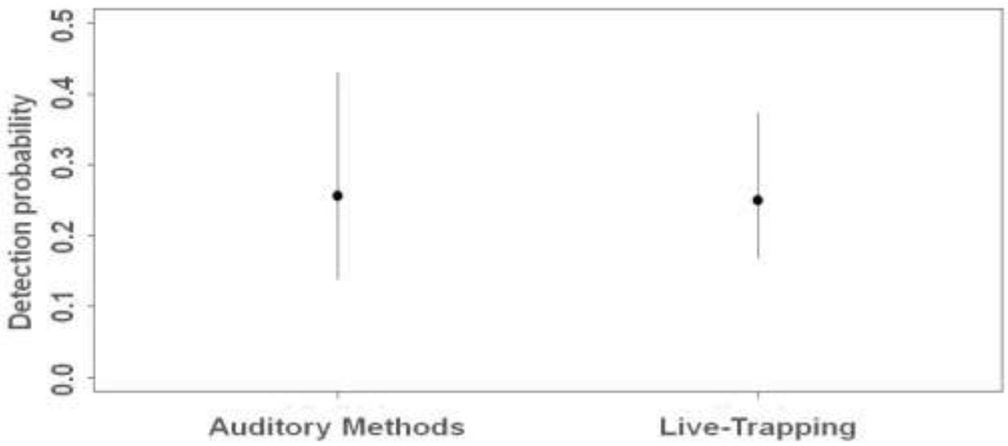

Figure 3.3 Predicted detection probabilities of American red squirrels (*Tamiasciurus hudsonicus*) using either live-trapping or point counts combined with playback count. Error bars denote 95% unconditional confidence intervals.

3.5.3 Costs of sampling methods

Total costs differed by several thousands of Canadian dollars between live-trapping ($39 631.81) and the two other sampling methods used in the present study ($31 364.48 and $14 050.50 for playback count and point count respectively, **Appendix 3.9.4**). This was not surprising as the number of hours spent in the field was between 1.1 and 3.3 times greater for live-trapping compared to either passive point counts or playback, respectively.

3.6 Discussion

There is a growing body of literature that focuses on the importance of accounting for imperfect detection probability when studying patterns of species distribution and population parameters (*e.g.*, MacKenzie et al. 2003; Mazerolle et al. 2007; Smith et al. 2007; Kéry and Schmidt 2008; Kellner and Swihart 2014). As detection can be greatly affected by the sampling protocol, studies have emphasised the importance of carefully defining the sampling period, allocating sufficient effort, and using appropriate sampling techniques (Drapeau et al. 1999; Otto and Roloff 2011). Squirrel occupancy has been studied using several sampling methods other than live-trapping (e.g. Buchanan et al. 1990; Fisher et al. 2005; Mortelliti and Boitani 2008; Gurnell et al. 2011; Allard-Duchêne et al. 2014), but to our knowledge, no one specifically compared the detection probability of alternative methods to live-trapping. In the present study, we quantified the detection probability of three different sampling methods, namely live-trapping, playback, and point counts. Given the sampling effort that was defined for all three sampling methods, live-trapping and point counts had the highest probability of detection compared to playback counts (**Figure 3.2**). However, we found no difference between live-trapping and point count methods. This indicates that point counts could be considered as an effective sampling method when focusing on squirrel site occupancy, which could often be conducted simultaneously to auditory ornithological surveys. Indeed, American red squirrels are opportunistic predators of bird nests in boreal forests, despite being mostly granivorous (Reitsma et al. 1990; Bayne and Hobson 2002). The abundance of nesting birds and nest densities decline in the presence of American red squirrels (Darveau et al. 1997; Martin and Joron 2003; Willson et al. 2003), potentially reducing the local distribution of some bird species (Siepielki 2006). Reliance upon point counts to investigate co-occurrence patterns of American red squirrels and nesting birds agrees with the view of Richmond et al. (2010), who recommend the use of a unique sampling technique for measuring occupancy of all species of interest.

Live-trapping has been traditionally used for sampling small mammals in mark-recapture studies (e.g., Harris et al. 1990; Pradel 1996) and as such, live-trapping enables the estimation of several population parameters that cannot be obtained by alternative methods. Nevertheless, our results suggest that using point counts to study site occupancy by American red squirrels presents several benefits. Point counts are non-invasive (Ralph et al. 1995) and easy to implement over a large number of sites. In our study, we estimate that point counts cost half as much as live-trapping, due to halving the travel time to sites. Besides, for similar effectiveness in detecting individuals, less invasive methods should always be preferred over invasive methods (Hubbard 2008; Gompper et al. 2006).

Although playback counts have slightly lower detection probabilities than the two other sampling techniques (**Figure 3.2**), there was no real difference according to multimodel inference. Live-trapping and territorial calls stem from different behaviours, but detection probability from live-trapping and auditory methods was surprisingly similar. These results emphasise that the playback count technique is worth considering when monitoring squirrel occupancy. Like point counts, the biological process behind playback counts is well suited to study occupancy (Burton et al. 2015). Both auditory methods rely on territorial behaviours displayed by squirrels. Unlike live-trapping which sample both resident squirrels and dispersing individuals, auditory methods mainly focus on individuals holding a territory. Nonetheless, the choice of recorded calls during playback counts may influence the intensity of territorial behaviour of squirrels. Responses to playback calls vary with the local density of squirrels (Shonfield et al. 2012), sex, and breeding status (Price et al. 1990). American red squirrels are also more likely to respond to territorial calls from an unknown individual than to those of neighbours (Price et al. 1990). It would thus be interesting to test whether detection probabilities vary with the type of call (alarm call or territorial call) being used during playback counts.

Sampling techniques must be adapted to the species of interest, but also to the environment in which sampling will be conducted. Site characteristics can influence the effectiveness of sampling techniques to detect species. Surprisingly, the density of large trees did not negatively affect the two auditory methods that we used, which disagrees with the conclusions of several studies (*e.g.*, Richards 1981; Pacifici et al. 2008) and with our own prediction. The detection probability of American red squirrels seemed to slightly increase with the density of large live trees regardless of the sampling method used to detect individuals. An increase in large trees (both dead and alive) may enable a denser population of red squirrels to establish territories or favour females sharing territories with their juveniles (Wheatley et al. 2002; Patterson and Malcolm 2010), because large trees represent important attributes in boreal forests, providing shelter and food for a number of animal species (Gauthier et al. 2008). However, we found no relationship between squirrel occupancy and the number of large live trees in our study.

Sampling period is another factor that could influence the detection of species with different sampling techniques. In this study, the detection probability of American red squirrels did not vary with sampling session, although we expected squirrels to vocalise more frequently in late summer, *i.e.*, when juveniles begin dispersing to find territories and when territory boundaries must be clearly advertised (Larsen and Boutin 1994). Juvenile dispersal potentially did not occur by the end of our study, and this would explain the lack of change in the probabilities of colonisation and local extinction when allowed to vary with the sampling session. Squirrels are active year-round, modifying their social behaviour at different periods of the year (e.g., peak in juvenile dispersal, food-hoarding - Steele 1998; Larsen and Boutin 1994; Wauters and Dhondt 1993). Likewise, changes in their environment (such as masting events) may alter their likelihood to enter live-traps (Selonen et al. 2015). Our study focused exclusively on the summer period, but extending the sampling to other times of the year might reveal different patterns.

Some studies advocate combining several techniques to increase the probability of detecting a species of interest (Garden et al. 2007; Petitot et al. 2014). Live-trapping and point counts are comparable in terms of detection probability. Pooling detection data that were obtained by playback and point counts did not substantially increase detection probability. However, the probability of detection (predicted average probability and SE) from the combined methods matched that obtained with our live-trapping effort. Our results emphasise the complementarity of point and playback count methods when studying occupancy by American red squirrels.

In this study, we showed that auditory methods are reliable in detecting American red squirrels. These results show promise for site occupancy studies of other vocal mammalian species such as eastern chipmunks (*Tamias striatus*) and Douglas squirrels (*Tamiasciurus douglasii*) (Smith 1978; Snyder 1982; Burke Da Silva et a, 1994). To a lesser extent, eastern gray squirrels (*Sciurus carolinensis*) and Eurasian red squirrels (*Sciurus vulgaris*) also occasionally vocalise (Lishak 1984; Randler 2006; Getschow et al. 2010). The sciurid species mentioned above are also nest predators (Reitsma et al. 1990; Callahan 1993; Newson et al. 2010; Mori et al. 2013). Formally estimating the detection probability of point and playback counts on *Tamiasciurus* and *Tamias* species would be valuable where individuals might influence the nesting success of birds. Likewise, similar studies should be conducted for both *Sciurus* species, after adapting the protocol to these two quieter species. Obtaining valid occupancy data of sciurid nest predators and breeding birds at the same sites is essential to investigate the co-occurrence of the two groups as well as examine their shared responses to habitat disturbance.

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3.9 Appendices

3.9.1 Appendix 1

Literature review of the use of pre-baiting in squirrel abundance or occupancy studies. These papers were found by typing the search terms "abundance", "demography", “occupancy“, “occurrence", "population density", "*Sciurus*", “squirrel“, and “*Tamiasciurus*“ in both Google Scholar and ISI Web of Knowledge.

REFERENCE	**SPECIES**	**PRE-BAITING**
Boutin et al., 1995*	*T. hudsonicus*	Unknown
Dantzer et al., 2012*	*T. hudsonicus*	Unknown
Fisher and Bradbury, 2006	*T. hudsonicus*	None
Gurnell et al., 2004	*S. vulgaris*	Yes (inside traps)
Haugland and Larsen, 2004	*T. hudsonicus*	Yes (inside traps)
Holloway and Malcom 2006	*T. hudsonicus*	None
Patterson and Malcom 2010	*T. hudsonicus*	Yes (outside traps)
Ransome and Sullivan 2004	*T. douglasii*	None
Ransome and Sullivan 2003	*T. douglasii*	Yes (outside traps)
Ransome et al. 2004	*T. hudsonicus*	None
Stuart-Smith et al. 1995*	*T. hudsonicus*	Yes (inside traps)
Sullivan and Moses 1986	*T. hudsonicus*	None
Trudeau et al. 2011	*G. sabrinus*	None

(suite)

REFERENCE	SPECIES	PRE-BAITING
Verbeylen et al. 2003	*S. vulgaris*	Not in all years
Walpole and Bowman 2011	*T. hudsonicus*	None
Wauters et al. 2008	*S. vulgaris*	Yes (inside traps)
Wheatley et al. 2002	*T. hudsonicus*	None

* long-term study from the Kluane project

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3.9.2 Appendix 2

Candidate set of dynamic occupancy models used to assess the effects of covariates on detection probability of American red squirrels (*Tamiasciurus hudsonicus*) sampled in black spruce forest of northwestern Quebec with three different sampling methods, *viz.*, live trapping, playback counts, and point counts.

Candidate models	**Occupancy (ψ)**	**Colonisation (γ)**	**Local extinction (ε)**	**Detection (*p*)**	**Estimated parameters (K)**
Three sampling methods - three primary periods - three secondary periods					
Colonisation and local extinction kept constant					
M0	ψ(Tree Density)	γ(.)	ε(.)	*p*(.)	5
M1	ψ(Tree Density)	γ(.)	ε(.)	*p*(Method)	7
M2	ψ(Tree Density)	γ(.)	ε(.)	*p*(Method$^+$)	9
M3	ψ(Tree Density)	γ(.)	ε(.)	*p*(Session)	7
M4	ψ(Tree Density)	γ(.)	ε(.)	*p*(Visit)	7

(suite)

Candidate models	**Occupancy (ψ)**	**Colonisation (γ)**	**Local extinction (ε)**	**Detection (*p*)**	**Estimated parameters (K)**
M5	ψ(Tree Density)	γ(.)	ε(.)	*p*(Session + Method)	9
M6	ψ(Tree Density)	γ(.)	ε(.)	*p*(Session + Method^{+})	11
M7	ψ(Tree Density)	γ(.)	ε(.)	*p*(Session + Visit)	9
M8	ψ(Tree Density)	γ(.)	ε(.)	*p*(Method : Tree Density)	10
M9	ψ(Tree Density)	γ(.)	ε(.)	*p*(Visit : Method)	13
Seasonal colonisation and constant local extinction					
M0col	ψ(Tree Density)	γ(Session)	ε(.)	*p*(.)	6
M1col	ψ(Tree Density)	γ(Session)	ε(.)	*p*(Method)	8

(suite)

Candidate models	**Occupancy (ψ)**	**Colonisation (γ)**	**Local extinction (ε)**	**Detection (*p*)**	**Estimated parameters (K)**
M2col	ψ(Tree Density)	γ(Session)	ε(.)	*p*(Method$^+$)	10
M3col	ψ(Tree Density)	γ(Session)	ε(.)	*p*(Session)	8
M4col	ψ(Tree Density)	γ(Session)	ε(.)	*p*(Visit)	8
M5col	ψ(Tree Density)	γ(Session)	ε(.)	*p*(Session + Method)	10
M6col	ψ(Tree Density)	γ(Session)	ε(.)	*p*(Session + Method$^+$)	12
M7col	ψ(Tree Density)	γ(Session)	ε(.)	*p*(Session + Visit)	10
M8col	ψ(Tree Density)	γ(Session)	ε(.)	*p*(Method : Tree Density)	11
M9col	ψ(Tree Density)	γ(Session)	ε(.)	*p*(Visit : Method)	14

(suite)

Candidate models	**Occupancy (ψ)**	**Colonisation (γ)**	**Local extinction (ε)**	**Detection (*p*)**	**Estimated parameters (K)**
Constant colonisation and seasonal local extinction					
M0ext	ψ(TREE DENSITY)	γ(.)	ε(SESSION)	*p*(.)	6
M1ext	ψ(TREE DENSITY)	γ(.)	ε(SESSION)	*p*(METHOD)	8
M2ext	ψ(TREE DENSITY)	γ(.)	ε(SESSION)	*p*(METHOD$^+$)	10
M3ext	ψ(TREE DENSITY)	γ(.)	ε(SESSION)	*p*(SESSION)	8
M4ext	ψ(TREE DENSITY)	γ(.)	ε(SESSION)	*p*(VISIT)	8
M5ext	ψ(TREE DENSITY)	γ(.)	ε(SESSION)	*p*(SESSION + METHOD)	10
M6ext	ψ(TREE DENSITY)	γ(.)	ε(SESSION)	*p*(SESSION + METHOD$^+$)	12
M7ext	ψ(TREE DENSITY)	γ(.)	ε(SESSION)	*p*(SESSION + VISIT)	10

(suite)

Candidate models	**Occupancy (ψ)**	**Colonisation (γ)**	**Local extinction (ε)**	**Detection (*p*)**	**Estimated parameters (K)**
M8ext	ψ(Tree Density)	γ(.)	ε(Session)	*p*(Method : Tree Density)	11
M9ext	ψ(Tree Density)	γ(.)	ε(Session)	*p*(Visit : Method)	14

Note: Covariate acronyms: Method, sampling method (live-trapping, playback count, or point count); Method^{+}, sampling method that takes into account whether an individual squirrel was trapped before conducting the two auditory methods (live-trapping, playback count after at least one capture, playback count after no capture, point count after at least one capture, or point count after no capture); Tree Density, number of live trees with a diameter larger than 10 cm; Session, sampling session (i.e. primary period - three in total); Visit, sampling visits (i.e. secondary period - three in total) within a sampling session. Parameters followed by (.) indicate that they are constant.

3.9.3 Appendix 3

Candidate set of dynamic occupancy models used to assess the effects of covariates on detection probability of American red squirrels (*Tamiasciurus hudsonicus*) sampled in black spruce forest of northwestern Quebec with live trapping and auditory methods (point and playback counts). Acronyms are defined in **Appendix 3.9.2**.

Candidate models	**Occupancy (ψ)**	**Colonisation (γ)**	**Local extinction (ε)**	**Detection (*p*)**	**Estimated parameters (K)**
Live-trapping vs playback and point counts pooled together - two primary periods - three secondary periods - Colonisation and local extinction kept constant					
M0pool	ψ(TREE DENSITY)	γ(.)	ε(.)	*p*(.)	5
M1pool	ψ(TREE DENSITY)	γ(.)	ε(.)	*p*(METHOD)	6
M2pool	ψ(TREE DENSITY)	γ(.)	ε(.)	*p*(METHOD^{+})	6
M3pool	ψ(TREE DENSITY)	γ(.)	ε(.)	*p*(SESSION)	6

(suite)

Candidate models	**Occupancy (ψ)**	**Colonisation (γ)**	**Local extinction (ε)**	**Detection (*p*)**	**Estimated parameters (K)**
M4pool	ψ(TREE DENSITY)	γ(.)	ε(.)	*p*(VISIT)	7
M5pool	ψ(TREE DENSITY)	γ(.)	ε(.)	*p*(SESSION + METHOD)	8
M6pool	ψ(TREE DENSITY)	γ(.)	ε(.)	*p*(SESSION + METHOD^{+})	9
M7pool	ψ(TREE DENSITY)	γ(.)	ε(.)	*p*(SESSION + VISIT)	8
M8pool	ψ(TREE DENSITY)	γ(.)	ε(.)	*p*(METHOD : TREE DENSITY)	10
M9pool	ψ(TREE DENSITY)	γ(.)	ε(.)	*p*(VISIT : METHOD)	7

3.9.4 Appendix 4

Cost analysis of sampling American red squirrels (*Tamiasciurus hudsonicus*) in black spruce forest of northwestern Quebec with live-trapping and auditory methods (point and playback counts). Costs of each sampling method were calculated independently based on the effort required to survey 60 sites over one sampling session (i.e. over 3 consecutive nights). All costs are given in Canadian dollars. Three main areas of cost expenditure were considered for each method: equipment, personnel , and travel between sites.

Costs	**Live-trapping**	**Playback count**	**Point count**
Equipment costs	5 646.31	1 075.26	765.83
Travel costs	5 005.83	4 685.83	3 692.83
Lodging costs	1 280.00	1 024.00	704.00
Personnel costs	28 022.67	24 576.39	8 567.84
Total	**40 004.81**	**31 364.48**	**14 050.50**

CHAPITRE IV

BOREAL SMALL MAMMALS SUGGEST EVIDENCE OF DENSITY-DEPENDENT PATTERNS WITH AREA-SENSITIVITY

EMILIE E. CHAVEL, LOUIS IMBEAU, MARC J. MAZEROLLE & PIERRE DRAPEAU

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4.1 Abstract

In recent years, habitat amount in fragmented landscapes has been shown to positively influence population size, species occurrence, and species diversity. Quantifying how sensitive bioindicator species respond to the amount of habitat in disturbed landscapes (i.e. area-sensitivity) has become a growing research focus to provide robust guidelines for ecosystem-based management. In this study, we modelled the occurrence of North American boreal small mammals in relation to the total amount of forest surrounding remnant forest patches in disturbed landscapes while controlling for local habitat associations. Over the summers of 2013 and 2014, we conducted four trapping sessions in 60 sites located in old forest remnant patches of old forests in both wildfires and aggregated clearcuts, and in continuous old forest blocks within the black spruce forest of northwestern Quebec, Canada. American red squirrels (*Tamiasciurus hudsonicus*), southern red-backed voles (*Myodes gapperi*) and masked shrews (*Sorex cinereus*) represented 85.5% of our total captures. We measured the amount of habitat (percentage of forest cover) within 100 concentric buffers around each capture grid using digital forest cover maps. Buffers varied in radius from 50 m to 5 km. We quantified area-sensitivity using dynamic models of single-species occupancy to estimate the probabilities of initial site occupancy, site extinction and site colonisation of each species according to both local habitat variables and surrounding habitat amount. We found no associations between initial site occupancy, site colonisation, or site extinction with local habitat features, possibly in response to habitat structure similarity of our three site types. Species studied had different life histories in terms of population dynamics and timing of juvenile dispersal, possibly explaining why each species had its individual response to the amount of habitat in the surrounding landscape. For the American red squirrel, we found no evidence of within-year area-sensitivity on initial site occupancy patterns, whereas negative area sensitivity to initial site occupancy between-years was observed for the southern red-backed vole. In contrast, we found positive area-sensitivity between-years site colonisation for this latter species at small spatial scales. For masked shrews, we detected negative area-sensitivity on initial site occupancy within-year. As populations were sampled at low density, we suspect that the sparse distribution of individuals may influence area-sensitivity patterns. Future studies should consider area-sensitivity with regards to both spatial and temporal scales. We encourage long-term monitoring of animal populations at multiple spatial scales to investigate the underlying ecological mechanisms of positive and negative area-sensitivity.

Key words: boreal forest; habitat amount; landscape scale; old-growth forest remnants; temporal scale

4.2 Résumé

La quantité d'habitat est reconnue pour exercer une influence positive sur la taille des populations, l'occurrence des espèces et par conséquent, la diversité des espèces présentes dans les paysages fragmentés. Quantifier la réponse des espèces bioindicatrices sensibles à cette quantité d'habitat disponible dans les paysages perturbés, fournirait des pistes robustes pour un aménagement écosystémique du territoire. Dans cette étude, nous avons modélisé l'occurrence de petits mammifères boréaux nord-américains en relation avec la quantité totale de forêt dans des paysages perturbés par la coupe et par le feu, tout en contrôlant les associations potentielles avec des variables locales d'habitat. Au cours des étés 2013 et 2014, nous avons mené quatre sessions de capture dans 60 sites répartis entre des îlots résiduels de vieille forêt dans des parterres de feu et de coupes forestières, avec pour témoins des massifs de vieilles forêts continues dans la pessière noire du nord-ouest du Québec, Canada. Les écureuils roux d'Amérique (*Tamiasciurus hudsonicus*), les campagnols à dos roux de Gapper (*Myodes gapperi*) et les musaraignes cendrées

(*Sorex cinereus*) représentaient 85,5 % des captures totales. Les données d'inventaires forestiers nous ont permis de mesurer la quantité d'habitat (pourcentage de forêt) dans 100 périmètres circulaires et concentriques centrés sur chacune des grilles de capture. Les périmètres délimités avaient un rayon variant de 50 m à 5 km, selon une incrémentation de 50 m. Nous avons quantifié la sensibilité de chacune des espèces à la quantité d'habitat en utilisant des modèles d'occupation dynamique à une espèce pour estimer les probabilités d'occupation initiale, d'extinction et de colonisation selon les conditions locales d'habitat et la quantité de forêt disponible. Nous n'avons trouvé aucune association entre l'occupation initiale, l'extinction ou la colonisation de sites et les variables locales d'habitat, possiblement en raison de la similarité structurelle entre les différents types de sites échantillonnés. Le cycle de vie des espèces étudiées diffère en termes de cyclicité d'abondance et de périodes de dispersion juvénile, ce qui expliquerait les réponses individuelles de chaque espèce à la quantité de forêt disponible dans le paysage. Pour l'écureuil roux d'Amérique, nous n'avons trouvé aucune évidence de réponse intra-annuelle d'occupation initiale. Pour le campagnol à dos roux de Gapper, nous avons observé une réponse négative de son occupation de site inter-annuelle à une quantité d'habitat croissante, mais non de son occupation de site intra-annuelle. En comparaison, nous avons trouvé une réponse positive à sa colonisation de sites à petite échelle. Pour les musaraignes cendrées, nous avons détecté une réponse négative constante sur son occupation de site. L'échantillonnage s'étant effectué sur des populations peu denses, nous soupçonnons également que la distribution clairsemée des individus a pu influencer les patrons de sensibilité à la quantité d'habitat disponible. Les recherches futures devraient considérer cette sensibilité à la quantité d'habitat comme dépendante de l'échelle spatiale ainsi que de l'échelle temporelle. Nous encourageons la réalisation de suivis de populations à long terme, à plusieurs échelles spatiales pour comprendre les mécanismes écologiques derrière une sensibilité positive et négative à la quantité d'habitat.

4.3 Introduction

Studies identifying habitat characteristics and mechanisms that are critical to maintain vertebrate populations have traditionally been conducted at the local scale (e.g. Dueser and Shugart 1978; Pough et al. 1987; Dupuis et al. 1995). In recent years, however, spatial heterogeneity at larger scales (i.e. effects of surrounding habitat amount, remnant patch size, and structural connectivity) has been considered to explain patterns of species occurrence that involve underlying biotic processes such as source-sinks dynamics and spatial aggregation of competitor species (Pickett and Cadenasso 1995; Mazerolle and Villard 1999; Jones 2011). The proportion of remnant habitat in managed landscapes (habitat amount) and its spatial arrangement (habitat configuration) have been identified as important determinants of the global loss of biodiversity (Czech and Krausman 1997; Lawler et al. 2002; Kerr and Cihlar 2004). Habitat loss, rather than fragmentation *per se*, is generally considered as having the upper hand in explaining population declines (Schmiegelow and Mönkkönen 2002; Fahrig 2003; but see Villard et al. 1999 for another perspective). Indeed, habitat area has been shown to have a positive influence on population size, species occurrence, and species diversity (Fahrig 2003, 2013). As a result, determining the spatial scale of individual species or community responses to habitat area has become a growing research focus (e.g. Holland et al. 2004; Desrochers et al. 2010; Drapeau et al. 2016) with the underlying objective to quantify the sensitivity of species with the amount of habitat in surrounding areas both to fulfil their life cycle and to carry out ecological functions (i.e. species area-sensitivity - Robbins 1979). In a context of large-scale anthropogenic changes of the environment (e.g. forest management, agriculture) affecting both the availability of habitat and its spatial configuration, empirical studies showing evidence of thresholds of area-sensitivity are required to inform conservation strategies (Linehan et al. 1995; Boutin and Hebert 2002; Wiens 2009).

In the eastern Canadian boreal forest, tree harvesting has become the dominant disturbance in several regions, exceeding wildfires in spatial coverage (Drapeau et al. 2009). Tree harvesting has changed the age structure of landscape mosaics with a net decrease in old forest cover types when compared with historical disturbance regimes (Bergeron et al. 2002; Cyr et al. 2009). To mitigate this decline in the proportion of old forest stands, ecologists have proposed ecosystem-based approaches that cast timber harvested landscapes within the range of variation of their natural disturbance regimes (Hunter 1993; Niemelä 1999; Bergeron et al. 2007). However, the implementation of thisforest management approach is, in its initial steps, and most of the retention of forest patches in former and current aggregated clearcuts have not been planned within an ecosystem management framework. Remnant patches of old forests may provide habitat conditions for wildlife, as is the case for fire skips in stand-replacing wildfires (Morissette et al. 2002; Nappi et al. 2010). To better forecast the planning of green retention under the new ecosystem-based approach, there is a need to assess how the current retention strategy of old remnant patches in aggregated clearcuts provides species with habitat conditions that may or may not differ with those in wildfires. Such assessments require going beyond the usual analyses relating species' presence-absence or relative abundance data with stand- and landscape-level habitat explanatory variables (McGarigal and McComb 1995; Drapeau et al. 2000; Brotons et al. 2003). These assessments should tackle a more in depth analysis on response variables such as initial site occupancy, site colonisation and site extinction rates of species in remnant habitats.

In this study, we used small mammals as a focal species group. Their general biology, habitat associations, and dispersal capacities suggest that they could be more sensitive to landscape characteristics than anticipated as their response to habitat varies at different scales (Schweiger et al. 1999; Manning and Edge 2004; Fauteux et al. 2012). Moreover, changes in landscape configuration could either disrupt individual dispersion or alter the spatial distribution of predators, both mechanisms eventually having an effect on small mammal populations (Bélisle et al 2001; Banks et al 2005). To our knowledge, very few studies have considered habitat area to understand small mammal area-sensitivity through quantitative analyses of initial site occupancy, site colonisation, and site extinction patterns of small mammals in forest patches (Ritchie et al. 2009). We modelled site occupancy of boreal small mammals in relation to the total amount of forest in the surrounding landscape while controlling for local habitat associations. Specifically, our first objective was to evaluate the importance of remnant patch forest structure for site occupancy by small mammals. We assessed the suitability of remnant patches given landscape conditions to provide habitat conditions comparable to those occurring following wildfires by measuring site occupancy of small mammals in post-fire and post-harvesting remnant stands. Our second objective was to measure the relationship between population parameters (i.e. initial site occupancy, site colonisation, and site extinction) and the amount of forest by using multiple-scale buffers surrounding our sampling sites. Population parameters were estimated from data collected in years of low mammalian density (i.e. when populations are presumably more associated to optimal habitats with the presence of critical resources). Evidence supporting area-sensitivity in small mammals would add further value to the reliability of these species as indicators of sustainable forest management (McLaren et al. 1998; Pearce and Venier 2005; Holloway and Smith 2011).

According to our objectives, we hypothesised that:

1) at the local scale, the occurrence of boreal small mammals would not be explained by patch origin (post-fire vs. post-harvest), but rather by forest structure attributes (such as downed woody debris and canopy cover) found in either post-fire or post-harvesting remnant stands (e.g. Orrock and Pagel 2002; Fauteux et al. 2012; Craig et al. 2014).

2) at low density, boreal small mammals are area-sensitive at a spatial scale greater than the local stand scale.

4.4 Methods

4.4.1 Study area

The study area covered a total of 8325 km^2 of black spruce-feather moss forest located in northwestern Quebec, Canada (79˚29’ W, 49˚00’ N - 75˚39’ W, 50˚22’ N - **Figure 4.1**). A subpolar continental climate characterises this boreal region, with mean monthly temperatures ranging from 20 °C to -16 °C and 850 mm of annual precipitation (Blouin and Berger 2002; Environment Canada 2015). The forest canopy is dominated by black spruce (*Picea mariana*). Jack pine (*Pinus banksiana*) and balsam fir (*Abies balsamea*) also occur, along with broadleaf species such as paper birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*). The understory is primarily composed of dwarf ericaceous shrubs (e.g. *Rhododendron groenlandicum*) and feather mosses (*Pleurozium schreberi*) forming a dense carpet, replaced by *Sphagnum* species as drainage conditions deteriorate due to paludification with time since fire (Fenton and Bergeron 2006). Indeed, the region is also characterised by recurrent and severe wildfires over vast areas (8000 km^2 on average - Payette 1992; Bergeron et al. 2004; Le Goff et al. 2008), although this major disturbance is increasingly replaced by various forest management and harvesting strategies (Imbeau et al. 2015).

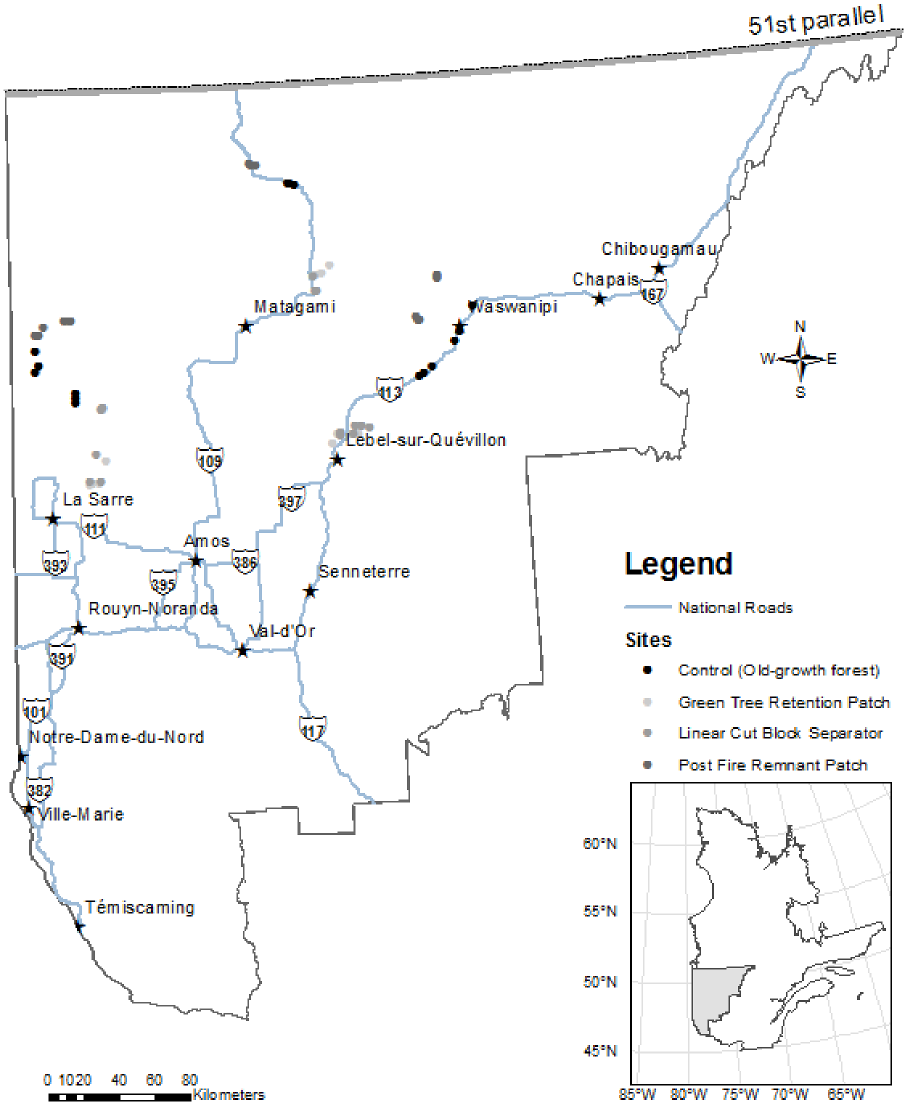

Figure 4.1 Location of the study sites in black spruce forest of northwestern Quebec, Canada.

