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UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

LES EFFETS RELATIFS DES VARIABLES CARACTÉRISANT LES PETITS  
ÉTANGS, ET DES INTERACTIONS AVEC LES PRÉDATEURS, SUR  
L'OCCUPATION ET L'ABONDANCE DES ESPÈCES DE TROIS GROUPES DE  
VERTÉBRÉS DANS LE NORD-DU-QUÉBEC

THÈSE

PRÉSENTÉE

COMME EXIGENCE PARTIELLE

DU DOCTORAT EN SCIENCES DE L'ENVIRONNEMENT

PAR

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AVRIL 2023

## AVANT-PROPOS

Cette thèse présente les travaux de recherche que j'ai réalisés dans le cadre du doctorat en sciences de l'environnement à l'Université du Québec en Abitibi-Témiscamingue (UQAT). Il s'agit d'une thèse par articles, qui comprend une introduction générale (Chapitre I), trois chapitres sous la forme d'articles scientifiques en anglais (Chapitres II à IV) et une conclusion générale (Chapitre V). Le premier article a été accepté pour publication, le deuxième article a été publié et le troisième article est en cours de préparation pour soumission. L'introduction et une conclusion générale sont rédigées en français.

Chapitre I. Introduction générale.

Chapitre II. Feldman, M. J., Mazerolle, M. J., Imbeau, L., et Fenton, N. J. (*article accepté le 14 septembre 2022*). Occupancy and abundance of pond-breeding anurans in boreal landscapes. *Journal of Herpetology*.

Chapitre III. Feldman, M. J., Mazerolle, M. J., Imbeau, L., et Fenton, N. J. (*article publié le 17 février 2023*). Beaver activity and red squirrel presence predict bird assemblages in boreal Canada. *Ornithology*, 140(2), ukad009.

Chapitre IV. Feldman, M. J., Mazerolle, M. J., Imbeau, L., et Fenton, N. K. (*en préparation*). Using camera traps to estimate habitat preferences and occupancy patterns of vertebrates in boreal wetlands of Northern Quebec. *Wetlands*.

Chapitre V. Conclusion générale.

En tant que principal contributeur à la collecte des données sur le terrain et à la rédaction de l'article, je suis le premier auteur des trois chapitres de cette thèse. Mon superviseur Louis Imbeau, ainsi que mes co-superviseurs Marc Mazerolle et Nicole Fenton ont été impliqués à toutes les étapes de cette thèse, c'est-à-dire le développement du protocole, l'interprétation des résultats et la rédaction du manuscrit. En outre, Marc Mazerolle a vérifié les analyses du chapitre II et a joué un rôle majeur dans l'analyse des données des chapitres III et IV.

Les trois principaux articles scientifiques (chapitres II, III et IV) ont été développés avec la collaboration et à partir de la contribution essentielle de chacun de leurs auteurs. Mon directeur de thèse Louis Imbeau (LI) et mes co-directeurs Nicole Fenton (NJF) et Marc Mazerolle (MJM) ont contribué de plusieurs façons tout au long du projet dans leurs champs d'expertises, et leur place dans les listes des auteurs sont fonction de leur implication respective dans la réalisation de chacun des chapitres.

Les annexes A et B comprennent un article de synthèse supplémentaire et une note scientifique, qui ont été élaborés et publiés au cours du développement de cette thèse. L'article de synthèse complémentaire inclus dans l'annexe A a fait l'objet de l'examen doctoral et a été élaboré parallèlement aux chapitres scientifiques de cette thèse grâce à l'étroite collaboration de mes directeurs de thèse et des membres du comité du projet de thèse (Philippe Marchand et Marcel Darveau). La décision d'inclure cette revue en annexe a été prise en raison de son sujet proche, bien que non strictement lié, aux principaux chapitres scientifiques de cette thèse. La note de l'Annexe B fait partie d'un événement de prédation inhabituel documenté par le suivi par piège à caméra au cours du chapitre IV entre des espèces figurant dans les chapitres II et III, et a donc été incorporée dans ce document de thèse.

Le lecteur y trouvera quelques répétitions, particulièrement dans la présentation de la région et du contexte de l'étude. Nous nous excusons pour cette redondance au cours de la lecture du présent travail.

## REMERCIEMENTS

Une thèse de doctorat est le résultat d'un cheminement long et difficile. Ce travail a été possible grâce à l'aide de nombreuses personnes, directement ou indirectement impliquées. Je tiens à remercier tous ceux qui ont fait partie de mon parcours de doctorant. Mes premiers remerciements vont tout d'abord à mes trois encadrants, Louis Imbeau, mon directeur de thèse, Marc Mazerolle et Nicole Fenton, qui ont co-supervisé mon travail. En 2018, ils m'ont accordé leur confiance et l'opportunité de les rejoindre à l'Université du Québec en Abitibi-Témiscamingue pour réaliser ce projet de doctorat. Ils m'ont remarquablement soutenu dans la réalisation de cette thèse. Louis m'a donné l'opportunité de travailler sur ce projet, puis la confiance dès le début et tout au long de mon doctorat. Merci pour tes encouragements, ta patience, ta disponibilité, tes conseils et ton ouverture pour parler de tout et de rien et faire évoluer mes réflexions. Ton soutien académique et humain a été essentiel.

J'ai également apprécié la codirection et la dimension humaine de Marc et Nicole, qui ont contribué à améliorer chaque étape de ce travail. Merci Marc, ton implication tout au long de ce projet a été indispensable dans son ensemble, et plus particulièrement dans l'analyse des données, un rôle que tu as assumé activement. Merci d'avoir répondu à mes millions de questions sur des sujets statistiques de manière rapide, concise et claire, ce qui m'a permis d'avancer. Merci aussi de m'avoir ouvert la porte de ton laboratoire. Je tiens également à remercier Nicole Fenton, ma co-superviseuse, pour son étonnante disponibilité considérant l'étendue de ses activités, et ses conseils et suggestions toujours pertinents. Tu m'as aidé à me sentir intégré depuis le début dans ton laboratoire de bryologie et de botanique, et à me nourrir des rencontres et des discussions au sein de ton groupe. Alors à vous trois, merci pour vos mots de soutien tout au long du chemin. Merci également pour vos courriels d'encouragement dans les

moments les plus difficiles ou les défis personnels. Vous m'avez aidé à clarifier mes idées lorsque j'étais un peu perdu ou confus, mais en respectant et en encourageant ma propre autonomie. Merci pour votre investissement.

Je tiens également à remercier les deux membres de mon comité de direction, Marcel Darveau et Philippe Marchand, pour leurs commentaires toujours pertinents sur le projet de thèse et la synthèse environnementale. Je remercie sincèrement les personnes qui m'ont beaucoup aidé dans toutes sortes de démarches et d'informations administratives durant ces années à l'UQAT, notamment Danièle Laporte et Marie-Hélène Longpré. Elles ont facilité ma démarche dans les méandres administratifs et logistiques du doctorat avec beaucoup d'efficacité et de bonne humeur, toujours si important pour les étudiants étrangers. Merci également à Sophie Laliberté pour son excellent travail et son intérêt et énergie constants. Merci à Julie Arsenault d'avoir répondu à mes nombreuses demandes de matériel de terrain, d'assistance technique et d'hébergement sur le terrain. Merci à Mélanie Desrochers pour son aide précieuse dans l'extraction des variables de végétation et de paysage et la cartographie de mes recherches.

Je tiens également à mentionner ma gratitude aux personnes qui m'ont accompagné sur le terrain, à Julie encore, et surtout à Rémi Chevallier. Merci, Rémi, tu es devenu un ami, et tu m'as accompagné dans cette aventure du début à la fin, merci pour tes efforts et ta passion sur le terrain ! Ce fut un grand plaisir de découvrir cette belle région avec toi et de partager tant d'heures sur la route. J'espère que nous aurons l'occasion de travailler à nouveau ensemble. Merci également à Pierre Fournier, qui s'est intéressé à mon projet, m'a donné des conseils pour le travail de terrain et avec qui nous continuons à avoir de riches discussions sur les bestioles en général.

Je suis reconnaissant aux organismes de financement d'avoir cru en ce projet et en ma capacité à le mener à bien. Je tiens tout particulièrement à remercier l'équipe environnementale de la mine Casa Berardi, de la mine Whabouchi et de la mine Renard pour leur accueil chaleureux et leur hospitalité durant mon travail de terrain. Cette recherche a été financée par la Chaire industrielle CRSNG-UQAT sur la biodiversité nordique en contexte minier. Au cours de cette thèse, j'ai aussi bénéficié du Fonds de Soutien au dépôt de thèse doctorale de l'UQAT.

Un grand merci à tous les amis rencontrés à l'UQAT pour la bonne humeur que nous avons partagée, pour nos pauses café et pour le soutien qu'ils m'ont apporté durant ces années, ce qui m'a permis de m'amuser les jours les plus difficiles. Merci à mes collègues (et maintenant amis) Alexandre, Andréanne, Charly, Daniela, Émilie, Enrique, Jeffrey, Juanita, Marc-Frederic, Xianbo, et bien d'autres pour les bons moments de science, de volley-ball et de détente passés avec vous. Un grand merci à *@Corrige-moi*, un système de relecture entre étudiants que nous avons créé avec des collègues et qui est toujours utilisé grâce aux nombreux étudiants qui collaborent entre eux pour améliorer leurs textes scientifiques. J'ai utilisé cette ressource tout au long de ma thèse. Remerciements particuliers à France-Lise Colin et Alexandre Nolin pour leur relecture approfondie de l'introduction et de la conclusion de la thèse en français et pour les corrections linguistiques qu'ils ont suggérées.

Je réserve mes derniers remerciements à ma famille pour son soutien dans mes projets malgré la distance physique imposée par l'éloignement. Ces moments avec ma famille étaient essentiels pour recharger mes batteries. Je remercie tout particulièrement mes parents de m'avoir encouragé à faire ce que je voulais faire de ma vie et d'avoir toujours accepté mes décisions. Je pense surtout à ma grand-mère Alicia, qui est un élément moteur dans ma vie. Une dédicace exclusive à ma partenaire de vie, Marie, qui m'accompagne depuis plusieurs années dans diverses aventures et qui a littéralement



mis son cœur et son âme dans cette thèse. Cela aurait été impossible sans toi, je t'aime. Merci pour ta confiance en moi, ton affection et ta compagnie, sans toi je ne serais certainement pas là. Ces deux enfants avec toi au milieu de mon doctorat m'ont donné la force de continuer.

## **DÉDICACE**

*A mes parents qui m'ont inculqué la  
valeur des études.*

*A ma femme Marie, mon fils Simon et  
ma fille Celeste.*

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## LISTE DES ABRÉVIATIONS, DES SIGLES ET DES ACRONYMES

AB	Données d'abondance
AIC	Critère d'information d'Akaike
AICc	Critère d'information d'Akaike corrigé pour les échantillons de petite taille
ALA	Atlas of Living Australia
ArcGIS	Aeronautical Reconnaissance Coverage Geographic Information System
ARU	Unités d'enregistrement automatique
BEAV	Étangs de castors échantillonnés
BHM	Modèles hiérarchiques bayésiens
BMS	Butterfly Monitoring Scheme
CBM	Community based monitoring
CI	Intervalle de confiance, généralement à 95%, acronyme issu du terme anglaise "Confidence Interval"
CONIF300	Pourcentage de forêt de conifères dans une zone tampon de 300 mètres autour de l'étang
CONIF1000	Pourcentage de forêt de conifères dans une zone tampon de 1000 mètres autour de l'étang
CRI	Intervalle de confiance bayésien
CRSNG	Conseil de recherches en sciences naturelles et en génie du Canada

CS	Science citoyenne
DECMIX300	Pourcentage de forêts de feuillus et de forêts mixtes dans une zone tampon de 300 mètres autour de l'étang.
DECMIX1000	Pourcentage de forêts de feuillus et de forêts mixtes dans une zone tampon de 1000 mètres autour de l'étang.
e.g.	<i>exempli gratia</i> (par exemple).
ESRI	Environmental Systems Research Institute
Fig	Figure
FaunENord	Organisation à but non lucratif
GAM	Modèles additifs généralisés
GBIF	Système mondial d'information sur la biodiversité
GLM	Modèles linéaires généralisés
GPS	Système de positionnement géographique
iButton	Temperature logger
i.e.	<i>id est</i> (c'est-à-dire)
IRF	Institut de Recherche sur les Forêts
IUCN	International Union for Conservation of Nature
JAGS	Just Another Gibbs Sampler
kHz	Kilohertz

LI	Louis Imbeau
LR	Approches de régression linéaire
MaxEnt	Maximum entropy modelling
MEA	Millennium Ecosystem Assessment
MCMC	Chaîne de Markov Monte Carlo
MDDELCC	Ministère du Développement durable, de l'Environnement et de la Lutte contre les changements climatiques
MF	Mariano Feldman
MUSE	Montpellier Université d'Excellence
NAAMP	North American Amphibian Monitoring Program
NBN	National Biodiversity Gateway
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"
PA	Données de présence-absence
PEAT	Étangs de tourbières échantillonnés
PO	Données de présence seulement
QAIC	Critère d'information d'Akaike sur la quasi-vraisemblance et corrigé pour les petits échantillons, acronyme issu du terme anglais "Quasi-likelihood Akaike's Information Criterion"

QAIC <sub>c</sub>	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
QC	Québec
ROC	Receiver operating characteristic curve
SABAP	Southern African Bird Atlas Project
SD	Écart-type
SDMs	Modèles de distribution des espèces
<i>sensu</i>	Dans le sens de
SM4	Song meter
Snowmelt	Nombre de jours après la fonte des neiges
Temp	Température de l'air
UQAT	Université du Québec en Abitibi-Témiscamingue
WET300	Pourcentage de milieux humides ouverts dans une zone tampon de 300 mètres autour de l'étang.
WET1000	Pourcentage de milieux humides ouverts dans une zone tampon de 1000 mètres autour de l'étang.
ZIP	Distribution de Poisson gonflée de 0 ou à distribution de Poisson avec une surabondance de 0

## LISTE DES SYMBOLES ET DES UNITÉS

%	Pourcentage
<	Inférieur à
>	Supérieur à
$\leq$	Inférieur ou égal à
$\geq$	Supérieur ou égal à
$\pm$	Valeur à la fois positive et négative
+	Réponse positive à la prédiction de la variable en question
—	Réponse négative à la prédiction de la variable en question
$\neq$	L'effet de réponse est variable et spécifique à l'espèce
=	Égal à
°C	Degré Celsius
° N	Degré de latitude Nord
° O	Degré de longitude Ouest
$\hat{c}$	Paramètre qui informe de la dispersion des données, paramètre introduit pour l'ajustement des données à la modélisation
cm	Centimètre
df	Degrés de liberté

h	Heure
ha	Hectare
HR	Humidité relative
Hum	Humidité
K	nombre de paramètres estimés dans un modèle statistique
km	Kilomètre
LL	Le maximum de log-vraisemblance
m	Mètre
min	Minute
mm	Millimètre
n	Nombre d'entités
p	Probabilité de détection dans les modèles d'occupation
Ph.D.	<i>Philosophiae doctor</i> (docteur en philosophie)
r	Valeur absolue du coefficient de corrélation de Pearson
s	Seconde
t	Test statistique utilisé pour comparer les moyennes de deux groupes.
$\omega_i$	Poids d'Akaike pour un modèle donné
$\Delta_i$	Différence d'AIC (d'AICc, de QAIC ou de QAICc) entre le meilleur modèle et un autre modèle donné



*	Niveau de signification faible
**	Niveau de significativité intermédiaire
***	Niveau de signification élevé
$\beta$	Estimé de régression pour une variable donnée
$\chi^2$	Test du chi carré
$\psi$	Paramètre d'occupation de site à une espèce

## RÉSUMÉ

Les milieux humides font partie des écosystèmes les plus menacés au monde. Dans les paysages boréaux, les milieux humides fournissent des services écologiques précieux et constituent des habitats de qualité pour plusieurs espèces. Dans le nord du Canada, les écosystèmes des milieux humides se transforment sous l'effet combiné des perturbations naturelles, du changement climatique et de l'utilisation des sols par l'humain. Ces territoires nordiques représenteront dans un avenir proche un potentiel croissant d'accès aux ressources naturelles, en particulier pour l'exploitation du bois, le développement hydroélectrique et les activités minières. Par conséquent, il peut en résulter une perte ou une réduction de l'habitat des espèces qui dépendent de certains types de milieux humides. Les milieux humides contenant de petits étangs (< 8 ha) sont particulièrement importants pour plusieurs vertébrés qui choisissent ces habitats pour se reposer, se nourrir et se reproduire, notamment les amphibiens, les oiseaux et les mammifères. Cependant, peu d'études ont porté sur la présence de vertébrés au sein des petits étangs et les connaissances sont donc encore fragmentaires. Nous manquons de connaissances sur les préférences en matière d'habitat, et sur l'influence des facteurs biotiques et abiotiques sur les espèces boréales. L'examen de ces facteurs est une première étape pour aborder la gestion des milieux humides et des espèces associées dans les milieux nordiques.

L'objectif général de cette thèse était de comparer l'utilisation des étangs de tourbières et des étangs de castors, et de quantifier l'influence des facteurs qui caractérisent ces habitats, ainsi que les interactions biotiques sur trois groupes de vertébrés: les amphibiens, les oiseaux et les mammifères. La région d'étude est située dans la forêt boréale canadienne, dans la région Eeyou-Istchee Baie James, dans le nord-ouest du Québec. Nous avons échantillonné 38 étangs de tourbières et 12 étangs de castors de mai à août 2018 et de mai à juillet 2019, avec deux campagnes d'échantillonnage par an.

Dans le chapitre II, nous avons examiné le rôle des facteurs propres à l'étang et au paysage sur l'occupation et l'abondance de trois espèces d'anoures à différents stades de leur cycle de vie, y compris les masses d'œufs, les juvéniles et les mâles chanteurs. Les résultats n'indiquent pas d'effets significatifs des variables explicatives sur la probabilité d'occupation des mâles chanteurs. Les individus métamorphosés de la grenouille du Nord (*Lithobates septentrionalis*) étaient plus abondants dans les étangs de plus petite surface et à pH moins acides. L'effort reproducteur de la grenouille des bois (*Lithobates sylvaticus*) était plus élevé dans les étangs de castors que dans les étangs de tourbières. Ce chapitre renforce l'idée que les étangs de castors sont des

environnements plus productifs pour les amphibiens que les étangs de tourbières. Les étangs de tourbières sont autant utilisés par les anoues juvéniles et adultes que les étangs à castors. Ce chapitre suggère aussi, étant donné que nous avons utilisé des méthodes visuelles et acoustiques complémentaires, que les amphibiens des latitudes nordiques sont des généralistes de l'habitat et ne sont pas limités à des facteurs spécifiques aux étangs et aux paysages.

Dans le chapitre III, nous avons évalué comment l'occupation des oiseaux différait entre les deux types d'étangs, et comment les oiseaux répondaient aux facteurs locaux et paysagers, ainsi qu'à la présence d'un important prédateur de nids : l'écureuil roux (*Tamiasciurus hudsonicus*). Les enregistrements acoustiques ont permis d'identifier un total de 96 espèces d'oiseaux que nous avons regroupées en quatre guildes : espèces de début de succession, des forêts matures, généralistes et des milieux humides. Les résultats indiquent que les étangs de castors abritent une plus grande richesse d'espèces d'oiseaux de celle des étangs de tourbières, une tendance principalement due aux espèces de début de succession. La richesse des espèces était plus faible en présence d'écureuils roux. Les espèces forestières matures ont réagi positivement à la couverture forestière dans un rayon de 1000 m autour de l'étang. Ce chapitre démontre donc que les assemblages d'oiseaux profitent de la modification de l'habitat par les castors et sont affectés négativement par la présence des écureuils roux. Cela peut être dû à un effet direct de prédation ou parce que certaines espèces ne partagent pas le même habitat que ce prédateur.

Le chapitre IV utilise une méthode d'échantillonnage passive différente, par pièges photographiques, pour comprendre comment les caractéristiques de l'habitat affectent les mammifères et les oiseaux qui utilisent les tourbières et les étangs de castors. Les données provenant de 150 stations de caméras ont documenté 11 espèces de mammifères de taille moyenne à grande et 45 espèces d'oiseaux. Les résultats ont montré que deux espèces de mammifères et quatre espèces d'oiseaux avaient des préférences inattendues pour les étangs de tourbières plutôt que pour les étangs de castors. La proximité des routes n'a pas affecté l'occupation des étangs. Nous avons démontré la pertinence de l'utilisation d'approches multi-espèces dans des régions où des informations de base sur la répartition des espèces ne sont généralement pas disponibles. Nous soulignons également que les pièges photographiques sont efficaces pour étudier les espèces d'oiseaux de milieu humide, en particulier les oiseaux aquatiques. Finalement, le couvert forestier n'a pas eu d'effet sur l'utilisation des étangs par les espèces, révélant ainsi une réponse différente selon les techniques d'observation utilisées dans cette thèse (visuelles et acoustiques) pour évaluer les réactions des espèces aux caractéristiques du paysage.

Cette thèse de doctorat constitue une référence sur les étangs utilisés par les vertébrés dans leur aire de répartition nordique et dans une zone géographique peu explorée. Ces travaux de recherche auront permis de faire progresser la compréhension de deux types majeurs de milieux humides dans la région boréale. Les tourbières, considérées jusqu'à présent comme des environnements pauvres et hostiles, peuvent abriter une diversité remarquable de vertébrés à divers stades de leur cycle de vie. Cependant, les étangs de castors semblent être plus productifs en masse d'œufs que les tourbières, bien que des études additionnelles soient nécessaires pour élucider la valeur différentielle des étangs de castors actifs et abandonnés. Un meilleur affinement des paramètres biologiques affectant la qualité de l'habitat pour diverses espèces et une reconnaissance plus large des interactions biotiques impliquant diverses espèces (prédation, compétition, par exemple) aideront à clarifier les modèles écologiques d'occupation des espèces. Dans un contexte de pressions anthropiques et climatiques croissantes sur les milieux humides boréaux, une meilleure compréhension des milieux humides permettra de mieux conserver ces habitats de grande qualité, ce qui profitera à un large ensemble d'espèces.

*Mots-clés* : milieux humides, petits étangs, Nord-du-Québec, étangs à castors, étangs de tourbières, qualité d'habitat, biodiversité, vertèbres boréaux, enregistreurs automatiques, pièges photographique, richesse en espèces.

# CHAPITRE I

## INTRODUCTION GÉNÉRALE

### 1.1 Milieux humides : fonctions et rôles

Les milieux humides sont des écosystèmes uniques qui se situent à l'interface entre les écosystèmes entièrement terrestres et les écosystèmes entièrement aquatiques (Mitsch et Gosselink, 2000). Ils sont présents dans de nombreuses régions du monde, mais se concentrent surtout dans l'hémisphère nord, entre les 45<sup>e</sup> et 75<sup>e</sup> parallèles, et dans les régions équatoriales (Scott et Jones, 1995). Ils occupent seulement 5 à 8 % de la surface terrestre mondiale (Mitsch et al., 2013; Mitsch et Gosselink, 2000), mais représentent environ 45 % de la valeur réalisée des écosystèmes naturels (Costanza et al., 1997). Bien que la définition des milieux humides varie à l'échelle mondiale, ces milieux se définissent comme des écosystèmes saturés d'eau ou inondés pendant une période suffisamment longue pour que des processus lacustres se produisent et influencent les composantes du sol ou de la végétation (Couillard et Grondin, 1986; Warner et Rubec, 1997). Sous les latitudes boréales, on reconnaît généralement cinq grandes catégories de milieux humides : les marais, les marécages boisés, les plans d'eau peu profonds, les forêts inondées de façon saisonnière, les tourbières ombrotrophes et les tourbières minérotrophes. Les milieux humides sont particulièrement connus pour fournir un large spectre de services écosystémiques vitaux pour la faune et l'homme (Costanza et al., 1989; Dahl et al., 1991; Mitsch et Gosselink, 2000). On entend par *services écosystémiques* les bénéfices pour les humains obtenus grâce aux processus hydrologiques et biogéochimiques se déroulant au sein d'habitats naturels (Díaz et al., 2018).

Les milieux humides offrent une multitude de fonctions et avantages importants pour l'environnement et la société. Grâce à différents processus biogéochimiques, les milieux humides agissent comme un filtre qui peut modifier la concentration des nutriments et les sédiments dans l'eau, et transformer les agents pathogènes et les produits chimiques en des formes moins nocives, contribuant ainsi à la recharge des eaux souterraines (Fisher et Acreman, 2004; Mitsch et Gosselink, 2000; Verhoeven et al., 2006). Ils peuvent capturer jusqu'à 90% des sédiments de ruissellement et ont une grande capacité à purifier et à améliorer la qualité de l'eau des bassins versants auxquels ils appartiennent (Phillips, 1989; Yan et al., 1998). D'un point de vue hydraulique, les milieux humides peuvent retenir et stocker de grandes quantités d'eau, limitant ainsi naturellement les inondations et les basses eaux (Miller et Frink, 1984). La végétation des milieux humides contribue également à réduire les forces d'érosion des côtes en aval, en atténuant l'action des vagues et en ralentissant les courants d'eau, en particulier pendant les inondations et les périodes de fortes pluies (Barnaud et Fustec, 2007). Les milieux humides jouent également un rôle indispensable dans l'adaptation au changement climatique en retenant un tiers du carbone terrestre et en aidant ainsi à réduire les émissions de gaz à effet de serre (Erwin, 2009; Kayranli et al., 2010; Sahagian et al., 1997).

Enfin, les milieux humides offrent une grande diversité de services écosystémiques, tels que des fonctions esthétiques, éducatives, scientifiques et culturelles, ainsi que des possibilités de loisirs et de tourisme, et constituent un habitat unique et critique pour 40% des espèces mondiales (Balcombe et al., 2005; Dahl et al., 1991; Margaryan et al., 2018; MEA, 2005). De multiples études, notamment celles de Cardinale et al. (2012) et de Cimon-Morin et al. (2016) ont évalué l'impact de la perte des milieux humides sur les fonctions qu'ils remplissent et les services écosystémiques qu'ils fournissent à l'échelle mondiale.

### 1.1.1 Fragmentation et perte de milieux humides

Bien que les milieux humides naturels aient une importance cruciale, ils sont aussi l'un des écosystèmes les plus menacés, car ils sont vulnérables aux perturbations anthropiques et naturelles (Hu et al., 2017). Ces écosystèmes sont souvent dégradés, fragmentés ou perdus en raison du développement industriel et infrastructurel intensif. La perte d'habitat (réduction de la quantité d'habitats) et la fragmentation (isolement de parcelles d'habitat) sont des processus qui modifient la distribution, l'abondance, la diversité et le maintien du biote des milieux humides. Dans ces écosystèmes, l'hydrologie est la principale variable déterminante pour la création et le maintien de leur biodiversité. Tous les impacts directs ou indirects qui modifient les régimes hydrologiques influencent donc la biodiversité. La fragmentation et la diminution de la connectivité causées par la perte d'habitat ont un impact négatif sur la survie de nombreux taxons, car elles réduisent le succès de la reproduction, modifient les interactions intra et interspécifiques et limitent la capacité de dispersion et de migration (Fahrig, 2017; Fischer et Lindenmayer, 2007; Tilman et al., 1994). En Amérique du Nord, la relation négative entre l'établissement humain et la densité des milieux humides est bien connue, ce qui signifie qu'à mesure que les activités humaines s'étendent, la mosaïque des milieux humides se transforme en un nombre réduit de parcelles de milieux humides plus isolées (Gibbs, 2000). Le Canada compte un total de 200 000 km<sup>2</sup> de milieux humides, dont environ 70 % ont été perdus ou dégradés depuis 1950, en raison de l'urbanisation, de l'agriculture et de l'expansion industrielle (Pellerin et Poulin, 2013; Queste, 2011).

Les impacts sur les milieux humides peuvent être classés en perturbations naturelles et perturbations anthropiques. Les perturbations naturelles incluent les fluctuations du niveau d'eau, le dépôt de sédiments, les incendies, les épidémies d'insectes et l'activité

des castors. Les perturbations anthropiques comprennent les changements de terrain dus au développement industriel, tels que le drainage, la fragmentation et l'apport de nutriments et de produits chimiques. En définitive, les impacts globaux sont le résultat d'une combinaison d'influences naturelles et anthropiques, parmi lesquelles le changement climatique est l'exemple le plus marquant (Niemi et al., 2004). L'augmentation de la température et la plus grande variabilité des précipitations dans les latitudes nordiques ont de graves conséquences pour les milieux humides et modifient les communautés végétales et animales (Gitay et al., 2011; Keller, 2011; Weltzin et al., 2000; Weltzin et al., 2003). Par exemple, les patrons de migration et de dispersion saisonnières des oiseaux peuvent changer, ce qui affecte considérablement leur survie (Žalakevičius et Švažas, 2005). En somme, la destruction et la dégradation des milieux humides entraînent l'élimination de nombreuses fonctions écologiques essentielles, réduisant l'accessibilité, la quantité et la qualité des habitats (Junk et al., 2006; MEA, 2005; Poulin et al., 2016).

#### 1.1.2 Qualité de l'habitat des milieux humides pour les vertébrés boréaux

L'habitat est défini comme « *les ressources et les conditions environnementales présentes dans une zone qui sont requises par les individus d'une espèce ou d'un groupe d'espèces pour accomplir le processus de vie, y compris la survie et la reproduction* » (Hall et al., 1997). D'autre part, la qualité de l'habitat correspond, quant à elle, à la capacité de l'environnement à fournir des conditions appropriées pour la survie des individus et des populations (Hall et al., 1997), laquelle est explicitement liée aux taux de survie et de reproduction d'une espèce donnée. La présente thèse utilisera les définitions des termes *habitat* et *qualité de l'habitat* proposées ci-dessus.



Les écosystèmes des tourbières font partie des habitats particulièrement touchés par la réduction et la disparition des milieux humides à l'échelle mondiale. Environ 3 à 4 % de la surface terrestre mondiale est occupée par des tourbières, ce qui représente près de 60 % de la superficie totale des milieux humides (Lappalainen, 1996). On distingue généralement deux types de tourbières, en fonction de la source d'eau qui influence la végétation : les tourbières minérotrophes et les tourbières ombrotrophes. Les premières sont alimentées à la fois par les précipitations et par les eaux circulantes enrichies en minéraux au contact des sols environnants. Les secondes sont principalement alimentées par les précipitations provenant de la pluie et de la neige. Les tourbières ombrotrophes d'Amérique du Nord sont généralement considérées comme pauvres en vertébrés et invertébrés par rapport aux autres habitats (Desrochers, 2001; Mazerolle et al., 2001). Pourtant, les informations de base sur la faune de ces écosystèmes sont très parcellaires. En ce qui concerne les vertébrés, les tourbières restent l'un des habitats terrestres le moins étudié.

Les tourbières contribuent à la diversité végétale et faunistique régionale, car de nombreuses espèces utilisent ces milieux pour au moins une partie de leur cycle de vie (Calmé et Desrochers, 1999; Desrochers, 2001; Larson et House, 1990; Mazerolle et al., 2001; Poulin et al., 1999). Au Canada, les tourbières occupent environ 17 % de la superficie terrestre, dont la quasi-totalité se trouve dans les régions boréale et subarctique (Poulin et al., 2004; Tarnocai, 2009). Moins de 1 % de la superficie des tourbières est exploitée au Canada, et l'extraction de la tourbe se concentre dans le sud-est du pays. La majeure partie de la tourbe qui est extraite est destinée au secteur horticole (Keys, 1992; Poulin et al., 2004). Bien que les milieux humides soient abondants dans la région boréale du Québec, représentant ainsi 12,9 % du territoire selon Pellerin et Poulin (2013), leur importance reste peu connue dans cette région. Au Québec, les tourbières représentent environ 85 % de la superficie des milieux humides, et environ 1,5 % de cette superficie a été perdue en raison des activités anthropiques.

Dans le Nord-du-Québec, les basses terres de la baie James et de la baie d'Hudson constituent le plus grand complexe de tourbières au Canada et comptent parmi les plus grands complexes de tourbières au monde (Abraham et Keddy, 2005; Riley, 2003). Les tourbières et les autres types de milieux humides composés de petits étangs (superficie inférieure à 8 ha) sont particulièrement vitaux pour plusieurs groupes d'animaux, comme les oiseaux aquatiques et les amphibiens, qui choisissent de préférence les petits étangs pour se reproduire (Gibbs et Melvin, 1993; Lemelin et al., 2010; Semlitsch et al., 2015). De plus, ils sont utilisés par de nombreuses espèces au cours de leur migration (Mack et Morrison, 2006). Ainsi, les milieux humides de la zone boréale offrent de nombreux étangs et petits plans d'eau qui sont reconnus comme des habitats importants pour de nombreuses espèces. Comme mentionné ci-dessus, les connaissances sur la faune des tourbières sont éparses et lacunaires. Au regard du rôle clé et irremplaçable que remplissent ces écosystèmes, il est donc primordial d'offrir une meilleure compréhension de la façon dont la qualité de leur habitat peut affecter la biodiversité des vertébrés.

## 1.2 Facteurs déterminants de l'occupation et de la richesse des espèces

La mesure biologique la plus simple et la plus fréquemment utilisée dans les études écologiques et les programmes de suivi est probablement la richesse en espèces, c'est-à-dire le nombre d'espèces dans une zone donnée (Gotelli et Colwell, 2001). Les caractéristiques de la richesse des espèces sont souvent le résultat d'une combinaison de processus écologiques et évolutifs (Mittelbach et al., 2007; Ricklefs, 1987; Wiens et Donoghue, 2004). Comprendre les processus régulant la richesse en espèces entre différents habitats est un objectif majeur de l'écologie et constitue la base des études sur l'écologie des communautés (Colwell et Coddington, 1994; May, 1988). La

richesse des espèces varie souvent le long des gradients environnementaux et géographiques, ainsi qu'entre les habitats d'une même région (Rahbek, 1995). Les processus qui modifient directement la richesse à un endroit donné sont le plus souvent étudiés à grande échelle, mais l'importance relative des facteurs qui expliquent les patrons de richesse reste incertaine à plus petite échelle (Field et al., 2009). Dans ce dernier cas, plusieurs études ont mis en évidence le grand potentiel des petits étangs pour accueillir un large éventail d'espèces aquatiques, terrestres et amphibiens (Akasaka et Takamura, 2012; Biggs et al., 2017; Gómez-Rodríguez et al., 2009; Oertli, 2010). La présence d'espèces dans les étangs résulte de différents facteurs abiotiques et biotiques intrinsèques et extrinsèques, qui déterminent la répartition des espèces et les assemblages de communautés. Ces facteurs incluent des facteurs géographiques (pool d'espèces, dispersion), des facteurs abiotiques (disponibilité des ressources, hétérogénéité environnementale, fréquence et intensité des perturbations) et des facteurs biotiques (compétition, prédation, facilitation). La compréhension de ces facteurs est cruciale pour la conservation et la gestion de la diversité dans le contexte d'un changement anthropique global croissant.

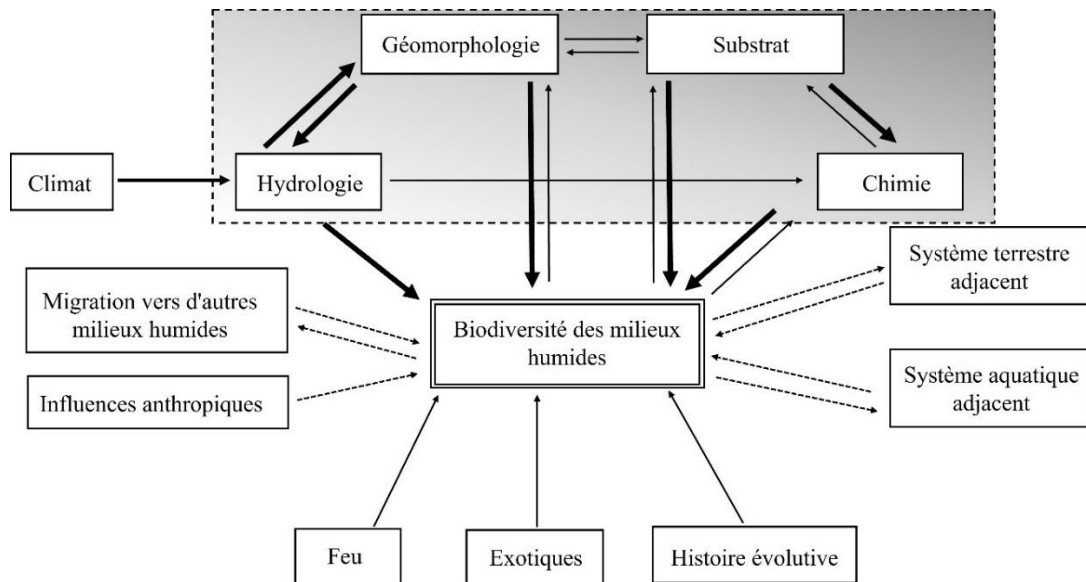


Figure 1.1. Schéma conceptuel montrant les principaux facteurs influençant la biodiversité dans les milieux humides. L'épaisseur des flèches indique l'importance relative du facteur et l'interaction entre les facteurs. Les quatre composantes dans la boîte ombragée interagissent entre elles pour créer l'hétérogénéité de l'habitat, et influencent la biodiversité du milieu humide à la fois collectivement et séparément. Tiré et modifié de Maltby et Barker (2009).

### 1.2.1 Facteurs géographiques et abiotiques

Les processus qui déterminent la richesse des espèces sont supposés varier dans le temps et dans l'espace. Les études examinant les patrons biogéographiques à grande échelle trouvent souvent des relations entre le nombre d'espèces présentes et la latitude d'un lieu donné (Rohde, 1992). Dans les grandes zones géographiques, la richesse des espèces est susceptible de diminuer avec la latitude; elle est donc plus élevée sous les tropiques (Gaston, 1996; Stevens, 1989). Par exemple, la richesse en espèces d'oiseaux diminue généralement en se déplaçant vers le nord (Kouki, 1999). Cependant, cela n'est pas dû à la latitude per se, mais à des variables positionnelles (élévation et

longitude, par exemple), à des conditions environnementales abiotiques (température et précipitations) et à des forces stochastiques (Willig et al., 2003). Par conséquent, considérer les gradients latitudinaux de manière isolée peut s'avérer inapproprié. Le climat est sans aucun doute un facteur majeur qui détermine la présence d'espèces le long d'un gradient nord-sud. Les variables environnementales qui influencent les facteurs biologiques et géographiques, tels que les régimes de température, les précipitations, le vent et le mouvement de l'eau, façonnent souvent les gradients de richesse des espèces. Les modèles de richesse des espèces à travers les gradients géographiques dépendent des interactions entre les intervalles de tolérance et la compétition des espèces.