We selected a total of 60 forested sites that were equally distributed among old-growth undisturbed forests (CONTROL - continuous forest over 100-years-old and of more than 200 ha), post-fire remnant patches (POSTFIRE - mean 3.1 ha; range 0.2 – 11.1 ha) left after wildfires that occurred over 20 years ago, green tree retention stands (GREENTREE – mean 0.8 ha; range 0.09 – 1.6 ha) left after recent clear-cuts (< 10 years), and linear cutblock separators (LINEARCUT - 60-100 m large, connected to old-growth forests) that separate clearcut areas. Sites were at least 500 m apart. Based on the average movement distance of American red squirrels (*Tamiasciurus hudsonicus*) which are the most vagile species found on our study area (Larsen and Boutin 1994), this distance of 500 m was sufficient to ensure independence among sites. Details regarding habitat structure and composition in these four site types are found in **Appendix 4.9.1**.

Although we initially selected four types of sites, we pooled GREENTREE and LINEARCUT sites together. These two types were pooled to increase species detection in site occupancy models as low species detection reported in GREENTREE sites prevented us from estimating site occupancy in this site type. Hereafter, we referred to GREENTREE and LINEARCUT sites as harvest retention patches (HARVEST). Habitat structure and composition characterising HARVEST sites are found in **Appendix 4.9.1** in comparison to both CONTROL and POSTFIRE sites.

4.4.2 Small mammal trapping design

Live-trapping was conducted in 2013 from July 23rd to August 15th, as well as from June 1st to August 21st, in 2014. We trapped over three consecutive nights and days, checking the traps twice a day (early morning and late afternoon) as small mammals are mostly nocturnal except for American red squirrels which start foraging just after sunrise (Merritt 1981; Whitaker 2004; Smith 2012). Each site was monitored with this trapping regime of three consecutive nights during one session over the summer 2013 (sampling session 1) and three sessions over the summer 2014 (3 nights in each of June - sampling session 2, July - sampling session 3, and August - sampling session 4). Trapping sessions in a given site were separated by 27 days over the summer 2014.

Sciurid species were trapped using Tomahawk (Tomahawk Live Trap llc ®) live-traps baited with peanut butter and apple pieces, providing food and water to trapped individuals. Cotton batting was also added in each trap to provide shelter. We established one transect line of six live-traps per site with a distance of 10 m between traps. Transects were 50 m long to accommodate our smallest retention and remnant patches. American red squirrels were also sampled using point and playback counts. These consisted of first listening for squirrels for 10 minutes after having checked traps and released any trapped individuals. Then, we called individuals using recorded red squirrels calls over a period of 10 min and noted any response to these playback calls (Chavel et al. 2017).

Cricetine species were trapped using Sherman (H.B. Sherman Traps, Inc. ®) live-traps supplied with peanut butter, apple pieces, and cotton batting. At each site, we established a trapping grid of 4 x 4 traps with a distance of 5 m between traps.

We observed incidental captures of amphibians and lethal captures of small mammals in pitfall traps deployed to sample arthropods (i.e. environmental data - see below), which allowed us to include soricids in subsequent analyses. We used 26 cl pitfall traps half-filled with salty water in which odourless soap was dissolved. Four pitfall traps were placed in each site, forming a 20 m-long square grid. In 2013, pitfall traps were checked the morning after three consecutive trapping nights. During the 2014 trapping sessions, pitfall traps were checked on three consecutive mornings. Trapping grids and transect lines were centred on each site (**Figure 4.2**).

Individuals captured alive were pit-tagged (Biomark ®), identified to sex and age using visual characteristics. All live individuals were subsequently released. Dead individuals were stored in a sealed plastic bag to confirm species identification according to tooth patterns and other cranial characteristics (Lupien 2001, 2002; Fauteux et al. 2014).

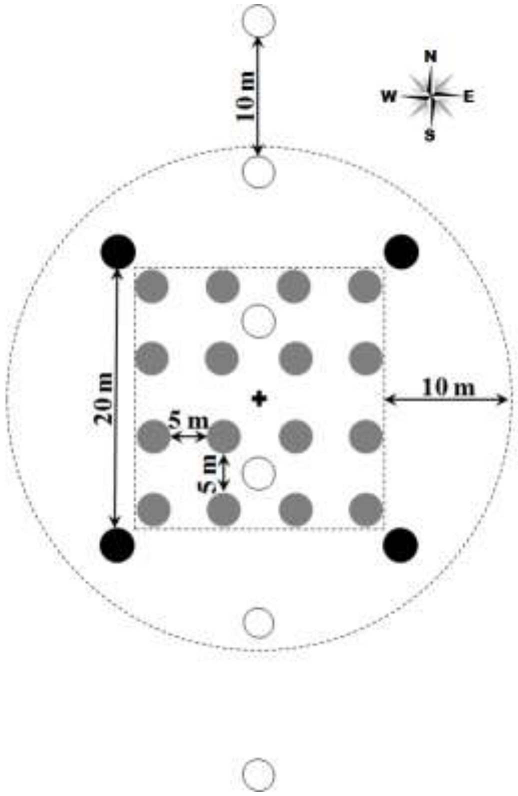

Figure 4.2 Schematic representation of a sampling site. The black cross (✚) represents the centre of all sampling plots where all weather variables were recorded. White circles (○) represent one Tomahawk live-trap, grey circles (●) represent one Sherman live-trap, black circles (●) represent one arthropod pitfall trap, the dotted square represents the quadrat in which tree and snag densities were recorded as well as volumes of downed woody debris, while the dotted circle represents one plot in which canopy cover and tree stand age were recorded. The presence of deciduous trees was assessed from the grid centre as well as 4 other points 15 m away from the grid centre and located at each cardinal point.

Shrews captured in Sherman live-traps were excluded from our analyses for two main reasons. First, most soricid species potentially found in the study area are too light to trigger the traps. Only heavier individuals could be caught which means that we could only sample a portion of the population. Secondly, identifying some species such as masked shrews (*Sorex cinereus*) and pygmy shrews (*S. hoyi*) is often impossible unless measuring tooth pattern and other cranial characteristics (Nagorsen 1996).

We considered each Sherman and Tomahawk trap as providing an effort of one trap night, except traps which were accidentally sprung and were consequently noted as providing an effort of 0.5 trap night (Nelson and Clark 1973). Likewise, all pitfall traps were considered as providing an effort of one trap night, unless dug out.

All manipulations adhered to the Canadian Council on Animal Care Guidelines and were approved by the Institutional Animal Care Review Committee, Université du Québec en Abitibi-Témiscamingue (UQAT, permit no. 2013-04-02).

4.4.3 Environmental data

4.4.3.1 Stand scale microhabitat associations

Microhabitats were characterised at the level of the Sherman grid (15 x 15 m). All sampling plots were centred on a single point (**Figure 4.2**), from where all weather variables were also recorded. Stand age (AGE) was obtained by coring ten of the largest live trees located within a plot 30 m in diameter. Core samples were extracted with a 400 x 5.15 mm increment borer and stand age was measured by counting growth rings on sanded samples through an Olympus SZX12 binocular (90-fold magnification).

Canopy cover (CANCOV) was measured using hemispherical photographs taken with a Nikon CoolPix 990 camera with a fisheye lens FC-E8 and using the “Threshold” tool on Adobe Photoshop Element 2.0 (Adobe Systems 2002). Nine photographs were taken per site, one in the grid centre, four at each grid corner, and four 10 m away from each grid side. Photographs were taken at both 20 and 150 cm off the ground (CANCOV 20 and CANCOV 150) as we expected sciurid species to be more impacted by the tree canopy, whereas we expected other small mammals to react to both tree and understory canopy. Both canopy covers were expressed in percentages (%).

We identified all tree species observed from the site centre as well as from four other points located 15 m away from it and facing each cardinal point. This measure was primarily taken to record the presence of deciduous trees (DECID - binary variable).

We counted all large standing trees (live and dead) within a 15 x 15 m quadrat. We defined large trees and snags as those with a diameter at breast height (dbh) equal or larger than 10 cm (Déry and Leblanc 2005). All snags shorter than 1.2 m were excluded from the count. We then obtained the total density of large live trees (TREEDENS) and the density of large snags (SNAGDENS). All values were expressed as a number of stems per hectare (stems.ha^{-1}). The volume of downed woody debris (DWD) was inventoried in a 15 m-sided triangle (Harvey and Brais 2007), following the methods and the decay classes described in Fauteux et al. (2012). Volumes of logs were calculated using the conic-paraboloid formula (Fraver et al. 2007) and were expressed in cubic meters per hectare (m^3.ha^{-1}).

Night temperatures were measured at each site by setting data loggers (Hydrochron iButton®, Maxim Integrated, San Jose, CA, USA) 1 m off the ground, in a shaded area, protected from the wind. Data loggers were set to record temperatures (°C) every 4 hours. Temperatures were recorded for every trapping session except for June 2014 due to technical problems. We only considered mean night temperatures that were obtained by separating nighttime from daytime temperatures according to the sunrise and sunset times (http://www.sunrise-and-sunset.com). Mean night temperature was then calculated for each trapping night. Night rainfall (mm) was measured daily using rain gauges.

Moon illumination was expressed as the percentage of visible moon. This environmental variable was determined according to the lunar calendar found on http://time.unitarium.com/moon/where.html, and by setting the UTC time at one hour after sunset on the day when traps were set (i.e. when nocturnal small mammals are most active).

Biomasses of arthropods (ARTHRO) and terrestrial molluscs (MOLLUSC), expressed in grams, were determined by sampling invertebrate communities at each site and each capture session, using the four pitfall traps described above and collecting their contents on a daily basis. Invertebrates were dried in a kitchen paper towel before being weighed.

4.4.3.2 Landscape association with the amount of forest at different scales

Species encountered at our study sites have been reported in different forest cover types, even though some of the species prefer old-growth or coniferous forests (Merritt 1981; Whitaker 2004; Smith 2012). As a consequence, we focused on the total amount of forest located around capture grids, regardless of forest composition and tree density. Forest cover was obtained using an ArcGIS layer updated in 2013 produced by the Ministère du Développement durable, de l’Environnement et de la Lutte contre les changements climatiques (MDDELCC) (Bissonnette and Lavoie 2015). Forested areas were defined as patches of trees with a minimum area of 0.1 ha, a canopy cover ≥ 10%, a stand height ≥ 2 m, and a stand age ≥ 20 years-old.

Percent area covered by forest was measured in a total of 100 concentric buffers defined around the centre of each capture grid, using all radii with increments of 50 m, from 50 m up to 5 km. We chose a maximum radius of 5 km because the two most vagile species encountered in our study sites (i.e. northern flying squirrels - *Glaucomys sabrinus* - and American red squirrels) may be impacted by landscape disturbances both within and beyond their home range (Larsen and Boutin 1994; Bowman et al. 2002; Ritchie et al. 2009). Grid resolution of the map (30 X 30 m) was kept constant among radii.

4.4.4. Statistical analyses

4.4.4.1. Stand scale microhabitat associations

We used dynamic single-species occupancy models to estimate the probabilities of initial site occupancy (ψ), site extinction (ε), site colonisation (γ), and detection (*p*) of each species (MacKenzie et al. 2003). We considered the populations of small mammals to be open because 1) cricetine juveniles are usually weaned and independent at about three weeks (Merritt 1981), and 2) juvenile American red squirrels begin to disperse within the first month after leaving the family den (Larsen and Boutin 1994; Steele 1998). All parameters were estimated with maximum likelihood using the *unmarked* package (Fiske and Chandler 2010) in R (version 3.0.1, R Development Core Team 2015).

We considered two time frames to analyse data, each one consisting of two primary periods. The first time frame accounts for between-year variations, and included data collected in late July-August 2013 (sampling session 1) and during August 2014 (sampling session 4). The second time frame accounts for within-year variations, and included data collected in July 2014 (sampling session 3) and again in August 2014 (sampling session 4). Data obtained in June 2014 (sampling session 2) were excluded as detections of most species were too low to obtain a reliable estimate of initial occupancy. In any of these two time frames, we considered a total of 67 models (**Appendix 4.9.2**). The probabilities of initial site occupancy, site colonisation, and site extinction were allowed to vary, one at a time, according to a set of seven hypotheses, and the detection probability was allowed to vary with one of three scenarios (**Table 4.1**).

We used an information-theoretic approach based on Akaike's Information Criterion for small samples (AIC_c) to compare candidate models (Burnham and Anderson 2002). The goodness-of-fit of occupancy models was tested by performing 10 000 bootstraps on the most global model using an extension of the MacKenzie and Bailey (2004) goodness-of-fit test for occupancy models, which was implemented in the *AICcmodavg* package (Mazerolle 2015). Slight overdispersion was suggested for all sets of analyses ($\hat{c}$ = [1.16; 2.04]) but one (i.e. *M.gapperi*, within-year analyses - $\hat{c}$ = 0.89). Multimodel inference was conducted on each variable that was contained in the top models to compute 95% unconditional confidence intervals and model-averaged predictions based on the entire set of candidate models.

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Table 4.1 List of hypotheses tested tested with 67 dynamic single-species occupancy models to analyse detection data of American red squirrel (*Tamiasciurus hudsonicus*), southern red-backed vole (*Myodes gapperi*), and masked shrew (*Sorex cinereus*), sampled in black spruce forest of northwestern Quebec.

Model structure	**Predictions**	**References**
Scenarios applied independently on either one of the parameters of initial occupancy (ψ), colonisation (γ), and extinction (ε)		
(.)	Probabilities of occupancy, colonisation, and extinction are constant.	N/A
(TYPE)	No differences in either initial occupancy or colonisation probabilities among site types.	Green-tree retention patches should act as refuges and sources of dispersers (Leblanc and Pouliot 2011; Robinson et al. 2013).
(EARLYDWD + LATEDWD)	Probabilities of occupancy and colonisation increase with increasing volumes of downed woody debris.	Small mammals use woody debris as cover, feeding grounds, and even as structures facilitating their movements (Moseley et al. 2008; Sullivan and Sullivan 2012; Craig et al. 2014).

(suite)

Model structure	**Predictions**	**References**
(CANCOV : LATEDWD)	Canopy cover mitigates the effects of late-decayed woody debris on probabilities of occupancy and colonisation.	Mammalian association with late-decayed downed woody debris can be partially released depending on the canopy cover (Fauteux et al. 2012).
(DECID)	Probabilities of occupancy and colonisation increase with the presence of broadleaf trees.	Some hypogeous fungi are related to the presence of broadleaf trees (Crites and Dale, 1998). Boreal small mammals either have a diet primarily composed of hypogeous fungi (Orrock and Pagel 2002) or opportunistically feed on them (Currah et al. 2000; Pyare and Longland 2001).
(CANCOV)	Probabilities of occupancy and colonisation increase with canopy cover.	Small mammals in our study sites are associated to features of old-growth forests (McLaren et al. 1998; Pearce and Venier 2005; Smith 2012).

(suite)

Model structure	**Predictions**	**References**
(CANCOV^2)	Probabilities of occupancy and colonisation increase with canopy cover up to an optimal value, and then decrease.	Old-growth forests are characterised by canopy openings favourable for small mammals (Crête et al. 1995).
(TREEDENS + SNAGDENS)	Probabilities of occupancy and colonisation increase with the presence of large trees and snags.	Sciurid species benefit from the presence of large snags as well as large live trees (Carey 1995; Darveau and Desrochers 2001; Vanderwel et al. 2010).
Set of scenarios applied on the detection parameter (*p*)		
(.)	Detection probabilities are constant.	N/A

(suite)

Model structure	**Predictions**	**References**
(SESSION + METHOD) *	For cricetine species only, detection probabilities increase from 2013 to 2014. Within-year (from July to August 2014), detection of all species (except sciurids) increases.	With an increasing density during a breeding season, there is a greater chance to detect at least one individual. Some cricetine species also cycle over four years (e.g. red-backed voles, Fauteux et al. 2015). We sampled individuals during the low and increasing phases of this cycle. Cyclicity in sciurids and soricids is unknown, but sciurids show no within-year change in their detection probability (Chavel et al. 2017).
	Detection probabilities of American red squirrels are not affected by the sampling technique.	Detection of American red squirrels is similar using either live-trapping, playback or point counts (Chavel et al. 2017).

(suite)

Model structure	Predictions	References
(RAIN + TEMP + MOON) **	Detection probabilities increase with rainfall.	Some small mammals are more active during rainy and warm nights (Vickery and Bider 1981).
	Detection probabilities of cricetine and soricid species increase with average night temperature up to 20 °C.	Small mammals benefit from positive ambient temperature below 20 °C, i.e. temperatures when body water loss becomes a severe issue (Getz 1961; McManus 1974; Cherry and Verner 1975).
	Detection probabilities of cricetine and soricid species decrease with increasing moon illumination.	Nocturnal small mammals are more likely to be predated during bright nights (Clarke 1983; Orrock et al. 2004).
(ARTHRO + MOLLUSC)	Detection probabilities (especially of insectivorous soricids) increase with the amount (weight) of ground-dwelling arthropods and to a lower extent, to the amount of molluscs.	Small mammals are either insectivorous or feed opportunistically on invertebrates (Merritt 1981; Whitaker and French 1984; Bellocq and Smith 1994; Pretzlaw et al. 2006).

(suite)

Notes: Covariate acronyms: Arthro, weight of ground-dwelling arthropods; CanCov, canopy cover taken either 150 cm off the ground to analyse squirrel data or 20 cm off the ground to analyse data from all other species (linear form); CanCov^2, canopy cover (quadratic form); Decid, presence of deciduous trees; EarlyDwd, early decayed downed woody debris; LateDwd, late decayed downed woody debris; Method, methods used to detect individuals (live-trapping, live-trapping + playback count, live-trapping + point count, live-trapping + point count + playback count); Mollusc, weight of terrestrial molluscs; Moon, percentage of moon illumination during each trapping night; Rain, rainfall measured after each trapping night; Session, trapping session (i.e. primary period - August 2013, July 2014, August 2014); SnagDens, density of snags with a dbh larger than 10 cm; Temp, average night temperatures for each trapping night; TreeDens, density of live trees with a dbh larger than 10 cm; Type, site type (control, post-fire remnant patch, harvest retention patch). Parameters followed by (.) indicate that they are constant. (*) Method was only used to analyse detection data of American red squirrels (*Tamiasciurus hudsonicus*). (**) Moon was not used to analyse detection of American red squirrels.

4.4.4.2. Landscape association with the amount of forest at different scales

We evaluated the relationship between species occurrence and forested areas (i.e. level of area-sensitivity) at the spatial scale used to measure habitat availability. Three parameters of species occurrence, namely initial site occupancy, site colonisation, and site extinction probabilities, were successively and independently evaluated. We used top-ranking models defined for each species in the first set of analyses (stand scale microhabitat associations - see above) to build on the following landscape modelling. We allowed initial site occupancy (ψ), site colonisation (γ), and site extinction (ε) to vary with the amount of forested areas measured in each concentric buffers around capture grids. Each of these three parameters was analysed by varying the amount of forested area in concentric buffers while holding the other parameters constant.

To quantify the response to forested areas (area sensitivity), we extracted the β estimates associated with the amount of forested area for each parameter (ψ, γ, ε), from each dynamic model. For each parameter, we used the βestimates of the amount of forested area in four candidate models (see below). To avoid correlations among consecutive measures of forested areas, we selected a series of β estimates, starting at the β estimates associated with the amount of forested area in the two smallest radii (0.050 and 0.100 km). We then selected β estimates associated with the amount of forested area in each radius that was the sum of the two preceding radii, i.e. radii of 0.150 km, 0.250 km, 0.400 km, 0.650 km, 1.050 km, 1.700 km, 2.750 km, and 4.450 km. We used this series of ten β estimates to in four candidate linear regressions.

The first regression allowed the dependent variable to be constant, and this model tested whether β estimates associated with the amount of forested area were independent of the radii of the concentric circles where forested area was measured. The second regression tested whether there was a linear relationship between β

estimates and circle radii. The third regression tested a quadratic relationship, assuming an optimal radius for patterns of area sensitivity. Finally, a logarithmic relationship between the dependent variable and the circle radii was tested according to a fourth regression using the log of circle radii and hypothesising that β estimates become more stable at larger scales. Parameters of the regressions were estimated by maximum likelihood using generalised least squares with an autoregressive first-order correlation structure using the nlme package (Pinheiro et al 2017). We conducted model selection and multimodel inference based on Akaike's Information Criterion for small samples (AIC_c) to compare these four candidate models (Burnham and Anderson 2002).

4.5 Results

4.5.1 Small mammal survey

We captured a total of 676 small mammals (280 rodents and 396 shrews - **Appendix 4.9.3**) during the trapping sessions of 2013 and 2014 with a total effort of 11055 Sherman trap-nights, 4229.5 Tomahawk trap-nights, and 2828.5 pitfall trap-nights. Three species represented 85.5% of our total captures: masked shrew (*S. cinereus* - 52.4%), southern red-backed vole (*M. gapperi* – 23.1%), and American red squirrel (*T. hudsonicus* - 10.0%). Other species that were sporadically trapped included, in decreasing abundance, pygmy shrew (*S. hoyi*), deer mouse (*P. maniculatus*), northern flying squirrel (*G. sabrinus*), eastern heather vole (*Phenacomys ungava*), Arctic shrew (*S. arcticus*), northern short-tailed shrew (*Blarina brevicauda*), field vole (*Microtus pennsylvanicus*), and smoky shrew (*S. fumeus*).

We captured twice as many small mammals in August 2014 as compared to August 2013 (number of individuals per 100 trap nights: $No/100TN_{session1}$ = 3.11, $No/100TN_{session4}$ = 7.08). More individuals were also caught from June to August

2014 (No/100TN$_{session2}$ = 0.63, No/100TN$_{session3}$ = 4.09, No/100TN$_{session4}$ = 7.08). We present species-specific detection results in **Appendix 4.9.3**. A similar pattern could be observed for the number of sites occupied by small mammals (i.e, model-averaged site occupancy [ψ] * number of sites) with an estimated 17 sites occupied in session 2, 52 sites occupied in session 3, and 56 occupied in session 4.This pattern was consistent among site types (**Appendix 4.9.4**).

4.5.2 Stand scale microhabitat associations

Detection data were too scarce for the algorithms to converge, except for three species, namely *T. hudsonicus*, *M. gapperi*, and *S. cinereus*. Moreover, between-years (August 2013, August 2014) and within-year (July 2014, August 2014) analyses could only be conducted for *M. gapperi*. Only within-year analyses could be carried out on both *T. hudsonicus* and *S. cinereus*.

For southern red-backed voles, detection probability varied with explanatory variables, but none of the variables were related to microhabitat. This held true in both analyses conducted on this species (i.e., between-years and within-year). The top-ranked model for between-year data had an Akaike weight of 0.31, and the model allowed the initial site occupancy probability to vary with the interaction between the canopy cover taken at 20 cm off the ground and the volume of LATEDWD (**Table 4.2**). In this model, the detection probability was allowed to vary with the trapping session. This latter variable produced the only effect on detection probability, with an increase from August 2013 to August 2014 (model-averaged effect size on logit scale: 2.12, 95% CI: [0.85, 3.39]; **Figure 4.3**).

Table 4.2 Ranking of dynamic single-species occupancy models for each of the three small mammal species based on their relative support (w_i). Two data sets (between-years and with-year) were analysed for southern red-backed voles (*Myodes gapperi*). Only models with a **Δ** < 4 are included in this table.

CANDIDATE MODELS	K	QAICc	Δ	Weight (ω)
M. gapperi **- Between-year variations (August 2013, August 2014)**				
ψ(LateDwd:CanCov)γ(.)ε(.) p(Session)	9	231.18	0.00	0.31
ψ(.)γ(TreeDens+SnagDens)ε(.) p(Session)	8	232.20	1.02	0.19
ψ(EarlyDwd+LateDwd)γ(.)ε(.) p(Session)	8	232.65	1.47	0.15
ψ(.)γ(.)ε(.)p(Session)	6	233.32	2.14	0.11
ψ(.)γ(EarlyDwd+LateDwd)ε(.) p(Session)	8	235.04	3.86	0.05
M. gapperi **- Within-year variations (July 2014, August 2014)***				
ψ(Type)γ(.)ε(.) p(Temp+Rain+Moon)	9	303.79	0.00	0.77
S. cinereus **- Within-year variations (July 2014, August 2014)**				
ψ(CanCov)γ(.)ε(.) p(Arthro+Mollusc)	8	352.60	0.00	0.21
ψ(.)γ(.)ε(.)p(.)	5	353.37	0.77	0.14

(suite)

CANDIDATE MODELS	**K**	**QAICc**	**Δ**	**Weight (ω)**
ψ(CanCov)γ(.)ε(.)*p*(Session)	7	353.62	1.02	0.13
ψ(.)γ(EarlyDwd+LateDwd)ε(.) *p*(Arthro+Mollusc)	9	355.35	2.75	0.05
ψ(.)γ(.)ε(.)*p*(Session)	6	355.75	3.15	0.04
ψ(TreeDens+SnagDens)γ(.)ε(.) *p*(Session)	8	355.82	3.225	0.04
ψ(TreeDens+SnagDens) γ(.)ε(.)*p*(Arthro+Mollusc)	9	355.83	3.24	0.04
***T. hudsonicus* - Within-year variations (July 2014, August 2014)**				
ψ(.)γ(.)ε(.)*p*(.)	5	165.49	0.00	0.24
ψ(.)γ(CanCov)ε(.) *p*(Arthro+Mollusc)	8	166.16	0.67	0.08
ψ(CanCov)γ(.)ε(.) *p*(Arthro+Mollusc)	8	166.29	0.80	0.08
ψ(CanCov^2)γ(.)ε(.) *p*(Arthro+Mollusc)	8	166.36	0.87	0.07
ψ(.)γ(.)ε(CanCov) *p*(Arthro+Mollusc)	8	166.62	1.13	0.06

(suite)

CANDIDATE MODELS	**K**	**QAICc**	**Δ**	**Weight (ω)**
ψ(CanCov)γ(.)ε(.) *p*(Session+Method)	8	167.13	1.64	0.05
ψ(.)γ(Decid)ε(.) *p*(Arthro+Mollusc)	8	167.31	1.82	0.05
ψ(.)γ(.)ε(CanCov^2) *p*(Arthro+Mollusc)	8	167.54	2.05	0.40
ψ(Decid)γ(.)ε(.) *p*(Arthro+Mollusc)	8	167.78	2.29	0.04
ψ(.)γ(.)ε(CanCov) *p*(Session+Method)	8	167.87	2.37	0.03
ψ(.)γ(CanCov)ε(.) *p*(Session+Method)	8	167.88	2.39	0.03
ψ(Decid)γ(.)ε(.) *p*(Session+Method)	8	168.19	2.70	0.03
ψ(.)γ(CanCov)ε(.)*p*(Rain+Temp)	8	168.43	2.94	0.03

(suite)

Notes: Covariate acronyms: Arthro, weight of ground-dwelling arthropods; CanCov, canopy cover taken either 150 cm off the ground to analyse squirrel data or 20 cm off the ground to analyse data from all other species (linear form); CanCov^2, canopy cover (quadratic form); Decid, presence of deciduous trees; EarlyDwd, early decayed downed woody debris; LateDwd, late decayed downed woody debris; Method, methods used to detect American red squirrels (live-trapping, live-trapping + playback count, live-trapping + point count, live-trapping + point count + playback count); Mollusc, weight of terrestrial molluscs; Moon, percentage of moon illuminated during each trapping night; Rain, rainfall measured after each trapping night; Session, trapping session (i.e. primary period - August 2013, July 2014, August 2014); SnagDens, density of snags with a dbh larger than 10 cm; Temp, average night temperatures for each trapping night; TreeDens, density of live trees with a dbh larger than 10 cm; Type, site type (control, post-fire remnant patch, harvest retention patch). Parameters followed by (.) indicate that they are constant. whereas (*) indicates that model adjustment was not necessary (c-hat < 1) and that consequently, we relied on the AICc instead of the QAICc.

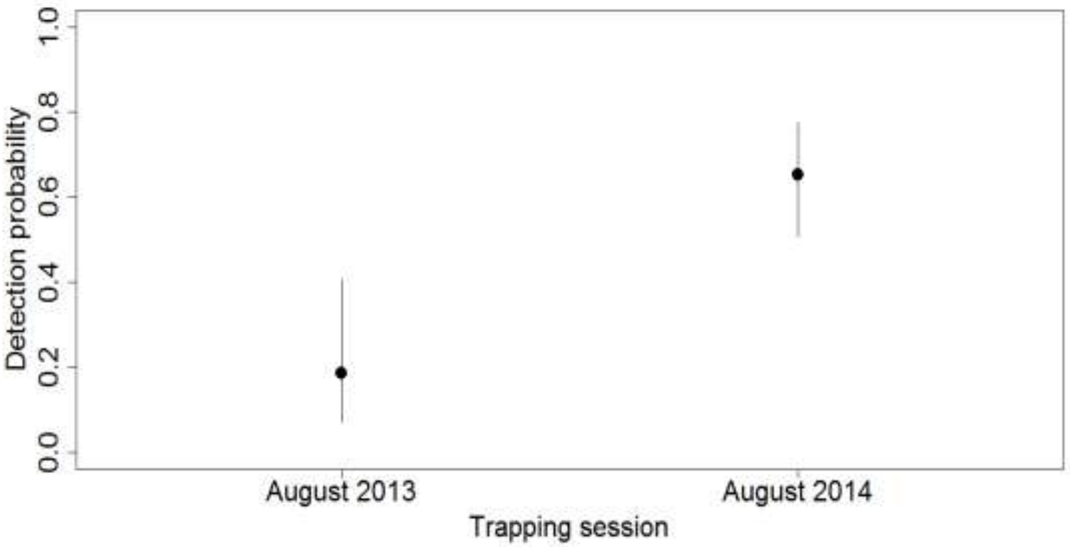

Figure 4.3 Between-years model-averaged detection probabilities of southern red-backed voles (*Myodes gapperi*) over the trapping sessions in August 2013 and August 2014. Error bars represent 95% unconditional confidence intervals.

The top-ranked model for within-year data allowed the initial site occupancy probability to vary with site type, whereas the detection probability included the effect of moon illumination, rain that fell within 24 h prior to sampling, and average night temperature. This model had 77% of the weight (**Table 4.2**). Multimodel inference showed that all covariates had only marginal support, except for the average night temperature. Indeed, detection probability of southern red-backed voles decreased with increasing average night temperature (model-averaged effect size on logit scale: -1.90, 95% CI: [-3.59, -0.22]; **Figure 4.4a**). Detection probability marginally decreased with moon illumination (model-averaged effect size on logit scale: -1.09, 95% CI: [-2.29, 0.11]; **Figure 4.4b**) and marginally increased with rainfall (model-averaged effect size on logit scale: 1.22, 95% CI: [-0.28, 2.71]; **Figure 4.4c**). Finally, southern red-backed voles occurred as often in control sites as in post-fire retention patches (model-averaged effect size of POSTFIRE compared to CONTROL on logit scale:-0.06, 95% CI: [-1.71, 1.59]). The species occurred marginally less often in green-tree retention patches (model-averaged effect size of HARVEST compared to CONTROL on logit scale: -1.89, 95% CI: [-4.24, 0.45]; **Figure 4.4d**)

The top-ranked model for the within-year data of masked shrews accounted for 21% of the weight, and it allowed the initial site occupancy probability to vary with the canopy cover taken 20 cm above the ground (**Table 4.2**). However, the null model followed this model closely. Unsurprisingly, multimodel inference revealed that none of the covariates had any support. Finally, the null model ranked highest for the within-year data of American red squirrels (**Table 4.2**), indicating that none of the variables influenced any of the parameters.