L'hétérogénéité environnementale peut également contribuer à la richesse des espèces locales en promouvant la diversité. Les environnements hétérogènes contiennent un plus large spectre de conditions potentiellement optimales pour un plus large ensemble d'espèces que les environnements plus homogènes. Dans les milieux humides, l'hétérogénéité environnementale résulte principalement des interactions entre l'hydrologie et la géomorphologie (Keough et al., 1999). Les variations des attributs hydrologiques, tels que l'amplitude, la durée, la fréquence et le rythme des inondations, contribuent à une grande hétérogénéité. À grande échelle, cette hétérogénéité se traduit par une variété de types de milieux humides (Maltby et Barker, 2009). L'hétérogénéité environnementale comprend les ressources (eau et nutriments du sol) et les conditions environnementales, telles que la température, les précipitations ou l'acidité de l'eau.

La complexité structurelle de l'habitat accroît les gradients environnementaux et le nombre de types d'habitats, ce qui favorise la cooccurrence d'un plus grand nombre d'espèces (Tews et al., 2004). En effet, les habitats hétérogènes sont plus susceptibles de fournir un abri et une protection contre les conditions environnementales défavorables à un plus grand nombre d'espèces. La théorie de la niche écologique,

associée à de nombreuses preuves empiriques provenant de nombreux groupes taxonomiques et fonctionnels, soutient une relation positive entre l'hétérogénéité de l'habitat et la richesse des espèces (MacArthur et MacArthur, 1961; Pausas et al., 2003; Shmida et Wilson, 1985). Des habitats plus diversifiés peuvent accueillir un plus grand nombre d'espèces grâce à la création de niches et au partage des ressources (Cramer et Willig, 2005; Tews et al., 2004). La superficie des habitats est également considérée comme un facteur déterminant de la richesse des espèces. Les recherches sur les relations entre les espèces et la superficie indiquent un plus grand nombre d'espèces dans les grands habitats : en effet, à mesure que la superficie augmente, des microhabitats supplémentaires sont ajoutés au système, ce qui facilite l'incorporation d'autres espèces dans les assemblages (Connor et McCoy, 1979; Rosenzweig, 1995).

La connectivité entre des milieux hétérogènes permet d'accroître la biodiversité dans les milieux humides (Gibbs et Melvin, 1993; Scheffer et al., 2006; Ward et al., 1999; Zamberletti et al., 2018). Bien que la biodiversité globale soit plus élevée à des niveaux intermédiaires de connectivité, la réponse varie selon les groupes taxonomiques (macrophytes, amphibiens, mollusques, insectes) (Tockner et al., 1999; Van den Brink et al., 2013). Par exemple, la connectivité augmente la richesse des espèces d'amphibiens, contrairement à la fragmentation des habitats (Lehtinen et al., 1999). La fragmentation des milieux humides réduit la connectivité en augmentant la longueur de la bordure du milieu humide.

### 1.2.2 Facteurs biotiques

À l'échelle locale, l'occurrence des espèces est influencée par plusieurs types d'interactions intra et interspécifiques qui comprennent des interactions au sein du

réseau alimentaire, la compétition pour les ressources, la facilitation, l'immigration et les perturbations humaines (Keddy et Fraser, 2000). Ces effets sont communément difficiles à mesurer, car ils impliquent souvent des interactions très complexes. Les interactions du réseau alimentaire régulent la diversité animale par des processus impliquant la spécialisation de la niche alimentaire, les habitats d'alimentation et la ségrégation temporelle et spatiale de l'alimentation. La grande diversité des espèces qui utilisent les ressources des milieux humides provient des différences morphologiques et des variations dans le comportement alimentaire des espèces ayant des habitats similaires (Kushlan, 1989).

Les plantes et les animaux contribuent également à augmenter l'hétérogénéité des habitats, en jouant un rôle actif. Tel est le cas des ingénieurs de l'écosystème, définis comme des organismes qui modulent directement ou indirectement la disponibilité des ressources pour les autres espèces en provoquant des changements physiques dans les matériaux biotiques ou abiotiques (Jones et al., 1994). En fait, les ingénieurs des écosystèmes créent de nouveaux habitats pour d'autres espèces ou groupes d'espèces, augmentant ainsi la richesse des espèces (Nummi et Holopainen, 2014).

La biodiversité des milieux humides est influencée par les interactions avec les systèmes terrestres et aquatiques environnants. Par exemple, de nombreux animaux des milieux humides (amphibiens, reptiles et oiseaux aquatiques) utilisent régulièrement ces habitats adjacents pour se nourrir, nicher ou se reproduire (Burke et Gibbons, 1995). Par conséquent, toute altération de l'habitat ou des ressources environnantes pourrait les affecter. Les activités industrielles anthropogéniques causent des altérations des milieux humides en modifiant les apports d'eau, de sédiments et de nutriments. La perturbation est donc l'une des principales composantes de l'environnement qui affecte les espèces des milieux humides (Mooney et Godron, 1983; Turner, 1987). La faible et la forte perturbation peuvent conduire à une faible diversité d'espèces, tandis que les

niveaux intermédiaires de perturbation maximisent la richesse des espèces (Keddy et Fraser 2000) . Dans le cas de perturbations de faible intensité, les espèces compétitives en excluent d'autres, tandis qu'à des niveaux élevés de perturbation, seules quelques espèces peuvent tolérer une telle perturbation. Des niveaux intermédiaires de perturbation maximisent la richesse des espèces, car l'abondance de l'espèce la plus dominante est réduite, ce qui permet aux autres espèces de s'établir (Palmer, 1994). La compétition interspécifique pour les ressources limitées peut limiter la diversité de la faune lorsque le nombre des compétiteurs supérieurs augmente (Hutchinson, 1959). Lorsque les ressources sont rares, un nombre limité d'espèces peut être présent dans un lieu ou un habitat donné.

### 1.3 Justification de la thèse

#### 1.3.1 Contexte social et géographique

Cette thèse est réalisée dans la région de la baie James de l'Eeyou Istchee du nord-ouest du Québec (Canada), située entre 49 ° et 55 ° N et 70 ° et 79 ° O. La région administrative du Nord-du-Québec est à la fois la plus grande région du Québec, avec une superficie de 707 333 km<sup>2</sup>, et la moins peuplée, puisqu'elle compte environ 46 600 habitants (Institut de la statistique du Québec, 2022). La région est en grande partie occupée par la Nation Crie, qui possède des droits de gestion spécifiques sur les ressources naturelles locales et continue de pratiquer intensivement la chasse, le piégeage, la cueillette et la pêche (Berkes et al., 1995; Royer et Herrmann, 2011). On trouve également dans le sud de cette région le territoire de la Première Nation



Abitibiwinni. Les deux nations représentent la majorité de la population totale de la région.

Le Nord-du-Québec est un vaste territoire dont l'accès routier est limité. Par conséquent, la biodiversité y est relativement peu étudiée par rapport à la partie sud, plus densément peuplée. La région de la présente étude comprend les basses terres de la baie d'Hudson et de la baie James, qui constituent l'un des plus grands milieux humides au monde (Abraham et Keddy, 2005). En général, la région abrite différents types d'étangs, bien que les tourbières minérotrophes et les tourbières ombrotrophes, constituent la majeure partie de cette région (Pellerin et Poulin, 2013). Les autres types d'étangs comprennent les marais, les marécages et les étangs de castors qui contiennent une grande diversité d'espèces (Warner et Asada, 2006). Comme ces milieux humides sont abondants et omniprésents dans le paysage, tout projet de développement les affectera d'une façon ou d'une autre.

Cette région boréale du Canada est de plus en plus affectée par les activités d'exploitation des ressources ainsi que par des facteurs naturels, tels que le climat, le feu et les insectes. Ces processus entraînent la réduction ou la perte d'habitats et représentent donc une menace importante pour la diversité des vertébrés. Les activités industrielles se concentrent ainsi dans la partie la plus méridionale du paysage boréal, les difficultés géographiques, comme l'éloignement et l'inaccessibilité des centres urbains, les coûts de transport et le climat défavorable, ayant limité l'expansion du développement dans les régions plus septentrionales (Foote et Krogman, 2006). Les régions du nord du Canada et du Québec n'ont pas encore été développées industriellement et conservent ainsi la majeure partie de leur biodiversité intacte. Toutefois, avec la croissance démographique, l'expansion urbaine et la diminution croissante des ressources disponibles dans les zones habitées, l'exploitation des ressources naturelles de ces territoires nordiques devrait s'intensifier dans un avenir

proche. Cette augmentation imminente des pressions environnementales risque de dégrader, voire de faire disparaître, des écosystèmes clés pour les vertébrés, notamment les milieux humides (Foote et Krogman, 2006; Schindler et Lee, 2010).

La région est principalement caractérisée par trois activités anthropiques, à savoir l'exploitation minière, l'hydroélectricité et l'exploitation forestière, cette dernière étant localisée exclusivement dans la partie méridionale (Société du Plan Nord, 2022). En effet, l'exploitation forestière n'est pas un enjeu majeur à l'échelle régionale, car cette région se situe majoritairement au nord de la frontière commerciale du Québec. À l'inverse, l'exploitation minière joue un rôle clé car il s'agit d'une des industries les plus importantes du Canada. Plusieurs développements miniers, tels que l'exploitation de l'or, du lithium et du diamant, sont en constante augmentation (Société du Plan Nord, 2022) et on estime que cette activité a un impact majeur sur certaines populations fauniques. L'exploration et l'extraction minière nécessitent le développement d'infrastructures importantes (Pellerin et Poulin, 2013), notamment des infrastructures linéaires, comme les routes et les chemins de fer destinés au transport des équipements et des minerais, ainsi que des lignes électriques. Il s'agit là de vecteurs de transformation des terres (Asselin, 2011; Forbes et al., 2004) pouvant entraîner la perte ou la fragmentation des habitats. De plus, les sites miniers abandonnés peuvent devenir une source potentielle de contamination des eaux et des sols (Johnston et al., 2003; Sprague et Vermaire, 2018).

Dans ce contexte, un certain nombre de contraintes telles que l'immensité et l'inaccessibilité du territoire, la rigueur du climat, la brièveté de la saison estivale et les difficultés logistiques et financières rendent la collecte de données de base sur la présence des espèces complexe et laborieuse. Toutefois, ces mêmes caractéristiques d'immensité et d'inaccessibilité du territoire offrent le grand avantage de pouvoir étudier des espèces dans des habitats peu perturbés ou relativement intacts. Comme

mentionné dans la première partie de cette introduction, les connaissances sur les tourbières des parties septentrionales du Québec progressent, mais un travail considérable reste à faire pour les étoffer et renforcer ainsi l'efficacité des décisions de conservation.

### 1.3.2 Modèles d'étude pour les espèces des milieux humides : amphibiens, oiseaux et mammifères

La présente thèse s'appuie sur la définition des espèces des milieux humides proposée par Gopal et Junk (2001), à savoir : « *toutes les plantes, tous les animaux et tous les micro-organismes qui vivent dans un milieu humide de façon permanente ou périodique, y compris les migrants provenant d'habitats adjacents ou éloignés, ou qui dépendent directement ou indirectement de l'habitat du milieu humide ou d'un autre organisme vivant dans le milieu humide* ». Jusqu'à présent, la recherche sur la biodiversité des étangs s'est concentrée de manière isolée sur les invertébrés, les amphibiens, les poissons et la sauvagine, mais de nombreuses autres espèces dépendent des habitats qu'offrent ces milieux pour se nourrir ou se reproduire, à différents moments de leur cycle de vie (Batzler, 2013; Brown et al., 2012; Withey et van Kooten, 2011). Dans un contexte boréal, les espèces des milieux humides peuvent être résidentes ou migrer périodiquement ou saisonnièrement vers les étangs. Beaucoup d'entre elles utilisent périodiquement les milieux humides directement et même si elles n'y résident pas, elles dépendent toujours du biote des milieux humides. En fait, les petits étangs jouent un rôle important dans la dynamique des métapopulations de divers taxons, en réduisant l'isolement entre les grandes parcelles d'habitat des milieux humides (Gibbs et Melvin, 1993; Semlitsch et Bodie, 1998).

Pour les amphibiens, la plupart des espèces au Québec possèdent un cycle de vie biphasique, impliquant une phase larvaire aquatique et un stade adulte principalement terrestre (Rodrigue et Desroches, 2018; Semlitsch, 2000; Wilbur, 1980). Généralement, les amphibiens ayant un cycle de vie complexe utilisent les habitats aquatiques, y compris les étangs, pour la ponte des œufs et le développement des larves (Calhoun et DeMaynadier, 2007; Vitt et Caldwell, 2013). Après la métamorphose, les juvéniles migrent vers un habitat terrestre périphérique pour atteindre la maturité et, une fois adultes, de nombreuses espèces passeront la majeure partie de leur vie en phase terrestre (Rittenhouse et Semlitsch, 2007; Rothermel et Semlitsch, 2002; Semlitsch, 2008). De nombreuses espèces présentent un degré de philopatrie, ce qui signifie qu'une grande partie des adultes reviennent se reproduire dans le même étang où ils sont nés (Pechmann et al., 2001). Les amphibiens dépendent également des habitats terrestres adjacents pour se nourrir, se protéger des prédateurs et, finalement, pour hiberner. Ainsi, l'accès à l'habitat terrestre environnant est essentiel pour compléter leur cycle de vie (Marsh et Trenham, 2001; Semlitsch, 2002). À plus grande échelle, le nombre et la position des étangs dans le paysage permettent de maintenir la connectivité, y compris l'immigration et la dispersion entre les populations (Semlitsch et Bodie, 1998). Comme ils ont un cycle de vie qui inclut l'utilisation d'habitats terrestres et aquatiques, les amphibiens sont souvent utilisés comme indicateurs biologiques, car ils servent de signes d'alerte de la dégradation à la fois des milieux terrestres et des milieux aquatiques (Welsh et Ollivier, 1998; West, 2018). Les amphibiens subissent un déclin mondial majeur, avec 41 % des espèces d'amphibiens du monde menacées et font l'objet de relativement peu d'efforts de conservation (Houlahan et al., 2000; IUCN, 2022; Stuart et al., 2004; Wake et Vredenburg, 2008). Plusieurs études ont montré que la perte et la fragmentation des habitats réduisent la richesse en espèces et l'abondance des populations d'amphibiens, ainsi que leur diversité génétique (Cushman, 2006; DeMaynadier et Hunter, 1995; Findlay et

Houlahan, 1997; Petranka et al., 1993). La perte et la fragmentation des habitats dues aux activités anthropiques restent les facteurs les plus fréquents à l'origine de ces déclin (Campbell et al., 2020; Green et al., 2020).

De nombreuses études montrent que les étangs et petits plans d'eau boréaux constituent des habitats essentiels pour de nombreuses espèces d'oiseaux (Desjardins et al., 2020; Holopainen, 2015; Weller, 1999). Les milieux humides contenant de petits étangs, présentent certaines caractéristiques favorables à l'établissement de la sauvagine, comme l'abondance de proies aquatiques, l'absence de stratification thermique et une exposition réduite au vent et aux vagues (Baschuk et al., 2012; Lemelin et al., 2010; Nummi et Poysa, 1995). Par exemple, plus de 35 espèces de sauvagine présentes au Québec utilisent les milieux humides comme halte migratoire et de reproduction (Lemelin et al., 2010). Un grand nombre d'oiseaux aquatiques migrent et se reproduisent pendant le printemps et l'été dans les abondants milieux humides boréaux (Faaborg et al., 2010).

Seulement une centaine d'espèces de mammifères ont besoin des milieux humides dans le monde et les exemples boréaux comprennent des espèces aquatiques ou semi-aquatiques telles que les rats musqués, les castors et les loutres (Lévêque et al., 2005; Prescott et Richard, 2016). Cependant, d'autres mammifères jouent des rôles écologiques importants dans les milieux humides (Fritzell, 1988) : les herbivores agissent comme des disperseurs de graines, et les carnivores peuvent réguler les abondances de proies par la prédation. Ces rôles écologiques ont des effets importants sur les fonctions des milieux humides comme le cycle des nutriments, le flux d'énergie, la qualité de l'eau et la régénération des forêts (Lacher et al., 2019; Terborgh et al., 2001). En outre, certaines espèces sont emblématiques et importantes pour les activités humaines liées à l'utilisation des milieux humides, comme la chasse, la pêche ou la photographie animalière.

L'intérêt d'utiliser les amphibiens, les oiseaux et les mammifères comme groupes de vertébrés pour élucider les associations habitat-espèces découle du manque de connaissances sur l'aire de répartition nordique des espèces (Warner et Asada, 2006), mais aussi de leur vulnérabilité à de nombreuses pressions naturelles et anthropiques qui menacent leur existence, particulièrement celle des amphibiens. Ces trois groupes de vertébrés constituent donc un modèle biologique original et robuste pour étudier la relation habitat-espèces dans les milieux humides contenant des petits étangs.

### 1.3.3 Facteurs affectant l'utilisation des habitats par les vertébrés

*La taille de l'étang* — Il est essentiel de comprendre le rôle de la superficie de l'habitat, car elle peut favoriser la diversité des espèces. Cependant, lorsqu'il s'agit des étangs, les informations actuelles suggèrent que la relation entre la surface et la richesse d'espèces est complexe. En effet, Oertli et al. (2002) ont montré que cette corrélation positive ne s'applique qu'aux odonates, tandis qu'elle n'a pas été confirmée pour les autres macroinvertébrés et amphibiens. Par conséquent, il est probable que d'autres facteurs jouent un rôle plus pertinent dans l'association entre la taille des étangs et la richesse en espèces, comme la qualité de l'eau, la présence des poissons, l'hydropériode ou le couvert végétal (Semlitsch et al., 2015). En somme, la relation entre la superficie de l'habitat et la diversité des espèces dans les étangs est complexe et doit être étudiée en prenant en compte plusieurs facteurs.

À l'échelle de l'espèce, l'influence de la surface des étangs n'est pas claire, puisque certaines études ont mis en évidence une association positive dans le cas des amphibiens se reproduisant dans les étangs (Findlay et al., 2001; Houlihan et Findlay, 2003), alors que d'autres études ont démontré une relation faible ou nulle (Hecnar et

M'Closkey, 1998; Snodgrass et al., 2000). Les amphibiens ont tendance à trouver un équilibre entre les petits étangs, plus susceptibles de s'assécher, et les grands étangs, plus susceptibles d'abriter des poissons prédateurs (Semlitsch et al., 2015; Skelly et al., 1999; Snodgrass et al., 2000). Dans le cas des oiseaux, plusieurs études sur l'utilisation de l'habitat ont signalé l'importance de la taille du plan d'eau pour les oiseaux d'eau (Adde et al., 2021). Les oiseaux d'eau non-piscivores utilisent plus les petits que les grands plans d'eau (Lemelin et al., 2010; Nummi et Poysa, 1995).

*La disponibilité des ressources alimentaires* — Les changements dans la structure de la végétation peuvent influencer la disponibilité des ressources alimentaires et affecter de manière différentielle les espèces se nourrissant dans diverses strates de végétation (Donkor et Fryxell, 1999; Pastor et Naiman, 1992). La disponibilité des ressources alimentaires peut être un déterminant de la qualité de l'habitat pour les espèces des milieux humides (Arcese et Smith, 1988). De nombreux processus écologiques peuvent provoquer des variations des ressources alimentaires, comme l'approvisionnement en graines, les infestations d'insectes et les perturbations naturelles, telles que les feux de forêt et la présence de castors (Edworthy et al., 2011; Fisher et Wilkinson, 2005; Koenig et Knops, 2000).