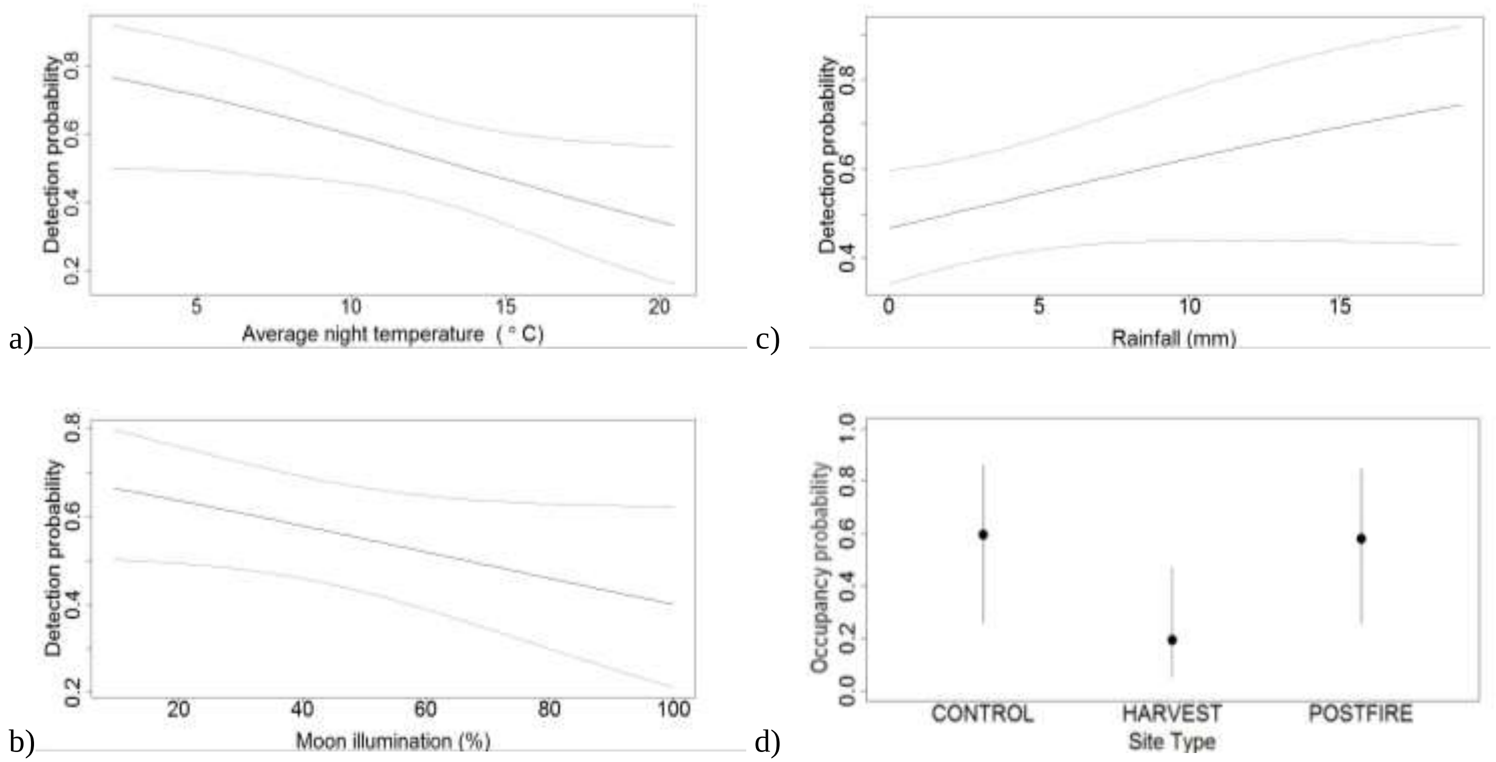

Figure 4.4 Within-year model-averaged detection probabilities of southern red-backed voles (*Myodes gapperi*), under different scenarios of night average temperature (a), rainfall (b), and moon illumination (c). Dotted lines represent 95% unconditional confidence intervals. Within-year occupancy probabilities of southern red-backed voles in old-growth forests (CONTROL), post-fire remnant patches (POSTFIRE), and both linear cutblock separators and green-tree retention stands pooled together (HARVEST) (d). Bars represent 95% unconditional confidence intervals.

4.5.3 Landscape association with the amount of forest at different scales

At a local scale, the amount of forest rapidly dropped from 63% to 40%, and then slowly rose to plateau at 56%. The remaining 44% included disturbed habitat, different bodies of water and human infrastructures such as roads and mines (**Figure 4.5**).

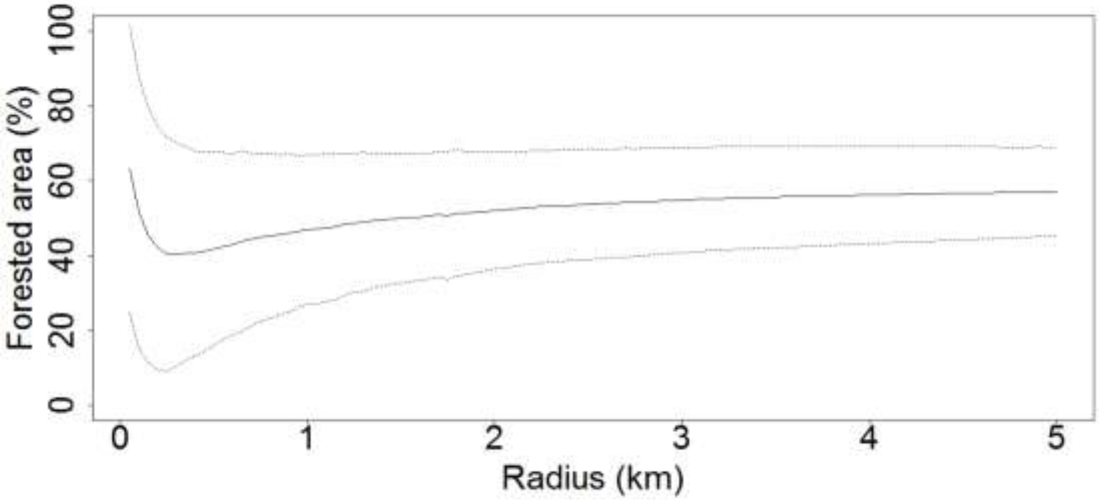

Figure 4.5 Percentage of forest around capture grids (n = 60) in concentric circular areas, with a radius varying from 0.05 to 5 km. Dotted lines represent 95% confidence intervals around the average values.

A total of 1 200 species-radius dynamic models ((3 parameters [ψ, γ, or ε] x 100 radii x 3 species captured within a year) + (3 parameters x 100 radii x 1 species captured between-years)) were built to observe changes in occupancy according to the spatial scale used to measure forested area. All models that allowed the probability of occupancy or the probability of site colonisation to vary with the amount of forest converged. In contrast, out of 400 models allowing site extinction to vary with forested areas, 83 models (12 and 71 models for *T. hudsonicus* and *S. cinereus*, respectively) produced unstable beta estimates with large SE, likely due to the scarcity of site extinction events for these two species (**Figure 4.6**). By considering a 90% CI (instead of the more conservative 95% CI), a marginal negative area-sensitivity was observed for the initial site occupancy patterns of both masked shrews (relatively constant at all radii, within-year) and southern red-backed voles (at radii greater than 1 km, between-year only; **Figures 4.6, 4.7**). Although we found no evidence of an effect of area-sensitivity on site extinction for red-backed voles, we found evidence (using a 90% CI) of marginal positive area-sensitivity in site colonisation for this species at small scales (between-years).

The top-ranked regression of beta estimates for between-year initial site occupancy by southern red-backed voles assumed a logarithmic relationship of area-sensitivity (90% of the weight). Multimodel inference indicated beta estimates increased with decreasing radii (model-averaged effect size on probability scale: 1.27, 95% CI: [0.29, 2.25], **Figures 4.6, 4.7**). On the other hand, the top-ranked regression for within-year initial site occupancy by masked shrews allowed a quadratic relationship (74% of the weight), but this relationship was only marginally supported and the effect itself was very low (model-averaged effect size on probability scale: 0.22, 95% CI: [-0.10, 0.54], **Figures 4.6, 4.7**).

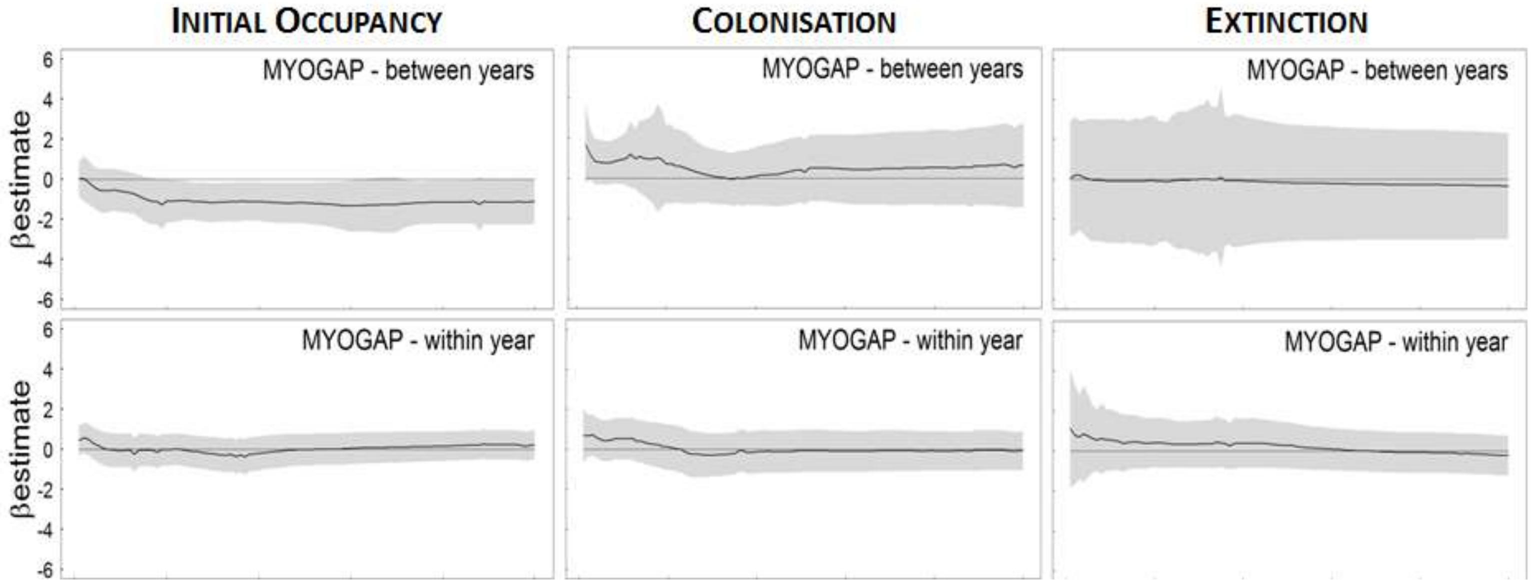

Figure 4.6 Area-sensitivity patterns of four small mammals species. Betas estimated for the amount of forested area contained in concentric circles around trapping grids were extracted from dynamic single species occupancy models where each parameter (occupancy ψ, colonisation γ, and extinction ε) was in turn allowed to vary with the amount of forested area. Shaded area corresponds to the 95% confidence intervals around beta estimates. Acronyms: MYOGAP, southern red-backed vole; SORCIN, masked shrew; TAMHUD, American red squirrel (*Tamiasciurus hudsonicus*); N/A, non-applicable.

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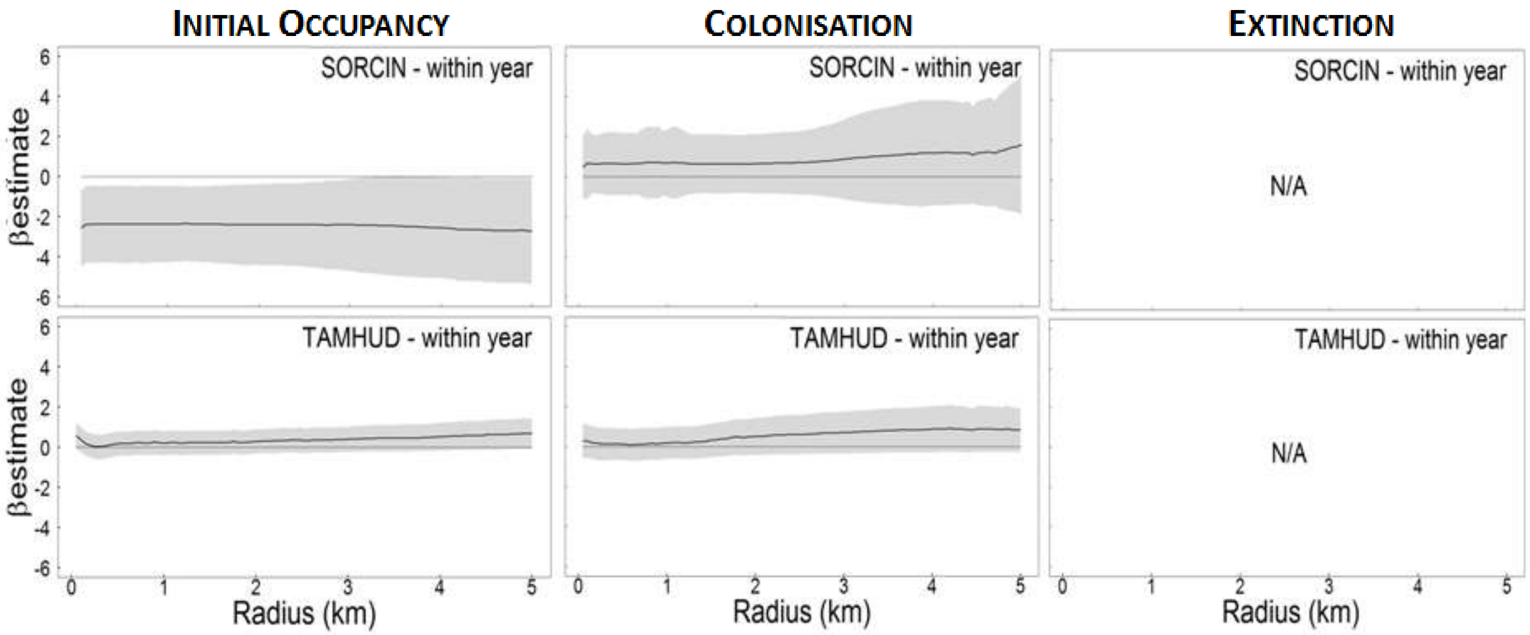
INITIAL OCCUPANCY
COLONISATION
EXTINCTION
SORCIN - within year
SORCIN - within year
SORCIN - within year
N/A
TAMHUD - within year
TAMHUD - within year
TAMHUD - within year
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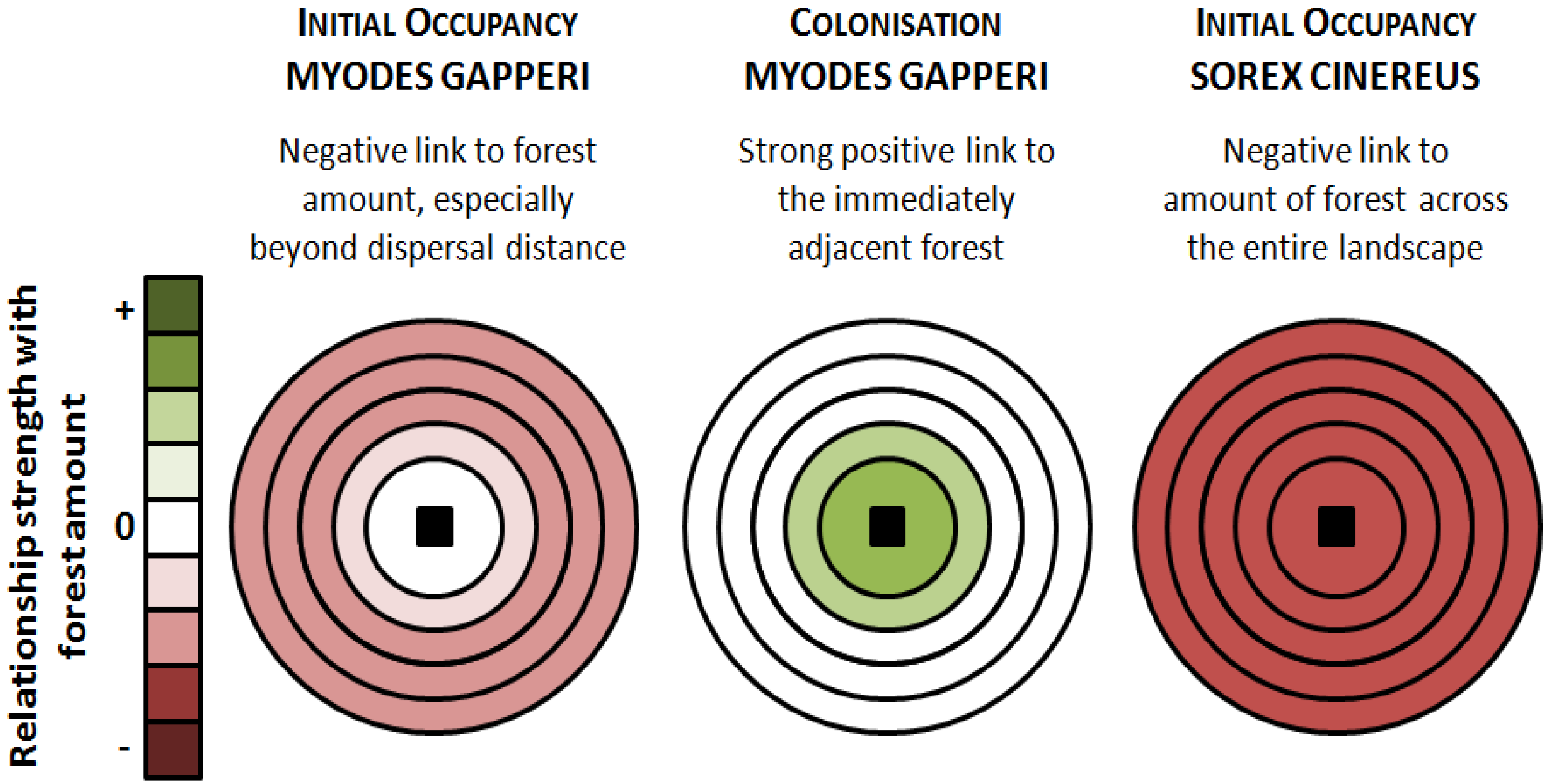

Figure 4.7. Schematic patterns of area-sensitivity by two small mammals species (southern red-backed vole - *Myodes gapperi* - and masked shrews - *Sorex cinereus*), measured in concentric circles extending from 1 to 5 km centred on trapping grids.

4.6 Discussion

The aim of the present study was to model initial site occupancy, site colonisation and site extinction of North American boreal small mammals as a function of the total amount of forest present in the surrounding landscape while controlling for local habitat conditions. The importance of both local and landscape scales in predicting species occurrence in boreal forest landscapes is being increasingly documented (Drapeau et al. 2000, 2016; Brotons et al. 2003; Mönkkönen et al. 2014). However, to our best knowledge, this study is the first to examine possible relationships between area-sensitivity and demographic parameters such as site colonisation and site extinction. To do so, we used an innovative statistical approach that accounts for imperfect detection probability. Furthermore, by highlighting a negative rather than a positive area-sensitivity pattern on a vertebrate, this study strongly suggests that a bottom-up process hierarchically structured around local scale density-dependence and landscape scale habitat amount can drive small mammals area-sensitivity in disturbed boreal landscapes.

4.6.1 Stand scale microhabitat associations

New clear-cutting strategies have been proposed over the past years in an attempt to better emulate the structures left by wildfires at both the stand and landscape scales (Niemelä 1999; Bergeron et al. 2007). According to ecosystem-based management, all the vegetation structure features and legacies critical for the occurrence of small mammals should be encountered within the same range of variability in all types of our study sites (Bergeron et al. 2007). Moreover, some small mammal species such as voles remain relatively unaffected by patch geometry as they have been reported to use patch-cut interior and are edge-tolerant species (Harper et al. 1993; Hayward et al. 1999; Tallmon and Mills 2004). We first hypothesised that at the local scale, the occurrence of North American boreal small mammals in remnant patches would mainly respond to their structural attributes rather than to site disturbance origin (wildfire vs. harvesting). Despite some minor differences, we found several similarities in the vegetation structure between old post-fire forest remnants and post-harvest green-tree retention patches. Accordingly, initial site occupancy patterns of small mammals did not vary with the landscape origin in which these remnants were embedded despite marginally lower initial site occupancy in post-harvest patches (HARVEST) for the southern red-backed vole. Unlike past studies that found associations of small mammals with habitat elements, occupancy patterns did not strongly vary with stand-level habitat variables most likely due to the limited range of variation of the vegetation structure in our study sites (Moseley et al. 2008; Sullivan and Sullivan 2012; Craig et al. 2014). Top-models highlighted the importance of environmental variables on detection probability. Indeed, the detection probability of southern red-backed voles varied mainly with climatic and light conditions propitious to nocturnal activities (e.g. foraging, searching for mates) as it was previously shown to a lower extent by other studies (McManus 1974; Vickery and Bider 1981).

4.6.2 Cyclicity of small mammals

Populations of some small mammal species show cyclic patterns (Boonstra and Krebs 2012; Krebs 2013), and in our study sites, populations of southern red-backed voles cycle over an average of four years (Cheveau et al. 2004; Fauteux et al. 2015). According to Fauteux et al. (2015), the years of 2013 and 2014 corresponded to the low phase of the population cycle and the phase of increase, respectively. The increase in the total number of all small mammals over the late-summer trapping session of these two consecutive years, from 2013 to 2014, suggests continuation of these previously documented small mammal cycles.

Sampling southern red-backed voles during the low and the increasing phases of the cycle implies that: 1) patterns of initial site occupancy might reveal local conditions critical for the species because at low densities, individuals will remain where the most needed resources occur (Fretwell and Lucas 1969; Hayward et al. 1999; Andreassen and Ims 2001), 2) patterns of site colonisation might get more obvious by the summer of the increasing phase, i.e. when populations have had time to build up to reach high densities and favour dispersal (van Horne 1983; Bondrup-Nielsen and Karlsson,1985), 3) site extinction might not be favoured. Indeed, sites with required resources are not yet over-crowded, and therefore individuals are not forced to leave such sites due to competition.

4.6.3 Area-sensitivity and small mammals

In a context of large-scale anthropogenic changes to forests (i.e. tree harvesting), testing whether small mammals are area-sensitive becomes critical, especially if they are considered reliable indicators of sustainable forest management (McLaren et al. 1998; Pearce and Venier 2005; Holloway and Smith 2011). Research on area-sensitivity has initially focused on presence-absence data of various species (mainly birds - Robbins 1979; Walk and Warner 1999; Desrochers et al. 2010) to later shift to species richness, density, and reproductive success (Donovan and Lamberson 2001; Davis 2004; Smith et al. 2011). These studies led us to hypothesise that small mammals could display scale-dependent area-sensitivity at spatial scales even greater than the one of their home range. In our study, we used an innovative approach to address the question of area-sensitivity of small mammals by using dynamic occupancy analyses to account for imperfect detection probability. Five main results emerge from our study: 1) both masked shrews and southern red-backed voles were marginally area-sensitive, whereas American red squirrel was not area-sensitive, regardless of the scale, 2) the main response was observed on initial site occupancy, whereas we found no patterns of area-sensitivity for site extinction, and only a slight response was observed on site colonisation patterns, 3) at all spatial scales, initial site occupancy decreased with an increase in the amount of available forest habitat, 4) responses observed on initial site occupancy of masked shrews were constant at all spatial scales whereas initial site occupancy of southern red-backed voles decreased with an increase in the buffer radius considered around the trapping grids and rapidly reached a plateau, and 5) there was a difference in the response depending on whether the analyses included between-years data or within-year data (i.e., analyses of southern red-backed vole data).

To our knowledge, most studies found area-sensitivity to arise as a positive relationship between habitat amount and species abundance or between habitat amount and species occurrence. Indeed, positive area-sensitivity has been recorded in butterflies (Fred and Brommer 2003; Baunerfeind et al. 2009), in amphibians and reptiles (Knutson et al. 1999; Guerry and Hunter 2002; Hager 1998), in grassland birds (Walk and Warner 1999; Davis 2004), and in forest birds (Trzcinski et al. 1999; Lee et al. 2002; Desrochers et al. 2010). Our study is one of the first to record negative area-sensitivity, i.e. species probability of occurrence at a site decreases with an increasing area of suitable habitat in the surrounding landscape. We believe that to interpret such an unexpected trend we have to consider area-sensitivity as being both a scale and density-dependent pattern. First, we considered red-backed voles which have been reported to cycle over a period of four years in sites located a few kilometres south of our study sites, and we sampled this species during the low and increasing phases of its abundance cycle (Fauteux et al. 2015). On the other hand, we also considered shrews for which there is generally no strong evidence of cyclicity, except maybe for common shrew (*Sorex araneus*) (Korpimäki et al. 2005, but see Henttonen et al. 1989 for another perspective). Long-term data on masked shrews are scarce (e.g. Fryxell et al. 1998). However, there are few reports showing masked shrews' abundance fluctuating with prey abundance (e.g. Innes et al. 1990; McCay and Storm 1997). We also observed such fluctuations in our study sites with 50% between-year and nearly 100% within-year population increases. Moreover, shrew abundance has often been reported to vary jointly with rodent abundance, although not as strong (e.g. Henttonen et al. 1989; Zub et al. 2012 in common shrews; Fryxell et al. 1998 in masked shrews). These observations concur with our own. Based on these two previous statements, we believe that the masked shrew populations we sampled were not as densely populated as they could have been. As a consequence, we considered fluctuating populations of red-backed voles sampled at low density, and potentially sparse shrew populations whereas all previous area-sensitivity studies carried out until now focused on species with relatively stable populations. We suggest that the negative trends we observed in the occupancy of both southern red-backed voles and masked shrews might be linked to the spatial distribution of individuals when local populations are at low density.

At low densities, individuals will first occupy the most suitable areas (Fretwell and Lucas 1969; Hayward et al. 1999; Andreassen and Ims 2001). Resources may be found where sampling grids are set, but with an increasing amount of suitable habitat in the surrounding landscape, the chance of detecting individuals at low density in such a grid decreases. As density increases, individuals disperse. All suitable areas become increasingly occupied, and successful sampling of species does no longer rely on chance. We hypothesise that the analysis of data covering the increasing phase and the peak of the cycle may reveal a weaker relationship between species' site occupancy and the amount of forested area. At the peak of the cycle of small mammal populations, we expect that the relationship between the initial site occupancy of a species and the amount of forested area would disappear, although this should be tested empirically. Both southern red-backed voles and masked shrews use disturbed and regenerating matrices around forested areas (Hayward et al. 1999; Fisher and Wilkinson 2005; Zwolak 2009). These environments will be more likely to be used when population size goes above the carrying capacity of a forested site. Thus, the amount of forest would no longer have an effect on their occurrence.

Although the disturbed and regenerating matrix around remnant forest sites can provide shelter to southern red-backed voles, forested areas hold habitat elements favoured by the species. Indeed, the between-year initial site occupancy pattern was negative for this species. Their between-year site colonisation pattern was positive at a local scale (radii under 500 m): the probability of individuals to disperse between the low phase and the build-up phase of their population cycle increases with a greater amount of forest in the surrounding landscape. We believe that this result highlights the importance of large amounts of forested areas within dispersal distance for southern red-backed voles when populations are building up and individuals are dispersing toward new sites. However, this result also shows that area-sensitivity cannot be studied by exclusively focusing on the effect of the habitat amount on the abundance or occurrence of a species.

Past studies have attempted to link species' life-history and strength of area-sensitivity (e.g. Henle et al. 2004; Desrochers et al. 2010; Őckinger et al. 2010), with limited results as most of these reports did not account for the scale- and density-dependence of area-sensitivity. Moreover, it is interesting to note that the three species studied had a different life-history in terms of population cycle and dispersal timing, possibly explaining why each species had its own response to the amount of habitat in the surrounding landscape. Populations of American red squirrels are not reported to fluctuate between years and individuals mostly start dispersing by the end of summer (Wauters and Dhondt 1993; Larsen and Boutin 1994; Steele 1998). For this species, we found no evidence of within-year area-sensitivity on initial site occupancy patterns. In contrast, populations of southern red-backed voles fluctuate between years and individuals start dispersing in late summer (Bondrup-Nielsen and Karlsson 1985). For southern red-backed voles, we observed between-years negative area-sensitivity on initial site occupancy but not within-year area-sensitivity. In contrast, area sensitivity was positive at small scales for between-year site colonisation. Finally, populations of masked shrews could fluctuate but masked shrews do not show any peak for dispersal during the season (Whitaker 2004). For this last group, we detected within-year negative area-sensitivity on initial site occupancy. Given these interspecific differences and responses in terms of area-sensitivity, we recommend sampling small mammals over one complete population cycle to better understand the trends described for American red squirrels, masked shrews, and southern red-backed voles. This would include sampling these species over four consecutive years from the beginning of June to the end of October in order to compare area-sensitivity during all four phases of a population cycle as well as when individuals are dispersing.

4.6.4 Conclusions

By comparing small mammals occurrence patterns in green-tree retention, post-fire remnant patches and old-growth forests, our study showed that old forest patches in harvested landscapes acted as refuges and sources of dispersers for small mammals to a degree similar to what occurs in post-fire remnant patches (Leblanc and Pouliot 2011; Robinson et al. 2013). Retention patches in conventional clear-cut agglomerations are thus playing a functional role for small mammal populations in human-disturbed landscapes which can be improved by ecosystem-based management through planning for the amount and spatial arrangement of old forest habitats at levels that better reflect the regional natural disturbance regimes (Drapeau et al. 2016).

We encourage long-term monitoring of populations of animals at multiple spatial scales to investigate ecological mechanisms behind positive and negative area-sensitivity patterns (Desrochers et al. 2010). Indeed, we found that area-sensitivity could be density-dependent for populations characterised by cyclic abundance patterns, such as the southern red-backed vole which is particularly interesting as it shows cyclic patterns in some parts of its range (Boonstra and Krebs 2012; Krebs 2013; Fauteux et al. 2015). However, further studies are required to investigate the relationship between occurrence of small mammals and habitat amount during the peak of their cycle.

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4.9 Appendices

4.9.1 Appendix 1

Habitat structure and composition encountered in the 60 sampling sites used to investigate the occurrence of small mammals in black spruce forests of northwestern Quebec.

4.9.1.1 Site selection

We selected a total of 60 forested sites that were equally distributed among old undisturbed forest (CONTROL - continuous forest over 100-years-old), post-fire remnant patches (POSTFIRE - mean 3.1 ha; range 0.2 – 11.1 ha) left after wildfires that occurred over 20 years ago, green tree retention stands (GREENTREE – mean 0.8 ha; range 0.09 – 1.6 ha) left after recent clear-cuts (< 10 years), and linear cutblock separators (LINEARCUT - 60-100 m large, connected to old-growth forests) that separate clearcut areas.

4.9.1.2 Statistical analyses

We first investigated potential relationships between numeric habitat variables and site type (CONTROL, POSTFIRE, GREENTREE and LINEARCUT) using one-way ANOVA. We subsequently conducted multiple comparisons with a Tukey contrast matrix to observe potential differences among sites and regarding each of the continuous habitat variables considered.

In the study, we pooled GREENTREE and LINEARCUT sites together to increase species detection in site occupancy models (low species detection reported in

GREENTREE sites prevented us from accurately analysing site occupancy in this site type). The resulting site type was named HARVEST. We then conducted a second set of one-way ANOVA analyses, coupled with multiple comparisons with a Tukey contrast matrix, to compare the three remaining site types to one another.

All analyses were conducted in R (version 3.0.1, R Development Core Team 2015).

4.9.1.3 Results

Some differences among measured habitat variables were identified in each site type but the most noticeable difference concerned site age (**Table 4.3**). Residual patches left after logging were younger than control and post-fire remnant patches, and lacked some structural attributes found in old-growth stands.

GREENTREE sites were characterised by dense monospecific forests of smaller diameter and shorter black spruces than all other sites. GREENTREE sites also had few large trees (dbh > 10 cm), low volumes of LateDwd, and small snags, mainly of early decay classes. LINEARCUT sites were characterised by the largest live trees and snags belonging to both coniferous and deciduous trees. Overstory cover were the greatest (no canopy openings) unlike understory covers which were reduced and not as rich in ericaceous shrubs as other site types. POSTFIRE sites were composed of old-growth forests as were our CONTROL sites, which presented canopy openings (as shown by a smaller basal area and less important overstory covers) as well as species-rich understory. Large live trees and snags could be encountered although their density was lower than the density of large live trees and large snags found in either LINEARCUT or POSTFIRE. Finally, HARVEST sites were similar to CONTROL and POSTFIRE sites across all habitat variables (**Figure 4.8**).

Table 4.3 Mean values (± sd) of site age as well as all site covariates introduced in models, according to site types (CONTROL, POSTFIRE, GREENTREE, LINEARCUT).