La profondeur de l'eau modifie également la disponibilité et la diversité des ressources alimentaires, notamment les poissons, les invertébrés et les graines (Connor et Gabor, 2006; Desgranges et al., 2006). Par exemple, les populations d'invertébrés sont une source de nourriture essentielle pour les espèces de sauvagine et d'oiseaux des marais, car ils constituent une ressource cruciale pour la croissance des jeunes (Murkin et Kadlec, 1986). L'émergence de ces jeunes insectes nourrit les migrateurs et constitue la principale source de nourriture pour de nombreux passereaux nicheurs. La présence de poissons dans un étang peut affecter l'abondance ou la richesse des invertébrés aquatiques (Mallory et al., 1994). Les apports allochtones, provenant de l'activité des

castors, augmentent les ressources alimentaires aquatiques, ce qui favorise les populations d'invertébrés qui soutiennent les poissons, les mammifères et les oiseaux aquatiques (Longcore et al., 2006; Nummi et Holopainen, 2014).

*La compétition et prédation* — Le fait que des espèces partagent la même niche écologique implique qu'elles partagent des ressources alimentaires communes; cette situation entraîne une compétition voire une prédation intragilde (Donadio et Buskirk, 2006). Dans le cas de la compétition, les individus d'une même espèce, ou de plusieurs espèces, utilisent une ressource commune dont la disponibilité est limitée (Tilman, 1990). Alors que les interactions compétitives se produisent au sein d'un même niveau trophique, les interactions de prédation peuvent se produire à différents niveaux trophiques (Holling, 1959). La prédation est une source primaire de mortalité et peut affecter la présence des espèces et la dynamique des populations dans un étang. La prédation affecte la distribution des proies, qui sont généralement distribuées de manière à limiter leur risque de prédation, comme se nourrir davantage dans des habitats couverts (Brown et Kotler, 2004; Morris et Gilroy, 2008). Le risque de prédation est influencé par l'abondance des prédateurs, la structure de l'habitat et le comportement prédateur-proie (Lima et Dill, 1990; Söderström et al., 1998).

Les amphibiens et les oiseaux doivent faire face à des prédateurs différents selon leur habitat. Le manque d'adaptations des amphibiens face aux prédateurs des poissons se traduit par une plus grande richesse des espèces d'anoues dans les zones humides sans poissons (Hecnar et M'Closkey, 1997; Kats et Ferrer, 2003). Les étangs peu profonds sont des habitats favorables pour les amphibiens, car ils ne sont pas colonisés par les populations de poissons et les grands invertébrés qui constituent une menace pour leurs œufs, leurs larves et leurs adultes. Les oiseaux, quant à eux, subissent la prédation des nids par de nombreux prédateurs, un facteur important qui influence l'écologie de leurs populations. Dans les régions boréales en particulier, la prédation des nids est un



élément crucial pour le succès de la nidification des oiseaux (Martin, 1988, 1992; Sherry et Holmes, 1992), qui doivent faire face à une variabilité importante en fonction des prédateurs, des habitats et des paysages auxquels ils sont exposés. Le principal prédateur de nids dans les forêts nordiques est l'écureuil roux (*Tamiasciurus hudsonicus*), bien que d'autres espèces puissent également jouer un rôle important localement (Bayne et Hobson, 2002; Sieving et Willson, 1998).

*Les étangs de castors* — L'activité des ingénieurs de l'écosystème augmente l'hétérogénéité de l'habitat dans un paysage. En Amérique du Nord, il n'y a pas d'ingénieur d'écosystème plus influent que le castor (Jones et al., 1994). Le castor est une espèce de rongeur clé de l'écosystème largement répandue dans les régions boréales du Canada (Müller-Schwarze, 2011). On le trouve également dans les bassins versants des cours d'eau du Nord-du-Québec, mais son abondance diminue vers le nord dans cette région. Les perturbations causées par le castor entraînent des changements dans la composition des espèces végétales, le déroulement de la succession, l'hydrologie des cours d'eau, la géomorphologie, ainsi que la chimie et la température de l'eau, ce qui affecte également l'habitat d'autres espèces (Rosell et al., 2005). L'activité des castors constitue donc une perturbation naturelle qui accroît l'hétérogénéité et la diversité du paysage (Cunningham et al., 2006; Westbrook et al., 2011).

Les castors ont besoin d'un approvisionnement constant en eau tout au long de l'année pour se protéger des prédateurs et accéder facilement à la nourriture, ce qu'ils régulent en construisant des barrages (Müller-Schwarze, 2011). Ces barrages inondent la végétation, modifient la succession des communautés aquatiques et forment ainsi de nouveaux étangs. La ressource en eau passe d'un cours d'eau à un étang lentique, ce qui augmente la quantité d'eau libre et de zones humides émergentes dans un bassin versant (Cunningham et al., 2006). Les étangs créés par les castors modifient les cycles

biogéochimiques à de grandes échelles spatiales et temporelles du paysage (Johnston et Naiman, 1990; Naiman et al., 1994). Dans ces étangs peu profonds et généralement stagnants, la pénétration de la lumière, augmentent la productivité primaire (Klotz, 1998). Les étangs de castors exposent une plus grande surface à la lumière du soleil, ce qui augmente le rayonnement thermique et les températures de surface des étangs (McRae et Edwards, 1994). La mort des arbres et la chute des feuilles contribuent à cette augmentation des nutriments dans l'eau (Naiman et al., 1986). Après quelques années, les étangs de castors actifs peuvent être abandonnés, ce qui peut entraîner la détérioration des structures du castor (c'est-à-dire la hutte, le barrage), modifiant ainsi les caractéristiques de l'habitat (Grover et Baldassarre, 1995). Les étangs de castors abandonnés peuvent également être transformés en prairies ouvertes dominées par des graminées et des carex (Neff, 1957). Cette nouvelle hétérogénéité du paysage créée par les étangs de castors actifs et abandonnés peut profiter à plusieurs espèces.

De nombreuses études ont montré que les castors exercent une influence positive sur de nombreuses populations animales, principalement parce qu'ils augmentent l'hétérogénéité de l'habitat dans l'espace et dans le temps. Par exemple, les barrages inondés de castors fournissent un couvert de nidification aux oiseaux aquatiques adjacents aux étangs (Gibbs et Melvin, 1993), tandis que les niveaux d'eau stables créent des zones pour l'élevage des couvées (Nummi, 1992; Nummi et Holopainen, 2014). De même, les oiseaux aquatiques profitent de l'abondance croissante des invertébrés comme source de nourriture, surtout pendant leur période de reproduction (McKinstry et al., 2001). Les conditions peu acides des étangs de castors peuvent stimuler le développement des larves et la physiologie des amphibiens (Müller-Schwarze, 2011; Skelly et Freidenburg, 2000). Dans le cas des mammifères, les étangs de castors fournissent aux mammifères semi-aquatiques un approvisionnement abondant en proies, des niveaux d'eau stables et un abri. Les prairies de castors

fournissent quant à elles une végétation succulente aux mammifères terrestres (Müller-Schwarze, 2011; Rosell et al., 2005).

*Les variables du paysage* — La biodiversité des zones humides est grandement influencée par les interactions avec les systèmes adjacents de hautes terres et d'eau libre. De nombreuses espèces d'amphibiens, de reptiles et certains oiseaux aquatiques des zones humides utilisent périodiquement les habitats environnants pour se nourrir, nicher ou se reproduire (Burke et Gibbons, 1995). Il est démontré que les variables au niveau du paysage, telles que la densité des routes ou la superficie des forêts et des milieux humides entourant les étangs de reproduction, sont corrélés avec la présence d'amphibiens et la richesse des espèces (Dodd et Cade, 1998; Findlay et Houlihan, 1997). De même, la présence de passereaux est affectée par l'étendue et la structure de la forêt environnante (Drapeau et al., 2000; Hobson et Schieck, 1999). La superficie de forêts adjacente peut être importante pour les spécialistes de la forêt, tandis que les habitats ouverts peuvent être pertinents pour les espèces en début de succession (Imbeau et Desrochers, 2002a; Lesmerises et al., 2013; Venier et al., 2014).

#### 1.3.4 Approche méthodologique et statistique

Plusieurs méthodes d'échantillonnage sont traditionnellement utilisées pour étudier les vertébrés et plus particulièrement les amphibiens, les oiseaux et les mammifères. Ces méthodes actives et standards comprennent les rencontres visuelles, l'échantillonnage par transects, les captures ou les comptages ponctuels (Gaines et al., 1999; Heyer et al., 2014; Ralph et al., 1995; Rockhill et al., 2016). L'une des principales avancées technologiques pour les études sur la faune sauvage au cours des deux dernières décennies est le développement d'unités d'enregistrement autonomes (*automatic*

*recording units*, ARU) qui permettent d'effectuer un suivi acoustique passif. Le suivi acoustique passif est un outil très répandu et très populaire pour le suivi à distance des oiseaux, mammifères, anoues et insectes qui vocalisent (de Solla et al., 2005; Furnas et Callas, 2015; Laiolo, 2010). En effet, les inventaires acoustiques passifs sont plus efficaces que les inventaires in situ traditionnels menés par des observateurs humains (Bridges et Dorcas, 2000), car ils peuvent atténuer les perturbations sur la faune en collectant des données à distance et obtenir une énorme quantité de données avec moins d'efforts. L'utilisation des ARU facilite le suivi des espèces à de plus grandes échelles spatiales et temporelles : les ARU peuvent être laissées sur le terrain pendant de longues périodes sans intervention, et peuvent être déployées pour étudier plusieurs zones simultanément. Les ARU peuvent être programmées pour enregistrer à différents moments de la journée, même la nuit dans le cas des espèces nocturnes, lorsque l'accès est plus difficile. Ceci est particulièrement utile dans le cas des espèces qui émettent des vocalisations relativement peu fréquentes ou irrégulières, et qui ne sont pas facilement détectées par d'autres méthodes. Les ARUs permettent de programmer un nombre illimité de visites répétées et peuvent être utilisées pour échantillonner des sites difficiles d'accès d'un point de vue logistique, comme l'est notre région d'étude. Les enregistrements nécessitent généralement une interprétation manuelle, bien que les méthodes de reconnaissance par ordinateur soient de plus en plus utilisées (Priyadarshani et al., 2018).

Dans les chapitres II et III, les ARU sont l'une des méthodes de détection utilisées pour caractériser les espèces d'amphibiens et d'oiseaux et les assemblages de taxons entiers. Dans le chapitre II, les ARU servent à déterminer les patrons d'occupation de trois espèces d'anoues, tandis que dans le chapitre III elles sont utilisées pour les espèces d'oiseaux et l'écureuil roux d'Amérique qui est susceptible d'influencer l'assemblage des espèces d'oiseaux à différents niveaux.

Cette thèse s'appuie également sur le relevé de pièges photographiques, une autre méthode de détection passive mais qui n'est pas une nouveauté dans le suivi de la faune (Kucera et Barrett, 2011). L'utilisation de pièges photographiques a élargi la portée et les possibilités de recherche, de gestion et de conservation de la faune sauvage dans le monde entier (Caravaggi et al., 2020; McCallum, 2013; Rowcliffe, 2017). Comme le démontre l'utilisation de cet outil dans le cas de plusieurs carnivores dans différents paysages (Kays et Slauson, 2008; Lesmeister et al., 2015), ces caméras non invasives sont bien adaptées à la détection d'espèces difficiles à piéger et à gérer, dont la densité est faible ou qui ont des habitudes nocturnes et secrètes. Cependant, comme toute méthode d'échantillonnage, les enregistreurs acoustiques et les pièges photographiques sont susceptibles à la détection imparfaite des espèces (Burton et al., 2015; Guillera-Arroita, 2017).

*L'importance de la détection imparfaite* — La détectabilité est une source d'erreur importante lors de l'estimation des paramètres biologiques d'intérêt. La capacité à détecter la présence ou le nombre d'individus d'une espèce donnée dans une unité d'échantillonnage est rarement parfaite ou constante dans le temps et l'espace (MacKenzie et al., 2002; MacKenzie et Royle, 2005), et est souvent affectée par un certain nombre de facteurs liés aux conditions d'échantillonnage (Guillera-Arroita, 2017; MacKenzie et al., 2017; Mazerolle et al., 2007; Pollock et al., 2002). Ce phénomène, dénommé détection imparfaite, est inhérent à la plupart des habitats et des écosystèmes. Plus précisément, on parle de détection imparfaite lorsqu'une espèce présente à un endroit d'échantillonnage n'est pas détectée et que l'on conclut erronément à son absence (MacKenzie et al., 2002). La détection imparfaite peut entraîner des biais dans les estimations des paramètres et donc dans les conclusions qui en dérivent (Guillera-Arroita et al., 2014; Kellner et Swihart, 2014).

De nombreux facteurs peuvent influencer la détectabilité des espèces émettant des sons, tels que les caractéristiques de la végétation environnante, les traits de vocalisation spécifiques, le matériel d'enregistrement et la méthode utilisée pour traiter les enregistrements audios. L'un des principaux obstacles à la réalisation de relevés acoustiques est le contrôle de la variation de la qualité des signaux sonores. Dans le contexte des pièges photographiques, la détection imparfaite peut agir au niveau de l'habitat utilisé par l'espèce, mais aussi au niveau du positionnement de la caméra (Burton et al., 2015; Findlay et al., 2020). En effet, la zone de détection peut varier en fonction du modèle de caméra, de la visibilité, de la hauteur, de l'angle d'installation, du comportement et de la taille de l'espèce (Findlay et al., 2020; Meek et al., 2016; Tourani et al., 2020).

Certains des problèmes associés à la détection imparfaite sont inhérents aux groupes de vertébrés étudiés. La détection imparfaite est particulièrement fréquente dans le cas des amphibiens parce qu'ils sont difficiles à détecter : en effet, ils sont souvent cryptiques, actifs à des moments où ils ne sont pas facilement observables et ne sont visibles qu'à certaines périodes de l'année (Mazerolle et al., 2007; Stebbins et Cohen, 1995; Vitt et Caldwell, 2013). La détectabilité des oiseaux dans les zones humides boréales est influencée, quant à elle, par le biais de l'observateur, la saison de reproduction, le type d'appel, le moment de la journée, le bruit de fond et les conditions météorologiques (Conway et Gibbs, 2001; Harms et Dinsmore, 2014; Stiffler et al., 2018). Une série de variables propres à certaines espèces peut influencer la capacité des chercheurs à détecter les individus. Par exemple, certaines espèces ayant un sens de l'odorat très développé peuvent être attirées par certains appâts olfactifs (c'est-à-dire, des proies) ou être repoussées par d'autres (par exemple, l'odeur humaine) (Séquin et al., 2003). D'autres facteurs météorologiques peuvent aussi affecter l'activité des espèces, comme les précipitations, l'heure de la journée ou la température (Chatterjee et al., 2021; Lesmeister et al., 2015; Tobler et al., 2008). Il est donc essentiel

de tenir compte de la détection imparfaite lors de la réalisation d'études sur ces groupes. Pour surmonter la détection imparfaite, des inventaires répétés des sites d'échantillonnage sont suggérés (Kéry et al., 2005). Dans notre cas, nous avons procédé à quatre périodes d'échantillonnage primaires (deux périodes d'échantillonnage entre les mois de mai et juin 2018 et 2019, et deux autres entre les mois de juin et août 2018 et 2019) et sept périodes d'échantillonnage secondaires au sein des quatre périodes d'échantillonnage primaires (c'est-à-dire sept jours consécutifs échantillonnés au sein de chaque période primaire).

*Approche statistique* — Au cours des deux dernières décennies, des outils statistiques ont été mis au point pour tenir compte de la détection imparfaite, notamment des méthodes de capture-marquage-recapture, des analyses de comptage et, plus particulièrement, des modèles d'occupation des sites (Burton et al., 2015; Mazerolle et al., 2007; Shannon et al., 2014). Les modèles d'occupation permettent d'étudier les populations d'espèces individuelles par rapport à leur occurrence, c'est-à-dire leur présence dans une proportion définie de zone ou d'habitat (MacKenzie et al., 2017). En prenant en compte la probabilité de détection, les modèles d'occupation de site à une saison estiment la probabilité d'occurrence d'une espèce sur un site tout en estimant l'influence des covariables sur cette probabilité sur un certain nombre de sites au cours d'une saison (MacKenzie et al., 2002). De même, les modèles *N*-mélange sont utilisés pour estimer l'abondance des individus d'une espèce pendant une saison donnée, tout en tenant compte de la probabilité de détection (Royle, 2004). Une telle approche est basée sur le comptage des individus de la même espèce observés sur un site, sans qu'il soit nécessaire de capturer et de marquer les individus (Mazerolle et al., 2007; Royle, 2004). Par conséquent, pour les espèces d'amphibiens du chapitre II, nous avons utilisé des modèles d'occupation de site à une saison pour estimer l'occupation de trois espèces qui se reproduisent en étang, et des modèles *N*-mélange pour estimer

l'abondance des masses d'œufs et des individus métamorphosés de certaines de ces espèces.

*Richesse des espèces* — Les effets du changement global sur la composition des communautés étant de plus en plus préoccupants, les informations au niveau des communautés sont de plus en plus nécessaires. Déterminer avec précision la richesse spécifique peut être compliqué étant donné la détectabilité variable de chaque espèce (Kéry et Schmidt, 2008). Les modèles multi-espèces permettent d'estimer la probabilité d'occupation et la probabilité de détection indépendamment pour chaque espèce et groupe ou au sein d'une communauté entière (Devarajan et al., 2020). Les stratégies de gestion et de conservation doivent prendre en compte toutes les espèces qui habitent un site donné, plutôt que de se limiter à celles qui fournissent suffisamment de données (Zipkin et al., 2010). Les espèces rares sont souvent négligées dans les études au niveau communautaire, principalement en raison de leurs faibles taux de détection (MacKenzie et al., 2017). Les modèles multi-espèces permettent d'intégrer des données sur les espèces rares, insaisissables ou à faible densité (Dorazio et Royle, 2005; Gelfand et al., 2005). C'est pourquoi, des modèles d'occupation multi-espèces ont été utilisés dans les chapitres III et IV de la présente thèse afin d'étudier les assemblages de trois groupes à différents niveaux, y compris de nombreuses espèces qui sont difficiles à détecter ou qui ne peuvent être détectées que pendant de courtes périodes. De plus, compte tenu des objectifs de cette thèse, nous avons l'intention de caractériser les petits étangs qui abritent des amphibiens, des oiseaux et des mammifères et d'évaluer l'utilisation de l'habitat pour ces trois groupes. L'étude qui a été menée dans le cadre de cette thèse s'appuie sur différents modèles : des modèles d'occupation à une saison, des modèles à  $N$ -mélange et des modèles hiérarchiques multi-espèces, selon les particularités de chaque chapitre.



### 1.3.5 Objectifs et structure de la thèse

L'objectif général de l'étude est de caractériser les étangs des tourbières et les étangs de castors afin d'évaluer et de comparer l'utilisation de ces deux types de milieux humides par trois groupes de vertébrés : les amphibiens, les oiseaux et les mammifères. Étant donné que l'utilisation des étangs par différents taxons est associée aux caractéristiques de chaque habitat, nous cherchons à déterminer la composition des communautés de ces ordres taxonomiques en comparant les facteurs d'habitat impliqués dans l'utilisation des étangs de chaque type par les espèces. Nous quantifions les différences d'occupation des espèces d'amphibiens (chapitre II), d'oiseaux (chapitres III et IV) et de mammifères (chapitre IV) dans les deux types d'étangs, dans le but d'utiliser ces connaissances comme base de référence à intégrer dans les futurs projets de conservation et de gestion à l'échelle régionale. Cette recherche permettra en fin de compte de mieux comprendre les milieux humides de la région boréale de l'est du Canada et plus particulièrement les petits étangs, afin d'améliorer la conservation de la diversité des vertébrés qui utilisent ces habitats et en dépendent.