VARIABLE	**CONTROL**	**POSTFIRE**	**GREEN TREE**	**LINEAR CUT**
AGE (years)	158.9 ± 55.6 (a)	168.5 ± 65.8 (a)	104.1 ± 43.6 (b)	108.3 ± 33.9 (b)
CANCOV20 (%)	74.0 ± 13.8 (a)	82.9 ± 7.7 (ab)	80.4 ± 11.0 (ab)	85.0 ± 6.3 (b)
CANCOV150 (%)	59.3 ± 22.6 (a)	70.0 ± 18.0 (ab)	69.1 ± 16.5 (ab)	78.1 ± 12.3 (b)
TREEDENS (no. trees. ha^{-1})	838.5 ± 619.0 (ab)	826.7 ± 499.7 (a)	583.7 ± 568.4 (a)	1407.4 ± 738.5 (b)
SNAGDENS (no. snags. ha^{-1})	83.0 ± 71.0 (a)	284.4 ± 428.2 (a)	71.1 ± 101.9 (a)	165.9 ± 108.2 (a)
EARLYDWD ($m^3.ha^{-1}$)	35.7 ± 42.2 (a)	144.2 ± 264.5 (a)	25.6 ± 52.1 (a)	121.8 ± 157.8 (a)
LATEDWD ($m^3.ha^{-1}$)	10.7 ± 21.2 (ab)	29.72 ± 43.1 (a)	4.05 ± 9.2 (b)	15.69 ± 19.8 (ab)

(suite)

Note: Site type acronyms: CONTROL, control (old-growth forest); GREENTREE, green-tree retention stand; LINEARCUT, linear cutblock separator; POSTFIRE, post-fire remnant patch. Variable acronyms: AGE, stand age; CANCOV20, canopy cover measured 20 cm off the ground; CANCOV 150, canopy cover measured 150 cm off the ground; EARLYDWD, volume of early decayed down woody debris; LATEDWD, volume of late decayed down woody debris; SNAGDENS, density of large snags; TREEDENS, density of large live trees. Values with same letters are not statistically different.

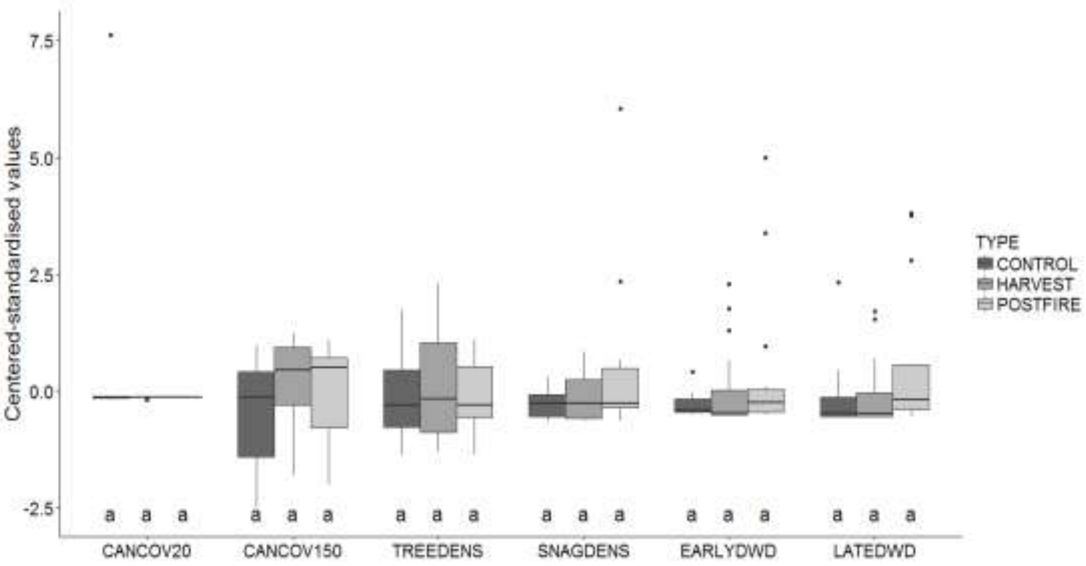

Figure 4.8 Median values and dispersion of all site covariates introduced in models, according to site types: CONTROL, control (old-growth forest); POSTFIRE, post-fire remnant patch; GREENTREE, green-tree retention patch which includes both linear cutblock separators (LINEARCUT) and green tree retention stands (GREENTREE). Variable acronyms: CANCOV20, canopy cover measured 20 cm off the ground; CANCOV150, canopy cover measured 150 cm off the ground; EARLYDWD, volume of early decayed down woody debris; LATEDWD, volume of late decayed down woody debris; SNAGDENS, density of large snags; TREEDENS, density of large live trees.

4.9.1.4 Litterature cited

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4.9.2 Appendix 2

List of 67 dynamic occupancy models used to assess site occupancy (ψ) of small mammals in black spruce forests as well as site colonisation (γ) and local extinction (ε).

Candidate models	**Occupancy**	**Colonisation**	**Local Extinction**	**Detection**	**K**
M0	ψ(.)	γ(.)	ε(.)	*p*(.)	4
M1	ψ(.)	γ(.)	ε(.)	*p*(Rain + Temp + Moon)	7
M2	ψ(.)	γ(.)	ε(.)	*p*(Session + Method)	7
M3	ψ(.)	γ(.)	ε(.)	*p*(Arthro + Mollusc)	6
OCCUPANCY MODELS with WEATHER VARIABLES on the detection parameter					
M4	ψ(Type)	γ(.)	ε(.)	*p*(Rain + Temp + Moon)	9
M5	ψ(EarlyDwd + LateDwd)	γ(.)	ε(.)	*p*(Rain + Temp + Moon)	9
M6	ψ(LateDwd : CanCov)	γ(.)	ε(.)	*p*(Rain + Temp + Moon)	10

(suite)

Candidate models	**Occupancy**	**Colonisation**	**Local Extinction**	**Detection**	**K**
M7	ψ(DECID)	γ(.)	ε(.)	*p*(RAIN + TEMP + MOON)	10
M8	ψ(CANCOV)	γ(.)	ε(.)	*p*(RAIN + TEMP + MOON)	8
M9	ψ(CANCOV ^{2})	γ(.)	ε(.)	*p*(RAIN + TEMP + MOON)	8
M10	ψ(TREEDENS + SNAGDENS)	γ(.)	ε(.)	*p*(RAIN + TEMP + MOON)	9
OCCUPANCY MODELS with TRAPPING VARIABLES on the detection parameter					
M11	ψ(TYPE)	γ(.)	ε(.)	*p*(SESSION + METHOD)	9
M12	ψ(EARLYDWD + LATEDWD)	γ(.)	ε(.)	*p*(SESSION + METHOD)	9
M13	ψ(LATEDWD : CANCOV)	γ(.)	ε(.)	*p*(SESSION + METHOD)	10
M14	ψ(DECID)	γ(.)	ε(.)	*p*(SESSION + METHOD)	10
M15	ψ(CANCOV)	γ(.)	ε(.)	*p*(SESSION + METHOD)	8

(suite)

Candidate models	**Occupancy**	**Colonisation**	**Local Extinction**	**Detection**	**K**
M16	ψ(CanCov^{2})	γ(.)	ε(.)	*p*(Session + Method)	8
M17	ψ(TreeDens + SnagDens)	γ(.)	ε(.)	*p*(Session + Method)	9
OCCUPANCY MODELS with INVERTEBRATES VARIABLES on the detection parameter					
M18	ψ(Type)	γ(.)	ε(.)	*p*(Arthro + Mollusc)	8
M19	ψ(EarlyDwd + LateDwd)	γ(.)	ε(.)	*p*(Arthro + Mollusc)	8
M20	ψ(LateDwd : CanCov)	γ(.)	ε(.)	*p*(Arthro + Mollusc)	9
M21	ψ(Decid)	γ(.)	ε(.)	*p*(Arthro + Mollusc)	9
M22	ψ(CanCov)	γ(.)	ε(.)	*p*(Arthro + Mollusc)	7
M23	ψ(CanCov^{2})	γ(.)	ε(.)	*p*(Arthro + Mollusc)	7
M24	ψ(TreeDens + SnagDens)	γ(.)	ε(.)	*p*(Arthro + Mollusc)	8
COLONISATION MODELS with WEATHER VARIABLES on the detection parameter					
M25	ψ(.)	γ(Type)	ε(.)	*p*(Rain + Temp + Moon)	9

(suite)

Candidate models	**Occupancy**	**Colonisation**	**Local Extinction**	**Detection**	**K**
M26	ψ(.)	γ(EARLYDWD + LATEDWD)	ε(.)	*p*(RAIN + TEMP + MOON)	9
M27	ψ(.)	γ(LATEDWD : CANCOV)	ε(.)	*p*(RAIN + TEMP + MOON)	10
M28	ψ(.)	γ(DECID)	ε(.)	*p*(RAIN + TEMP + MOON)	10
M29	ψ(.)	γ(CANCOV)	ε(.)	*p*(RAIN + TEMP + MOON)	8
M30	ψ(.)	γ(CANCOV ^{2})	ε(.)	*p*(RAIN + TEMP + MOON)	8
M31	ψ(.)	γ(TREEDENS + SNAGDENS)	ε(.)	*p*(RAIN + TEMP + MOON)	9
COLONISATION MODELS with TRAPPING VARIABLES on the detection parameter					
M32	ψ(.)	γ(TYPE)	ε(.)	*p*(SESSION + METHOD)	9
M33	ψ(.)	γ(EARLYDWD + LATEDWD)	ε(.)	*p*(SESSION + METHOD)	9

(suite)

Candidate models	**Occupancy**	**Colonisation**	**Local Extinction**	**Detection**	**K**
M34	ψ(.)	γ(LateDwd : CanCov)	ε(.)	*p*(Session + Method)	10
M35	ψ(.)	γ(Decid)	ε(.)	*p*(Session + Method)	10
M36	ψ(.)	γ(CanCov)	ε(.)	*p*(Session + Method)	8
M37	ψ(.)	γ(CanCov ^{2})	ε(.)	*p*(Session + Method)	8
M38	ψ(.)	γ(TreeDens + SnagDens)	ε(.)	*p*(Session + Method)	9
COLONISATION MODELS with INVERTEBRATE VARIABLES on the detection parameter					
M39	ψ(.)	γ(Type)	ε(.)	*p*(Arthro + Mollusc)	8
M40	ψ(.)	γ(EarlyDwd + LateDwd)	ε(.)	*p*(Arthro + Mollusc)	8
M41	ψ(.)	γ(LateDwd : CanCov)	ε(.)	*p*(Arthro + Mollusc)	9
M42	ψ(.)	γ(Decid)	ε(.)	*p*(Arthro + Mollusc)	9
M43	ψ(.)	γ(CanCov)	ε(.)	*p*(Arthro + Mollusc)	7
M44	ψ(.)	γ(CanCov ^{2})	ε(.)	*p*(Arthro + Mollusc)	7

(suite)

Candidate models	Occupancy	Colonisation	Local Extinction	Detection	K
M45	ψ(.)	γ(TREEDENS + SNAGDENS)	ε(.)	*p*(ARTHRO + MOLLUSC)	8
EXTINCTION MODELS with WEATHER VARIABLES on the detection parameter					
M46	ψ(.)	γ(.)	ε(TYPE)	*p*(RAIN + TEMP + MOON)	9
M47	ψ(.)	γ(.)	ε(EARLYDWD + LATEDWD)	*p*(RAIN + TEMP + MOON)	9
M48	ψ(.)	γ(.)	ε(LATEDWD : CANCOV)	*p*(RAIN + TEMP + MOON)	10
M49	ψ(.)	γ(.)	ε(DECID)	*p*(RAIN + TEMP + MOON)	10
M50	ψ(.)	γ(.)	ε(CANCOV)	*p*(RAIN + TEMP + MOON)	8
M51	ψ(.)	γ(.)	ε(CANCOV ^{2})	*p*(RAIN + TEMP + MOON)	8

(suite)

Candidate models	**Occupancy**	**Colonisation**	**Local Extinction**	**Detection**	**K**
M52	ψ(.)	γ(.)	ε(TREEDENS + SNAGDENS)	*p*(RAIN + TEMP + MOON)	9
EXTINCTION MODELS with TRAPPING VARIABLES on the detection parameter					
M53	ψ(.)	γ(.)	ε(TYPE)	*p*(SESSION + METHOD)	9
M54	ψ(.)	γ(.)	ε(EARLYDWD + LATEDWD)	*p*(SESSION + METHOD)	9
M55	ψ(.)	γ(.)	ε(LATEDWD : CANCOV)	*p*(SESSION + METHOD)	10
M56	ψ(.)	γ(.)	ε(DECID)	*p*(SESSION + METHOD)	10
M57	ψ(.)	γ(.)	ε(CANCOV)	*p*(SESSION + METHOD)	8
M58	ψ(.)	γ(.)	ε(CANCOV ^{2})	*p*(SESSION + METHOD)	8
M59	ψ(.)	γ(.)	ε(TREEDENS + SNAGDENS)	*p*(SESSION + METHOD)	9

(suite)

Candidate models	Occupancy	Colonisation	Local Extinction	Detection	K
EXTINCTION MODELS with INVERTEBRATE VARIABLES on the detection parameter					
M60	ψ(.)	γ(.)	ε(TYPE)	*p*(ARTHRO + MOLLUSC)	8
M61	ψ(.)	γ(.)	ε(EARLYDWD + LATEDWD)	*p*(ARTHRO + MOLLUSC)	8
M62	ψ(.)	γ(.)	ε(LATEDWD : CANCOV)	*p*(ARTHRO + MOLLUSC)	9
M63	ψ(.)	γ(.)	ε(DECID)	*p*(ARTHRO + MOLLUSC)	9
M64	ψ(.)	γ(.)	ε(CANCOV)	*p*(ARTHRO + MOLLUSC)	7
M65	ψ(.)	γ(.)	ε(CANCOV^2)	*p*(ARTHRO + MOLLUSC)	7
M66	ψ(.)	γ(.)	ε(TREEDENS + SNAGDENS)	*p*(ARTHRO + MOLLUSC)	8

(suite)

Note 1: Covariate acronyms: ARTHRO, weight of ground-dwelling arthropods; CANCOV, canopy cover taken either 150 cm off the ground to analyse squirrel data or 20 cm off the ground to analyse data from all other species (linear form); CANCOV^2, canopy cover (quadratic form); DECID, presence of deciduous trees; EARLYDWD, early decayed downed woody debris; LATEDWD, late decayed downed woody debris; METHOD*, methods used to detect individuals (live-trapping, live-trapping + playback count, live-trapping + point count, live-trapping + point count + playback count); MOLLUSC, weight of terrestrial molluscs; MOON**, percentage of moon illuminated during each trapping night; RAIN, rainfall measured after each trapping night; SESSION, trapping session (August 2013, July 2014, August 2014); SNAGDENS, density of snags with a dbh larger than 10 cm; TEMP, average night temperatures for each trapping night; TREEDENS, density of live trees with a dbh larger than 10 cm; TYPE, site type (control, post-fire remnant patch, harvest patch). Parameters followed by (.) indicate that they are constant

Note 2: * Different methods were only used to detect squirrels; ** Moon illumination was not used to analyse squirrel data.

4.9.3 Appendix 3

Number of individuals caught, by species, by trap type and by trapping session. Trapping session corresponds to August 2013, trapping session 2 to July 2014 and trapping session 3 to August 2014.

	August 2013 (Session 1)			**July 2014 (Session 3)**			**August 2014 (Session 4)**		
Mammalian species	Sherman	Tomahawk	Pitfall	Sherman	Tamahawk	Pitfall	Sherman	Tomahawk	Pitfall
Glaucomys sabrinus	1	0	0	0	0	0	6	10	0
Tamiasciurus hudsonicus	0	3	0	0	24	0	2	36	0
Myodes gapperi	16	0	0	54	0	0	72	0	0
Microtus pennsylvanicus	0	0	0	0	0	0	1	0	0
Peromyscus maniculatus	5	0	0	10	0	0	11	0	0
Phenacomys ungava	0	0	0	8	0	1	4	0	0

(suite)

Mammalian species	**August 2013 (Session 1)** Sherman	Tomahawk	Pitfall	**July 2014 (Session 3)** Sherman	Tamahawk	Pitfall	**August 2014 (Session 4)** Sherman	Tomahawk	Pitfall
Blarina brevicauda	2	0	1	0	0	0	0	0	0
Sorex cinereus	0	0	101	5	0	82	12	0	151
Sorex hoyi	0	0	13	1	0	6	0	0	7
Sorex arcticus	0	0	1	0	0	3	0	0	4
Sorex fumeus	0	0	0	0	0	0	0	0	1

4.9.4 Appendix 4

Number of sites occupied by any species of small mammal depending on the site type and trapping session. Trapping session corresponds to August 2013, trapping session 2 to July 2014 and trapping session 3 to August 2014.

Site type (/no of sites sampled)	**Trapping session 1**	**Trapping session 2**	**Trapping session 3**
CONTROL (/15)	3	10	10
POSTFIRE (/15)	7	9	11
GREENTREE (/15)	3	8	9
LINEARCUT (/15)	5	8	12
TOTAL (/60)	18	35	42

Note: Site type acronyms: CONTROL, control (old-growth forest); GREENTREE, green-tree retention patch; LINEARCUT, linear cutblock separator; POSTFIRE, post-fire remnant patch.

CHAPITRE V

DOES HABITAT AMOUNT IN NATURALLY DISTURBED OR MANAGED LANDSCAPES INFLUENCE SMALL MAMMAL CO-OCCURRENCE?

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5.1 Abstract

Habitat amount in fragmented landscapes positively influences population size, species occurrence, and species diversity. However, ecological mechanisms such as interspecific competition could themselves be area-sensitive. In this study, we focused on small mammals co-occurrence patterns in relation to habitat amount within naturally disturbed and managed landscapes. During the summer 2014, we sampled 60 sites located in old forest remnant patches within the black spruce forest of northeastern Canada. We analysed the co-occurrence of northern flying squirrels (*Glaucomys sabrinus*) and American red squirrels (*Tamiasciurus hudsonicus*), two potential competitors, in relation to the total amount of forest in surrounding landscapes up to 5 km, while controlling for associations to local habitat variables. We conducted similar analyses with the co-occurrence of southern red-backed voles (*Myodes gapperi*) and masked shrews (*Sorex cinereus*), a potential predators of juvenile voles. Whereas analyses of co-occurrence of voles and shrews did not show effects with the amount of habitat in the surrounding landscape, we observed positive area-sensitivity on the co-occurrence pattern of squirrels at the landscape scale. Our results question the suitability of current retention strategies in maintaining species co-occurrence. In addition, these results encourage the investigation of area-sensitivity not only on species presence and abundance, but also on ecological mechanisms that drive species interactions.

Key words: Area-sensitivity; boreal forest; two-species co-occurrence occupancy models; habitat amount; landscape scale; old-growth forest remnants

5.2 Résumé

La quantité d'habitat exerce une influence positive sur la taille des populations, l'occurrence des espèces et par conséquent, la biodiversité présente dans les paysages fragmentés. Cependant, des mécanismes tel que la compétition interspécifique pourraient eux-mêmes dépendre de la quantité d'habitat dans le paysage. Nous nous sommes penchés sur les patrons de co-occurrence de petits mammifères boréaux en fonction de la quantité d’habitat contenue dans des paysages perturbés naturellement ou par l'aménagement forestier. L'échantillonnage s'est déroulé pendant l’été 2014, dans 60 sites situés dans des îlots résiduels de vieilles forêts de la pessière noire du nord-est du Canada. Nous avons analysé la co-occurrence du grand polatouche (*Glaucomys sabrinus*) et de l'écureuil roux d'Amérique (*Tamiasciurus hudsonicus*), deux compétiteurs potentiels, en relation avec la quantité de forêt comprise dans plusieurs rayons allant jusqu`à 5 km, tout en contrôlant les associations avec des variables locales d'habitat. Des analyses similaires ont été réalisées avec le campagnol roux de Gapper (*Myodes gapperi*) et la musaraigne cendrée (*Sorex cinereus*)), un prédateur potentiel des jeunes de campagnols. La co-occurrence de la paire campagnol-musaraigne ne variait pas avec les méthodes de récolte. Toutefois, la co-occurrence des deux espèces de sciuridés semblait positivement liée à la quantité de forêt, plus particulièrement à grande échelle. Nos résultats remettent en question l'efficacité de certaines stratégies d'aménagement forestier favorisant la co-occurrence d'espèces. Ces résultats encouragent également les études d'impact de la quantité d'habitat sur d'autres mécanismes écologiques régulant les interactions entre les espèces.

5.3 Introduction

Area-sensitivity, i.e. the dependence of a species on the amount of habitat in surrounding areas (Galli et al. 1976; Robbins 1979), has become a growing research focus. Indeed, habitat area has a positive influence on population size, species occurrence, and species diversity (Fahrig, 2003, 2013), on different taxa such as arthropods (Margules et al. 1994), birds (Robbins et al. 1989; Villard et al. 1999), reptiles and amphibians (Kolozsvary and Swihart 1999; Diaz et al. 2000), and mammals (Lynch and Whigham 1984; Michalski and Peres 2007). On one hand, area-sensitivity has mainly been studied in birds, focusing on population density and reproductive success of single species at a time (Donovan and Lamberson 2001; Davis 2004; Smith et al. 2011a). To our knowledge, very few studies have looked into species occurrence as being area-sensitive (Trzcinski et al. 1999; Walk and Warner 1999; Desrochers et al. 2010; Chavel et al 2017), and only two authors have linked area-sensitivity with mechanisms such as resource tracking, movements, predation, or competition, that regulate animal population and species occurrence (Andrén 1994; Andrén et al. 1997; Desrochers et al. 2010).

On the other hand, area-sensitivity has also been addressed when analysing community composition and species richness (Öckinger and Smith 2006; Martensen et al. 2012), as a response to various mechanisms such as predation and parasitism (Brittingham and Temple 1983; Robinson et al. 1995), food shortage (Burke and Nol 1998; Zanette et al. 2000), reduced breeding opportunities (Villard et al. 1993; Burke and Nol 2000; Ribic et al. 2009), and changes in dispersal strategies (Lynch and Whigham 1984; Schtickzelle et al. 2006).

Community composition can be viewed as multiple species co-occurrence. This leads to the idea that species co-occurrence could also be area-sensitive. Specifically, a minimum area of habitat should be available for two or more species to co-occur, whether these species need similar resources (interspecific competition), interact in a predator/prey relationship (predation) or attract predators leading to the population decrease of only one prey species (apparent competition).

In this study, we focused on small mammal species inhabiting boreal forests, a system disturbed by wildfires and tree harvesting on a recurrent basis (Hunter 1993, Niemelä 1999; Bergeron et al. 2007). This landscape presents a habitat mosaic highly suitable for conducting research on area-sensitivity. Moreover, estimating co-occurrence of small mammal species in both post-fire and post-harvest sites provides an assessment of habitat conditions under current retention strategies of old remnant patches in aggregated clearcuts of managed landscapes with regards to conditions in patches originating from wildfires. Such assessment is critical to plan green retention under ecosystem-based approaches.

We relied on small mammals to investigate area-sensitivity of species co-occurrence for three main reasons. First, small mammals are potentially reliable ecological indicators of sustainable forest harvesting (McLaren et al. 1998; Pearce and Venier 2005; Holloway and Smith 2011). Second, the general biology, local habitat associations, and dispersal abilities of small mammals suggest that they could be more sensitive to landscape characteristics than anticipated, especially given that their response to habitat variables varies at different scales (Schweiger et al. 1999; Manning and Edge 2004; Fauteux et al. 2012). Third, small mammal communities can be impacted by all three mechanisms stated above (interspecific competion, predation and apparent competition), and co-occurrence patterns of species may be related to the amount of habitat in surrounding areas (Hallett et al 1983; Kelt et al 1995; Morris 1999).

Interspecific competition can influence small mammal occurrence and abundance, especially if resources are limited. Yet, the amount of resources is dependent on the amount of habitat where these resources are found. For instance, a greater availability of coarse woody debris translates into more refuges, denning sites, and food available for various small mammals, increasing the probability of species to co-occur (Fauteux et al. 2013). When interspecific competition organises small mammal populations, species co-occurrence benefits from greater amounts of habitat (linear positive area-sensitivity relationship).Predation has been documented among small mammals species, especially predatory behaviour of shrews on voles which has been observed for short-tailed shrews (*Blarina brevicauda*) (Eadie 1952; Getz et al. 1992) and suspected from common shrews (*Sorex araneus* - Liesenjohann et al. 2011). Although not predatory, aggressive encounters have also been documented in vole communities (Turner et al. 1975), generally reporting both the dominance of one species over the other (Grant 1970; Conley 1976; Myllymaki 1977; De Jonge 1983; Wolff 1985) and the avoidance of the subordinate species (Hoffmeyer 1973; Heske and Repp 1985; Eccard and Ylönen 2003). Aggressive behaviour is also well documented in squirrel species, mostly due to a general intolerance of squirrels in sharing nesting grounds with other sciurid species. Indeed, it has been reported in eastern grey squirrels, *Sciurus carolinensis*, toward European red squirrels, *Sciurus vulgaris* (Ackerman and Weigl 1970), in southern flying squirrels, *Glaucomys volans*, towards northern flying squirrels (Weigl 1978), and in American red squirrel towards northern flying squirrels (Smith 2012). Increasing amount of habitat, in theory, would lead to less encounters between species, and therefore decreasing aggressive behaviours from one another. More habitat with more resources would also lead shrews to rely on their main food sources (i.e. insects) and decrease their predatory behaviour towards vole juveniles. Here as well, when predatory and aggressive behaviours impact small mammal populations, species co-occurrence may benefit from greater amounts of habitat (linear positive area-sensitivity relationship).

Finally, new evidence report apparent competition between some small mammal species, such as white-footed mice (*Peromyscus leucopus*) and meadow voles (*Microtus pennsylvanicus* - Schmidt et al. 2005), between field voles (*Microtus agrestis*) and Ondrias voles (*Microtus epiroticus* - Norrdahl and Korpimäki 1993), and between southern red-backed voles (*Myodes gapperi*) and deer mice (*Peromyscus maniculatus* - Le Borgne et al. 2018). Apparent competition explains how populations of a given prey species decreases with predation following the increase of another prey species population which attracted predators (Holt 1997). More habitat with more resources may benefit a "dominant" species, leading to an increase in number of this species, followed by the arrival of predators and the subsequent predation of the "subordinate" species. When apparent competition determine species distribution in a landscape, species co-occurrence does not benefit from greater amounts of habitat, but from intermediate amounts of habitat in the landscape (quadratic positive area-sensitivity relationship).

We modelled co-occurrence of American boreal small mammals in relation to the total amount of old-growth forest in the surrounding landscape while controlling for local habitat. We analysed the probability of co-occurrence for two pairs of small mammal species that have potential interspecific interactions. Smith (2012) hypothesised that American red squirrel and northern flying squirrel could compete for similar resources, especially for nesting sites. In contrast, southern red-backed vole (*Myodes gapperi*) and masked shrews (*Sorex cinereus*) do not compete for similar resources. Instead, masked shrews could influence vole breeding success through predatory behviour. Thus, shrews potentially influence the space used by voles in forest habitats (Fulk 1972; Liesenjohann et al. 2011).

Specifically, our first objective was to evaluate the importance of remnant forest patch structure for mammalian co-occurrence at the stand scale for both post-fire and post-harvesting remnant stands. We hypothesised that the co-occurrence of boreal small mammals at local scale is not explained by patch origin (post-fire vs. post-harvest), as harvested remnant sites should mimic naturally disturbed remnant sites in structure and composition. Rather the co-occurrence of boreal small mammals at local scale should be explained by local structural attributes such as downed woody debris found in either post-fire or post-harvesting remnant stands (e.g. Orrock and Pagel 2002; Fauteux et al. 2012; Craig et al. 2014). Our second objective aimed to quantify the relationship between species co-occurrence and the amount of forest by using multiple-scale buffers surrounding our sampling sites. We hypothesised that co-occurrence of boreal small mammals is positively related to habitat amount at greater scales than the local scale.

5.4 Methods

5.4.1 Study area

The study area covered a total of 8325 km^2 of black spruce-feather moss forest located in northwestern Quebec, Canada (79˚29’ W, 49˚00’ N - 75˚39’ W, 50˚22’ N - **Figure 5.1**). A subpolar continental climate characterises this boreal region, with mean monthly temperatures ranging from -16 °C to 20 °C and 850 mm of annual precipitation (Blouin and Berger 2002; Environment Canada 2015). The forest canopy is dominated by black spruce (*Picea mariana*). Jack pine (*Pinus banksiana*) and balsam fir (*Abies balsamea*) also occur, along with broadleaf species such as paper birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*). The understory is primarily composed of dwarf ericaceous shrubs (e.g. *Rhododendron groenlandicum*) and feather mosses (*Pleurozium schreberi*) forming a dense carpet, replaced by *Sphagnum* species as drainage conditions deteriorate due to paludification with time since fire (Fenton and Bergeron 2006). Wildfires are the main natural recurrent disturbance in this region even though they are being increasingly replaced by various forest management and harvesting strategies (Imbeau et al. 2015).

We selected a total of 60 forested sites that were equally distributed among old undisturbed forest (CONTROL - continuous forest over 100-years-old and of more than 200 ha), post-fire remnant patches (POSTFIRE - mean size 3.1 ha; range 0.2 - 11.1 ha) left after wildfires that occurred over 20 years ago (fire mean size 16816 ha; range 1932 - 40713 ha), green tree retention stands (GREENTREE – mean size 0.8 ha; range 0.09 - 1.60 ha) left after recent clear-cuts (< 10 years; mean size 6.3 ha; range 0.5 - 41.0 ha), and linear cutblock separators (LINEARCUT - 60-100 m large, 250-900 long, connected to old-growth forests) that separate clearcut areas. Sites were at least 500 m apart. Based on the average movement distance of American red squirrels (*Tamiasciurus hudsonicus*) and northern flying squirrels (*Glaucomys* *sabrinus*) which are the most vagile species found on our study area (Larsen and Boutin 1994; Reunanen et al. 2000; Weigl 2007), this distance of 500 m was sufficient to ensure independence among sites. Details regarding habitat structure and composition in these four site types are found in Chavel et al. (2017a).

Although we initially selected four types of sites, we pooled GREENTREE and LINEARCUT sites together. These two types were pooled to increase species detection in site occupancy models because low species detection in GREENTREE sites. Hereafter, we referred to GREENTREE and LINEARCUT sites as harvest retention patches (HARVEST). Habitat structure and composition characterising HARVEST sites are found in Chavel et al. (2017a) and compared with both CONTROL and POSTFIRE sites.

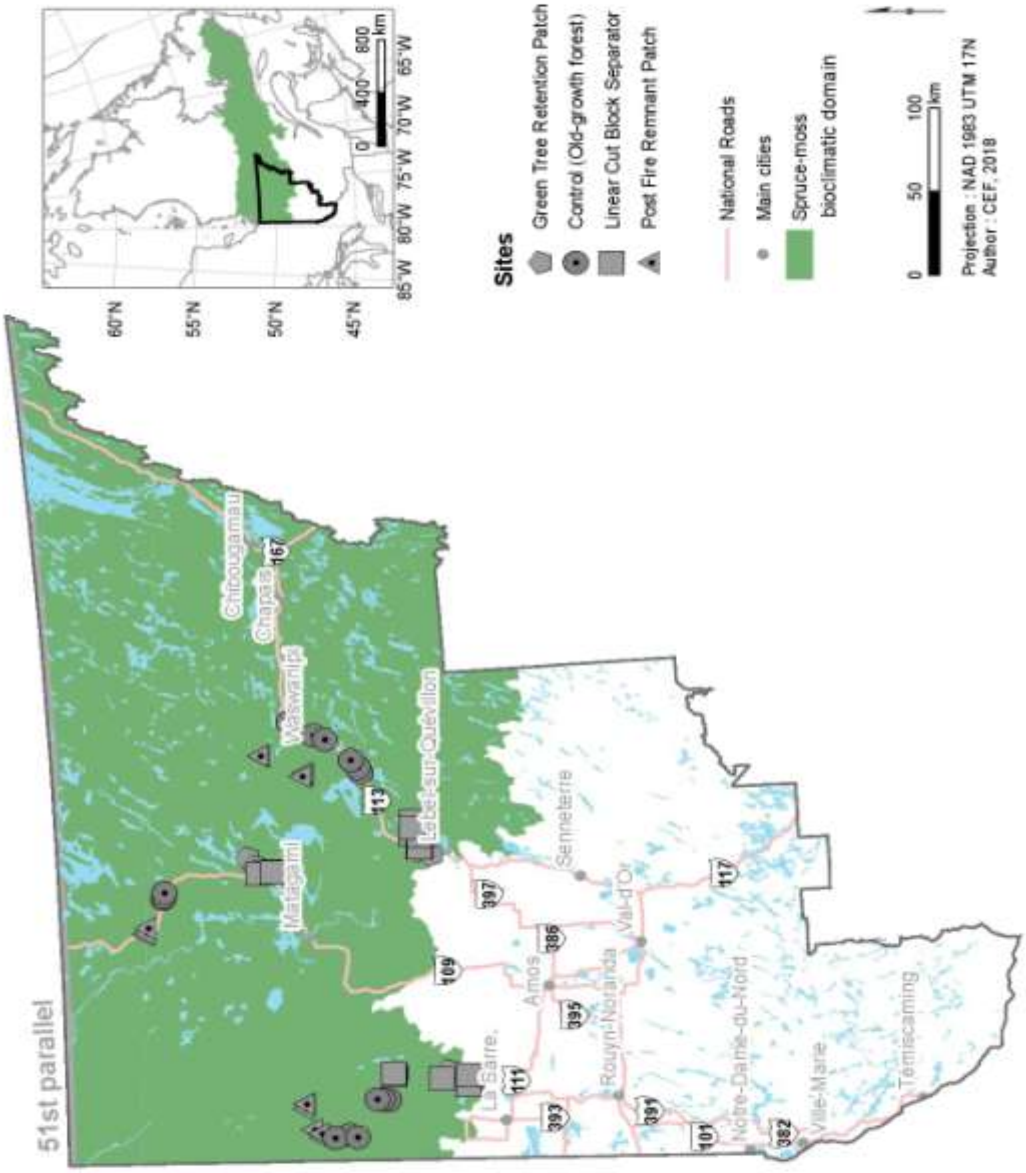

Figure 5.1 Location of the study sites in black spruce forests of northwestern Quebec, Canada.