Bien que le rôle des étangs de castors ait fait l'objet d'études substantielles quant à leurs effets sur de nombreux groupes de vertébrés (Grover, 1993; Rosell et al., 2005; Stringer et Gaywood, 2016), les recherches sont rares dans les régions boréales nordiques où les perturbations humaines sont faibles. De plus, aucune étude basée sur une approche multi-espèces n'a été menée dans le Nord-du-Québec dans le cas des oiseaux et des mammifères. Les tourbières (en particulier les tourbières ombrotrophes) sont considérées comme des habitats hostiles pour certains groupes taxonomiques, en raison de leur acidité inhérente, de leur faible disponibilité en nutriments et caractère humide (Desrochers, 2001; Mazerolle et al., 2001). Ces écosystèmes sont donc étonnamment peu explorés pour les groupes de vertébrés. Par conséquent, le manque

d'informations sur la présence des vertébrés dans le nord-est du Canada, l'aire de répartition nordique de nombreuses espèces, la rareté des données sur l'utilisation des milieux naturellement perturbés par les castors nordiques, le statut vulnérable des populations d'amphibiens et l'absence d'approches multi-espèces ont motivé la préparation de cette thèse.

Pour atteindre les objectifs fixés, l'analyse est menée à trois échelles taxonomiques et méthodologiques, à savoir les anoues et les oiseaux par une approche acoustique (chapitres II et III) et les mammifères et les oiseaux par une approche visuelle (chapitre IV). La séquence des chapitres représente une chronologie méthodologique et taxonomique. Outre l'introduction générale et la conclusion, la thèse est divisée en trois chapitres élaborés sous forme d'articles scientifiques :

- Le chapitre II vise à estimer l'occupation et l'abondance de trois espèces d'anoues se reproduisant en étang et à quantifier l'influence des facteurs liés à l'étang et au paysage au cours des différents stades de leur cycle de vie, y compris les masses d'œufs, les individus métamorphosés et les mâles chanteurs.
- Dans le chapitre III, nous avons mené une étude communautaire sur un ensemble d'oiseaux afin d'examiner comment l'occupation des espèces d'oiseaux différait entre les deux principaux types d'étangs et répondait aux facteurs d'habitat et de paysage, ainsi qu'à la présence d'un prédateur de nid. Ici, nous avons évalué les réponses à trois niveaux (espèces, guildes et communauté) et déterminé si la richesse était affectée par les covariables d'occupation.
- Dans le chapitre IV, nous utilisons une méthodologie passive différente (pièges photographiques) pour estimer l'occupation des étangs par les mammifères de

taille moyenne et grande et les oiseaux, et évaluer comment l'hétérogénéité de l'habitat, la quantité d'habitats et les caractéristiques anthropogéniques affectent l'occupation de chaque espèce détectée parmi les deux taxons.

La conclusion générale du chapitre V synthétise les résultats des chapitres ci-dessus, discute de la relation qu'ils entretiennent et aborde leurs implications. Enfin, nous fournissons des recommandations et des suggestions pour de futures recherches sur les petits étangs. En outre, deux annexes ont été ajoutées. La première est une revue quantitative de la contribution des données de science citoyenne largement utilisées aux modèles de distribution des espèces, dans laquelle nous discutons de leurs variations et des lacunes taxonomiques à l'échelle mondiale. La seconde annexe décrit pour la première fois un événement de prédation spécifique par un oiseau migrateur très répandu dans la région d'étude, le Grand Chevalier (*Tringa melanoleuca*) sur des anoues comme proies dans sa distribution nordique. Cet événement a été enregistré à l'aide de pièges photographiques dans le cadre du chapitre IV.

## CHAPITRE II

### OCCUPANCY AND ABUNDANCE OF POND-BREEDING ANURANS IN BOREAL LANDSCAPES

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Accepted in *Journal of Herpetology* (September 2022)

## 2.1. Abstract

As resource extraction moves north across the globe, wetland ecosystems in Canada are increasingly degraded due to disturbances associated with anthropogenic activities, including timber harvesting, hydroelectric development, and mining. These activities may particularly affect amphibian species that depend on certain wetland types for breeding, such as peatland and beaver ponds. We assessed the influence of pond and landscape level characteristics on amphibian use of 50 ponds in northern Quebec, Canada in 2018 and 2019. Using acoustic recorders and visual counts, we estimated the occupancy of calling males and the abundance of metamorphosed individuals and egg masses of three amphibian species: Wood Frogs (*Lithobates sylvaticus*), Mink Frogs (*Lithobates septentrionalis*), and Spring Peepers (*Pseudacris crucifer*). We quantified the influence of variables such as pond type, area, fish presence, acidity, and landscape features on occupancy and abundance. We found no effect of explanatory variables on the probability of occupancy of calling males of the three species. Detection probability of Spring Peeper choruses increased with air temperature. The abundance of Mink Frog metamorphosed individuals decreased with increasing pond area and increased with water pH. Wood frog reproductive effort, quantified as egg mass abundance, was more than four times greater in beaver ponds than in peatland ponds. Our survey results provide a reference to guide management decisions regarding the conservation of amphibian assemblages in increasingly disturbed wetlands of Northern Canada.

*Key words:* Call survey; Egg mass counts; *Lithobates septentrionalis*; *Lithobates sylvaticus*; *N*-mixture model; Northern Quebec; *Pseudacris crucifer*; Visual survey.

## 2.2. Résumé

Comme l'extraction des ressources se déplace vers le nord de la planète, les écosystèmes des milieux humides du Nord canadien sont de plus en plus dégradés en raison des perturbations associées aux activités anthropiques, notamment la récolte du bois, le développement hydroélectrique et les activités minières. Ces activités peuvent affecter particulièrement les espèces d'amphibiens qui dépendent de certains types de milieux humides pour la reproduction, comme les étangs de tourbières et les étangs de castors. Nous avons évalué l'influence des caractéristiques au niveau de l'étang et du paysage sur l'utilisation par les amphibiens de 50 étangs du nord du Québec, Canada, en 2018 et 2019. À l'aide d'enregistreurs acoustiques et de décomptes visuels, nous avons estimé l'occupation des mâles chanteurs et l'abondance des individus métamorphosés et des masses d'œufs de trois espèces d'amphibiens : la Grenouille des bois (*Lithobates sylvaticus*), la Grenouille du Nord (*Lithobates septentrionalis*) et la Rainette crucifère (*Pseudacris crucifer*). Nous avons quantifié l'influence des variables de l'étang telles que le type d'habitat, la superficie de l'étang, la présence de poissons, le pH de l'eau et les variables du paysage sur l'occupation et l'abondance. Nous n'avons trouvé aucun effet des variables explicatives sur la probabilité d'occupation des mâles chanteurs des trois espèces. La probabilité de détection des chorales des Rainettes crucifère augmentait avec la température de l'air. L'abondance des individus métamorphosés de Grenouilles du Nord diminuait avec l'augmentation de la superficie des étangs et augmentait avec le pH de l'eau. L'effort reproducteur de la Grenouille des bois, quantifié par l'abondance de masses d'œufs, était plus de quatre fois supérieur dans les étangs de castors que dans les étangs de tourbières. Les résultats de notre étude constituent une référence pour orienter les décisions de gestion concernant la conservation des assemblages d'amphibiens dans les milieux humides de plus en plus perturbés du nord du Canada.

### 2.3. Introduction

Worldwide, wetlands are often the main breeding habitat type for many amphibian species and are crucial for the maintenance of amphibian biodiversity (Semlitsch, 1998; Snodgrass et al., 2000). In recent years, the decline in abundance of extensive wetland areas has presumably isolated amphibian communities (Alford and Richards, 1999; Houlihan et al., 2000). Pond-breeding amphibians in temperate climates depend on specific habitats, as they require distinct environments for each life stage at different times of the year (Semlitsch, 1998, 2002; Wilbur, 1980). For such species, the removal of either aquatic or adjacent terrestrial habitats can prevent the completion of their life cycle (Trenham and Shaffer, 2005).

In boreal landscapes, wetlands support amphibian species at their northern range limits. In these northern wetlands, the breeding season is short. However, wetlands in northern areas are under growing pressure from human activities involving the exploitation of resources, mainly due to the expansion of timber harvesting, hydroelectric development, and mining (MEA, 2005; Timoney, 2003; Venier et al., 2014). Consequently, forest fragmentation and wetland loss are spreading northward and exerting pressure on the persistence of pond-breeding amphibian populations (Lesbarrères et al., 2014).

Typical breeding habitats of boreal amphibians are permanent or ephemeral standing water embedded in forested landscapes (Okonkwo, 2011; Stevens et al., 2006). Boreal regions in Canada harbor different types of wetlands including peatland and beaver ponds (Pellerin and Poulin, 2013). Use of peatland ponds as breeding ponds by amphibians in southern Canada have received some attention at temperate latitudes (Mazerolle, 2001, 2005; Mazerolle and Cormier, 2003; Stockwell and Hunter, 1989).

However, investigations on factors driving occupancy and abundance of amphibians in boreal peatlands remain scarce (Annich et al., 2019; Browne et al., 2009). A growing body of evidence suggest that beaver ponds in boreal regions are used by many amphibian species throughout their entire life cycle (Cunningham et al., 2007; Stevens, 2006; Stevens et al., 2007).

As ecosystem engineers, beavers (*Castor canadensis*) can drastically modify an entire water body by building lodges and dams (Jones et al., 1994; Rosell et al., 2005). Therefore, they create new breeding areas for amphibians (Dalbeck et al., 2007), enhance landscape heterogeneity, and increase connectivity between remaining populations by decreasing the distance between ponds (Cunningham et al., 2007). Beavers could be used as a surrogate indicator species for locating populations and identifying amphibian habitat, which can be especially useful in remote boreal regions (Stevens et al., 2007). Beaver and peatland ponds at northern latitudes may offer distinct conditions for amphibian species that may influence occupancy dynamics and distributions.

The occurrence and abundance of pool-breeding amphibians not only vary with pond conditions, but also with characteristics of the surrounding landscape (e.g., Mazerolle et al., 2005; Scherer et al., 2012; Van Buskirk, 2005). At the local pond level, species occurrence is influenced by abiotic and biotic factors, including hydroperiod (Babbitt et al., 2003; Snodgrass et al., 2000; Veysey et al., 2011), wetland size and hydrology (Babbitt and Tanner, 2000; Babbitt, 2005), and levels of competition and predation risk (Hecnar and M'Closkey, 1997; Werner and McPeck, 1994). At the landscape level, site occupancy is often affected by factors related to movement of individuals among local populations and the extent of surrounding terrestrial or wetland areas (e.g., Guerry and Hunter, 2002; Mazerolle et al., 2005; Sawatzky et al., 2019). However, these previous investigations were conducted in specific contexts and locations, and there is a lack of



studies in northern regions, where the breeding period is much shorter than in southern areas (e.g., D'Aoust-Messier, 2012; Homan et al., 2004; Lehtinen et al., 1999). Therefore, understanding how heterogeneous habitats influence different life stages of amphibians in a poorly studied region is essential to develop conservation and management strategies.

In this study, we assessed factors affecting site occupancy and abundance of pond-breeding anuran species in two distinct boreal wetland landscapes in northern Quebec. Specifically, i) we compared characteristics of beaver ponds and peatland ponds at the pond and landscape levels, and ii) we quantified the influence of these local and landscape factors on the occupancy and abundance of three pond-breeding species. We hypothesized that factors at the pond level may influence species occurrence and abundance as the two habitats may differ in key attributes, including pond type, water acidity, water depth, pond size, and presence of fish predators (Annexe A, Table A.1). Because peatland ponds are acidic and amphibian eggs and larvae are sensitive to low water pH (Payette and Rochefort, 2001; Pierce, 1985; Zoltai and Vitt, 1995), we predicted that beaver ponds were more likely to be occupied by breeding amphibians and support higher abundances of individuals than peatland ponds. We predicted that anuran occupancy would decrease with fish presence, as fish prey on egg masses and tadpoles (Egan and Paton, 2004; Holbrook, 2014; Teplitsky et al., 2003). At the landscape level, we predicted that occupancy increased with the proportion of the surrounding area covered by forest and wetland as these habitats are used by adult and juveniles for foraging and hibernation (Semlitsch, 1998, 2002; Semlitsch and Bodie, 2003). Accordingly, species with affinities for terrestrial habitats (e.g., American Toads, Spring Peepers, Wood Frogs) should experience stronger forest effects than primarily aquatic species (e.g., Mink Frogs, Green Frogs).

## 2.4. Materials and Methods

### 2.4.1. Study area

We conducted this work in the Eeyou Istchee James Bay region in northwestern Quebec (Canada) between 49° to 53° N, and 71° and 79° W (Fig. 2.1A). The study area covers approximately 400,000 km<sup>2</sup> and is part of a traditional Cree and Abitibiwinni First Nation territory. Study sites were distributed among three sectors along a northeastern gradient from a landscape dominated by black spruce (*Picea mariana*) conifer stands in the southwest to a landscape of open forest dominated by small black spruce categorized under the Taiga shield ecozone in the far northeast (Ducruc et al., 1976; Lord and Robitaille, 2013). Southwestern sites of the study area were located within commercial black spruce forests and were part of the Hudson Bay Lowlands which contains the highest density of wetlands in North America (Fraser and Keddy, 2005). In addition to climate change and wildfire regime dynamics (Bergeron et al., 2004; Payette and Rochefort, 2001), the region faces anthropic threats, including timber harvesting in the south and hydroelectric development, but most commonly from mining activities, which require major road and infrastructure developments (Anielski and Wilson, 2005; Ménard et al., 2013).

Vegetation surrounding peatland ponds can be classified as belonging to minerotrophic fens or ombrotrophic bogs (Fig. 2.1B). Common species dominating the shrub layer (< 3 m) were black spruce and tamarack (*Larix laricina*). The main vascular plant groups in the low shrub layer (10-30 cm) include species of Ericaceae (e.g., *Chamaedaphne calyculata*, *Kalmia angustifolia*, *Rhododendron groenlandicum*) and to a lesser extent various Cyperaceae species (e.g., *Eriophorum vaginatum*, *Trichophorum cespitosum*, *Carex exilis*). Bryophytes are the most prevalent plant species on these peatlands, with a continuous carpet of Sphagnum mosses dominating the ground layer including

species as *Sphagnum angustifolium*, *S. cuspidatum*, and *S. magellanicum* complex (Payette et Rochefort, 2001). Beaver ponds were more common at the southern latitudes of the study region and vegetation in these ponds consisted of a dense cover of mixed forest dominated by black spruce, trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), balsam fir (*Abies balsamea*), graminoids, and flooded vegetation (Fig. 2.1C).

Mean temperature ranges from about -3 to 1 °C annually (8 to 22 ° C in summer) and annual precipitation in the region ranges from 700 to 1100 mm (Ouranos, 2021). Snow generally covers the region from mid-September to mid-May. We selected a total of 50 ponds < 2 ha in size that were distributed among the three 2500 km<sup>2</sup> sectors. To maintain independence among sites, sampled ponds were more than 800 m apart. We considered this distance appropriate as most adult amphibian species in the region migrate within 300 m of breeding sites (Semlitsch and Bodie, 2003). Among the 50 ponds, 12 were beaver ponds and 38 were peatland ponds (Fig. 2.1).

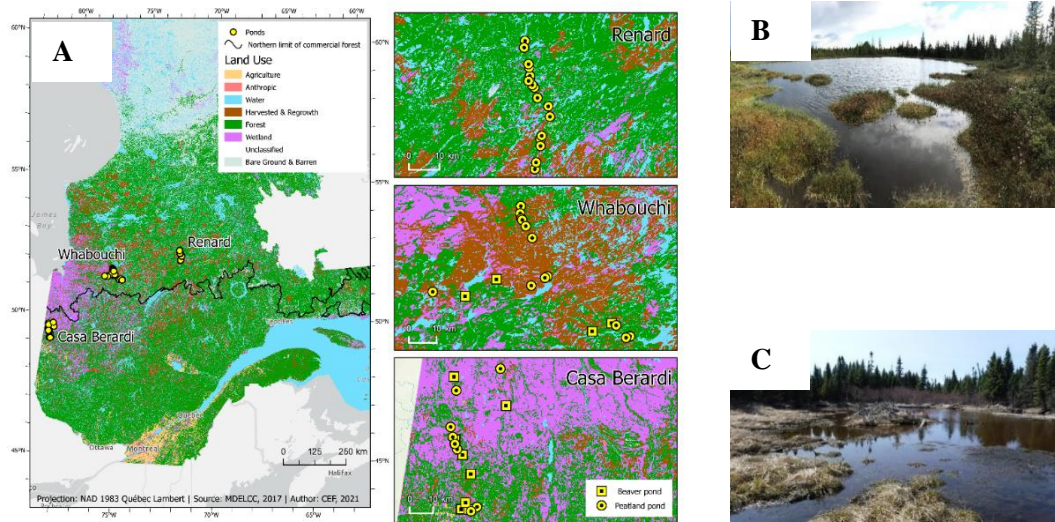


Figure 2.1. (A) Location of the 50 ponds (38 peatland and 12 beaver ponds) in three study sectors of Northern Quebec, Canada, sampled for pond-breeding anurans in 2018 and 2019. Photographs of representative main habitats in the study region: (B) Peatland ponds and (C) Beaver ponds. Photo credit: Remi Chevallier (B), and MF (C).

#### 2.4.2. Sampling methods

We sampled the same 50 ponds over two years. We performed two surveys per year, May to August 2018 and May to July in 2019. Visits during a given year were separated by 35 to 50 days. During each pond visit, we sampled amphibians using acoustic surveys with automated recorders to detect calling anuran males and visual surveys to count egg masses and metamorphosed individuals (i.e., juveniles and adults). The study area comprised different types of wetlands, but the landscape is dominated by a mosaic of peatlands. Forested areas occurred mostly in the southern portions of the study area, where beaver ponds are more commonly found. We planned to stratify the random selection of peatland and beaver ponds within each of the three regions of the study area. We selected an equal number of peatland and beaver ponds in the southern portion

of the study area (Casa Berardi; Fig. 2.1A). However, moving northward, beaver ponds meeting our selection criteria were less common than peatland ponds in the two other regions of the study area. Therefore, we increased the number of peatland ponds in the two other regions to compensate for the scarcity of beaver ponds. This resulted in a final sample consisting of 12 beaver ponds and 38 peatland ponds.

#### 2.4.3. Acoustic surveys

We visited sites in a south to north direction to match surveys times with the species' peak calling periods in each sector. Thus, we conducted anuran call surveys at all sites in May, June and July, which corresponded to the expected breeding times of all potential species in the region. As each species has a specific and short breeding season, we conducted call surveys based on their breeding phenologies. We deployed an automated acoustic recorder at each pond (SM4 Song meter, Wildlife Acoustics Inc., Maynard, MA, USA) to record male anuran calls in May to June and June to July in 2018 and 2019. During each visit, recorders were positioned 2 - 10 m from the water's edge and fastened approximately 1.5 m above ground to trees or wooden stakes. Each device was programmed to record at 2100 h, during 3-min for seven consecutive days. To reduce observer effects, one person listened to all 3-min recordings to identify species calls (Fig. 2.2). Each 3-min recording was also visualized as a spectrogram to help locate and identify calls using the Audacity program (Audacity Team, version 3.1.3; Koehler et al., 2017). Therefore, we completed four groups of sampling surveys of seven consecutive days for 50 ponds, yielding a total of 84 min for each pond. We analyzed recordings to identify species calls for each 3-min recording (Fig. 2.2).