5.4.2 Small mammal trapping design

Live-trapping was conducted in 2014 from July 30th to August 21st. Groups of 12 sites were monitored by trapping each site over three consecutive nights and days and checking the traps twice a day (early morning and late afternoon). Sciurid species were trapped using Tomahawk (Tomahawk Live Trap llc ®) live-traps baited with peanut butter and apple pieces, providing food and water to trapped individuals. Cotton batting was also added in each trap to provide shelter. We established one transect line of six live-traps per site with a distance of 10 m between traps. Transects were 50 m long to accommodate our smallest retention and remnant patches. American red squirrels were also sampled using point and playback counts. These consisted of first listening for squirrels for 10 minutes after having checked traps and released any trapped individuals. Then, we played recorded red squirrel calls over a period of 10 min and noted any response to these playback calls (Chavel et al. 2017b).

Cricetine species were trapped using Sherman (H.B. Sherman Traps, Inc. ®) live-traps supplied with peanut butter, apple pieces, and cotton batting. At each site, we established a trapping grid of 4 x 4 traps with a distance of 5 m between traps. We observed incidental lethal captures of soricid species in pitfall traps deployed to sample arthropods (i.e. environmental data in a concurrent study), which allowed us to include soricids in subsequent analyses. We used 26 cl pitfall traps half-filled with salty water in which odourless soap was dissolved. Pitfall traps were checked on three consecutive mornings and closed when not trapping. Four pitfall traps were placed in each site, forming a 20 m-long square grid. Trapping grids and transect lines were centred on each site (**Figure 5.2**).

Individuals captured alive were pit-tagged (Biomark ® HTP9 9mm 134.2 kHz ISO FDX-B), identified to sex and age using visual characteristics. All live individuals were subsequently released. Dead individuals were stored in a sealed plastic bag to confirm species identification according to cranial characteristics (Lupien 2001, 2002; Fauteux et al. 2014). Shrews captured in Sherman live-traps were excluded from our analyses for two main reasons. First, most soricid species potentially found in the study area are too light to trigger the traps. Only heavier individuals could be caught which means that we could only sample a portion of the population. Secondly, identifying some species such as masked shrews (*Sorex cinereus*) and pygmy shrews (*S. hoyi*) is often impossible unless measuring cranial characteristics.

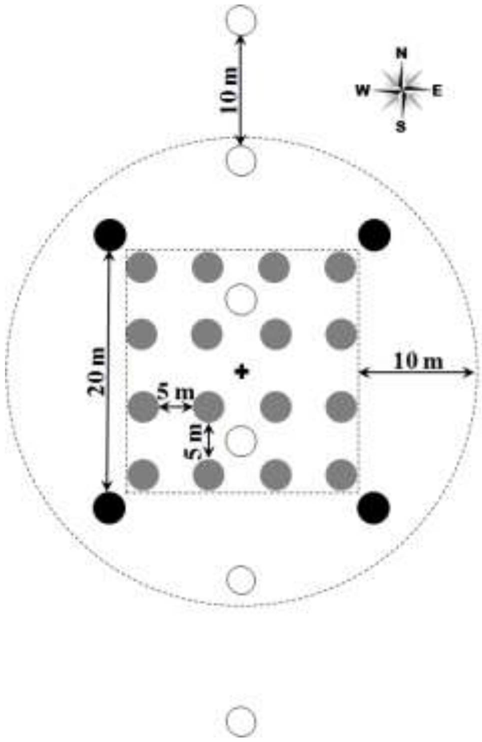

Figure 5.2 Schematic representation of a sampling site. The black cross (✚) represents the centre of all sampling plots where all weather variables were recorded. White circles (○) represent one Tomahawk live-trap, grey circles (◍) represent one Sherman live-trap, black circles (●) represent one arthropod pitfall trap, the dotted square represents the quadrat in which tree and snag densities were recorded as well as volumes of downed woody debris, while the dotted circle represents one plot in which canopy cover and tree stand age were recorded. The presence of deciduous

trees was assessed from the grid centre as well as 4 other points 15 m away from the grid centre and located at each cardinal point.

We considered each Sherman and Tomahawk trap as providing an effort of one trap night, except traps that were accidentally sprung and were consequently noted as providing an effort of 0.5 trap nights (Nelson and Clark 1973). Likewise, all pitfall traps were considered as providing an effort of one trap night, unless dug out. All manipulations adhered to the Canadian Council on Animal Care Guidelines and were approved by the Institutional Animal Care Review Committee, Université du Québec en Abitibi-Témiscamingue (UQAT, permit no. 2013-04-02).

5.4.3 Environmental data

5.4.3.1 Stand scale microhabitat associations

Sites were categorised as either connected to old-growth forest or isolated in a disturbed matrix (binary variable - CONFIGURATION). Connected sites included linear cutblock stands and control sites. Isolated sites included post-fire remnant patches and green-tree retention patches.

The volume of downed woody debris (DWD) was inventoried in a 15 m-sided equilateral triangle (Harvey and Brais 2007), following the methods and the decay classes described in Fauteux et al. (2012 - **Figure 5.2**). Volumes of logs were calculated using the conic-paraboloid formula (Fraver et al. 2007) and were expressed in cubic meter per hectare ($m^3 \cdot ha^{-1}$). We then summed the volumes of DWD of the two earliest decay classes together (early-decayed downed woody debris - EARLYDWD) as well as the volumes of DWD of the two latest decay classes (late-decayed downed woody debris - LATEDWD).

Large snags, described as snags with a diameter at breast height (dbh) equal or larger than 10 cm (Déry and Leblanc 2005) and with a minimum height of 1.2 m (breast height) were counted within a 15 x 15 m quadrat. Densities of large snags (SNAGDENS) could then be calculated and values were expressed as a number of stems per hectare (stems.ha^{-1}).

Nocturnal temperatures were recorded at 4 hour intervals at each site with data loggers (Maxim's Hydrochron iButton®) set one meter off the ground in a shaded area protected from the wind. We computed average night temperature for each trapping night from data collected exclusively during nighttime. Only night tempreratures were considered as the bulk of species where nocturnal mammals. American red squirrels were the only exception as this species is mainly active at sunrise and sundown (Steele 1998). We identified nighttime temperatures according to sunrise and sunset times of our study area throughout the sampling season (http://www.sunrise-and-sunset.com).

5.4.3.2 Amount of forest at different spatial scales

Species encountered at our study sites occur in different forest cover types, although some of the species prefer old-growth or coniferous forests (Merritt 1981; Wells-Gosling and Heaney 1984; Steele 1998; Whitaker 2004). Thus, we focused on the total amount of forest located around capture grids, regardless of forest composition and tree density. Forest cover was obtained using an ArcGIS layer updated in 2013 produced by the Ministère du Développement Durable, de l'Environnement et de la Lutte contre les Changements Climatiques (MDDELCC) (Bissonnette and Lavoie 2015). Forested areas were defined as patches of trees with a minimum area of 0.1 ha, a canopy cover ≥ 10 %, a stand height ≥ 2 m, and a stand age ≥ 20 years.

Percent area covered by forest was measured in a total of 100 concentric buffers defined around the centre of each capture grid, using all radii with increments of 50 m, from 50 m up to 5 km. We chose a maximum radius of 5 km because the two most vagile species encountered in our study sites (i.e. northern flying squirrels and American red squirrels) may be impacted by landscape disturbances both within and beyond their home range (Larsen and Boutin 1994; Bowman et al. 2002; Ritchie et al. 2009). Grid resolution of the map (30 x 30 m) was kept constant among radii.

5.4.4 Analyses

5.4.4.1 Stand scale microhabitat associations

We used single-season, two-species occupancy models, and we used the conditional two-species occupancy parameterization (Richmond et al. 2010), rather than the unconditional one (MacKenzie et al. 2006) because we assumed that the probability of occupancy by the least interacting species in each pair was conditional on the occupancy of the most interacting species. Specifically, we considered the masked shrew as the dominant species (given its presumed predation pressure on juvenile voles) relative to the southern red-backed vole, whereas the American red squirrel was treated as a superior competitor over the northern flying squirrel. These models include three occupancy parameters namely ψ^{A} (probability of occupancy of species A), ψ^{BA} (probability of occupancy of species B given A is present), and ψ^{Ba} (probability of occupancy of species B given A is absent). The models include five detection parameters: p^{A} (detection probability for species A when species B is absent), p^{B} (detection probability for species B when species A is absent), r^{A} (detection probability for species A when both species are present), r^{BA} (detection probability for species B when both species are present and detected), and r^{Ba} (detection probability for species B when both species are present but species A remains undetected). However, with an increasing number of covariates on both occupancy and detection parameters, two-species occupancy models quickly become parameter-rich, and optimisation algorithms are less likely to converge. Thus, we reduced the five detection parameters to two, in two thirds of the candidate models. Specifically, we constrained the probabilities of detection of species A regardless of the presence of species B ($p^A = r^A$) and we also constrained the probabilities of detection of species B regardless of the presence and detection of species A ($p^B = r^{BA} = r^{Ba}$). This approach also made more sense biologically because 1) detection of one squirrel species should not be influenced by the detection of the other (one is nocturnal and the other diurnal - Wells-Gosling and Heaney 1984; Steele 1998), and 2) masked shrews and southern red-backed voles were sampled using two different methods.

Using the information recorded during our visits to the sites, we built detection histories for each species at each site and each of the three days of survey. For shrews, voles, and flying squirrels, a detection (1) involved the detection of the species in a trap, and 0 otherwise. For American red squirrels, we combined the trapping data and both auditory surveys to determine detection.

The probabilities of occupancy were allowed to vary according to a maximum set of eleven hypotheses of stand scale microhabitat associations, and the detection probability was allowed to vary with one of three scenarios (**Table 5.1**). Due to ecological differences between the pairs of species, we considered fewer models in the analysis of the co-occurrence of masked shrews and southern red-backed voles than between squirrel species. Specifically, we did not consider the density of large snags as a potential explanatory variable on occurrence patterns of shrews and voles because they are not arboreal and not known to use standing dead wood, unlike squirrels (Wells-Gosling and Heaney 1984; Steele 1998; Hackett and Pagels 2003). Because of these differences, we considered a total of 39 models (**Appendix 5.9.1**) to analyse the co-occurrence patterns between American red squirrels and northern flying squirrels and, we considered 33 models to analyse co-occurrence between masked shrews and southern red-backed voles (**Appendix 5.9.2**).

Parameters were estimated using maximum likelihood implemented in PRESENCE 12.5 (Hines 2006). We used an information-theoretic approach based on Akaike's Information Criterion for small samples (AIC_c) to compare candidate models (Burnham and Anderson 2002). We conducted multimodel inference on each explanatory variable appearing in the top models to compute 95% unconditional confidence intervals and model-averaged predictions based on the entire set of candidate models using the AICcmodavg package available in R 3.4.2 (Mazerolle 2017, R Development Core Team 2017).

To determine how likely two species were to co-occur compared to what would be expected if their distributions were totally independent, we used the species interaction factor (SIF, Richmond et al 2010), calculated as following:

$$\text{SIF} = \psi^{BA} / (\psi^{A} \text{ x } \psi^{B})$$

ψ^{A} represents the probability of occupancy of species A, ψ^{B} represents the probability of occupancy of species B regardless of the presence of species A, and ψ^{BA} represents the probability of occupancy of species B given A is present.A SIF < 1 indicates that species B is less likely to occur when species A is present. On the other hand, a SIF > 1 suggests that species B is more susceptible to be present at a site when species A is also present.

Table 5.1 List of biological hypotheses tested with conditional two-species occupancy models to analyse detection data of American red squirrel (*Tamiasciurus hudsonicus*) and northern flying squirrel (*Glaucomys sabrinus*) as well as masked shrew (*Sorex cinereus*) and southern red-backed vole (*Myodes gapperi*). All species were sampled in black spruce forest of northwestern Quebec.

Model structure	Predictions	References
Scenarios applied on the parameters of occupancy (ψ)		
$\psi^{A}(.)\psi^{BA}(.)\psi^{Ba}(.)$	Probabilities of occupancy are different but constant, regardless of the species and interactions between species.	N/A

(suite)

Model structure	Predictions	References
$\psi^{A}(.)\psi^{BA}(\mathrm{DWD_{TOT}}*)$ $\psi^{Ba}(\mathrm{DWD_{TOT}}*)$	Occupancy probability of northern flying squirrels increases with increasing volumes of downed woody debris, regardless of the presence of American red squirrels. Occupancy probabilities of American red squirrels are constant.	Although fungivore small mammals generally use woody debris as feeding grounds (presence of fungi - Loeb 1996; Fauteux et al. 2012), the response of northern flying squirrel remains to be tested regardless of the presence of a potential competing species.
	Occupancy probabilities of southern red-backed voles increases with increasing volumes of downed woody debris, regardless of the presence of masked shrews. Occupancy probabilities of masked shrews are constant.	Southern red-backed voles use woody debris as cover and nesting grounds (Loeb 1996; Craig et al. 2014).

(suite)

Model structure	Predictions	References
$\psi^{A}(.)\psi^{BA}(\mathrm{DWDTOT})$ $\psi^{Ba}(\mathrm{DWDTOT})$	Probabilities of occupancy increase with increasing volumes of downed woody debris for northern flying squirrels, but is lower in the presence of American red squirrels. Occupancy probabilities of American red squirrels are constant.	Although American red squirrels are mostly granivorous (Steele 1998), they can opportunistically feed on fungi (growing onto woody debris) and compete with northern flying squirrels, which are primarily fungivore (Wells-Gosling and Heaney 1984; Wheatley 2007).
	Probabilities of co-occurrence of southern red-backed voles and masked shrews decrease with increasing volumes of downed woody debris as greater volumes of downed woody debris can lead to more encounters between species and decreased predatory behaviour from shrews. Occupancy probabilities of shrews are constant.	Shrews use woody debris as hunting grounds for insects (Loeb 1996; Craig et al. 2014). Shrew species can prey upon vole juveniles (Getz et al. 1992).

(suite)

Model structure	Predictions	References
$\psi^{A}(.)\psi^{BA}(\text{EARLYDWD*})$ $\psi^{Ba}(\text{EARLYDWD*})$	Occupancy probabilities of northern flying squirrels increase with increasing volumes of early-decayed downed woody debris, regardless of the presence of American red squirrels. Occupancy probabilities of American red squirrels are constant.	Although fungivore small mammals are generally known to use woody debris as feeding grounds (presence of fungi - Loeb 1996; Fauteux et al. 2012), the response of northern flying squirrel remains to be tested regardless of the presence of a potential competing species.
	Probabilities of occupancy by southern red-backed voles increase with increasing volumes of early-decayed downed woody debris, regardless of the presence of masked shrews. Occupancy probabilities of masked shrews are constant.	Southern red-backed voles use woody debris as cover and nesting ground (Loeb 1996; Craig et al. 2014).

(suite)

Model structure	Predictions	References
$\psi^{A}(.)\psi^{BA}(\text{E}\textsc{arly}\text{DWD})$ $\psi^{Ba}(\text{E}\textsc{arly}\text{DWD})$	Occupancy probabilities increase with increasing volumes of early-decayed downed woody debris for northern flying squirrels, but is lower in the presence of American red squirrels. Occupancy probabilities of American red squirrels are constant.	Although American red squirrels are mostly granivorous (Steele 1998), they can opportunistically feed on fungi (growing onto woody debris) and compete with northern flying squirrels, which are primarily fungivore (Wells-Gosling and Heaney 1984; Wheatley 2007).
	Occupancy probabilities increase with increasing volumes of early-decayed downed woody debris for southern red-backed voles, but is lower in the presence of masked shrews. Occupancy probabilities of masked shrews are constant.	Shrews use woody debris as hunting ground (Loeb 1996; Craig et al. 2014). Shrew species have been observed to prey upon vole juveniles (Getz et al. 1992).

(suite)

Model structure	Predictions	References
$\psi^{A}(.)\psi^{BA}(\text{LATEDWD*})$ $\psi^{Ba}(\text{LATEDWD*})$	Occupancy probabilities of northern flying squirrels increase with increasing volumes of late-decayed downed woody debris, regardless of the presence of American red squirrels. Occupancy probabilities of American red squirrels are constant.	Although fungivore small mammals generally use woody debris as feeding grounds, and especially late-decayed woody debris (presence of fungi - Loeb 1996; Fauteux et al. 2012), the response of northern flying squirrel remains to be tested regardless of the presence of a potential competing species.
	Occupancy probabilities of southern red-backed voles increase with increasing volumes of late-decayed downed woody debris, regardless of the presence of masked shrews. Occupancy probabilities of occupancy of masked shrews are constant.	Southern red-backed voles use woody debris as cover and nesting grounds (Loeb 1996; Craig et al. 2014).

(suite)

Model structure	Predictions	References
$\psi^{A}(.)\psi^{BA}(\mathrm{LATEDWD})\psi^{Ba}(\mathrm{LATEDWD})$	Occupancy probabilities increase with increasing volumes of late-decayed downed woody debris for northern flying squirrels, but is lower in the presence of American red squirrels. Occupancy probabilities of American red squirrels are constant.	Although American red squirrels are mostly granivorous (Steele 1998), they can opportunistically feed on fungi (growing onto woody debris) and consequently compete with northern flying squirrels, which are primarily fungivore (Wells-Gosling and Heaney 1984; Wheatley 2007).
	Occupancy probabilities increase with increasing volumes of late-decayed downed woody debris for southern red-backed voles, but is lower in the presence of masked shrews. Occupancy probabilities of masked shews are constant.	Shrews use woody debris as hunting grounds (Loeb 1996; Craig et al. 2014). Shrew species have been observed to prey upon vole juveniles (Getz et al. 1992).

(suite)

Model structure	Predictions	References
$\psi^{A}(.)\psi^{BA}(\textsc{SnagDens*})$ $\psi^{Ba}(\textsc{SnagDens*})$#	Occupancy probabilities increase with the presence of large snags for northern flying squirrels, regardless of the presence of American red squirrels. Occupancy probabilities of American red squirrels are constant.	Sciurid species benefit from the presence of large snags (Carey 1995; Darveau and Desrochers 2001; Vanderwel et al. 2010).
$\psi^{A}(.)\psi^{BA}(\textsc{SnagDens})$ $\psi^{Ba}(\textsc{SnagDens})$#	Occupancy probabilities increase with the presence of large snags for flying squirrels, but is lower in the presence of red squirrels. Occupancy probabilities of American red squirrels are constant.	Squirrels species compete for nesting cavities (Smith 2012).

(suite)

Model structure	Predictions	References
$\psi^{A}(.)\psi^{BA}(\text{TYPE*})\psi^{Ba}(\text{TYPE*})$	There is a marginal difference in occupancy among site types for northern flying squirrel or southern red-backed vole, regardless of the presence of American red squirrel or masked shrew respectively.	Green-tree retention patches should act as refuges and sources of dispersers (Leblanc and Pouliot 2011; Robinson et al. 2013). However, if both red squirrels and masked shrews (Species A in both sets of analyses) remained unaffected by site types on these precise sampling sites, southern red-backed voles occurred less often in post-harvest sites (marginal effect - Chavel et al. 2017a). Flying squirrel response to site is unknown.
$\psi^{A}(.)\psi^{BA}(\text{TYPE})\psi^{Ba}(\text{TYPE})$	There is a marginal difference in occupancy among site types for northern flying squirrel or southern red-backed vole, but lower in sites where American red squirrel or masked shrew respectively is present.	Green-tree retention patches should act as refuges and sources of dispersers (Leblanc and Pouliot 2011; Robinson et al. 2013).

(suite)

Model structure	Predictions	References
$\psi^{A}(.)\psi^{BA}(\text{CONFIGURATION*})$ $\psi^{Ba}(\text{CONFIGURATION*})$	Occupancy probabilities of northern flying squirrel or southern red-backed vole increase when sites are connected to or part of a continuous old-growth forest instead of being isolated in a disturbed matrix, regardless of the presence of American red squirrel or masked shrew respectively. Occupancy probabilities of American red squirrel or masked shrews are constant.	Northern flying squirrels require trees to glide across an area (Vernes 2001). Although southern red-backed voles can use regenerating matrices, they favour old-growth forests for the resources they are associated with (Hayward et al.1999; Merrit 1981)

(suite)

Model structure	Predictions	References
$\psi^{A}(.)\psi^{BA}$(CONFIGURATION) ψ^{Ba}(CONFIGURATION)	Probabilities of occupancy of northern flying squirrel or southern red-backed vole increase when sites are connected to or part of a continuous old-growth forest instead of being isolated in a disturbed matrix, but the increase is higher in the presence of American red squirrel or masked shrew respectively. Probabilities of occupancy of American red squirrels or masked shrews are constant.	In the presence masked shrews (especially if the population is large), southern red-backed voles make use of the regenerating matrices around forested sites (Hayward et al.1999)
Set of scenarios applied on the detection parameter (*p*)		
$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	Detection probabilities are different but constant, regardless of the species and interactions between species.	N/A

(suite)

Model structure	Predictions	References
$p^A(.)p^B(\textsc{Temp})$§	Detection probabilities of southern red-backed voles decrease with average night temperatures. Probabilities of detection of masked shrews are constant.	Although small mammals benefit from positive ambient temperature below 20 °C (Getz 1961; McManus 1974; Cherry and Verner 1975), Chavel et al. (2017a) demonstrated that southern red-backed voles sampled on the same sites were negatively affected by mean nocturnal temperatures.
	Detection probabilities of northern flying squirrels increase with average night temperatures. Detection probabilities of Amerian red squirrels are constant.	Capture success of northern flying squirrels is positively correlated with temperatures (Vernes 2004).

(suite)

Model structure	Predictions	References
$p^{A}(.)p^{B}(.)$§	Detection probabilities for a given species are constant and independent from the presence of the other species.	Squirrel species were sampled at different times of the day. Ground-dwelling species were sampled using different methods.

Notes: Covariate acronyms: CONFIGURATION, distinction between site connected to or included in an undisturbed old-growth forest (CONTROL and LINEARCUT) from retention patches (GREENTREE and POSTFIRE); DWDTOT, total volumes of downed woody debris, regardless of their decay status; EARLYDWD, early decayed downed woody debris; LATEDWD, late decayed downed woody debris; SNAGDENS, density of snags with a dbh larger than 10 cm; TEMP, average night temperatures for each trapping night; TREEDENS, density of live trees with a dbh larger than 10 cm; TYPE, site type (control, post-fire remnant patch, harvest retention patch). Parameters followed by (.) indicate that they are constant.

*Model includes a separate intercept for ψ^{BA} and ψ^{Ba}, but a common slope of the explanatory variable to notify the difference in occupancy by Species B (northern flying squirrel or southern red-backed vole) in the presence or absence of Species A (American red squirrel or masked shrew, respectively).

#Models that are only applied to the pair of American red squirrel and northern flying squirrel.

§Model constrains parameters p^{A} and r^{A} into p^{A}, whereas parameters p^{B}, r^{BA}, r^{Ba} are constrained to p^{B}.

5.4.4.2 Amount of forest at different spatial scales

Building on the top-ranking two-species occupancy models obtained in the assessment of stand scale microhabitat associations (see above), we then quantified the relationship between species co-occurrence and forested areas (i.e. level of area-sensitivity) at each of the 100 spatial scales radius of 0.05 km to 5 km. Here, we focused on the effect of the percent of forested habitat at a given spatial scale on the probability of occupancy of species B when A is present(ψ^{BA}) to reduce convergence issues in the two-species occupancy models. We ran the models iteratively for each spatial scale and extracted the β estimate corresponding to the percent of forest habitat on the ψ^{BA} parameter.

We investigated the patterns of the effect of the percent of forest habitat across the different spatial scales by regressing the β estimates above against the spatial scale. To avoid correlations among consecutive measures of forested areas, we selected a series of β estimates, starting at the β estimates associated with the amount of forested area in the two smallest scales (radii of 0.050 and 0.100 km). We then selected β estimates associated with the amount of forested area in each radius that was the sum of the two preceding radii, i.e. radii of 0.150 km, 0.250 km, 0.400 km, 0.650 km, 1.050 km, 1.700 km, 2.750 km, and 4.450 km. We used this series of ten β estimates in four candidate regressions, according to Desrochers et al. (2010) who described different types of relationships between area-sensitivity and scales at which habitat area is measured, while proposing ecological mechanisms explaining these relationships. The first regression allowed the dependent variable to be constant, and this model tested whether β estimates associated with the amount of forested area at a given scale were independent of the spatial scale. The second regression tested a linear relationship between β estimates and the spatial scale. The third regression tested a quadratic relationship, assuming an optimal radius for patterns of area sensitivity. Finally, we tested a logarithmic relationship between the dependent variable and the circle radii in a fourth regression, using the log of circle radii and hypothesing that β estimates stabilise at larger scales. Regression parameters were estimated by maximum likelihood using generalised least squares with an autoregressive first-order correlation structure implemented in the nlme package (Pinheiro and Bates 2000). We conducted model selection and multimodel inference based on Akaike's Information Criterion for small samples (AIC_c) to compare these four candidate models.

5.5 Results

5.5.1 Small mammal survey

We captured a total of 305 small mammals (142 rodents and 163 shrews - **Appendix 5.9.3**) with a total effort of 2624.5 Sherman trap-nights, 1013.5 Tomahawk trap-nights and 671.5 pitfall trap-nights (7.08 individuals per 100 trap nights, and 42 sites with at least one detection). Four species represented 90.9% of our total captures: masked shrew (*S. cinereus* - 49.5%), southern red-backed vole (*M. gapperi* - 23.6%), American red squirrel (*T. hudsonicus* – 12.5%), and northern flying squirrel (*G. sabrinus* - 5.3%). Other species that were sporadically trapped included in decreasing abundances, deer mouse (*P. maniculatus*), pygmy shrew (*S. hoyi*), eastern heather vole (*Phenacomys ungava*), Arctic shrew (*S. arcticus*), field vole (*Microtus pennsylvanicus*), and smoky shrew (*S. fumeus*).

American red squirrels and northern flying squirrels were detected in 15 and 9 sites, respectively. Auditory methods enabled to detect American red squirrels in five sites where live-trapping did not detect the species. American red squirrels and northern flying squirrels were detected together in 14.3% of the sites where either species was detected (**Appendix 5.9.4**). Masked shrews and southern red-backed were detected in

47 and 23 sites, respectively. Masked shrews and southern red-backed voles were detected together in 40.0% of the sites where either species was detected.

5.5.2 Stand-scale microhabitat associations

A total of only 8 models (out of 33) converged when analysing the southern red-backed vole and masked shrew data. The top-ranked model (41% of the Akaike weight) allowed the occupancy probability of southern red-backed voles to vary with the volumes of early-decayed woody debris and to be different depending on whether masked shrews were present or not (ψ^{BA}(EarlyDwd) and ψ^{Ba}(EarlyDwd)) (**Table 5.2**). In this model, the occupancy probability of masked shrews was constant (ψ^{A}(.)), as were the two detection probabilities considered (p^{A}(.)p^{B}(.)).

Table 5.2 Ranking of conditional single-season, two-species occupancy models for each of the following pairs: 1) American red squirrel (*Tamiasciurus hudsonicus*) and northern flying squirrel (*Glaucomys sabrinus*) and 2) masked shrew (*Sorex cinereus*) and southern red-backed vole (*Myodes gapperi*). Ranking was based on the relative support (wi) of each model. Only models with a $\Delta < 4$ are included in this table.

CANDIDATE MODELS	K	AICc	Δ	Weight (ω)
S. cinereus* and *M. gapperi				
ψ^{A}(.)ψ^{BA}(EarlyDWD)ψ^{Ba}(EarlyDWD) p^{A} (.)p^{B}(.)	7	423.47	0.00	0.41
ψ^{A}(.)ψ^{BA}(.)ψ^{Ba}(.)p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)	8	424.58	1.11	0.24

(suite)

CANDIDATE MODELS	**K**	**AICc**	**Δ**	**Weight (ω)**
$\psi^{A}(.)\psi^{BA}(\text{EarlyDWD})\psi^{Ba}(\text{EarlyDWD})p^{A}(.)p^{B}(\text{Temp})$	8	426.12	2.65	0.11
$\psi^{A}(.)\psi^{B}(\text{Congiguration})p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	9	426.74	3.27	0.08
$\psi^{A}(.)\psi^{B}(\text{EarlyDWD})p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	9	427.15	3.68	0.07
$\psi^{A}(.)\psi^{B}(\text{DWDtot})p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	9	427.32	3.85	0.06
T. hudsonicus* and *G. sabrinus				
$\psi^{A}(.)\psi^{B}(\text{Configuration})p^{A}(.)p^{B}(.)$	6	253.46	0.00	0.19
$\psi^{A}(.)\psi^{BA}(.)\psi^{Ba}(.)p^{A}(.)p^{B}(.)$	5	253.83	0.37	0.14
$\psi^{A}(.)\psi^{B}(\text{LateDWD})p^{A}(.)p^{B}(.)$	6	254.58	1.12	0.10
$\psi^{A}(.)\psi^{B}(\text{DWDtot})p^{A}(.)p^{B}(.)$	6	255.18	1.72	0.07
$\psi^{A}(.)\psi^{B}(\text{EarlyDWD})p^{A}(.)p^{B}(.)$	6	255.36	1.90	0.06
$\psi^{A}(.)\psi^{B}(\text{Configuration})p^{A}(.)p^{B}(\text{Temp})$	7	255.63	2.17	0.06
$\psi^{A}(.)\psi^{B}(\text{Type})p^{A}(.)p^{B}(.)$	7	255.75	2.29	0.05
$\psi^{A}(.)\psi^{BA}(.)\psi^{Ba}(.)p^{A}(.)p^{B}(\text{Temp})$	6	256.00	2.54	0.05

(suite)

CANDIDATE MODELS	**K**	**AICc**	**Δ**	**Weight (ω)**
$\psi^{A}(.)\psi^{B}(\text{SNAGDENS})p^{A}(.)p^{B}(.)$	6	256.23	2.77	0.04
$\psi^{A}(.)\psi^{B}(\text{LATEDWD})p^{A}(.)p^{B}(\text{TEMP})$	7	256.88	3.42	0.03
$\psi^{A}(.)\psi^{BA}(\text{LATEDWD})\psi^{Ba}(\text{LATEDWD})p^{A}(.)$ $p^{B}(.)$	7	257.15	3.69	0.03
$\psi^{A}(.)\psi^{B}(\text{DWDTOt})p^{A}(.)p^{B}(\text{TEMP})$	7	257.41	3.95	0.02

Notes: acronyms: CONFIGURATION, distinction between site connected to or included in an undisturbed old-growth forest (CONTROL and LINEARCUT) from retention patches (GREENTREE and POSTFIRE); DWDTOT, total amount of decayed downed woody debris; EARLYDWD, early decayed downed woody debris; LATEDWD, late decayed downed woody debris; SNAGDENS, density of snags with a dbh larger than 10 cm; TEMP, average night temperatures for each trapping night; TYPE, site type (control, post-fire remnant patch, green-tree retention patch). Parameters followed by (.) indicate that they are constant.