We listened to the full length of each 3-min recording and noted the highest calling score detected, based on the North American Amphibian Monitoring Program (NAAMP) for each species: 0- No frog calls heard; 1- Individuals can be counted with no overlap in calls; 2- Some overlap of calls but individuals can be distinguished; 3- Full chorus, continuous and overlapping, individuals cannot be distinguished. These call indices were later converted to a binary variable as species detected or not, except for Spring Peepers which were detected in almost all of our recordings. For the latter species, we analyzed the probability of having many individuals (call index 3: Spring Peeper chorus) and how it varied across different explanatory variables.

The anuran fauna in our study area consisted of six species: Wood Frogs (*Lithobates sylvaticus*), Spring Peepers (*Pseudacris crucifer*), Mink Frogs (*Lithobates septentrionalis*), American Toads (*Anaxyrus americanus*), Northern Leopard Frogs (*Lithobates pipiens*), and Green Frogs (*Lithobates clamitans*; Bider, 1976; Desroches and Rodrigue, 2004; Fortin et al., 2012). We focused on the species that were most frequently observed at our sites, namely Wood Frogs, Spring Peepers, and Mink Frogs. The other three species were too rare for analysis and were discarded (detected at fewer than 10 of the 50 ponds). Species that were detected at the sites but not analyzed (i.e., fish, salamanders, frogs) were included in Annexe A (Table A.2 and A.3).

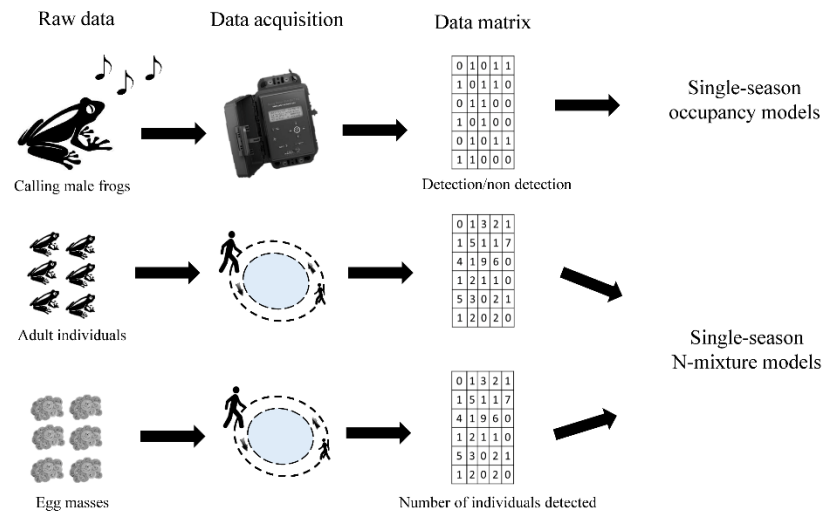


Figure 2.2. Workflow of the anuran data collected and analytical approach.

#### 2.4.4. Visual surveys

We conducted visual surveys in 2018 and 2019 during the recording periods at each pond to count egg masses (first visit of the year only) and metamorphosed individuals along the perimeter of each pond (Fig. 2.2). Visual surveys were conducted between 0900 and 1700 and consisted in walking slowly along the shore of the ponds and scanning within approximately 1 m spanning over the shoreline and the water for egg masses and metamorphosed individuals. Surveys were conducted simultaneously by the same two independent observers on all pond visits during the two years (Egan and Paton, 2004; Grant et al., 2005; Heyer et al., 2014). During a given visit, two observers started at the same point on the pond perimeter and walked in opposite directions along the entire perimeter. Both observers independently counted metamorphosed individuals and egg masses. Egg mass counts were conducted in 2018 (18 May -- 12 July) and 2019 (17 May -- 16 June). We detected egg masses of four amphibian species

at the ponds sampled: Mink Frogs, American Toads, Wood Frogs, and mole salamanders (*Ambystoma* sp.). As eggs for the other three species were rarely detected, we only analyzed egg masses of Wood Frogs.

#### 2.4.5. Pond and landscape-level variables

We recorded pond characteristics that may be important predictors of occurrence and abundance of pond-breeding amphibians based on previous studies. We considered several variables that can be separated into characteristics that describe habitat use (pond-level variables) and those related to the landscape surrounding the pond (landscape-level variables; Table 2.1).



Table 2.1. Summary of pond and landscape variables considered to explain the presence of calling frog males and the abundance of metamorphosed individuals and the number of egg masses (reproductive effort) of *Lithobates sylvaticus*, *Pseudacris crucifer* and *Lithobates septentrionalis* sampled at 50 beaver and peatland ponds in Northern Quebec in 2018 and 2019. Variables affecting detection were also included.

Level	Variable	Description and unit	Reference
Pond	Area	Pond area (ha)	Hecnar, 2004; Semlitsch and Bodie, 1998
	Depth	Mean water depth (cm)	Laan and Verboom, 1990
	Acidity	Mean water pH (pH)	Freda, 1986; Vatnick and al., 1999
	Fish	Fish presence (detection/non detection)	Mallory et al., 1994; Hecnar and M'Closkey, 1997
Landscape	Forest	Percentage of forest higher than 4 m within buffer areas (%)	Marsh and Trenham, 2001; Semlitsch and Bodie, 2003
	Wetland	Percentage of wetlands of all types within buffer areas (%)	Semlitsch and Bodie, 2003
Detection	Sound quality	Subjective evaluation of the quality of the acoustic recording (good or not good)	Koehler et al., 2017
	Air temperature	Average air temperature per hour (° C)	Heyer et al., 2014; Oseen and Wassersug, 2002
	Humidity	Average relative humidity per hour (% HR)	Bellis, 1962; Green, 1997
	Snowmelt	Number of days elapsed since snowmelt	Schmidt, 2005
	Observer	(Observer 1 or 2)	Allredge et al., 2006

For pond-level variables, we determined the area of each pond in ArcGIS 10.8 (ESRI, Redlands, California, USA) from coordinates taken along the shore with a geographical positioning system unit (GPS Etrex 20X  $\pm$  3 m accuracy, Garmin Ltd.) in June and July 2019. Furthermore, we measured the water depth 1 m from the pond edge at 10 points along the perimeter using a 2-m wooden ruler. We measured the pH (Oakton EcoTestr

pH 2, Ottawa, Canada) from three randomly selected points within the first 30 cm of the water column. Measures of water depth and pH were taken at each pond on each visit and averaged for each pond before analyses. We sampled each pond for fish, as they can be predators of amphibians (Hecnar and M'Closkey, 1997; Hopey and Petranka, 1994). To do so, we used three Silver Creek galvanized minnow traps (6.25 mm mesh size with openings of 2 cm) randomly positioned in each pond 1 - 2 m from the shore (Mallory et al., 1994). Traps were deployed during one visit on the second year of sampling. We removed traps after 2 or 3 days and identified individuals at the species level when possible. Specimens were photographed to facilitate identification and were returned to the water immediately.

We assessed landscape-level covariates from satellite imagery obtained from the ecological mapping of vegetation in meridional and northern Quebec (Berger and Leboeuf, 2013; Leboeuf et al., 2012a). We limited our analysis to concentric buffer areas of 300 and 1000 m along pond perimeters. These buffer sizes encompass the terrestrial habitat use adjacent to the pond and the migration and dispersal distances of most species in our study area (Dodd, 1996; Marsh and Trenham, 2001; Semlitsch and Bodie, 2003). Within buffers, we calculated the percent cover of forest areas of two forest types (deciduous and mixed forest combined, and coniferous), as well as the percent cover of open wetlands, including peatlands, ponds, marshes, and shallow water (Berger and Leboeuf, 2013; Leboeuf et al., 2012b). We assumed that the average vegetation and wetland cover at all sites was consistent between years.

#### 2.4.6. Observation variables

We examined parameters that potentially affected our detection of amphibians during each visit (Mazerolle et al., 2007). For acoustic surveys, we considered the quality of the recording, air temperature, relative humidity, and number of days after snowmelt (Annexe A, Table A.1). The quality of the recording was categorized with two levels (good or not) based on the level of saturation in recordings and background noise that could interfere with detection. Oversaturation occurs when the volume reaches maximum amplitude in the recording and prevents reliable information from being extracted (Koehler et al., 2017). Background noise could include wind, rain, vehicle traffic, flying insects, or sound produced by other animals. We measured air temperature (average per hour) at each pond using a temperature logger (iButton, Mont-St-Hilaire, QC, Canada) fixed to a wooden stake near the edge of the pond. Relative humidity (%) was obtained from a weather station located at each mining site. To account for asynchrony in the start of the breeding season along our latitudinal gradient, we considered the number of days elapsed since snowmelt. Snowmelt date was defined as the first day of 7 consecutive days in which the mean daily temperatures were above 0 °C. For visual count surveys, we considered the days elapsed since snowmelt and an observer effect (Annexe A, Table A.1).

#### 2.4.7. Statistical analyses

For comparing characteristics between pond types, we used a two-sample t-test with Bonferroni adjustment ( $p < 0.05/9 = 0.0055$ ). For the analysis of occupancy from call data, we used the 3-minute recordings taken on 7 consecutive days during two periods

per year (May-June and June-July) to estimate pond occupancy from anuran call data. We used single-season occupancy models (MacKenzie et al., 2002; MacKenzie et al., 2017) to test the influence of pond and landscape-level variables on occupancy of anuran species. We formulated models based on a set of variables likely to affect site occupancy ( $\psi$ ) and probability of detection ( $p$ ) (Annexe A, Appendix 1) (MacKenzie et al., 2003; Popescu and Gibbs, 2009). We used single-season  $N$ -mixture models (Royle, 2004) to estimate the abundance of metamorphosed individuals and egg masses of amphibians. These models enable the estimation of abundance and imperfect detection probability (Royle, 2004). We used a zero-inflated Poisson (ZIP) to model the abundance of each species.

For both state variables of occupancy and abundance in our models, we constructed 11 hypotheses based on the various factors known to influence amphibian habitat use and abundance (Table 2.1 and Annexe A, Table A.1). We did not include pairs of variables that were highly correlated ( $|r| > 0.60$ ) (Schloerke et al., 2018). We centered and scaled numerical variables by subtracting the mean and dividing by the standard deviation. Observations from both sampling years were combined for all analyses. To account for potential differences among the two sampling seasons, we included a year effect on the state variable in all models. We tested the effect of three scenarios on detection probability in our models (Annexe A, Table A.1). Thus, the combinations of 11 hypotheses on a state variable (occupancy, abundance) and scenarios on detection probability yielded a total of 33 models. To determine the influence of explanatory variables on the state variables, we performed model selection using the Akaike information criterion corrected for small samples and overdispersion (QAICc) (Mazerolle, 2006). We used the shrinkage estimator to conduct multimodel inference (Burnham and Anderson, 2002). We considered that a variable had an effect when 95% unconditional confidence intervals around the estimate excluded zero (Burnham and Anderson, 2002). We assessed the goodness of fit of the highest ranked model of each

analysis using the MacKenzie and Bailey test for occupancy models and the chi-squared test for N-mixture models with 5000 parametric bootstrap samples (MacKenzie and Bailey, 2004; Mazerolle, 2015). Parameters were estimated by maximum likelihood in R version 3.5.0 using the unmarked package (Fiske and Chandler, 2011; R Core Team, 2019).

## 2.5. Results

### 2.5.1. Comparisons of habitat variables between site types

Acidity, pond size and water pH were similar between beaver and peatland ponds (Table 2.2). At the landscape level, peatland ponds had less deciduous and mixed forest within 300 m ( $t = 3.99$ ,  $df = 48$ ,  $P = < 0.001$ ), than beaver ponds, although they did not differ within 1000 m and for the cover of coniferous forest between pond type for both buffer sizes (Table 2.2). The cover of open wetlands within 300 m and within 1000 m did not differ between pond type (Table 2.2).

Table 2.2. Mean, standard deviation ( $\pm 1$  SD) and range of the pond and landscape variables at 12 beaver ponds and 38 peatland ponds in Northern Québec, Canada. Comparisons were conducted with two sample t-tests for all variables.

Pond variables	Beaver ponds (n = 12)			Peatland ponds (n = 38)		
	Mean (SD)	Min	Max	Mean (SD)	Min	Max
Acidity (pH)	6.08 (0.46)	5.27	6.93	5.89 (0.67)	4.62	7.05
Pond area (ha)	0.68 (0.54)	0.11	1.84	0.74 (0.46)	0.14	1.87
Water depth (cm)	52 (12.8)	26.58	69.55	82.3 (40.5)	29.55	176.52
Landscape variables						
Deciduous and mixed forest (%) within 300 m - DECMIX300 *	18.3 (20.9)	0.00	62.29	1.97 (7.84)	0.00	38.21
Deciduous and mixed forest (%) within 1000 m - DECMIX1000	18.6 (22)	0.00	62.60	6.50 (12.5)	0.00	60.02
Coniferous forest (%) within 300 m - CONIF300	40.9 (26.5)	0.00	85.53	40.2 (35)	0.00	100.00
Coniferous forest (%) within 1000 m - CONIF1000	40.0 (24)	0.00	77.31	40.9 (29.7)	0.00	91.48
Open wetlands (%) within 300 m - WET300	7.06 (7.83)	0.00	24.85	10.1 (18.1)	0.00	76.09
Open wetlands (%) within 1000 m - WET1000	4.62 (4.69)	0.04	14.98	11.8 (11.6)	0.00	48.50

Levels of significance with Bonferroni adjustment

### 2.5.2. Single-season occupancy models

Of the 50 ponds surveyed, we detected calls of Wood Frogs in 43% (2018) and 50% (2019) of ponds. For the Spring Peeper chorus, we detected evidence of calls in 47% (2018) and 88% (2019) of all ponds. We detected calls of Mink Frogs in 43% (2018) and 40% (2019) of all ponds. Similar patterns of occupancy for the three species were observed in beaver ponds and peatland ponds. Anuran males were as likely to call in peatland and beaver ponds (Fig. 2.3). Additionally, we did not find evidence of an

effect of pond and landscape-level variables on site occupancy for the three species. These results are detailed below.

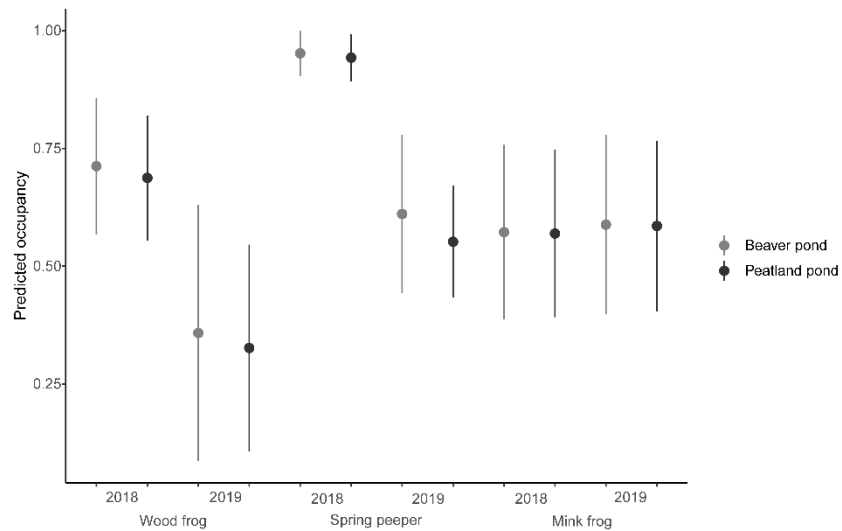


Figure 2.3. Model-averaged prediction of occupancy for three anurans species (Wood Frogs, Spring Peeper chorus and Mink Frogs) based on acoustic data from 12 beaver ponds (in grey) and 38 peatland ponds (in black) in Northern Québec in 2018 and 2019. Error bars denote 95% confidence intervals around estimates.

#### 2.5.2.1. Wood frogs

Analysis of Wood Frogs call data focused on sampling days in May and June because this corresponds to the breeding season of the species in our study area. The top-ranked model consisted of the effect of the proportion of forest cover within a buffer of 1000 m (DECMIX1000 + CONIF1000) on site occupancy and the quality of the recording on detection probability ( $\omega_i = 0.18$ ; Table 2.3). The goodness of fit test suggested moderate overdispersion ( $\chi^2 = 174.5$ ;  $P = 0.078$ ;  $\hat{c} = 1.39$ ). The null model was among the most parsimonious model with a delta QAICc  $< 2$ , indicating a lack of effect of

local and landscape variables on occupancy ( $\omega_i$ : 0.12; Annexe A, Table A.2). Wood Frogs occupancy did not vary with any of the variables we considered (Annexe A, Table A.3). Similarly, detection probability did not vary with any of the variables we considered (Annexe A, Table A.4).

Table 2.3. Most parsimonious occupancy models explaining the probability of occupancy of three anuran species in beaver and peatland ponds in Northern Quebec (Canada) in 2018 and 2019. Models were ranked based on the Akaike Information Criteria corrected for small samples and overdispersion (QAICc). Only models with a delta QAICc < 2 are presented with their respective Akaike weights ( $\omega_i$ ), log-likelihood (LL), and number of estimated parameters (K). Note that all models included a year effect on occupancy.

Models	LL	K	QAIC <sub>c</sub>	$\Delta$ QAIC <sub>c</sub>	$\omega_i$
<i>Wood frogs (<math>\hat{c} = 1.39</math>)</i>					
$\psi(\text{DECMIX1000} + \text{CONIF1000})p(\text{Quality})$	-153.20	8	324.00	0.00	0.18
$\psi(\text{DECMIX300} + \text{CONIF300})p(\text{Quality})$	-153.45	8	324.50	0.50	0.14
$\psi(\text{Null})p(\text{Quality})$	-155.96	6	324.83	0.83	0.12
$\psi(\text{Habitat type})p(\text{Quality})$	-155.17	7	325.58	1.58	0.08
$\psi(\text{Predation})p(\text{Quality})$	-155.37	7	325.96	1.96	0.07
<i>Spring Peeper chorus (<math>\hat{c} = 1.52</math>)</i>					
$\psi(\text{Predation})p(\text{Temp} + \text{Hum})$	-209.63	7	434.49	0.00	0.37
$\psi(\text{Habitat type})p(\text{Temp} + \text{Hum})$	-210.29	7	435.81	1.32	0.19
$\psi(\text{Null})p(\text{Temp} + \text{Hum})$	-211.68	6	436.28	1.79	0.15
<i>Mink frogs (<math>\hat{c} = 1.77</math>)</i>					
$\psi(\text{Null})p(\text{Temp} + \text{Hum})$	-103.52	6	219.95	0.00	0.26
$\psi(\text{DECWET300})p(\text{Temp} + \text{Hum})$	-103.24	7	221.72	1.77	0.11

DECMIX300: Deciduous and mixed forest (%) within 300 m; DECMIX1000: Deciduous and mixed forest (%) within 1000 m; CONIF300: Coniferous Forest (%) within 300 m; CONIF1000: Coniferous Forest (%) within 1000 m; Quality: Sound quality; Temp: Temperature; Hum: Humidity.