Multimodel inference showed that southern red-backed vole occupancy did not change with EARLYDWD, regardless of the presence of masked shrew (model-averaged estimate, [95% CI]: -0.02, [-0.20, 0.16]). Using values of covariates on ψ^{A}, ψ^{BA}, and ψ^{BA}, extracted from one site characterised by a mean value for each of these covariates, multimodel inference on the species interaction factor showed that the occurrence of the southern red-backed vole was independent of the presence of the masked shrew (model-averaged estimate, [95% CI]: 1.08, [0.90, 1.26]).

A total of 30 models (out of 39) converged when analysing the American red squirrel and northern flying squirrel data. The top-ranked model (19% of the Akaike weight) estimated a single effect of the binary variable "CONFIGURATION" on the occupancy probability of northern flying squirrels regardless of the presence of American red squirrels (Table 2). In this model, the occupancy probability of American red squirrels was constant ($\psi^A(.)$), as were the two detection probabilities considered ($p^A(.)p^B(.)$). This top-ranking model was closely followed by the null model (**Δ** = 0.37). According to multimodel inference, there was no evidence for an effect of isolation on northern flying squirrel occupancy. This species was as likely to occur in sites surrounded by a disturbed matrix than in sites connected or that were part of a continuous old-growth forest (model-averaged estimate, [95% CI]: -0.33, [-1.78, 1.12]). Multimodel inference on the species interaction factor confirmed that the northern flying squirrel and American red squirrel occurred independently (model-averaged estimate, [95% CI]: 1.46, [0.42, 2.51]).

5.5.3 Amount of forest at different spatial scales

From the local to landscape scales, the amount of forest across all sites rapidly dropped from 63% to 40%, then slowly rose to plateau at 56%. The remaining 44% of the buffers included disturbed habitat, different bodies of water, and human infrastructures such as roads and mines (**Figure 5.3a**). A more detailed look at the amount of forest around each of the four site types (CONTROL, POSTFIRE, GREENTREE, and LINEARCUT), revealed that GREENTREE sites had the most severe drop in surrounding habitat amount at the local scale (from 37% to 16 % within the first 200 m) but also reached amounts of habitat similar to CONTROL and

LINEARCUT sites at larger scales, i.e. 59% (**Figure 5.3b**). In contrast, POSTFIRE SITES remained at 46%.

For each pair of species (*G. sabrinus-T. hudsonicus, S. cinereus-M. gapperi),* all 100 two-species occupancy models (1 parameter [(ψ^{BA})] x 100 radii) built to observe changes in occupancy according to the spatial scale converged, except one (radius 1400 m for the *S. cinereus-M. gapperi* pair). Models produced stable β estimates with small standard errors (**Figure 5.4**).

After computing a 95% confidence interval around each β estimate, positive area-sensitivity appeared on the probability of occupancy of northern flying squirrel when American red squirrel was present (ψ^{BA}) at large scales (≥ 3.85 km, **Figure 5.4**). Area-sensitivity on the probability of occupancy of northern flying squirrel when American red squirrel was present increased with radii as the top-ranked regression of beta estimates assumed a quadratic relationship (98% of the Akaike weight), and it was supported by multimodel inference (model-averaged effect size on probability scale: 0.06, 95% CI: [0.04, 0.08]). However, this increase was relatively low, going from an area-sensitivity of 0.007 to an area-sensitivity of 0.066.

On the other hand, a 95% confidence interval around the estimate at each scale suggested a marginal positive area-sensitivity of the probability of occupancy of southern red-backed voles when masked shrews are present, but only at very small scales (≤ 0.15 km). The relationship between β estimates and spatial scale changed from positive to negative above 1.15 km (**Figure 5.4**). Unsurprisingly, we found no area-sensitivity in the beta estimates, as the top-ranked model consisted of only the intercept with 49% of the Akaike weight.

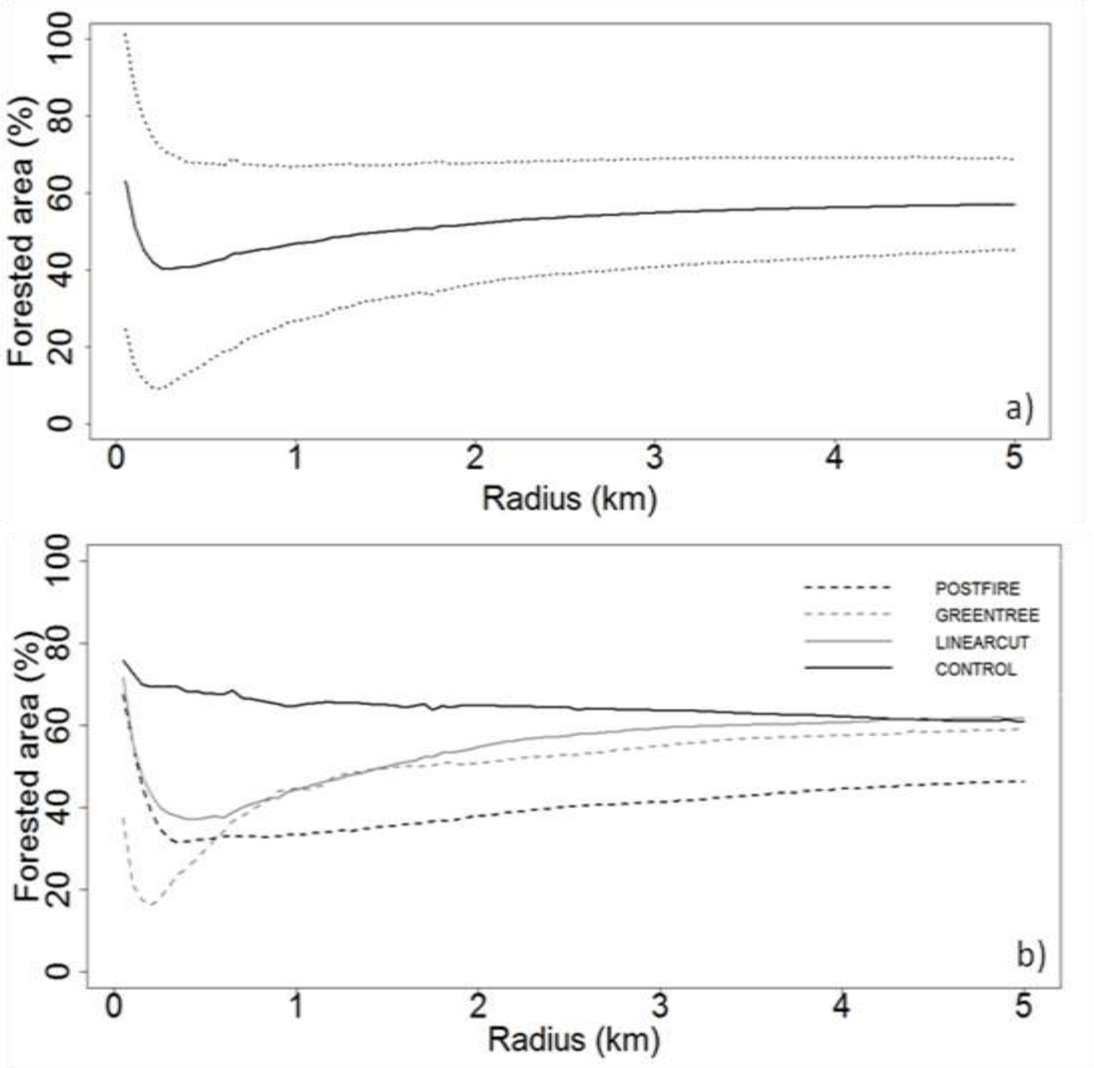

Figure 5.3 Percentage of forest around capture grids (n = 60) in concentric circular areas, with a radius varying from 0.05 to 5 km., a) for all sites and b) according to each site type (CONTROL, old-growth forest; POSTFIRE, post-fire remnant stand; GREENTREE, green-tree retention stand; and LINEARCUT, linear cutblock stands). Dotted lines in a) represent 95% confidence intervals around the arithmetic means.

Focusing on the SIFs, there were slight differences between the two pairs of small mammals under scope. While SIF estimates remained more or less equal to 1 across all scales for the pair of ground-dwelling mammals, they always decreased with increasing amounts of forest for the pair of sciurids (**Figure 5.5**). For both pairs however, the 95% confidence intervals systematically included the value 1 (i.e. showing independence between the two species).

5.6Discussion

In this study, we modelled co-occurrence patterns of American boreal small mammals as a function of the total amount of forest present in the surrounding landscape. There is a growing body of literature focusing on species co-occurrence, patterns that are generally investigated in relation to local habitat variables (Vernes 2003; Gibson and McKenzie 2009; Fauteux et al. 2013). In parallel, the importance of both local and landscape scales in predicting species occurrence in boreal forest landscapes is being increasingly documented (Drapeau et al. 2000, 2016; Brotons et al. 2003; Mönkkönen et al. 2014). To our knowledge, species co-occurrence, and especially small mammal co-occurrence, has not been directly examined as conditional upon habitat variables measured at both local and landscape scales. It is also the first study to use an innovative statistical approach that accounts for imperfect detection probability to apprehend species interactions according to the amount of habitat within disturbed landscapes.

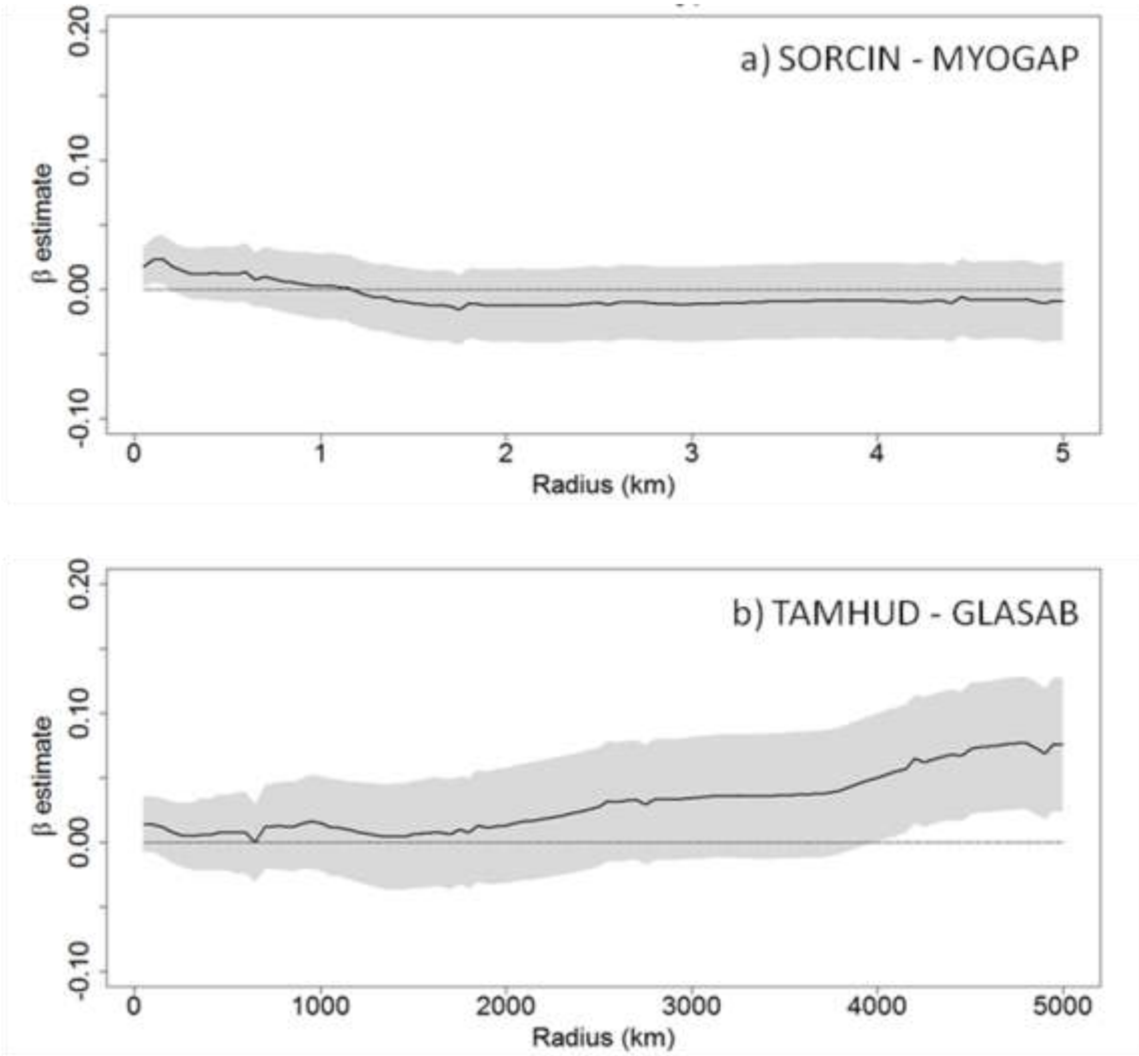

Figure 5.4 Area-sensitivity patterns on co-occurrence of small mammal species. The pairs of species represented on each graph were respectively a) American red squirrel (*Tamiasciurus hudsonicus* - TAMHUD) and northern flying squirrel (*Glaucomys sabrinus* - GLASAB), and b) masked shrew (*Sorex-cinereus* - SORCIN) and southern red-backed vole (*Myodes gapperi* - MYOGAP). Betas estimated for the amount of forested area contained in concentric circles around trapping grids were extracted from conditional single-season, two-species occupancy models where the probability of species B given species A is present (ψ^{BA}) was allowed to vary with the amount of forested area. Shaded area corresponds to the 95% confidence intervals around beta estimates. Acronyms: GLASAB, northern flying squirrel; MYOGAP, southern red-backed vole; SORCIN, masked shrew; TAMHUD, American red squirrel.

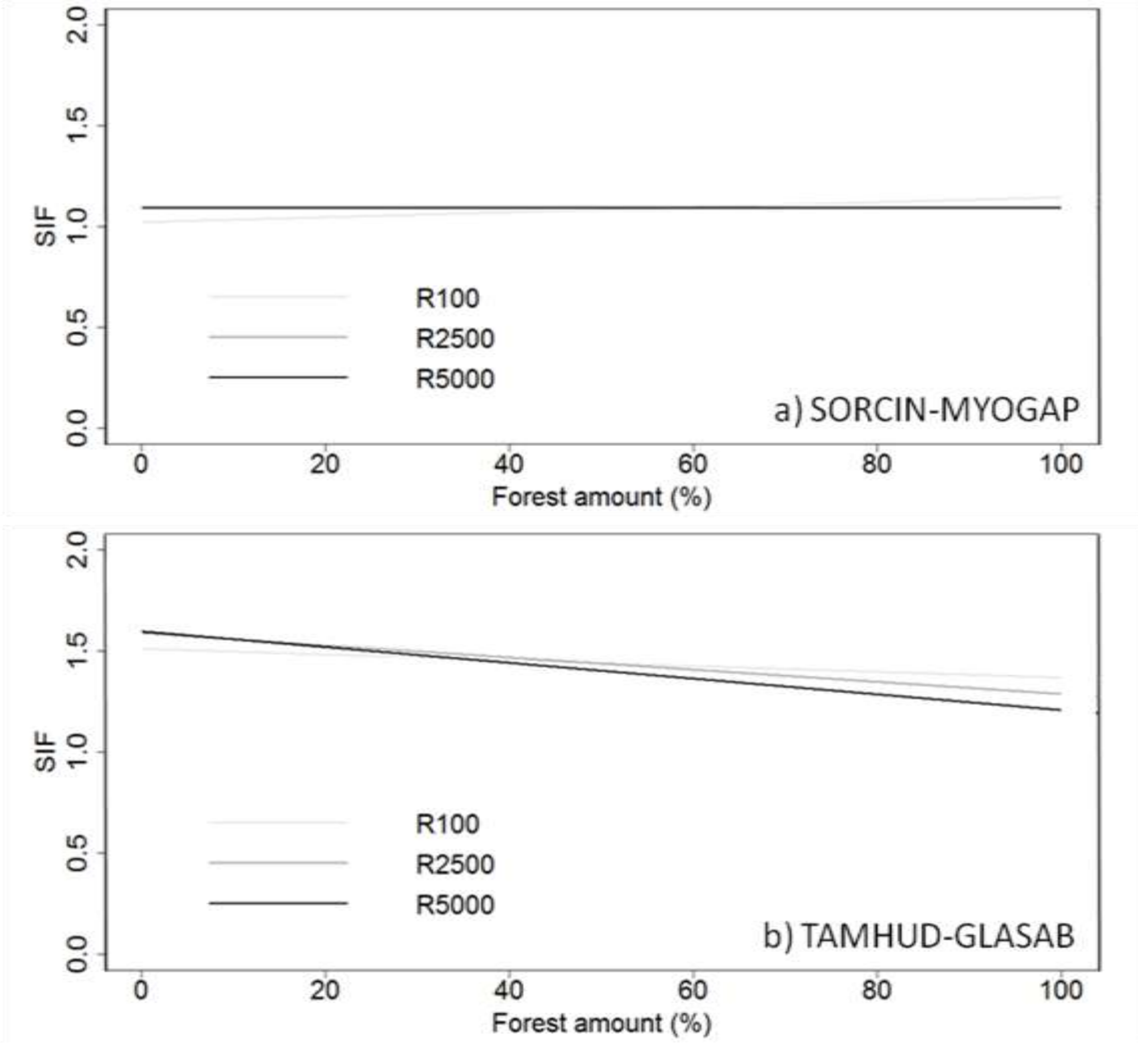

Figure 5.5 Linear regressions of Species Indicator Factors (SIF = ϕ) against the amount of forested areas measured at six radius (R100 = 100 m, R2500 = 2500 m, R5000 = 5000 m), for both pairs of small mammals a) SORCIN (masked shrew, *Sorex cinereus*) - MYOGAP (southern red-backed vole, *Myodes gapperi*) and b) TAMHUD (American red squirrel, *Tamiasciurus hudsonicus*) - GLASAB (northern flying squirrel, *Glaucomys sabrinus*). Note that for the vole-shrew pair, linear regressions corresponding to R2500 et R5000 overlap. 95% confidence intervals around SIF values were not drawn for better graph clarity, but all intervals included the value 1, corresponding to the species dependence/ independence cut-off.

5.6.1 Southern red-backed voles and masked shrews

For these two species of ground-dwelling small mammals, our first hypothesis on factors affecting occupancy at the local scale was not supported. Patch origin (post-fire *vs.* post-harvest) was indeed not a strong predictor of species co-occurrence, but neither was downed woody debris although it has been reported as a critical habitat component for small mammals (Orrock and Pagel 2002; Fauteux et al. 2012; Craig et al. 2014) which is favouring co-occurrence of boreal small mammals species (Fauteux et al. 2013). The lack of association between occupancy or co-occurrence and volumes of downed woody debris is most likely due to the limited range of variation of these habitat structural features in our study sites, as previously reported (Chavel et al. 2017a). Still, we cannot conclude to the absence of an effect of patch origin on species co-occurrence, for two main reasons. First, none of our models that included site type converged when analysing the vole-shrew dataset. The raw data indicated that southern red-backed voles were never sampled on their own in post-harvest sites (both GREENTREE and LINEARCUT stands).

Second, combining data from the two types of post-harvest sites may have diluted the effects of harvesting. Our analyses do not provide answers regarding the suitability of each type of harvesting strategy in sheltering both voles and shrews. Instead, our analyses show that species co-occurrence increases with the amount of habitat at the stand scale, i.e. within the first 200 meters. Coincidentally, GREENTREE stands largely differed with other site types in the amount of habitat that surrounds them (**Figure 5.3b**). Although GREENTREE stands are composed of mature or old-growth forest suitable for southern red-backed voles (according to ecosystem-based management - Merritt 1981; Bergeron et al. 2007), the surrounding amount of habitat is scarce compared to LINEARCUT stands. Based on our area-sensitivity results, we suggest that GREENTREE stands do not offer opportunities for southern red-backed voles to thrive whether the ubiquitous and abundant masked shrew already inhabits or not the area (Whitaker 2004). It is possible that GREENTREE stands are inappropriate for southern red-backed voles, regardless of the presence of masked shrews. Further studies and formal analyses should be carried out to verify this hypothesis, as we could not test it with our data.

5.6.2 Northern flying squirrels and American red squirrels

Our results offered a few leads regarding futures studies on both on sciurid co-occurrence patterns and the northern flying squirrel occurrence. By focusing on the relationship between species co-occurrence and amount of habitat, we found that northern flying squirrel did co-occur with its potential competitor, i.e. the American red squirrel. Indeed, American red squirrels do not appear to exclude northern flying squirrels from sites, despite the general intolerance of squirrels in sharing nesting grounds with other sciurid species (Ackerman and Weigl 1970; Weigl 1978; Smith 2012). This lack of exclusion is most likely due to the adaptability of northern flying squirrels in their nest choice in boreal forests, using either tree cavities, external leaf nests or ground nests (Wells-Gosling and Heaney 1984; Carey et al. 1997; Trudeau et al. 2011). This multiple-use had actually been recently documented in areas about 80 km south of our sites with a preference of northern flying squirrels for leaf and ground nests, including during winter time when individuals are most vulnerable to climatic conditions (Trudeau et al. 2011). Moreover, these two sciurid species occupy different niches in terms of food and activity peaks. Indeed, American red squirrels are mainly granivorous, whereas northern flying squirrels are almost exclusively fungivores (Ferron et al. 1986; Maser et al. 1986; Steele 1998; Lehmkhul et al. 2004). American red squirrels are diurnal, whereas northern flying squirrels are nocturnal (Steele 1998; Wells-Gosling and Heaney 1984).

According to our results, northern flying squirrels are more likely to occupy sites where American red squirrels are also present. Northern flying squirrels are considered old-growth specialists (Wells-Gosling and Heaney 1984). American red squirrels are more generalist and prefer mature forests, but they commonly occur in old-growth stands (Steele 1998; Fisher and Wilkinson 2005). SIF values greater than one but with a 95% confidence including this value, simply reflect sympatry of these two species. American red squirrels do not facilitate northern flying squirrel settlement. Instead, our results suggest that the two species co-exist if they have to, due to reduced amount of habitat in fragmented landscapes. This statement is further confirmed by the decrease in SIF values with increasing amount of habitat.

We suspected that site isolation could be an issue for sciurid species, and especially for northern flying squirrels as they require standing trees to accommodate their gliding mode of locomotion (Flaherty et al. 2008). Habitat connectivity can be a key factor for flying squirrels as their probability of occurrence decreases with open habitat within one kilometer (e.g. Mönkkönen et al. 1997; Smith et al. 2011b). Stand scale analyses suggested that including an explanatory variable such as site isolation, best explained the data collected. Looking at the raw data then, northern flying squirrel were hardly found in GREENTREE stands, i.e. the smallest type of sites and isolated in the disturbed matrix). They are also almost absent from POSTFIRE sites (i.e. isolated sites slightly larger than GREENTREE stands). On the other hand, northern flying squirrels were most abundant in LINEARCUT stands. At the local scale, these sites were not much larger than GREENTREE stands and had as much amount of forests surrounding them as POSTFIRE stands (**Figure 5.3b**). LINEARCUT stands mainly differed by their connection to continuous old-growth forest, although this "connection" is usually beyond the local scale. As flying squirrels are impacted by habitat as far as 6 km away (Ritchie et al. 2009), having LINEARCUT stands connected to old-growth forest, could benefit the species.

At local scale, size and site isolation could impact northern flying squirrels. At larger scales, however, the amount of habitat might be a better predictor of flying squirrel occurrence. Statistical models built to observe the effect of the habitat amount were based on the top-ranking model from the stand-scale analysis. For the pair of sciurids, the top-ranking model included a common slope of the explanatory variable referring to site isolation for northern flying squirrel occupancy (ψ^{BA} and ψ^{Ba}). We therefore included a common slope for the explanatory variable referring to habitat amount. As a result of not having independent parameters describing flying squirrel occurrence in the presence or absence of American red squirrel, we believe that **Figure 5.4** represents northern flying squirrel occurrence rather than sciurid co-occurrence. The results then show that, in addition to being impacted to habitat changes in at larger distances (Ritchie et al. 2009), northern flying squirrels benefit from larger amounts of habitat beyond their dispersal distance (Mönkkönen et al. 1997). Coincidentally, LINEARCUT stands have one of the highest amount of surrounding forest habitat at large scales. One question then comes to mind: are northern flying squirrels more likely to occur in linear cutblock stands because these sites are connected or because they are surrounded by more forest habitat than other sites? This is the heart of the debate on "habitat amount hypothesis vs. size/isolation" (Fahrig 2013; Torrenta and Villard 2017). On one side, spatial configuration (size and isolation) of habitat patches is viewed as a strong predictor of species occurrence and richness. On the other side, habitat amount could replace these two predictor variables (size and isolation) as spatial configuration is believed to be driven by a sample area effect while habitat amount drives species site colonisation and extinction at the landscape scale (Fahrig 2013). Further enquiries are required to answer our question above. Local connected patches, instead of single isolated habitat patches, might represent more adequate spatial units to rely on, when planning ecosystem-based strategies of forest management. A better understanding of northern flying squirrel relationship with landscape habitat variables could support that idea.

5.6.3 Conclusions

Studying area-sensitivity of co-occurrence patterns seems to be a promising approach given the growing interest for scaling community patterns to understand community structure processes (Weiher and Keddy 2001). We aimed at pinpointing the scale at which it would be relevant to study co-occurrence for pairs of species, and determining at which level habitat loss can have a critical impact on species interactions. We first showed that caution should be taken when studying co-occurrence. Pairs of species should be carefully selected for their changes in co-occurrence patterns to offer valid conclusions regarding harvesting strategies and their relevance in maintaining biodiversity. For southern red-backed vole and masked shrew populations, studying occurrence patterns independently (Chavel et al. 2017a) or conjointly as co-occurring species (present study) led to similar conclusions. Squirrels co-occurrence patterns, on the other hand, might be linked to either landscape configuration or the amount of habitat, depending on the study area spatial scale. Our study therefore provides direction for further research on spatial configuration of remnant forested patch within clear-cuts to maintain populations of old-growth specialists. This study also highlights the importance of studying populations at multiple scales before implementing ecosystem-based management strategies.

5.7 Acknowledgements

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5.9 Appendices

5.9.1 Appendix 1

List of 39 dynamic single-season, conditional two-species occupancy models used to assess site co-occurrence (ψ^{BA}) of American red squirrels (*Tamiasciurus hudsonicus*) and northern flying squirrels (*Glaucomys sabrinus*) in black spruce forests of western Quebec, Canada.

Candidate models	**Occupancy (ψ)**	**Detection (*p*)**	**Estimated parameters (K)**
M0	$\psi^{A}(.)\psi^{BA}(.)\psi^{Ba}(.)$	$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	8
M1	$\psi^{A}(.)\psi^{B}(\mathrm{DWDTOT})$	$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	9
M2	$\psi^{A}(.)\psi^{BA}(\mathrm{DWDTOT})$ $\psi^{Ba}(\mathrm{DWDTOT})$	$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	10
M3	$\psi^{A}(.)\psi^{B}(\mathrm{EARLYDWD})$	$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	9
M4	$\psi^{A}(.)\psi^{BA}(\mathrm{EARLYDWD})$ $\psi^{Ba}(\mathrm{EARLYDWD})$	$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	10
M5	$\psi^{A}(.)\psi^{B}(\mathrm{LATEDWD})$	$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	9

(suite)

Candidate models	**Occupancy (ψ)**	**Detection (p)**	**Estimated parameters (K)**
M6	$\psi^{A}(.)\psi^{BA}(\textsc{LateDWD})\psi^{Ba}(\textsc{LateDWD})$	$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	10
M7	$\psi^{A}(.)\psi^{B}(\textsc{SnagDens})$	$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	9
M8	$\psi^{A}(.)\psi^{BA}(\textsc{SnagDens})\psi^{Ba}(\textsc{SnagDens})$	$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	10
M9	$\psi^{A}(.)\psi^{B}(\textsc{Type})$	$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	10
M10	$\psi^{A}(.)\psi^{BA}(\textsc{Type})\psi^{Ba}(\textsc{Type})$	$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	12
M11	$\psi^{A}(.)\psi^{B}(\textsc{Configuration})$	$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	9
M12	$\psi^{A}(.)\psi^{BA}(\textsc{Configuration})\psi^{Ba}(\textsc{Configuration})$	$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	10
M13	$\psi^{A}(.)\psi^{BA}(.)\psi^{Ba}(.)$	$p^{A}(.)p^{B}(.)$	5
M14	$\psi^{A}(.)\psi^{B}(\textsc{DWDtot})$	$p^{A}(.)p^{B}(.)$	6
M15	$\psi^{A}(.)\psi^{BA}(\textsc{DWDtot})\psi^{Ba}(\textsc{DWDtot})$	$p^{A}(.)p^{B}(.)$	7

(suite)

Candidate models	Occupancy (ψ)	Detection (p)	Estimated parameters (K)
M16	$\psi^{A}(.)\psi^{B}(\text{EarlyDWD})$	$p^{A}(.)p^{B}(.)$	6
M17	$\psi^{A}(.)\psi^{BA}(\text{EarlyDWD})$ $\psi^{Ba}(\text{EarlyDWD})$	$p^{A}(.)p^{B}(.)$	7
M18	$\psi^{A}(.)\psi^{B}(\text{LateDWD})$	$p^{A}(.)p^{B}(.)$	6
M19	$\psi^{A}(.)\psi^{BA}(\text{LateDWD})$ $\psi^{Ba}(\text{LateDWD})$	$p^{A}(.)p^{B}(.)$	7
M20	$\psi^{A}(.)\psi^{B}(\text{SnagDens})$	$p^{A}(.)p^{B}(.)$	6
M21	$\psi^{A}(.)\psi^{BA}(\text{SnagDens})$ $\psi^{Ba}(\text{SnagDens})$	$p^{A}(.)p^{B}(.)$	7
M22	$\psi^{A}(.)\psi^{B}(\text{Type})$	$p^{A}(.)p^{B}(.)$	7
M23	$\psi^{A}(.)\psi^{BA}(\text{Type})\psi^{Ba}(\text{Type})$	$p^{A}(.)p^{B}(.)$	9
M24	$\psi^{A}(.)\psi^{B}(\text{Configuration})$	$p^{A}(.)p^{B}(.)$	6
M25	$\psi^{A}(.)\psi^{BA}(\text{Configuration})$ $\psi^{Ba}(\text{Configuration})$	$p^{A}(.)p^{B}(.)$	7

(suite)

Candidate models	**Occupancy (ψ)**	**Detection (p)**	**Estimated parameters (K)**
M26	$\psi^{A}(.)\psi^{BA}(.)\psi^{Ba}(.)$	$p^{A}(.)p^{B}(\text{Temp})$	6
M27	$\psi^{A}(.)\psi^{B}(\text{DWDtot})$	$p^{A}(.)p^{B}(\text{Temp})$	7
M28	$\psi^{A}(.)\psi^{BA}(\text{DWDtot})$ $\psi^{Ba}(\text{DWDtot})$	$p^{A}(.)p^{B}(\text{Temp})$	8
M29	$\psi^{A}(.)\psi^{B}(\text{EarlyDWD})$	$p^{A}(.)p^{B}(\text{Temp})$	7
M30	$\psi^{A}(.)\psi^{BA}(\text{EarlyDWD})$ $\psi^{Ba}(\text{EarlyDWD})$	$p^{A}(.)p^{B}(\text{Temp})$	8
M31	$\psi^{A}(.)\psi^{B}(\text{LateDWD})$	$p^{A}(.)p^{B}(\text{Temp})$	7
M32	$\psi^{A}(.)\psi^{BA}(\text{LateDWD})$ $\psi^{Ba}(\text{LateDWD})$	$p^{A}(.)p^{B}(\text{Temp})$	8
M33	$\psi^{A}(.)\psi^{B}(\text{SnagDens})$	$p^{A}(.)p^{B}(\text{Temp})$	7
M34	$\psi^{A}(.)\psi^{BA}(\text{SnagDens})$ $\psi^{Ba}(\text{SnagDens})$	$p^{A}(.)p^{B}(\text{Temp})$	8
M35	$\psi^{A}(.)\psi^{B}(\text{Type})$	$p^{A}(.)p^{B}(\text{Temp})$	8

(suite)

Candidate models	**Occupancy (ψ)**	**Detection (*p*)**	**Estimated parameters (K)**
M36	$\psi^{A}(.)\psi^{BA}(\text{Type})\ \psi^{Ba}(\text{Type})$	$p^{A}(.)p^{B}(\text{Temp})$	10
M37	$\psi^{A}(.)\psi^{B}(\text{Configuration})$	$p^{A}(.)p^{B}(\text{Temp})$	7
M38	$\psi^{A}(.)\psi^{BA}(\text{Configuration})\ \psi^{Ba}(\text{Configuration})$	$p^{A}(.)p^{B}(\text{Temp})$	8

Note: Covariate acronyms: Configuration, distinction between site connected to or included in an undisturbed old-growth forest (Control and LinearCut) from retention patches (GreenTree and PostFire); DWDtot, total amount of decayed downed woody debris; EarlyDwd, early decayed downed woody debris; LateDwd, late decayed downed woody debris; SnagDens, density of snags with a dbh larger than 10 cm; Temp, average night temperatures for each trapping night; Type, site type (control, post-fire remnant patch, green-tree retention patch). Parameters followed by (.) indicate that they are constant.