### 2.5.2.2. Spring peeper male chorus

Data for Spring Peepers spanned the same period as for Wood Frogs. The top-ranked model included the effects of the presence of fish on occupancy probability and of weather on detection probability ( $\omega_i = 0.37$ ; Table 2.3). The fit of this model suggested low overdispersion ( $\chi^2 = 189.51$ ;  $P = 0.0032$ ;  $\hat{c} = 1.52$ ). The null model also had some support ( $\omega_i: 0.15$ ; Table 2.3), explaining why we found no variation of the occupancy of Spring Peeper choruses with habitat or landscape variables. Spring Peeper choruses were more likely to occur in 2018 than in 2019 ( $\beta_{\text{Year}}: -2.6$ , 95% CI: [-4.56; -0.65], Fig. 2.3). Spring Peepers' occupancy did not vary with the remaining variables we considered (Annexe A, Table A.3). Detection probability of Spring Peepers' choruses increased with air temperature ( $\beta_{\text{Temp}}: 1.08$ , 95% CI: [0.66; 1.51], Fig. 2.4). Detection probability of Spring Peepers did not vary with any of the other variables we considered (Annexe A, Table A.2).

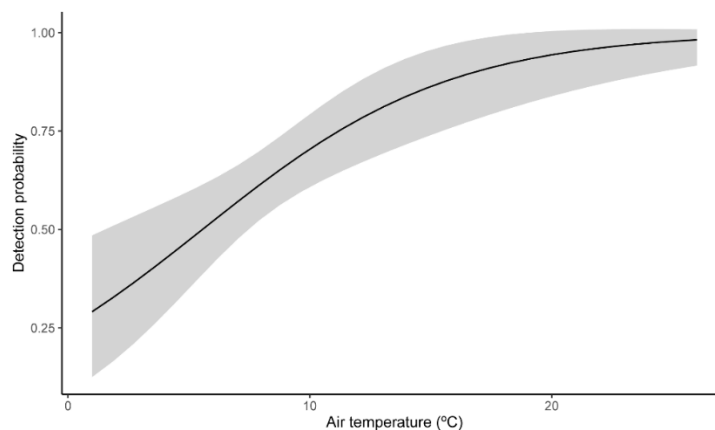


Figure 2.4. Variation in detection probability of Spring Peeper choruses with air temperature in 50 beaver and peatland ponds in Northern Quebec sampled during the summer of 2018 and 2019. Area shaded in gray denote 95% unconditional confidence intervals.

### 2.5.2.3. Mink frogs

The breeding season of Mink Frogs in our study area matched the timing of the surveys for the second period (June to July) as the species is active later in the season than Wood Frogs and Spring Peepers. The null model had the most support, indicating that the occupancy of the species did not vary with local and landscape variables ( $\omega_i = 0.26$ , Table 2.3). The goodness-of-fit test of this model suggested low overdispersion ( $\chi^2 = 206.40$ ;  $P = 0.077$ ;  $\hat{c} = 1.77$ ). Mink Frog occupancy did not vary with any of the variables we considered (Annexe A, Table A.1). Similarly, detection probability did not vary with any of the variables we considered (Annexe A, Table A.2).

### 2.5.3. Single-season N-mixture model

We detected egg masses of Wood Frogs in 41% (2018) and 52% (2019) of the ponds during the visual surveys. We also detected metamorphosed individuals of Wood Frogs in 62% (2018) and 50% (2019), and metamorphosed individuals of Mink Frogs in 50% (2018) and 42% (2019) of the ponds. We observed an average (SD) of  $9.18 \pm 25.97$  (range: 0-143) of Wood Frogs egg masses per pond in 2018 and  $6.8 \pm 18.88$  (range: 0-141) in 2019. We observed an average of  $1.2 \pm 2.85$  (range: 0-18 individuals) metamorphosed individuals of Wood Frogs in 2018 and  $0.8 \pm 1.57$  (range: 0-8 individuals) in 2019. We detected  $0.97 \pm 2.84$  (range: 0-22 individuals) metamorphosed individuals of Mink Frogs in 2018 and  $1.3 \pm 4.46$  (range: 0-27 individuals) in 2019.

### 2.5.3.1. Wood frog egg masses

Because Wood Frogs are early breeders, we retained only the first visits of each year for analysis. The top model for predicting reproductive effort included the pond type and the addition of observer effect and days elapsed since snowmelt on detection probability ( $\omega_i = 0.97$ ; Table 2.4). This model had high overdispersion ( $\chi^2 = 6373.96$ ;  $P = 0.0002$ ;  $\hat{c} = 3.62$ ). This model was followed closely by the model that included pond type and the effect of the observer on detection probability (Table 2.4). Reproductive effort of Wood Frog was higher in beaver ponds than in peatland ponds ( $\beta_{\text{Habitat type}}: -1.86$ , 95% CI: [-2.46; -1.27; Fig. 2.5). The number of Wood Frog egg masses did not vary with the other variables we considered (Annexe A, Table A.3). Detection probability of Wood Frog egg masses did not vary with either the number of days since snowmelt, or the observer (Annexe A, Table A.4).

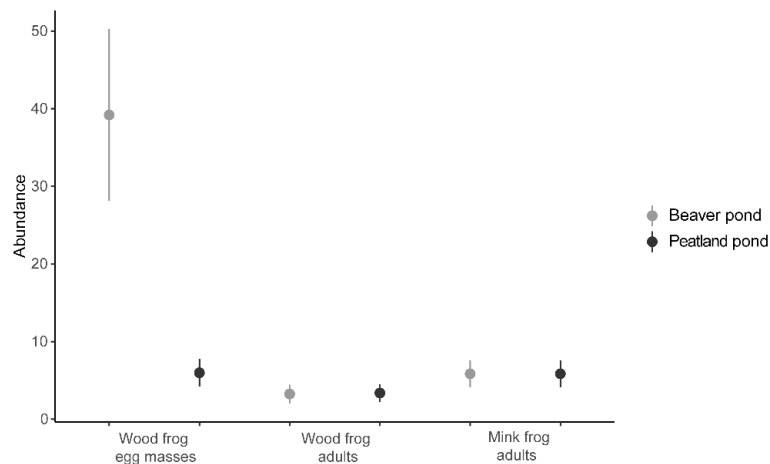


Figure 2.5. Model-averaged predictions of abundance for egg masses of Wood Frog egg masses (left), Wood Frog metamorphosed individuals (middle), Mink Frog metamorphosed individuals (right) from 12 beaver ponds (in grey) and 38 peatland ponds (in black) in Northern Québec in 2018 and 2019. Error bars denote 95% confidence intervals around estimates.

Table 2.4. Most parsimonious N-mixture models explaining the abundance of Wood Frog egg masses, Wood Frog and Mink Frog metamorphosed individuals in beaver and peatland ponds sampled in Northern Quebec, Canada in 2018 and 2019. Model selection has been corrected for overdispersion ( $\hat{c}$ ). Only models with a delta QAICc < 2 are presented with their respective Akaike weights ( $\omega_i$ ), log-likelihood (LL), and number of estimated parameters (K).

Models	LL	K	QAIC	$\Delta$ QAI	$\omega_i$
<i>Wood Frog egg masses</i> ( $\hat{c} = 3.62$ )					
$\psi(\text{Habitat type})p(\text{Snowmelt} + \text{Observer})$	-282.87	8	583.38	0.00	0.59
$\psi(\text{Habitat type})p(\text{Observer})$	-284.88	7	585.01	1.63	0.26
<i>Wood Frog metamorphosed individuals</i> ( $\hat{c} = 2.27$ )					
$\psi(\text{Predation})p(\text{Temp} + \text{Hum})$	-119.18	8	255.95	0.00	0.22
$\psi(\text{Null})p(\text{Temp} + \text{Hum})$	-120.85	7	256.93	0.98	0.13
$\psi(\text{DECMIX300} + \text{CONIF300})p(\text{Temp} + \text{Hum})$	-118.79	9	257.60	1.65	0.10
<i>Mink frog metamorphosed individuals</i> ( $\hat{c} = 3.06$ )					
$\psi(\text{Water and pond characteristics})p(\text{Snowmelt})$	-209.74	9	439.49	0.00	0.52
$\psi(\text{Water and pond characteristics})p(\text{Temp} + \text{Hum})$	-209.23	1	440.92	1.43	0.25

DECMIX300: Deciduous and mixed forest (%) within 300 m; DECMIX1000: Deciduous and mixed forest (%) within 1000 m; CONIF300: Coniferous Forest (%) within 300 m; CONIF1000: Coniferous Forest (%) within 1000 m; Temp: Temperature; Hum: Humidity.

### 2.5.3.2. Wood frog metamorphosed individuals

Because of very few detections on the first visit (mean per pond: 0.25; range: 0-5 metamorphosed individuals), we only used data from the second visit in each year in the analysis of counts of Wood Frog adults and juveniles. The top-ranked model consisted of predation on abundance and an effect of temperature and humidity on detection probability ( $\omega_i = 0.22$ ; Table 2.4). This model had moderate overdispersion ( $\chi^2 = 619.66$ ;  $P < 0.001$ ;  $\hat{c} = 2.27$ ). However, the null model also had some support

(Table 2.4). Thus, there was no evidence of effects of the habitat and landscape variables on the abundance of Wood Frog metamorphosed individuals. Abundance of Wood Frog metamorphosed individuals did not vary with any of the variables we considered (Annexe A, Table A.3). Similarly, detection probability of Wood Frog metamorphosed individuals did not vary with any of the variables we considered (Appendice A, Table A.4).

#### 2.5.3.3. Mink frog metamorphosed individuals

We considered both visits during each of the two years of sampling for the analysis of Mink Frog metamorphosed individuals. We excluded outliers from two ponds in 2018 since they led to model fitting problems (range 88-130 individuals). The top model included water and pond characteristics on abundance and an influence of days since snowmelt on detection probability (Table 2.4). This model had high overdispersion ( $\chi^2 = 3067.452$ ;  $P = 0.0002$ ;  $\hat{c} = 3.06$ ). This model was followed closely by the model with the same structure but with the inclusion of the effect of weather conditions on detection probability (Table 2.4). The abundance of Mink Frog metamorphosed individuals decreased with increasing pond area ( $\beta_{\text{Pond area}}: -0.28, 95\% \text{ CI: } [-0.46; -0.11]$ ; Fig. 2.6A) and increased with increasing pH ( $\beta_{\text{pH}}: 0.54, 95\% \text{ CI: } [0.31; 0.77]$ ; Fig. 2.6B). Abundance of Mink Frog metamorphosed individuals did not vary with the other variables we considered (Appendice A, Table A.3). Detection probability of Mink Frog metamorphosed individuals did not vary with any of the variables we considered (Appendice A, Table A.4).

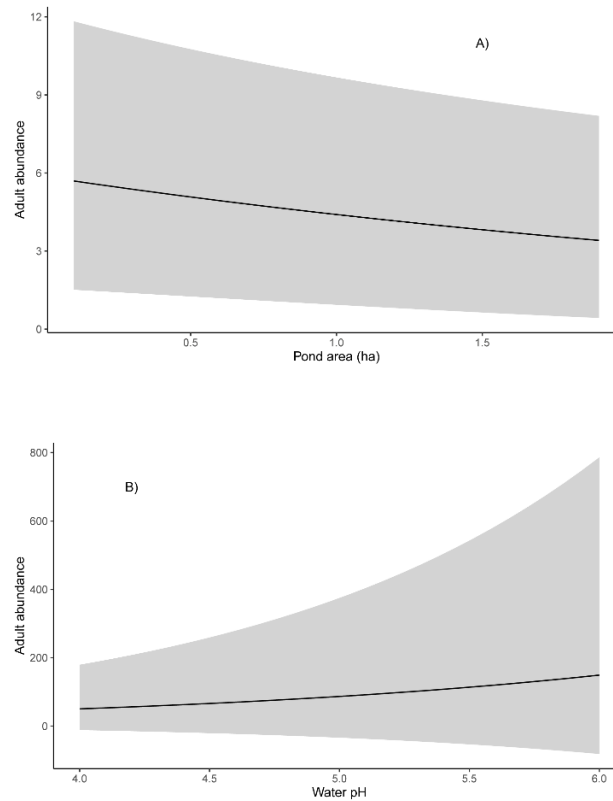


Figure 2.6. Model-averaged predictions of the abundance of Mink Frog metamorphosed individuals in 50 beaver and peatland ponds in northern Quebec sampled during the summer of 2018 and 2019 decreasing with (A) pond area and increasing with (B) water acidity. Areas shaded in gray denote 95% unconditional confidence intervals.

## 2.6. Discussion

Understanding how ecological constraints shape patterns of occupancy can improve predictions of range dynamics and species conservation. Yet, information on ecological factors for boreal amphibians at their northern range limit remains scarce. Here, we examined the role of abiotic and biotic factors in regulating habitat suitability for three pond breeding anurans during different stages of their life cycle in a poorly studied

region. Because anurans are sensitive to low water pH, we expected that occupancy by calling anurans, the abundance of terrestrial individuals, and the abundance of egg masses would be higher in beaver ponds than in peatland ponds (Russell et al., 1999; Stevens et al., 2006). Our results show that Wood Frogs were more likely to breed in beaver ponds than in peatland ponds. For all three species targeted, we did not find evidence of an effect of pond and landscape level variables on calling male frogs and terrestrial individuals. These findings were somewhat inconsistent as the habitat associations uncovered do not generally match those of earlier studies (e.g., Babbitt, 2005; Egan and Paton, 2004; Guerry and Hunter, 2002). However, the abundance of Mink Frog adults and juveniles decreased with pond size and increased with water pH. The present study provides new insight for combining different field methods to evaluate the presence and the abundance of pond-breeding anurans to detect patterns at aquatic and terrestrial life stages.

Beaver ponds are preferred reproductive sites for amphibians (Cunningham et al., 2007; Dalbeck et al., 2007). Thus, we expected a higher occupancy of calling anurans and abundance of terrestrial individuals and egg masses in beaver ponds than in peatland ponds (Russell et al., 1999; Stevens et al., 2006). Indeed, the number of Wood Frog egg masses in beaver ponds was more than four times higher than in peatland ponds. Larger numbers of egg masses in beaver ponds than peatland ponds suggests that Wood Frogs are highly successful in beaver ponds and agrees with earlier reports in boreal landscapes (Anderson et al., 2015; Cunningham et al., 2007; Stevens et al., 2007; Zero and Murphy, 2016). Stevens et al. (2006) noted that older beaver ponds (> 25 years) are selected by breeding Wood Frogs. Thus, abandoned or old beaver ponds may be even more important for anuran reproduction, but this hypothesis should be tested with data collected along a temporal gradient of beaver ponds. Old ponds without dam maintenance are usually fish-free habitat that hold shallow waters and emergent vegetation that facilitates egg mass attachments and facilitate larval development

(Darrow et al., 2004; Egan and Paton 2004; Porej and Hetherington, 2005; Stevens, 2006). Many studies report that beaver ponds improve water quality and amphibian productivity (Naiman and Melillo 1984; Smith et al., 1991; Rosell et al., 2005). Beaver activity such as dam construction, flooded timber material, and clearing of shade-producing riparian vegetation, increase water temperature, as well as nutrient and organic matter storage in pond sediments (Dillon et al., 1991; Naiman et al., 1994; Skelly and Freidenburg, 2000). These conditions may promote a better larval performance and faster development (Herreid and Kinney, 1967; Noland and Ultsch, 1981), reducing the time exposed to aquatic predators and increasing total larval production (Stevens et al., 2006; Wilbur, 1980).

Contrary to our predictions, we found no support that the occupancy or abundance of metamorphosed individuals varied with pond-level variables, except for the abundance of Mink Frogs which showed a relationship with pond area and water pH. Mink Frog metamorphosed individuals were more abundant in small and less acidic ponds. The importance of water conditions for this species is not surprising, as it is mostly aquatic and therefore more affected by water characteristics (Dodd, 2013). This negative association between Mink Frogs and pond area is unclear and contradicts previous reports of a positive effect (Findlay et al., 2001; Houlahan and Findlay, 2003; Popescu and Gibbs, 2009). The positive relationship between Mink Frog abundance and water pH was expected, as this species frequently avoids acidic conditions (Karns, 1992). In addition, we showed that the occurrence of Spring Peeper choruses was higher in 2018 than in 2019. Rather than variation in pond conditions during sampling periods, we believe this difference is due to annual variation in local weather conditions in the study region. More favorable conditions in 2018, such as the volume or timing of precipitations, could have favored calling activity in 2018. Indeed, the average rainfall during April and May was higher in 2018 (1.37 mm) than in 2019 (1.01 mm) in stations



near our sites. Calling intensity of Spring Peepers is positively related to the amount of rain and the species tends to call during rain events (Milne et al., 2013).

We did not detect any relationship between fish presence and anuran state variables of metamorphosed individuals or egg masses. This result was surprising and does not support our initial hypothesis of negative predatory fish effects. Although many studies have noted that the presence of aquatic predators has negative effects on pond use by amphibians (e.g., Egan and Paton, 2004; Hecnar and M'Closkey, 1997; Kiesecker, 1996;), most of them focus primarily on large size predatory fish (e.g., Eaton et al., 2005). We propose three explanations for the lack of observed relationship between anuran patterns and fish presence. First, this result could be associated with the preferred food resources of the species in the fish communities occurring in the ponds sampled, which consisted mostly of small-bodied cyprinids. Cyprinids are flexible omnivores that can consume amphibian larvae and eggs. However, cyprinids are not considered important amphibian predators, compared to centrarchids, salmonids, or pikes (Hecnar and M'Closkey, 1997). A second explanation, though speculative, could involve a release on amphibian predation by fish resulting from a shift of the latter to aquatic insect prey present at the sites (Peterson and Blaustein, 1992). Third, large fish species such as northern pike known as important amphibian predators (Hecnar and M'Closkey, 1997) may have been present in the study ponds, but excluded by winterkill triggered by hypoxic conditions (Eaton et al., 2005; Schlosser and Kallemeyn, 2000) or caused by beaver dams that limit fish movements (Stevens et al., 2007). Furthermore, the minnow traps used in our study had an entry hole of 2 cm, which could have prevented large fish from entering traps, although no juveniles of large fish species were ever captured in our traps. This size limit may have led to an underrepresentation of large fish in our data.

Along the same vein as pond variables, we found no evidence of a relationship between landscape level characteristics and site occupancy on anurans. Wetlands surrounding breeding ponds are important for terrestrial individuals because they may serve as source habitats or refuge for breeding and non-breeding stages during dry breeding seasons (DiMauro and Hunter, 2002; Knutson et al., 1999; Kolozsvary and Swihart, 1999). The proximity of terrestrial and aquatic habitats is crucial because it provides habitat for amphibian species to forage and hibernate (Guerry et Hunter, 2002). For example, adjacent percent of forest cover often explain site occupancy for many anurans species (Mazerolle et al., 2005; Weir et al., 2005). Yet, we found no evidence of such effects. This result has different implications for all three species studied and must be viewed in the context of annual life history. Whereas all species breed in ponds, Wood Frogs and Spring Peepers move into moist forest areas to forage and hibernate (Baldwin et al., 2006; Regosin et al., 2003). Thus, we should expect forest variables to influence terrestrial metamorphosed individuals of these two species. The lack of effect may have been due to the low variability in the proportion of deciduous and mixed forest cover surrounding the ponds (Table 2.2), particularly in northern sites located beyond the limit of commercial forest (Fig. 2.1A). Another possibility is that Wood Frog may be affected by forest cover at scales larger than 1000 m, and thus undetected here due our choices of buffer size. Our results, and those of previous studies for Wood Frog at northern latitudes, suggest that anuran occupancy is independent of forest cover in circular buffers around breeding ponds and closed canopy forest (Bishir et al., 2018; Reiter et al., 2008; Taylor and Paszkowski, 2018). In contrast to terrestrial hibernators, Mink Frog remains at the breeding site year-round, feeding on aquatic prey and hibernating into deeper waters (Hecnar, 2004). Mink Frog showed no response to landscape variables surrounding ponds in our study, consistent with observations of Guerry and Hunter (2002). These mixed effects involving terrestrial and aquatic hibernators implies that analyses must discriminate among annual life history periods

of each species to document habitat needs. Conservation of non-breeding habitats are just as critical for pond-breeding amphibians as their breeding habitat (Cunningham et al., 2007; Fellers and Kleeman, 2007; Marsh and Trenham, 2001).