5.9.2 Appendix 2

List of 33 dynamic single-season, conditional two-species occupancy models used to assess site co-occurrence (ψ^{BA}) of masked shrews (*Sorex cinereus*) and southern red-backed voles (*Myodes gapperi*) in black spruce forests of western Quebec, Canada.

Candidate models	**Occupancy (ψ)**	**Detection (*p*)**	**Estimated parameters (K)**
M0	$\psi^{A}(.)\psi^{BA}(.)\psi^{Ba}(.)$	$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	8
M1	$\psi^{A}(.)\psi^{B}$(DWDtot)	$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	9
M2	$\psi^{A}(.)\psi^{BA}$(DWDtot) ψ^{Ba}(DWDtot)	$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	10
M3	$\psi^{A}(.)\psi^{B}$(EarlyDWD)	$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	9
M4	$\psi^{A}(.)\psi^{BA}$(EarlyDWD) ψ^{Ba}(EarlyDWD)	$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	10
M5	$\psi^{A}(.)\psi^{B}$(LateDWD)	$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	9
M6	$\psi^{A}(.)\psi^{BA}$(LateDWD) ψ^{Ba}(LateDWD)	$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	10
M9	$\psi^{A}(.)\psi^{B}$(Type)	$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	10

(suite)

Candidate models	Occupancy (ψ)	Detection (*p*)	Estimated parameters (K)
M10	$\psi^{A}(.)\psi^{BA}(\text{Type})\psi^{Ba}(\text{Type})$	$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	12
M11	$\psi^{A}(.)\psi^{B}(\text{Configuration})$	$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	9
M12	$\psi^{A}(.)\psi^{BA}(\text{Configuration})$ $\psi^{Ba}(\text{Configuration})$	$p^{A}(.)p^{B}(.)r^{A}(.)r^{BA}(.)r^{Ba}(.)$	10
M13	$\psi^{A}(.)\psi^{BA}(.)\psi^{Ba}(.)$	$p^{A}(.)p^{B}(.)$	5
M14	$\psi^{A}(.)\psi^{B}(\text{DWDtot})$	$p^{A}(.)p^{B}(.)$	6
M15	$\psi^{A}(.)\psi^{BA}(\text{DWDtot})$ $\psi^{Ba}(\text{DWDtot})$	$p^{A}(.)p^{B}(.)$	7
M16	$\psi^{A}(.)\psi^{B}(\text{EarlyDWD})$	$p^{A}(.)p^{B}(.)$	6
M17	$\psi^{A}(.)\psi^{BA}(\text{EarlyDWD})$ $\psi^{Ba}(\text{EarlyDWD})$	$p^{A}(.)p^{B}(.)$	7
M18	$\psi^{A}(.)\psi^{B}(\text{LateDWD})$	$p^{A}(.)p^{B}(.)$	6
M19	$\psi^{A}(.)\psi^{BA}(\text{LateDWD})$ $\psi^{Ba}(\text{LateDWD})$	$p^{A}(.)p^{B}(.)$	7

(suite)

Candidate models	**Occupancy (ψ)**	**Detection (*p*)**	**Estimated parameters (K)**
M22	$\psi^{A}(.)\psi^{B}(\text{Type})$	$p^{A}(.)p^{B}(.)$	7
M23	$\psi^{A}(.)\psi^{BA}(\text{Type})\psi^{Ba}(\text{Type})$	$p^{A}(.)p^{B}(.)$	9
M24	$\psi^{A}(.)\psi^{B}(\text{Configuration})$	$p^{A}(.)p^{B}(.)$	6
M25	$\psi^{A}(.)\psi^{BA}(\text{Configuration})$ $\psi^{Ba}(\text{Configuration})$	$p^{A}(.)p^{B}(.)$	7
M26	$\psi^{A}(.)\psi^{BA}(.)\psi^{Ba}(.)$	$p^{A}(.)p^{B}(\text{Temp})$	6
M27	$\psi^{A}(.)\psi^{B}(\text{DWDtot})$	$p^{A}(.)p^{B}(\text{Temp})$	7
M28	$\psi^{A}(.)\psi^{BA}(\text{DWDtot})$ $\psi^{Ba}(\text{DWDtot})$	$p^{A}(.)p^{B}(\text{Temp})$	8
M29	$\psi^{A}(.)\psi^{B}(\text{EarlyDWD})$	$p^{A}(.)p^{B}(\text{Temp})$	7
M30	$\psi^{A}(.)\psi^{BA}(\text{EarlyDWD})$ $\psi^{Ba}(\text{EarlyDWD})$	$p^{A}(.)p^{B}(\text{Temp})$	8
M31	$\psi^{A}(.)\psi^{B}(\text{LateDWD})$	$p^{A}(.)p^{B}(\text{Temp})$	7

(suite)

Candidate models	**Occupancy (ψ)**	**Detection (*p*)**	**Estimated parameters (K)**
M32	$\psi^{A}(.)\psi^{BA}$(LateDWD) ψ^{Ba}(LateDWD)	$p^{A}(.)p^{B}$(Temp)	8
M35	$\psi^{A}(.)\psi^{B}$(Type)	$p^{A}(.)p^{B}$(Temp)	8
M36	$\psi^{A}(.)\psi^{BA}$(Type)ψ^{Ba}(Type)	$p^{A}(.)p^{B}$(Temp)	10
M37	$\psi^{A}(.)\psi^{B}$(Configuration)	$p^{A}(.)p^{B}$(Temp)	7
M38	$\psi^{A}(.)\psi^{BA}$(Configuration) ψ^{Ba}(Configuration)	$p^{A}(.)p^{B}$(Temp)	8

Note: Covariate acronyms: Configuration, distinction between site connected to or included in an undisturbed old-growth forest (Control and LinearCut) from retention patches (GreenTree and PostFire); DWDtot, total amount of decayed downed woody debris; EarlyDWD, early decayed downed woody debris; LateDWD, late decayed downed woody debris; SnagDens, density of snags with a dbh larger than 10 cm; Temp, average night temperatures for each trapping night; Type, site type (control, post-fire patch, green-tree retention patch). Parameters followed by (.) indicate that they are constant.

5.9.3 Appendix 3

Summary of captures of different mammal species at the sites in black spruce forests of western Quebec.

Mammalian species	**August 2014**		
	Sherman	Tomahawk	Pitfall
Glaucomys sabrinus	6	10	0
Tamiasciurus hudsonicus	2	36	0
Myodes gapperi	72	0	0
Microtus pennsylvanicus	1	0	0
Peromyscus maniculatus	11	0	0
Phenacomys ungava	4	0	0
Sorex cinereus	12*	0	151
Sorex hoyi	0	0	7
Sorex arcticus	0	0	4
Sorex fumeus	0	0	1

Note: *individuals not included in analyses

5.9.4 Appendix 4

Number of sites reported with at least one detection, given by site type and whether species were seen alone or co-occurring. Species trapped in black spruce forests of western Quebec, Canada, were American red squirrels (*Tamiasciurus hudsonicus*), northern flying squirrels (*Glaucomys sabrinus*), masked shrew (*Sorex cinereus*) and southern red-backed vole (*Myodes gapperi*).

Site type (/no of sites sampled)	**Species A**	**Species B**	**Both species**
American red squirrel (Species A) and northern flying squirrel (Species B)			
CONTROL (/15)	3	1	0
POSTFIRE (/15)	3	0	1
GREENTREE (/15)	3	0	1
LINEARCUT (/15)	3	5	1
TOTAL (/60)	12	6	3

Site type **(/no of sites sampled)**	**Species A**	**Species B**	**Both species**
Masked shrew (Species A) and southern red-backed vole (Species B)			
CONTROL (/15)	4	1	7
POSTFIRE (/15)	2	2	8
GREENTREE (/15)	10	0	3
LINEARCUT (/15)	11	0	2
TOTAL (/60)	27	3	20

Note: Site type acronyms: CONTROL, control (old-growth forest); GREENTREE, green-tree retention patch; LINEARCUT, linear cutblock separator; POSTFIRE, post-fire remnant patch.

CHAPITRE VI

CONCLUSION GÉNÉRALE

"*Le concept [d'aménagement écosystémique] est complexe [...] il requiert la prise en compte de nombreuses caractéristiques qui peuvent varier selon les régions et en fonction de l'échelle spatiale ou temporelle*" (J.W.Fyles 2008).

Le travail présenté ici s'inscrit dans ces lignes. Nous avons cherché à comprendre la dynamique de population de micromammifères, plus particulièrement leur occurrence, en considérant la pluralité des échelles spatiales dans lesquelles ces espèces évoluent. De manière plus audacieuse, nous nous sommes basés sur l'échantillonnage de populations en période de faible densité en espérant pointer :

1. les attributs de structure et de composition du peuplement critique à leur maintien et,
2. les conséquences pour les micromammifères qu'occasionne une perte d'habitat dans le paysage.

6.1 Chapitres théoriques *vs* chapitre méthodologique

Dans le cadre de cette thèse, nous avons souhaité baser nos analyses sur des modèles statistiques récents (modèles d'occupation dynamique) qui incluent, entre autres, un paramètre de détection (MacKenzie et al. 2006). Lors d'un échantillonnage, le nombre de sites occupés est nécessairement sous-estimé, et le degré de cette sous-estimation dépend des caractéristiques de l'habitat, des conditions d'échantillonnage mais également de la méthode d'échantillonnage employée (MacKenzie et al. 2003; MacKenzie 2006). Le paramètre de détection permet alors de corriger cette sous-estimation en utilisant les informations extraites d'observations répétées. Néanmoins, cette correction ne remplace pas l'utilisation d'un protocole d'échantillonnage adapté qui minimise avec précision les non-détections, permettant alors des analyses d'autant plus robustes.

Dans le chapitre III de ce mémoire, nous avons voulu explorer la fiabilité de plusieurs protocoles d'échantillonnage de l'écureuil roux d'Amérique. Il révèle ainsi que pour étudier l'occurrence de ce sciuridé (et strictement l'occurrence), les méthodes auditives (point d'écoute et repasse) permettent de détecter aussi efficacement la présence d'individus que la méthode plus traditionnelle de capture vivante, et ce, malgré les différences d'effort et de procédés écologiques impliqués par ces méthodes (Burton et al. 2015). Ce résultat implique alors que l'occurrence de l'écureuil roux et les problématiques associées peuvent être étudiées de manière plus intensives et extensives, sans la lourdeur logistique et financière associée à la capture vivante, grâce à de simples données binaires de présence/absence et les nouveaux modèles statistiques développés pour ce type d’historiques de détection. Ce chapitre, loin des question de quantité d'habitat et dynamique de populations, nous a cependant permis d'explorer l'aspect méthodologique qui nous semblait important dans le cadre de cette thèse doctorale. Ils'agit également d'une contribution méthodologique à la portée plus large en écologie animale que le seul domaine de l'étude des mammifères. En effet, l'écureuil roux d'Amérique est un prédateur de nid de passereaux. Etudier la co-occurrence d'espèces aviaires avec ce mammifère en utilisant des méthodes d'échantillonnage communes à ces espèces est dorénavant encouragé.

6.2 Ilots de rétention et échelle du peuplement

Pour ancrer notre étude, nous avons choisi le contexte de la forêt boréale québécoise où la flore, dominée par les épinettes noires, les bryophytes et les éricacées, subit régulièrement les perturbations associées aux grands feux de forêt (Payette 1992; Bergeron et al. 2004). Puisque l'ambition principale de l'aménagement écosystémique au Québec est d'exploiter durablement les ressources sylvicoles tout en maintenant la biodiversité et la fonctionnalité des écosystèmes forestiers (Gauthier et al. 2008 ; Grenon et al. 2010), la coupe avec protection de la régénération et des sols (CPRS) devrait s'inspirer des patrons de paysage générés par les grand feux (Bergeron et al. 2007; Simard et al. 2008). Hors, à leur implémentation, ces types d'aménagement encore largement pratiqués, s'inspiraient non pas des feux et des patrons qu'ils dessinaient à grande échelle, mais à leurs effets à l'échelle du peuplement, prélévant en une seule récolte la majorité du couvert forestier Cet aménagement dessina au sein des parterres de coupe des bouquets et des îlots d'arbres (nommés GREENTREE dans le manuscrit pour leur appellation anglaise "green-tree retention stands") dans la vicinité de séparateurs de coupe (appellation anglaise "linear cut-block separators", abrégé dans le manuscrit sous LINEARCUT), soit des corridors d'arbres de forêt mature ou âgée. Cette rétention, et plus particulièrement la rétention linéaire des séparateurs de coupe, était alors définie comme provisoire, puisqu’une option de récolte pouvait être mise dès lors que les parterres de coupes alentours atteignaient trois mètres de hauteur.

En positionnant nos grilles de capture à la fois dans ces deux types de sites aménagés (GREENTREE et LINEARCUT) et dans des îlots résiduels post-feu (POSTFIRE, d'après "post-fire retention stands" selon l'appellation anglaise), nous avons pu les comparer directement entre eux, ainsi qu'aux vieilles forêts (CONTROL), habitat de prédilection pour des espèces indicatrices de ce milieu telles que le campagnol à dos roux de Gapper et le grand polatouche (Merritt 1981; Weigl 2007). Cette approche nous a alors permis de montrer que :

1. des espèces forestières généralistes et opportunistes telles que l'écureuil roux d'Amérique et la musaraigne cendrée occupaient ces quatre types de sites, et ceci indépendamment des variables environnementales mesurées dans cette thèse pour caractériser localement les peuplements (Chapitre IV).

2. le campagnol à dos roux de Gapper, quant à lui, ne profite pas des îlots post-coupe, quelque soit la disponibilité des attributs structurels reconnus pour être critiques au maintien de l'espèce (ChapitreIV). Bien que cela n'aie pas été formellement analysé par manque de données, une observation similaire se fait par rapport au grand polatouche. De plus, il semblerait que ces îlots, quatre fois plus petis en moyenne que les îlots post-feu, ne présenteraient pas suffisamment d'habitat forestier dans leur vicinité pour maintenir localement ces deux espèces (Chapitre V).

3. des espèces de milieux ouverts tels que le campagnol des champs (*Microtus pennsylvanicus*) n'ont pas envahi les plus petits sites de forêt résiduelle dans lesquels nous les avons échantillonnés. Cette observation, bien qu'absente de nos trois chapitres, est un résultat en soi, et indiquerait que l'aménagement CPRS ne favorise pas ces espèces caractéristiques des milieux ouverts qui ont le potentiel de limiter l'occupation des sites par les espèces forestières tel que le campagnol à dos roux de Gapper (Grant 1969). Ce résultat, en revanche, nous a néanmoins contraints à revoir l'organisation de cette thèse dès la première année, pour ainsi transformer un des chapitres initiaux reposant sur la présence des espèces de milieux ouverts en un chapitre méthodologique.

Aménager des îlots résiduels dans la gamme de taille étudiée ne permettrait donc pas de maintenir dans un peuplement récolté des espèces spécialisées, contrairement aux séparateurs de coupes, qui toutefois ne reproduisent pas les conditions "insulaires" des peuplements épargnés par les grands feux de forêt. En théorie, les îlots résiduels post-coupe constitueraient des refuges et sources de recolonisation d'un paysage récolté (Grenon et al. 2010; Robinson et al. 2013). Notre constat, qui va en l'encontre de cette théorie, a aussi été rapporté dans des études conjointes à notre projet qui affirment que plusieurs espèces de bryophytes échantillonnées ne se retrouvent pas dans des îlots, qu'ils soient des îlots post-feu ou post coupe (Castonguay 2016; Barbé et al. 2017). Ainsi le méta-projet dans lequel cette thèse s'intègre soulève encore plusieurs questions : est-ce une question de structure interne de l'îlot post-coupe (en lien avec un âge de peuplement potentiellement plus jeune au sein de ces îlots résiduels)? Sa taille a-t-elle un effet (les îlots post-coupe étant généralement plus petits que les autres habitats résiduels)? Son emplacement dans le parterre de coupe a-t-il un effet (isolation)? Ou une combinaison de ces trois facteurs explique-t-elle mieux les patrons observés?

Plusieurs études se sont déjà appliquées à identifier les ressources critiques pour le maintien des micromammifères. L'une d'entre elles est la disponibilité du bois mort, et plus particulièrement du bois mort dégradé (Fauteux et al. 2012; Craig et al. 2014). Curieusement, cette variable n'a pas été retenue dans les modèles de notre étude. Il est vrai que les quantités échantillonnées étaient majoritairement en-dessous de celles rapportées dans d'autres études (Moseley et al. 2008; Sullivan and Sullivan 2012; Craig et al. 2014), occultant peut-être l'importance de cette ressource d'un point de vue statistique. Cependant, nous soupçonnons aussi que pour nos îlots post-coupe, les quantités de bois mort en dehors des îlots fournissaient une ressource de choix pour les soricidés et critecidés. Rappelons que musaraignes et campagnols (dont le campagnol à dos roux de Gapper) utilisent les matrices perturbées (naturellement ou suite à une coupe - Hayward et al. 1999; Fisher and Wilkinson 2005; Zwolak 2009). Il ne serait pas illogique de penser que de grosses quantités de bois mort dans le pourtour des petits îlots de coupe entraînent le déplacement des individus du centre de ces peuplements résiduels vers la matrice récoltée adjacente aux îlots. Nous proposons qu'une étude soit réalisée pour formellement vérifier formellement cette hypothèse.

Les questions de taille et d'emplacement des îlots demandent, quant à elles, des études à l'échelle du paysage, échelle rarement exploitée lorsque l'espèce focale est un micromammifère à faible capacité de dispersion. Cependant, comprendre les effets de la configuration spatiale des îlots sur les petits mammifères présente l'opportunité de s'inscrire dans un débat récent, opposant les variables prédictives traditionnelles d'aire et d'isolement à la quantité d'habitat (Fahrig 2013; Rybicki et Hanski 2013). Il s'agirait alors d'échantillonner la communauté de petits mammifères d'îlots de taille différentes et plus ou moins isolés dans la matrice perturbée, et de modéliser l'occurrence des espèces ainsi que la richesse de leur communauté selon ces deux variables. Nous confronterions alors des modèles d'occupation tenant des tailles et isolements d'ilôts à des modèles qui tiendraient principalement compte de la quantité d'habitat mesurée à une échelle fixe (Torrenta et Villard 2017).

6.3 Occurrence de population, quantité d'habitat et échelles spatiales

La quantité de l'habitat est reconnue pour exercer une influence positive sur la taille des populations, le taux de reproduction, la présence des espèces et par conséquent, la biodiversité présente dans les paysages fragmentés (Robbins 1979; Fahrig 2003). Cependant, nous nous sommes posé la question à savoir si certains mécanismes (occurrence, compétition) qui organisent les communautés pourraient eux-mêmes être considérés comme dépendants de la quantité d'habitat dans le paysage. Poussés par l'étude innovante de Ritchie et collègues (2009) qui démontrait que les écureuils volants pouvaient être impactés par l'état de la forêt en-dehors de leur domaine vital, nous avons souhaité comprendre quels impacts pouvaient avoir la quantité d'habitat d'un paysage perturbé sur ces mécanismes régulateurs de populations et à quelle échelle ils opéraient. Cet objectif s'est alors précisé à la lecture de Desrochers et al. (2010) qui s'appliqua à définir les courbes de sensibilité à la quantité d'habitat de différentes espèces selon les mécanismes régulateurs de populations.

Dans le chapitre IV, nous nous sommes donc penchés sur des mécanismes intraspécifiques tels que l'occupation, la colonisation et le départ (extinction locale) de site, tandis que la compétition interspécifique était au cœur du chapitre V. Un des résultats les plus marquants a été la mise en évidence d'une relation négative entre l'occupation de site et la quantité d'habitat disponible dans le paysage, et ceci quelque soit l'échelle à laquelle nous nous placions (Chapitre IV). L' "area-sensitivity", nom communément employé par la communauté scientifique pour parler de cette relation à la quantité d'habitat (Robbins 1979), est principalement rapporté comme une relation positive : plus il y a d'habitat disponible, plus la population étudiée s'épanouit. Seules quelques études présentent des résultats négatifs et aucune ne se penche sur la signification de cette relation (ex. Desrochers et al. 2010). Dans notre cas, et en ce qui concerne l'occupation de site, une explication nous vient immédiatement à l'esprit. La relation nous renseignerait-elle sur la répartition spatiale des individus ? Ainsi une relation négative pourrait indiquer que cette répartition serait suffisamment vaste pour que nous ne puissions échantillonner la population avec une grille relativement petite de 15 m par 15 m qui recouvre une aire inférieure aux domaines vitaux des petits mammifères strictement terrestres échantillonnés (Blair 1941 ; Lackey et al. 1985 ; Whitaker 2004). Un moyen de vérifier cette hypothèse serait alors d'étudier la relation avec des grilles d'échantillonnage de différentes surfaces. Il serait alors intéressant, dans un contexte d'aménagement écosystémique, de rapporter des éventuels changements de répartition en fonction des types de sites, conjointement avec l'étude proposée dans le paragraphe 1.

Néanmoins, rappelons que la répartition est, d'un point de vue comportemental, fonction de l'abondance (Fretwell 1969). Nous avons échantillonné les populations de micromammifères de faible densité (Fauteux et al. 2015), ce qui conduit à l'hypothèse suivante : l' "area-sensitivity", en plus d'être spatialement dépendante, ne serait-elle pas aussi densité-dépendante ? Plus encore, la relation négative que nous avons rapportée, pourrait-elle évoluer avec des changements de densité qu'occasionnent par exemple les cycles de populations de certaines espèces de micromammifères (Krebs 2013) ?

Le chapitre V, quant à lui, a tenté de comprendre les relations de co-occurrence entre deux espèces en fonction de la quantité d'habitat. Bien que plusieurs mécanismes peuvent expliquer les relations de co-occurrence et peuvent être plus ou moins prévalents selon les quantités d'habitat disponibles, ce chapitre n'avait pas la prétention de les différentier ni même de souligner lequel de ces mécanismes prédominait sur les relations de co-occurrence entre petits mammifères. Nous n'avons donc pas pu déterminer l'impact de la compétition interspécifique pour des resources (Fauteux et al. 2013), de la prédation entre petits mammifères (Eadie 1952; Getz et al. 1992 Liesenjohann et al. 2011), des comportements d'aggression (Turner et al. 1975 ; Myllymaki 1977 ; Eccard and Ylönen 2003 ; Smith 2012), ni même d'une compétition apparente (Norrdahl and Korpimäki 1993; Schmidt et al. 2005).

En revanche, les résultats principaux nous montre que les associations d’espèces sont corrélées à plusieurs échelles spatiales. D'un côté, le campagnol à dos roux de Gapper semble attaché à l'échelle locale (ce qui corrobore avec les résultats du chapitre IV), et, malgré qu'il puisse utiliser une matrice perturbée, préfère une plus grande quantité de forêt dans des distances équivalentes à celle de sa dispersion. En revanche, le grand polatouche se retrouve à des sites, semble-t-il connectés à la vieille forêt, et qui à l'échelle du paysage, comportent autant d'habitat à l’échelle du paysage que les vieilles forêts continues. Tout comme Ritchie et al. (2009), nous confirmons donc que les écureuils volants, malgré leur capacité de dispersion restreinte, sont impactés par le paysage situé au-delà de leurs domaines vitaux.

6.4 Limites de l'étude

Une des forces de cette études réside dans la taille de notre échantillonnage, soit un total de 60 sites, considérés comme indépendants, de quatre origines différentes ($n_{\text{témoins}}$ = 15, $n_{\text{îlotspostfeu}}$ = 15, $n_{\text{îlotspostcoupe}}$ = 15, $ns_{\text{éparateurs}}$ = 15). Moins de 20 sites sont généralement sélectionnés pour l'étude des populations d'écureuils (revue de littérature associée à l'Annexe 1 du Chapitre III) alors que pour les micromammifères de type campagnol, moins de 10 sites sont généralement utilisés (ex : Andreassen and Ims 2001; Keinath and Hayward 2003; Sullivan and Sullivan 2012).

Cependant nous nous sommes appuyés sur des analyses statistiques complexes qui exigeaient de contraindre le nombre de variables pouvant être introduites dans les modèles, et ce, malgré notre fort effectif par rapport aux autres études habituellement réalisées sur les petits mammifères. Un nombre plus élevé de sites aurait donc permis de préciser certains intervalles de confiance tout en augmentant le poids donné aux inférences et d'autre part autoriser l'ajout de variables, notamment au chapitre V. En effet les modèles utilisés dans ce chapitre comptent à eux seuls huit paramètres, ce qui limitait à 5 (dans certains cas jusqu'à 10) l'ajout de variables explicatives d'après le nombre de sites échantillonnés.

Un plus grand effectif aurait également permis de contrôler certains biais introduits par le choix des sites. En effet, il aurait par exemple été souhaitable de comparer des îlots de taille similaire. Avec des îlots post-coupe généralement plus petits que des îlots post-feu, nous avons pu introduire des effets de bordure, que nous n'avons pu contrôler dans notre modélisation. Le temps écoulé depuis la dernière perturbation constitue sans doute un autre biais important puisque certains petits mammifères, y compris des spécialistes comme le campagnol à dos roux de Gapper, peuvent utiliser la matrice en régénération. Globalement, la matrice autour de nos îlots post-coupe était plus jeune de 20 ans en moyenne que celle des îlots post-feu, or 20 ans est précisément un laps de temps qui différencie la colonisation de la matrice par certaines espèces, dont l'écureuil roux d'Amérique (Allard-Duchêne et al. 2014). Cette dernière étude rapporte donc une utilisation "précoce" de l'habitat post-coupe par rapport à l'habitat post-feu. En quoi alors, comparer des îlots post-coupe à des îlots post-feu dont les matrices ont 20 ans d'écart pourrait-être compromettant ? Le problème vient de la différence de dynamique des populations dans ces deux types de matrices. Alors que dans le contexte d'une perturbation naturelle, la recolonisation de la matrice et donc la dynamique des îlots de rétention se cale sur la succession secondaire et les associations spécifiques qu'ont les espèces animales à des habitats (Fox 1990), dans un contexte post-coupe, de nombreux écarts au scénario "naturel" s'observent. Notamment, les abondances sont plus fortes en matrices post-coupe, et des espèces de vieilles forêts peuvent se retrouver dans les premiers stades de succession (Fisher and Wilkinson 2005). A cause de ces différences de dynamique, nous recommandons donc, pour éviter tout biais "temporel", de comparer des îlots de matrices de même âge.

L'approche comparative directe entre des sites perturbés naturellement ou suite à un aménagement forestier représente une autre force. Cependant, nos sites n'appartiennent pas au même massif forestier, ce qui pourrait représenter une autre limite de la présente étude, pour des raisons de dynamiques forestières propres à chaque massif (Houllier et al. 1991). Par exemple, nous avons constaté que nous n'avions pas des volumes de débris de bois mort équivalent à d'autres études.

Finalement, nous préconisons un échantillonnage à plus long terme et, si possible en automne. Certains petits mammifères sont connus pour leur cycle de population (Krebs 2013), comme le campagnol à dos roux de Gapper que nous avons échantillonné pendant les phases creuse et ascendante de son cycle. Cette faible densité a pu affecter les réponses spécifiques des petits mammifères aux questions que nous nous sommes posées. Nous avons également échantillonné en été. Certaines espèces ont des pics de dispersion en automne, et à nouveau, les relations entre l'occurrence et la quantité d'habitat peuvent varier en fonction de la saison.

6.5 Perspectives et aménagement CPRS

Comprendre le rôle des îlots résiduels dans le maintien de la biodiversité après une perturbation, qu'elle soit d'origine naturelle ou anthropique, a motivé la collaboration entre plusieurs directeurs de recherche et étudiants. En regroupant alors les résultats de trois thèse doctorales et un mémoire de maîtrise, nous comprenons que l'aménagement en grandes agglomérations de coupe de type CPRS avec rétention de bouquets ou d'îlots est loin de s'inscrire pleinement dans une stratégie d'aménagement écosystémique.

Notamment, le recrutement du bois mort (ressource critique pour les petits mammifères et plusieurs autres espèces fauniques et florales) diffère selon la taille des îlots résiduels post-perturbation, ne permettant pas à ces îlots de jouer un rôle d'habitat refuges pour les petits mammifères et la biodiversité lorsque ces derniers sont trop petits car ils ne maintiennent pas leurs caractéristiques d'habitat (Moussaoui et al. 2016; Moussaoui 2017). En effet, plus la taille des îlots diminue, plus ces îlots sont vulnérables aux vents jusqu'en leur cœur. De moins en moins de bois mort est alors disponible avec les années, ne favorisant pas l'occupation de ces îlots par la biodiversité (petits mammifères et bryophytes) associée aux différentes structures de vielles forêts, dont le bois mort (Craig et al. 2014; Barbé 2017).

Les îlots naturels ou aménagés sont perçus comme des refuges et sources de recolonisation (Grenon et al. 2010; Robinson et al. 2013). Cependant, cette thèse comme celle consacrée aux bryophytes en îlots post-feu (Barbé et al. 2017) ont démontré que ce n'était pas toujours le cas. En effet, si les îlots de rétention ne sont pas des refuges de biodiversité, les îlots post-feu sont néanmoins au cœur de la dynamique de recolonisation d'un milieu perturbé pour les bryophytes. Dans le cas des petits mammifères qui ont une recolonisation de la matrice perturbée plus tardive que les bryophytes, les îlots de rétention, et principalement les îlots de rétention en parterre de coupe, ne constituent ni refuge ni source de recolonisation. Au mieux, ils pourraient représenter une halte dans la recolonisation progressive de la matrice coupée depuis des sites de vielles forêts ou des réels sites refuges comme les séparateurs de coupe. Au niveau local, encourager le maintien de séparateurs de coupe et d'îlots résiduels de grande taille (Moussaoui 2017), avec une complexité structurale modérée (Barbé 2017), et de maintenir des longs cycles de coupe (Catonguay 2016), permettrait alors de maintenir des habitats-sources pour la recolonisation du milieu perturbé, sources qui ne tariraient pas puisque les îlotsmaintiendraient leur caractéristiques structurales au cours de nombreuses années. Le redimensionnement à la hausse des îlots représenterait alors aussi une augmentation de la quantité d'habitat forestier (Chavel et al. 2017), quantité qui semblerait ne pas être comprise dans la variabilité naturelle de l'écosystème définie par les perturbations naturelles (Bergeron et al. 2007). Comme nous l'avons vu dans notre travail, la quantité d'habitat joue un rôle clef sur les dynamiques de populations des petits mammifères et ne doit par conséquent, être négligée si les CPRS îlots ont pour vocation de s'inscrire dans l'aménagement écosystémique. Dans un contexte où les îlots aménagés ne pourraient pas voir leur taille augmenter, nous encourageons alors une réduction des tailles de parterres de coupe, toujours entourés de séparateurs de coupe, et de rapprocher les parcelles de rétention les unes des autres pour augmenter la quantité totale de forêt dans la vicinité des îlots.

Grâce à nos travaux, étudiants et comités directeurs avons ébauché des pistes à suivre pour améliorer la stratégie d'aménagement de type CPRS bouquets ou îlots. Nous avons démontré qu'il ne fallait pas se cantonner à notre point de vue "humain" sur ces soi-disant espèces à "capacité de dispersion réduite" qui en réalité sont sensibles à des échelles allant bien au-delà de leur domaines vitaux (Barbé et al. 2016 ; Chavel et al.

2017 - Chapitre IV). À l'instar des bryophytes et petits mammifères qui interagissent (Annexe A), notre collaboration a avant tout confirmé que la dynamique forestière et celles des populations de bryophytes ou de petits mammifères devaient être au cœur du débat et ainsi optimiser les stratégies d'aménagement écosystémique des pessières noires à mousse.

ANNEXE A

DISPERSAL OF BRYOPHYTES AND FERNS IS FACILITATED BY SMALL MAMMALS IN THE BOREAL FOREST

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A.1 Abstract

Bryophytes and pteridophytes are important contributors to ecosystem services in boreal regions. Abiotic agents are considered their main dispersers, but recent studies suggest that biotic agents including invertebrates, birds, and large mammals might also be efficient dispersal agents. Dispersal of cryptogams by ground-dwelling small mammals is often assumed to occur, but has yet to be demonstrated. In this study, we present the first evidence of boreal cryptogam species being dispersed by ground-dwelling small mammals. In 2013 and 2014, we recorded bryophyte cover and fern presence in 35 sites in black spruce forest. We also collected diaspores by brushing the fur of 99 ground-dwelling small mammals live-trapped in the same sites. Diaspores were then germinated on nutrient agar for six months. Viable diaspores of five bryophyte species and one fern species were successfully grown. No association was found between the cryptogam community sampled on site and the diaspore community grown on artificial substrate. Unlike abiotic agents that randomly disperse cryptogams, small mammals are more likely to transport diaspores to suitable substrates where microhabitat requirements for germination are met. Our results highlight the need to consider a broad spectrum of dispersal agents when focusing on the community dynamics of cryptogams.

Key words: boreal forest, cryptogams, microhabitat requirements, medium-range dispersal, rodents

A.2 Résumé

Les cryptogames (bryophytes et pteridophytes) représentent une composante fondamentale des régions boréales, et leur dispersion à moyenne et longue distance dépend principalement d'agents abiotiques. Des études récentes suggèrent pourtant l'importance d'agents biotiques tels que les invertébrés, les oiseaux et les grands mammifères comme vecteur de dispersion. La dispersion des cryptogames par les micromammifères est régulièrement admise mais n'a encore jamais été formellement examinée. Dans cette étude, nous présentons la première preuve tangible du transport des cryptogames boréaux par des micromammifères. Au cours des étés 2013 et 2014, nous avons estimé le couvert des bryophytes et la présence des fougères (communauté in situ) dans 35 sites en pessière noire à mousses. Conjointement, nous avons brossé le pelage de 99 micromammifères de cinq espèces différentes capturés vivants dans les mêmes sites. Le matériel végétal collecté a été disposé durant six mois sur un gel nutritif d’agar afin d’étudier la germination. Nous avons observé la germination de cinq espèces de bryophytes et d'une espèce de fougère. Nous n’avons trouvé aucune association entre la communauté de cryptogames in situ présente dans les sites et la communauté germée sur un substrat artificiel. Contrairement à la dispersion aléatoire par des agents abiotiques, la dispersion par les micromammifères est plus susceptible de transporter les diaspores vers des substrats propices à leur germination. Nos résultats soulignent l’importance de considérer la dispersion par les micromammifères dans l’étude des dynamiques des communautés de cryptogames.

A.3 Introduction

Bryophytes [i.e., true mosses, liverworts and sphagna, following Crum (2001)] and ferns play important roles in the functioning of the boreal forest. They provide many organisms with shelter and food (Davidson et al. 1990; Haines and Renwick 2009), and they contribute to numerous ecosystem services. For instance bryophytes and ferns are implied in water filtration, nutrient retention, nitrogen fixation (through the association of some bryophytes and aquatic ferns with cyanobacteria), and they also provide germination substrates for tree seeds (Baker et al. 2003; Bay et al. 2013; Clark et al. 2005; DeLuca et al. 2007; George and Bazzaz 1999; Turetsky et al. 2012). The dispersal capacities of bryophytes and ferns remains a controversial topic, as some studies have reported dispersal distances of only a few meters for bryophytes and ferns (Söderström 1987; Tájek et al. 2011), whereas other studies have demonstrated their ability to travel between 20 and 100 km and beyond (De Groot et al. 2012; Hylander 2009; Sundberg 2013). Both bryophytes and ferns reproduce sexually and asexually, although vegetative reproduction is less common among ferns than bryophytes. Although still debated, it is assumed that the sexual "dust-like spores" of bryophytes are effective dispersal agents contributing to long distance dispersal. In contrast, vegetative propagation by asexual agents such as gemmae and specialized brood-leaves or by vegetative fragments of leaves and stems mainly supports short-distance dispersal and local population maintenance (c.f. Boch et al. 2013; Eckert 2002; Löbel and Rydin 2009; Muñoz et al. 2004; Pohjamo et al. 2006). Fragments of mature individuals can also grow into new individuals (Benscoter 2006; Mälson and Rydin 2007; Rochefort et al. 2003). Bryophytes and ferns are believed to disperse mainly through abiotic agents, such as water and wind (Johansson et al. 2014; Muñoz et al. 2004). Dispersal by biotic agents also occurs, with evidence of transport by birds (Davison 1976; Lewis et al. 2014; Osorio-Zuñiga 2014), large mammals and bats (Heinken et al. 2001; Parsons et al. 2007, Pauliuk et al. 2011), as well as invertebrates (Kimmerer and Young 1995; Marino et al. 2009; Rudolphi 2009). Such transport may be exozoochorous (i.e., external attachment on animal) or endozoochorous (i.e., internal, passing through the digestive tracts), and consumption of both bryophytes and pteridophytes has been shown (Arosa et al. 2010; Boch et al. 2013). Although one study has indirectly linked bryophyte abundance to the dynamics of small mammal populations (Rydgren et al. 2007), and some authors have speculated that small mammals transport bryophytes (Carey 2003; Kimmerer 1994), to our knowledge, external dispersal of bryophytes and ferns by ground-dwelling small mammals (a form of mammiochory) has yet to be demonstrated.

As boreal ground-dwelling small mammals are in continuous contact with the cryptogam layer during their daily activities, we hypothesize that dispersal of cryptogam species by small mammals is likely to occur. We predict 1) that cryptogam diaspores are frequently dispersed by all species of small mammals without any exclusive species-specific associations, 2) that the cryptogam species found on small mammal fur may reflect the extant cryptogam community found on sites, and 3) that distinct life traits (e.g., formation of large carpets, production of copious quantities of diaspores) may render some cryptogam species more susceptible to be dispersed by small mammals than other cryptogam species.

A.4 Methods

A.4.1 Study area and sampling

The study area covers a total of 8325 km^2 (79˚29’W, 49˚00’N – 75˚39’W, 50˚22’N) in the western black spruce (*Picea mariana*)-feather moss (*Pleurozium schreberi*) forest of Québec eastern Canada (Grondin 1996). This boreal region is characterized by a subpolar continental climate. Average annual temperature and precipitation are respectively 1 °C and 927.8 mm (1981 to 2010), recorded at the nearest weather station, Lebel-sur-Quévillon, Québec (Environment Canada 2015). The main tree species are black spruce (*P. mariana*), jack pine (*Pinus banksiana*) and balsam fir (*Abies balsamea*), along with occasional broadleaf species such as white birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*). The understory is primarily composed of ericaceous species (e.g., *Rhododendron groenlandicum*). True mosses form a dense carpet and are slowly replaced by *Sphagnum* species as drainage conditions deteriorate due to paludification with time since fire (Fenton & Bergeron 2006). The region is also characterized by large, recurrent and severe wildfires (8000 ha on average; Bergeron et al. 2004), although fire is increasingly being replaced by forest management practices as the primary agent of disturbance (Imbeau et al. 2015).

We selected a total of 35 sites distributed among old undisturbed forest stands (over 100 years old), post-fire remnant patches (3.9 ha [range: 0.4 - 11.1]) left after wildfires that occurred over 20 years ago, green tree retention patches (0.7 ha [range: 0.1 - 1.3]) left after recent clear-cutting (< 10 years), and linear cutblock separators (60-100 m large, connected to old-growth forests) that separate clearcut areas. Sites were at least 500 m apart, based on the average movement distance of the most mobile species (Larsen and Boutin 1994), to ensure that any two sites were independent.

Live-trapping was conducted between July 23rd and August 15th in 2013 and between June 1st and August 21st in 2014, with both Tomahawk live-traps (8.0 x 8.0 x 41.0 cm - Tomahawk Live Trap llc ®) and Sherman live-traps (7.5 x 9.0 x 23.0 cm - H.B. Sherman Traps, Inc. ®). Tomahawk live-traps were used to trap arboreal mammalian species such as American red squirrels (*Tamiasciurus hudsonicus*) and northern flying squirrels (*Glaucomys sabrinus*). Sherman live-traps enabled us to trap smaller ground-dwelling mammals such as southern red-backed voles (*Myodes gapperi*). All traps were baited with peanut butter and apple pieces, which provide water and food to the trapped individuals. Cotton batting was also added to each trap to provide shelter and insulation in order to ensure better survival. We established one transect of six Tomahawk live-traps per site with a distance of 10 m between traps. Transects were 50 m long in order to accommodate our smallest sites. Then we established a 15 m square trapping grid of 16 Sherman live-traps centred on the transect line with traps spaced at 5 m intervals (**Figure A.1**).

We trapped during 72 consecutive hours, checking the traps twice a day (early morning and late afternoon). Each site was monitored with this trapping regime during one trapping session in 2013 (three nights). In 2014, three trapping sessions were completed (three nights in each of June, July, and August). Toothbrushes were used to collect the potential diaspores (i.e., spores, gemmae, vegetative fragments) on the fur of the trapped small mammals. Each small mammal was gently brushed on their back, belly and paws with a new toothbrush for two minutes. We then sealed each toothbrush in a new labelled plastic bag. All individuals were released after brushing. Diaspores were visible neither on the mammalian fur nor used toothbrushes. All manipulations adhered to the Canadian Council on Animal Care Guidelines and were approved by the Institutional Animal Care Review Committee at the Université du Québec en Abitibi-Témiscamingue (UQAT, permit no. 2013-04-02).

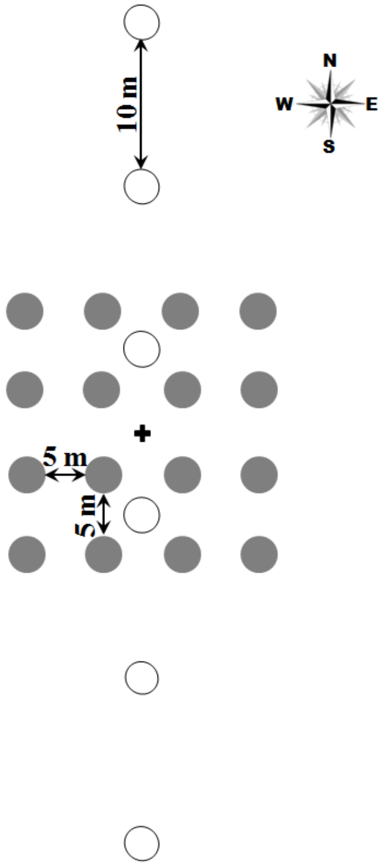

Figure A.1 Representation of the trapping station at each site. The filled cross (✚) represents the trapping station centre, empty circles (○) represent one Tomahawk live-trap, filled circles (●) represent one Sherman live-trap.

The extant bryophyte and fern community composition of the 35 sites was estimated using three 1-m² (1 x 1 m) quadrats placed randomly within the Sherman trapping grid. Percent cover of each bryophyte species present was visually estimated. Species represented by only one individual were noted as trace (i.e., less than 1% of cover of the 1 m² quadrat). Only the presence/absence of fern species was recorded.

We germinated the diaspores collected on an agar substrate following the "emergence method" used by Ross-Davis and Frego (2004). In the laboratory, we washed each toothbrush with deionized water over a Petri plate 90 mm in diameter to extract potential diaspores. Each Petri plate contained 78.5 cm² of nutrient agar prepared in sterile laboratory conditions [Parker Thompson's basal nutrient medium of Klekowski (1969), described by *C-Fern* Project © (1995–2014)]. After the extraction, Petri plates were covered and placed randomly in germination chambers for six months (from September 2013 to March 2014 after the 2013 trapping session and from September 2014 to March 2015 after the 2014 trapping session), under continuous spectrum Verilux ® (48" and 32 Watt) fluorescent light tubes with a 12 h/12 h light/dark regime. Petri plates were misted with deionized water as needed to prevent them from drying out. Germination chamber temperature was maintained at 22 °C. When the nutrient agar became too thin, the entire content of the Petri plate was transferred to a new Petri plate with fresh nutrient medium. When the growing bryophytes and ferns were too tall for Petri plates to contain they were placed in individual transparent plastic pots. Development of bryophyte gametophytes was assessed twice a week following germination. Minor contamination by fungus or algae was manually removed from the nutrient agar with forceps. In the case of a major contamination, where the Petri plate was entirely covered by fungus or algae and survival of the protonemata was compromised, protonema were removed from the plate, bathed in deionized water and transplanted in a new Petri plate. Three control Petri plates with virgin nutrient agar were placed in the germination chambers every three months for the duration of the 6-month emergence period to identify potential contaminants (air-borne diaspores). No species developed on any of the control plates, indicating that sample plates had not been contaminated during the laboratory growing period. Cryptogam culture with this method was generally successful, even though it introduces a bias towards cryptogam species able to germinate in artificial conditions.

All individuals were identified in the laboratory following Faubert (2013, 2014) for bryophytes. Ferns were identified following Martineau (2014). Due to the artificial growing conditions in Petri plates, bryophytes lacked some critical features for species identification, which is why some specimens were only identified to genus, in particular sphagna and members of the genera *Pohlia* sp. and *Polytrichum* sp.

A.4.2 Statistical analyses

Data from 2013 and 2014 were pooled for analyses. Furthermore, we made no distinction among the types of sites where small mammals were trapped due to the low sample size in each site type (old-growth forests, post-fire remnant patches, green-tree retention patches and linear cut-block separators). We consequently pooled data for all small mammals. We conducted analyses according to cryptogam species taxonomic groups and life forms: liverworts, sphagna, and true mosses, divided into acrocarpous and pleurocarpous groups. No distinction was made between individuals germinated from spores or gemmae because we could not distinguish among these two forms of diaspores on Petri plates. Vegetative fragments (i.e., stem and leaf fragments) deposited on Petri plates were also considered. To avoid overestimating the number of dispersed diaspores, cryptogam individuals were counted using the number of individual protonema and vegetative fragments instead of the number of stems produced, given that a single protonema can generate several stems in one Petri plate. As it is difficult to distinguish protonema once the plant is fully developed, monthly photographs of the plates were used to identify individual protonema. We counted the number of protonema germinated from spores/gemmae as well as the number of vegetative fragments in each Petri plate. Species abundance was calculated as the number of individual of each species per Petri plate. The extant community present on each site was described using the mean percent cover of each bryophyte species recorded in three 1-m² quadrats. Ferns were considered present if observed in at least one of the three 1-m² quadrats per site.

We compared the composition of the extant community and the diaspore community grown in Petri plates using Kendall rank correlations (Legendre and Legendre 2012). The individuals identified to genus in the Petri plates were compared to the species from the same genus in the extant community (e.g., *Polytrichum* sp. from Petri plates were compared to *Polytrichum commune* sampled on site). As there was no linear pattern between the two variables and because some variables included outliers, the Kendall rank correlation was more appropriate than the Pearson product-moment correlation to quantify the association between the abundance of species grown in Petri plates and percent cover of species in the extant community. Similarly, to assess whether the abundance of species grown in Petri plates was linked to their presence onsite, we used a second Kendall rank correlation on the abundance of the cryptogam species grown in Petri plates and their cover in small mammal trapping grids. We obtained the *p*-value of each Kendall rank correlation coefficient by randomization after 1000 iterations. This approach consisted of permuting the original data for each variable to break the pairwise structure of the data in agreement with the null hypothesis of no correlation and computing the test statistic at each iteration. All analyses were conducted in R 3.0.1 statistical software (R Core Team 2015).

A.5 Results

A total of 99 small mammals were trapped and brushed, including southern red-backed voles (*Myodes gapperi*), American red squirrels (*Tamiasciurus hudsonicus*), deer mice (*Peromyscus maniculatus*), northern flying squirrels (*Glaucomys sabrinus*) and common heather voles (*Phenacomys ungava*) (**Table A.1**).

Approximately half of the trapped individuals carried viable bryophyte and pteridophyte diaspores that germinated within six months (i.e., 50.5%; **Table A.1**). We counted a total of 172 individuals on Petri plates, germinated from spores/gemmae or identified as vegetative fragments such as leaf or stem pieces. Six bryophyte species (*Ceratodon purpureus*, *Platygyrium repens*, *Pleurozium schreberi*, *Pohlia* sp., *Polytrichum* sp. and *Sphagnum* sp.) and one pteridophyte species (*Dryopteris* cf. *carthusiana)* were recorded, along with 11 unidentifiable protonema (**Figure A.2** and **Table A.2**).

Table A.1 Number of Petri plates incubated with material brushed from five small mammal species trapped in the boreal forest. A separate Petri plate was used for each small mammal individual and represents the number of small mammals carrying viable diaspores.

Mammal species	Total Petri plates incubated (n)	Petri plates with germination (n)	Petri plates with germination (%)
Glaucomys sabrinus / northern flying squirrel	11	6	54.5
Tamiasciurus hudsonicus / American red squirrel	28	14	50.0
Myodes gapperi / red-backed vole	40	20	50.0
Peromyscus maniculatus / deer mouse	18	8	44.4
Phenacomys ungava / common heather vole	2	2	100.0
Total	99	50	50.5

Sphagna represented 68.6% of the identified bryophyte protonemata. Three acrocarpous and two pleurocarpous species were encountered consisting of 22.1% and 9.3% of the identified protonemata, respectively. No liverworts developed on the Petri plates. The number of mammalian species transporting a given bryophyte or fern species ranged from one to all five small mammal species (**Table A.2**). Mammalian species transported from eight to 64 diaspores from two to five different bryophyte or fern species. We found no association between bryophyte species and mammalian species. However, the one fern species was exclusively found on the fur of American red squirrels.

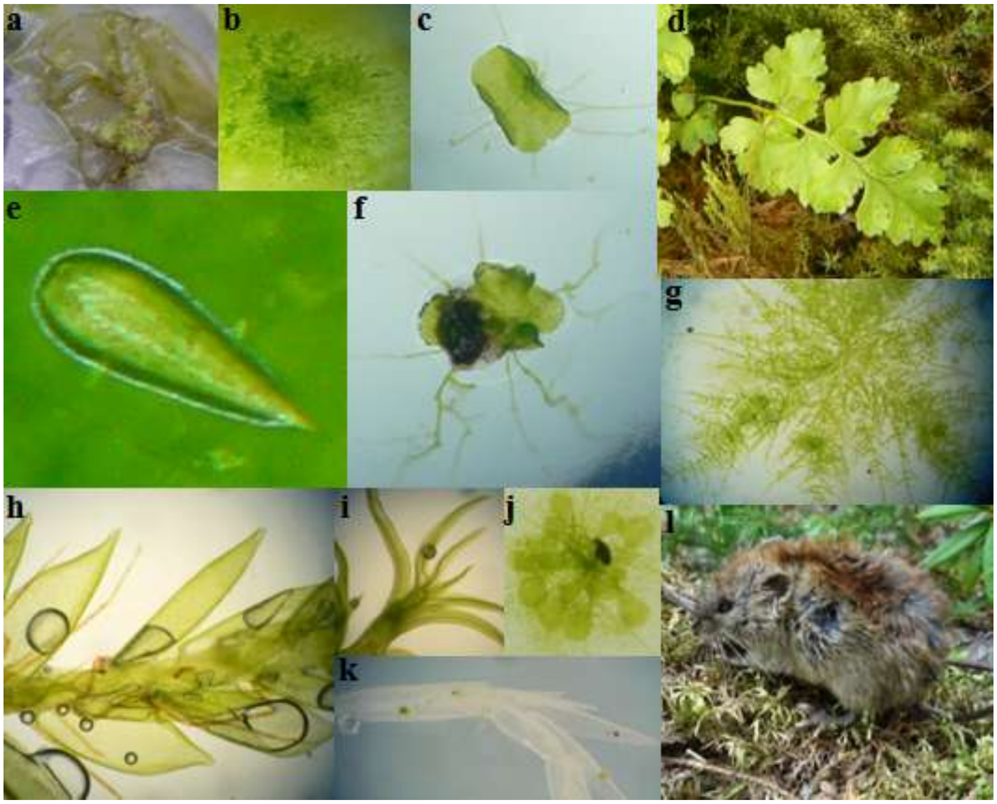

Figure A.2 Photography of cryptogam species grown *ex situ* (a–k) and of one southern red-backed vole found *in situ* in *Pleurozium schreberi* (l). Protonemata (a–c, f–g and j); Juvenile *Dryopteris* cf. *carthusiana* (d); Leaf and branch of *Sphagnum* sp. (e and k); Stem of *P. schreberi* (h); Stem of *Polytrichum* sp. (i); Southern red-backed vole (*Myodes gapperi*) (l). Photo credits: M. Barbé (a–k); D. Fauteux (l)

Table A.2 List of bryophyte and fern species brushed from five small mammal species trapped in boreal forests (n = 99 individuals trapped). Values refer to the number of bryophyte individuals grown in Petri plates counted as number of protonemata germinated from spores/gemmae or as number of vegetative fragment. As one Petri plate may contain several protonema, the values in brackets represent the number of Petri plates in which the cryptogam species were found. In species richness of bryophytes and ferns protonemata of *Sphagnum* sp. and *Sphagnum* leaves were grouped together and unidentified protonemata and unidentified stems/leaves were omitted because we could not determine if they were new species or not. [†], Acrocarp; [‡], Pleurocarp; [§], Fern.

Bryophyte species	*Glaucomys sabrinus* / northern flying squirrel	*Tamiasciurus hudsonicus* / American red squirrel	*Myodes gapperi* / southern red-backed vole	*Peromyscus maniculatus* / deer mouse	*Phenacomys ungava* / common heather vole	Sum of diaspores	Number of species as dispersal agents
Ceratodon purpureus[†]	0	1 (1)	0	3 (1)	0	4	2
Platygyrium repens[‡]	2 (1)	0	0	0	0	2	1
Pleurozium schreberi[‡]	0	10 (2)	1 (1)	0	0	11	2
Pohlia spp.[†]	0	0	11 (1)	8 (2)	0	19	2
Polytrichum spp.[†]	1 (1)	1 (1)	3 (2)	1 (1)	2 (1)	8	5
Sphagnum spp.	6 (5)	19 (10)	18 (11)	47 (4)	6 (1)	96	5

(suite)

Bryophyte species	*Glaucomys sabrinus* / northern flying squirrel	*Tamiasciurus hudsonicus* / American red squirrel	*Myodes gapperi* / southern red-backed vole	*Peromyscus maniculatus* / deer mouse	*Phenacomys ungava* / common heather vole	Sum of diaspores	Number of species as dispersal agents
Protonemata unidentified	2 (4)	3 (1)	5 (4)	1 (1)	0	11	4
Dryopteris cf. *carthusiana*§	0	2 (2)	0	0	0	2	1
Sphagnum sp. leaves*	2 (2)	4 (1)	6 (5)	4 (2)	0	16	4
Stems/Leaves unidentified*	0	1 (1)	2 (1)	0	0	3	2
Sum of individuals germinated from spores/gemmae + vegetative fragments	11+2	36+5	38+8	60+4	8		
Cryptogam species richness per small mammal species	3	5	4	4	2		

In the extant community, we found 16 bryophyte taxa: five pleurocarpous, seven acrocarpous and two liverwort species (**Figure A.3**). This value represents the minimum species richness of the sites, true species richness was probably much higher. Two bryophyte species found in Petri plates were not encountered in the extant community: *C. purpureus* and *P. repens*. Sphagna were present in all sites. Various ferns were present as isolated individuals. Sphagna dominated both the pool of diaspores collected and the species cover on site. However, there was no association between the species composition of bryophytes and ferns on site and the species composition grown in Petri plates (Kendall tau = 0.05, *p*-value = 0.752, **Figure A.3**). Similarly, we found no association between the abundance of bryophyte and fern species grown in Petri plates and their cover on site (Kendall tau = 0.69, *p*-value = 0.078).

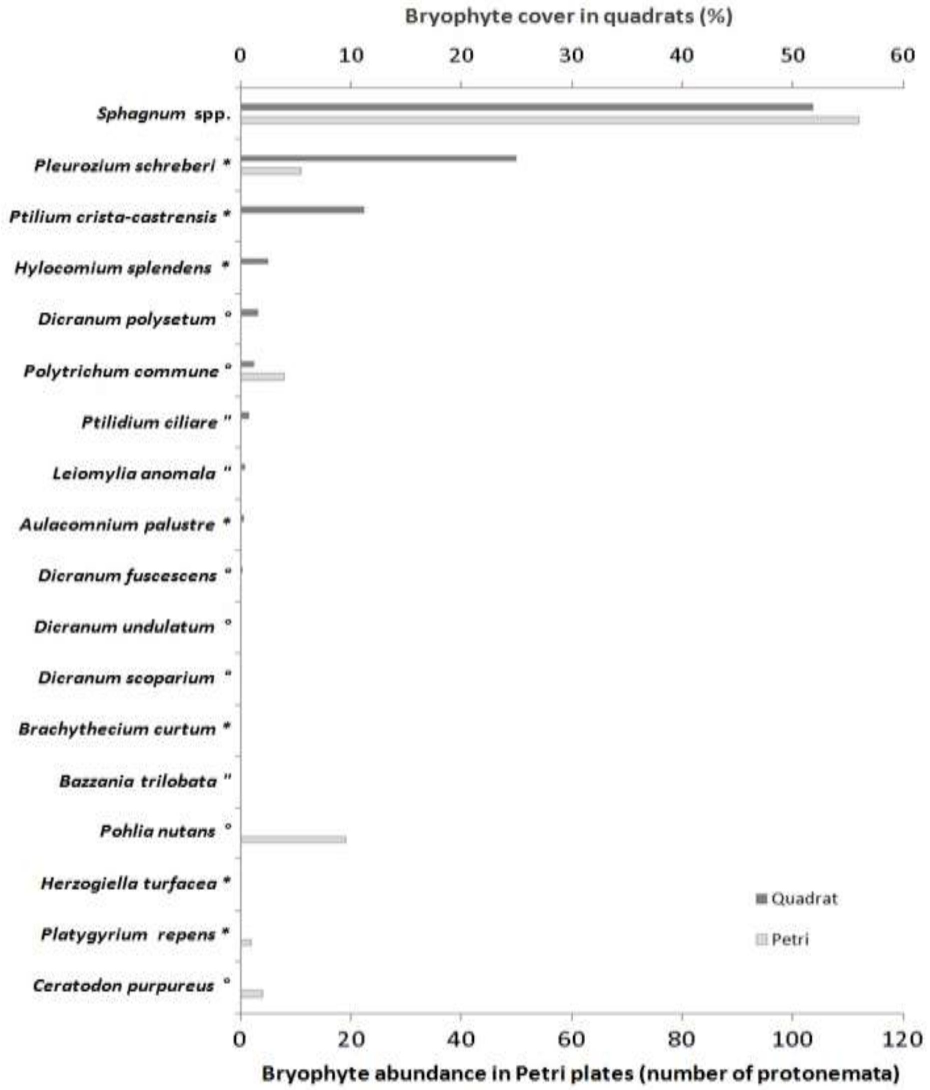

Figure A.3 Comparison of bryophyte cover sampled onsite and bryophyte abundance in Petri plates. Dark grey bars, mean bryophyte cover (%) per 1-m^2 quadrats; light grey bars, bryophyte abundance in Petri plates (number of protonemata from spores/gemmae + number of vegetative fragments in the case of *Sphagnum* sp.). Species are ranked by percent cover on site; species reported on site but with no apparent bars on the graph were present as less than 1% of cover and are noted as trace (Tr), except for the underlined species that were not recorded on site. †, Acrocarp; ‡, Pleurocarp; ¶, Liverwort. The fern *Dryopteris* cf. *carthusiana* is not displayed on the graph because only the presence/absence of fern was recorded on site without consideration of their percent cover.

A.6 Discussion

Southern red-backed voles, American red squirrels, and deer mice were the most abundant mammal species in our study sites. We found that these three species along with northern flying squirrels and common heather voles were dispersal agents for true mosses, sphagna and ferns. We also found that small mammals can transport several species of bryophytes and in some cases, a copious amount of viable diaspores of individual bryophyte species. Our results demonstrate that ground-dwelling small mammals are not occasional dispersal agents but instead represent important dispersers of bryophytes and ferns. Furthermore, ground-dwelling small mammals are in direct contact with the cryptogam layer and this may enhance the dispersal of cryptogams that rarely produce spores or that are poorly dispersed by the wind.

Mammalian species transported a fraction of species from the pool of bryophyte genera available on sites. Keeping in mind that some of the taxa that germinated were not identified to species due to germinating constraints, the pool of species found in Petri plates only represented 20% of the species encountered on site. This represents less than half of what was found by Pauliuk et al. (2011) who collected 40% of the bryophytes species found in European dry grassland ecosystems on large mammals. One factor explaining the low percent transported may be that none of the species collected are known to have developed features on their diaspores to actively rely on zoochory for dispersal (e.g., spore ornamentation, colorful spores, and sticky or odorous secretion to attract animal species; Demidova and Filin 1994; Ignatov and Ignatova 2001; Rudolphi 2009). Alternatively, if the main agent transported was spores, species phenology may have impacted our results, as not all cryptogam species produced dispersal agents during our trapping sessions. For instance, the over-abundance of sphagna diaspores may be explained by the coincidence of diaspore release and our experiment (Sundberg and Rydin 2002).

In contrast, two species germinated in Petri plates that were not found in the extant community, namely *Ceratodon purpureus and Platygyrium repens*. These species may have become attached to the fur of the small mammals when they dig in the moss layer and mineral soil searching for food such as seeds and insects (Merritt 1981). This activity may result in some spores present in the soil propagule bank becoming attached to their fur.

The only species of fern transported by a small mammal, *D.* cf *carthusiana,* is common in the boreal forest and produces large amounts of spores easily dispersed by wind (Rünk et al. 2012). However, ferns also reproduce by vegetative fragments and alternative diaspores (c.f. Boch et al. 2013), which may be brushed off by passing animals. In the present study, American red squirrels are the largest species trapped on our study sites and the only one that carried fern spores. Despite this, we found no apparent exclusive association between cryptogams and small mammals, which can possibly be explained by the low number of individuals trapped for some mammalian species.

Small mammal transport offers two main advantages over wind transport. First, as small mammals and bryophytes share the same types of microhabitats (Fauteux et al. 2012; Lõhmus et al. 2007; Mills and Macdonald 2004) small mammals offer oriented dispersal of the diaspores over the landscape. In contrast, during wind dispersal all diaspores are randomly deposited in microhabitats up to several kilometres away during wind dispersal (Lönnell 2011; van Zanten and Gradstein 1988). Secondly, ground-dwelling small mammals can transport species that are not efficient at wind dispersal, due to either low sporophyte production or sporophyte morphology. Ground-dwelling small mammals can transport cryptogam diaspores within their home range (from several meters for deer mice, up to 3.5 km for red squirrels; Bowman et al. 2002; Larsen and Boutin 1994, 1995; Wells-Gosling and Heaney 1984). Cryptogams could also be transported beyond small mammal home ranges during mammalian species dispersal and establishment of new home ranges. As a possible example, we brushed one individual that was carrying *C. purpureus*, 80 m away from the closest *C. purpureus* colony found in a concurrent study performed on the same study sites (Barbé et al. 2016).

We showed that ground-dwelling small mammals disperse bryophytes and ferns. However, additional species could be identified. Indeed, some species do not germinate on the agar substrate and others may have germinated after 6 months. However, as a concomitant study performed with the same protocol yielded the germination of 46 bryophyte species (Barbé et al. 2016). We argue that the reduced pool of species from this study is not due to the germination protocol. The composition of the bryophyte aerial propagule rain will differ among seasons with species phenology (Hock et al. 2004; Ross-Davis and Frego 2004; Stark 2002). Moreover, weather conditions such as relative humidity, night temperatures and rainfall might also have influenced cryptogam phenology via spore release (Glime 2014; Johansson et al. 2015), small mammal activity (Wróbel and Bogdziewicz 2015) and diaspore adherence to fur. In addition, other constraints associated with the sampling methods could have affected the results such as the use of cotton balls for the small mammal trapping in which diaspores might have been deposited during the many hours spent by the animals in the traps. In the future, we recommend to also collect the cotton balls provided in the traps. Finally, it may be important to consider the effectiveness of toothbrushes at removing diaspores that are electrostatically charged. Alternative collection methods on the fur might yield different species, and this topic could be explored in future studies.

To our knowledge, we provide the first direct evidence of epizoochory involving bryophytes and ferns and ground-dwelling small mammals in boreal forest ecosystems. The daily interaction between small mammals and the cryptogam layer could contribute to the directed transport of bryophyte and fern diaspores over medium distances and towards suitable substrates. Persistence of bryophyte and fern metapopulations depends on dispersal across the forest matrix and small mammals are identified as "mobile link organisms" (sensu Couvreur et al. 2004) that may participate in connecting fragmented bryophyte and fern populations. Our results open the door for a timely revision of bryophyte and fern dispersal mechanisms, extending the notion of epizoochory by ground-dwelling small mammals to other cryptogams such as horsetail, lichen or liverwort species.

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