Timing of breeding at these northern latitudes occurs over a relatively short period, often associated to seasonal fluctuations in environmental conditions such as temperature, humidity, and snowmelt (Oseen and Wassersug, 2002). This suggests a narrow window of activity when anurans are available for detection. However, we detected weak relationships between detection probability and weather covariates. As expected, detection probability of Spring Peeper chorus increased with air temperature (Steelman and Dorcas, 2010). This result is consistent with Spring Peeper breeding ecology and indicates that surveys conducted at temperatures above 8 °C have a probability of detecting Spring Peeper choruses greater than 0.5. A positive effect of air temperature on calling activity was also expected for Wood Frog and Mink Frog (Oseen and Wassersug, 2002; Weir et al., 2005). The lack of a relationship in our surveys could be due to a limited range of temperatures during the recordings for these species. Additionally, the detection probability for all the species we investigated did not vary with the days elapsed since snowmelt. This result could be due to our surveys coinciding with the peak activity periods for each species and life stage – late spring breeders (Wood Frog and Spring Peeper) and summer breeder (Mink Frog).

This study was constrained by a number of factors. Comparisons between pond types are difficult to interpret given the imbalance between both groups – there were three times more peatland ponds than beaver ponds. However, increasing the number of ponds was challenging due to logistical aspects including equipment, remote locations, and distances between all three sectors of our study area. Peak anuran activity at these northern latitudes occurs over short periods and preferred calling times during the day vary by species. Our choice of an acoustic survey at 21h00 from an automated recorder

could have reduced our ability to detect American Toads or choruses of Mink Frogs, which are known to be more active later in the evening (Annich et al., 2019; Bevier et al., 2004). In addition, since we sampled ponds in a south to north direction, our sampling window may have underestimated calling males and egg masses of Wood frog on early visits, especially in ponds sampled further north of the study area. Despite such limitations, we believe our results provide valuable baseline information in this boreal region.

Land-use patterns in remote boreal regions are creating increasing disturbance. A key step in predicting amphibian occupancy and abundance patterns will require a better understanding of factors leading to within-site and between-years variations, particularly for species at the northern limit of their distribution. Our study highlights the complementarity of visual and acoustic methods to detect boreal amphibians at different life stages. Overall, we found few effects of measured habitat covariates in our study. These results suggest that the three species investigated are habitat generalist in the study area and are not restricted to specific habitat conditions. We observed pond-level effects on the Mink Frog, which suggest that small and less acidic ponds represent a suitable habitat for metamorphosed individuals. Our results also add to an already increasing body of evidence supporting positive effects of beaver activity on pond-breeding anurans in North America. We believe our findings can contribute to develop conservation and management projects for anurans in changing boreal environments, near the northern extent of their ranges.

## Acknowledgment

We thank R. Chevallier and J. Arsenault for their assistance with fieldwork and M. Desrochers for providing valuable assistance to extract spatial data in a georeferenced information system. M-F. Indorf provided additional information for vegetation description at our sites. We also thank Hydro-Quebec and FaunENord for providing part of the data from its weather stations throughout James Bay region. Comments from anonymous reviewers from the *@Corrige-moi* group and UQAT Bryology lab improved earlier drafts of this manuscript. Funding was provided by the Natural Sciences and Engineering Research Council (NSERC) of Canada—Université du Québec en Abitibi-Témiscamingue (UQAT) industrial research chair on northern biodiversity in a mining context.

## CHAPITRE III

### BEAVER ACTIVITY AND RED SQUIRREL PRESENCE PREDICT BIRD ASSEMBLAGES IN BOREAL CANADA

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Published in *Ornithology*, ukad009 (2023)

### 3.1. Graphical abstract

Using acoustic recording, we detected 96 bird species in 50 ponds in Northern Quebec, Canada. Our analysis revealed that species richness was higher in beaver ponds compared to peatland ponds, and lower in the presence of red squirrel, a potential nest predator. For illustrative purposes, we show here three early successional species affected by both major drivers, namely Wilson's Warbler, Common Yellowthroat, and Yellow Warbler. We analyze and discuss the effects of local and landscape factors on different levels of boreal bird assemblages.



### 3.2. Abstract

Wetlands and predation in boreal ecosystems play essential roles throughout the breeding season for bird assemblages. We found a positive association of beaver activity and a negative influence of American red squirrels (*Tamiasciurus hudsonicus*) on bird assemblages. We used a multispecies hierarchical model to investigate whether bird species occupancy and community-level attributes differ between two major wetland habitats in boreal Canada: beaver ponds and peatland ponds. In addition to including variables such as forest cover and latitude, we adopted a structural equation model approach to estimate the occupancy of American red squirrels and its potential influence on bird communities. Using automated recording stations deployed at 50 ponds, we detected 96 bird species in 2018 and 2019. Bird species were grouped into four taxonomic guilds according to their habitat successional requirements: early successional species, late successional species, generalists, and wetland species. Beaver ponds harbored higher species richness, a pattern driven primarily by early successional species. The occupancy of almost a quarter of the species was lower in the presence of red squirrels. Late successional species responded positively to the cover of forest surrounding the pond. Our results highlight the value of considering acoustic data of red squirrels to quantify habitat quality in boreal forests. We conclude that beaver activity shapes bird assemblages through modification of their habitat, and that some bird guilds respond are associated negatively with the presence of American red squirrels.

*Keywords:* Beaver activity, red squirrels, bird assemblages, boreal ecosystems, automated recordings, multispecies hierarchical model.



### 3.3. Résumé

Les milieux humides et la prédation des écosystèmes boréaux jouent un rôle essentiel tout au long de la saison de reproduction pour les assemblages d'oiseaux. Nous avons trouvé une association positive entre les assemblages d'oiseaux et l'activité des castors, mais une association négative entre les assemblages d'oiseaux et la présence des écureuils roux d'Amérique (*Tamiasciurus hudsonicus*). Nous avons utilisé un modèle hiérarchique multi-espèces pour étudier si les communautés d'oiseaux diffèrent entre deux importants types de milieux humides du Canada boréal : les étangs de castors et les étangs de tourbières. Au-delà de l'inclusion de variables telles que le couvert forestier et la latitude, nous avons adopté une approche de modèle d'équation structurelle pour estimer l'occupation de l'écureuil roux d'Amérique et son influence potentielle sur les communautés d'oiseaux. En utilisant des stations d'enregistrement automatisées déployées sur 50 étangs, nous avons détecté 96 espèces d'oiseaux en 2018 et 2019. Les espèces d'oiseaux ont été regroupées en quatre guildes taxonomiques en fonction de leurs exigences en matière de succession de l'habitat : espèces de début de succession, espèces de fin de succession, généralistes et espèces des milieux humides. Les étangs de castors abritaient une plus grande richesse d'espèces que celle des étangs de tourbières, une tendance principalement liée aux espèces de début de succession. L'occupation de près d'un quart des espèces était plus faible en présence de l'écureuil roux. Les espèces de fin de succession ont répondu positivement à la couverture de la forêt entourant l'étang. Nos résultats soulignent l'intérêt de considérer les données acoustiques de l'écureuil roux pour quantifier la qualité de l'habitat dans les forêts boréales. Nous concluons que l'activité des castors façonne les assemblages d'oiseaux en modifiant leur habitat et que certaines guildes d'oiseaux sont associées négativement à la présence de l'écureuil roux d'Amérique.

*Mots clés* : Activité du castor, écureuil roux, assemblages d'oiseaux, écosystèmes boréaux, enregistrements automatiques, modèle hiérarchique multi-espèces.

### 3.4. Lay summary

- Studies of bird assemblages and their responses to local and landscape factors in boreal landscapes can inform wetland conservation.
- The aim of our study was to assess how bird occupancy differed between two major pond types and responded to habitat, landscape factors, and potential predators in boreal assemblages in northeastern Canada.
- We detected 96 species using automated recorders deployed at 50 ponds in 2018 and 2019.
- Species richness was higher in beaver ponds than peatland ponds. Species richness was lower in the presence of red squirrel, a potential nest predator, and decreased with increasing latitude.
- Our results highlight the importance of beavers and factors associated with the red squirrel presence in shaping bird assemblages in boreal landscapes.

### 3.5. Introduction

Wetland ecosystems are high quality habitats for a wide range of wildlife species (Hansson et al., 2005; Lesbarrères et al., 2014; Weller, 1999), but are suffering from global impacts due to human land conversion and climate change pressures (Davidson, 2014; Gibbs, 2000; Tarnocai 2009). Wetland loss and degradation have contributed to

the global decline of wetland-dwelling birds (Davidson, 2018; Quesnelle et al., 2015). Wetlands with permanent and seasonal water bodies and adjacent inland terrestrial environments play a key role throughout the breeding season for bird assemblages (Desgranges et al., 2006; Kantrud and Stewart, 1984; Naugle et al., 2001). For example, these wetlands attract several species associated with aquatic habitats, such as waterfowl (Lemelin et al., 2010), and are important for long-distance migratory species that benefit from adjacent habitats (Junk et al., 2006). This indivisible complex of aquatic and terrestrial habitats usually entails a greater diversity and richness than those formed exclusively by water (i.e. ponds or lakes) or by uplands habitats such as forest patches (e.g., Drapeau et al., 2000; Gopal, 2009; Gutzwiller and Anderson, 1987). Therefore, determining the relationships between bird assemblages and wetland habitat characteristics is of paramount importance for management and conservation decisions.

Wetlands in boreal landscapes are largely intact, but anthropogenic activities, including forestry, mining and energy resource extraction, are important and growing stressors that can reduce the quality of breeding habitats and modify forest vegetation composition (Foote and Krogman, 2006; Poulin et al., 2004; Wetland International, 2022). However, we lack basic ecological information regarding species-habitat associations for wetland-dwelling species beyond the northern limit of commercial forest harvesting. For instance, boreal landscapes of northern Canada are home to different types of wetlands, although peatlands comprise most of the wetlands in this region (Payette and Rochefort, 2001; Pellerin and Poulin, 2013). Fens and bogs represent the two main types of peatlands. Minerotrophic or fen peatlands are mainly fed by rain and flow from adjacent aquatic environments previously exposed to mineral soils, and consequently the pH typically varies from 5.5 to 7.5 (Leboeuf et al., 2012b; Payette and Rochefort, 2001; Zoltai and Vitt, 1995). In contrast, water and nutrients in ombrotrophic peatlands or bogs come mostly from atmospheric sources and have a pH ranging from approximately 4.0 to 5.5 (Payette and Rochefort, 2001). To date,

relatively few bird species, including migratory birds, have been reported in Canadian peatlands (Calmé and Desrochers, 2000; Desrochers, 2001; Junk et al., 2006). Given the dominance of peatlands in many boreal regions and increasing pressures from anthropogenic activities such as forestry and mining, there is a need to characterize the assemblage of bird species associated with structurally diverse peatlands.

Bird species assemblages in peatlands are likely to differ from those found in less acidic ponds, such as ponds modified by North American beavers (*Castor canadensis*). Beavers have a substantial impact on wetland dynamics that positively affects overall bird diversity (Grover and Baldassarre, 1995; Lemelin et al., 2010; Nummi and Holopainen, 2014). Beaver activities change the water level, which stimulates plant growth and increases invertebrate production (McKinstry et al., 2001), thus increasing food sources for a variety of waterfowl species and their broods (McCall et al., 1996; Nummi, 1992; Nummi and Hahtola, 2008). Beaver dams increase shallow water areas that can enhance nest concealment and reduce predation (Brown et al., 1996). Newly modified habitats provide snags and flooded trees, which attract birds like woodpeckers for nesting and feeding (Grover and Baldassarre, 1995). Indeed, Aznar and Desrochers (2008) reported higher levels of songbird biodiversity in abandoned beaver ponds than in adjacent riparian habitats. Beaver ponds may therefore increase regional avian diversity. Yet, we are aware of only a few studies comparing bird assemblages in ponds that are influenced or unaffected by beaver activity in North American boreal forest (e.g., Aznar and Desrochers, 2008; Desjardins et al., 2021; McKinstry et al., 2001). To our knowledge, no previous study has investigated the relative importance of beaver ponds and peatland ponds for habitat use by boreal birds. Increased knowledge of these habitats could contribute to the conservation of these species in their northern breeding habitats.

During the breeding period, nesting success is a critical stage that can influence the viability of bird populations (Hoekman et al., 2002; Smith et al., 2011; Vickery et al., 1992). Nest predation is typically the dominant cause of nest failure in birds (Martin and Li, 1992; Martin, 1993; Sherry and Holmes, 1992). Hence, predation risk structures breeding bird assemblages by conditioning nest site selection and limiting breeding success (Martin and Roper, 1988; Martin and Joron, 2003; Sieving and Willson, 1998). Direct encounters with predators may discourage birds from using certain nesting sites (Dinkins et al., 2012). Among nest predators, American red squirrels (*Tamiasciurus hudsonicus*) are recognized as dominant passerine nest predators in mature coniferous boreal forest of North America (Bayne and Hobson, 2002; Darveau et al., 1997). Bird nesting success decreases in forests where red squirrels are present (Darveau et al., 1997; Martin and Joron, 2003). Moreover, densities of ground and shrub-nesting birds decrease with increasing abundance of red squirrels (Sieving and Willson, 1998; Willson et al., 2003). These studies suggest that red squirrel occurrence influences both habitat selection and structure of bird assemblages (Darveau et al., 1997; Willson et al., 2003), although the effects may vary among prey species (Martin and Joron, 2003). However, current knowledge of red squirrel predation is usually mostly based on artificial nests, which are more conspicuous, smell differently, and lack parental protection, possibly leading to an overestimation of predation levels (Buler and Hamilton 2000; Rangen et al. 2000; Willson and Brittingham, 1998). This gap highlights the need to formally quantify predation by squirrels in future studies, particularly in forests where the species is abundant.

In addition to local effects, researchers have sought to explain processes operating at the landscape level by considering the amount of surrounding habitat on species abundance and distribution (De Camargo et al., 2018; Fahrig, 2001; Prugh et al., 2008). Both local habitat conditions and landscape characteristics adjacent to wetlands may also determine the structure of bird assemblages in these boreal landscapes (Froneman

et al., 2001; Sedgwick and Knopf, 1990; Strong and Bock, 1990). Indeed, the extent and structure of the surrounding forest often has a dominant influence on passerine presence and abundance in boreal ecosystems (Drapeau et al., 2000; Hobson and Schieck, 1999; Saab, 1999). Similarly, boreal species of woodpeckers vary with decreasing cover of old-growth coniferous forest in a landscape (Hutto and Gallo, 2006; Imbeau and Desrochers, 2002b; Koivula and Schmiegelow, 2007).

In this paper, our objectives were to assess the response of bird assemblages in wetlands to local-scale habitat and landscape factors in boreal regions. Specifically, we determined whether species occupancy and richness differed between two pond types, namely peatland ponds and beaver ponds. We also quantified the response of bird assemblages at these wetlands to the presence of a nest predator, as well as to latitude and the surrounding forest cover. We hypothesized that species occupancy varies with pond type, but depends on species habitat preferences (Alza, 2014; Desgranges et al., 2006; Calmé and Desrochers, 1999). Beavers may create favorable habitat for certain groups such as waterfowl or cavity-nesting birds. Therefore, we predicted that beaver ponds have a higher bird species richness and different bird assemblages than peatland ponds. We also hypothesized that occupancy of bird species decreases in the presence of American red squirrels, a known nest predator for most boreal species. Because of the various factors that operate across large geographical areas (Soininen et al., 2007), we expected species richness to decrease with increasing latitude. Finally, we expected differences in occupancy as a function of surrounding forest cover. Late successional species may react positively to increases in forest cover because they rely on tree substrates for breeding and feeding. As terminology in community ecology is ambiguous, we use here the terms “assemblage” *sensu* Fauth et al. (1996) when referring to a phylogenetic subgroup of species of a community (i.e. bird assemblage) and “taxonomic guild” *sensu* Stroud et al., (2015) to refer to a group of taxonomically

related species that exploit the same class of resources in a similar way (i.e. early successional species, late successional species).

### 3.6. Methods

#### 3.6.1. Study area

We conducted the study in the Eeyou Istchee James Bay region of northwestern Quebec (Canada) between the latitudes of 49° and 53° N, encompassing an area of about 400,000 km<sup>2</sup>. The study area experiences a subpolar and subhumid climate with a short growing season, decreasing in days with latitude from south to north (Lord and Robitaille, 2013). Mean annual temperatures range from -0.5 °C to -4 °C, decreasing gradually from south to north and also with elevation. The typical mean temperatures during the field work were 9 °C in May, 14 °C in June, 16 °C in July, and 17 °C in August (World Weather Online, 2021). The annual mean amount of precipitation in the region ranges from 700 to 900 mm. Most of the snow falls generally from August to April (World Weather Online, 2021).

The study region is distributed across three ecozones, including the Hudson Plains, the Boreal Shield, and the Taiga Shield (Environment Canada, 2015; Lord and Robitaille, 2013). The Hudson Plains comprise the southern portion of the study area and contain one of the highest density of wetlands in the world (Fraser and Keddy, 2005). This landscape is characterized by a mosaic of forest mainly dominated by black spruce (*Picea mariana*) stands. The Boreal Shield portion is characterized by rocky hills mostly covered by coniferous forests of spruce-moss stands and abundant small to medium-sized lakes with peatlands (Environment Canada, 2013a). The northernmost portion of the study region extends into the Taiga Shield ecozone (Ducruc et al., 1976;

Lord and Robitaille, 2013) with an undergrowth dominated by lichens of *Cladonia* spp. (Environment Canada, 2013b). Spruce-lichen woodlands are prevalent in this forest where black spruce occurs at lower density than in spruce-moss woodlands (Environment Canada, 2013b). The entire study area features numerous lakes and rivers and different types of wetlands, the latter are dominated by a complex mosaic of peatlands. Beavers are ubiquitous within the study region, although their abundance is higher in the southwestern sites and decreases along the northeast gradient.

We randomly selected 50 ponds in all three ecozones. To do so, we identified three sectors. The most southern sector (Casa Berardi) is encompassed by the Hudson Plains and located within commercial forests. The central sector (Whabouchi) is found in the Boreal Shield and the most northern sector (Renard) is within the Taiga Shield (Fig 3.1). Sixteen ponds were located in the vicinity of the Casa Berardi site, and 17 in each area surrounding Whabouchi and Renard sectors (Fig. 3.1). Ponds were selected based on the criteria of accessibility (<1 km from the road), size (<2 ha), and habitat type (peatland or beaver pond). We retained 38 peatland ponds and 12 beaver ponds with similar size and depth (peatland ponds: 0.11–1.84 ha, 26.58–69.55 cm, beaver ponds: 0.14–1.87 ha, 29.55–176.52 cm). We maintained at least 800 m between two ponds to ensure independence of our observations. The inclusion of the peatland type was not possible because some peatlands included areas that were ombrotrophic and others that were minerotrophic (Bourgeau-Chavez et al., 2017).



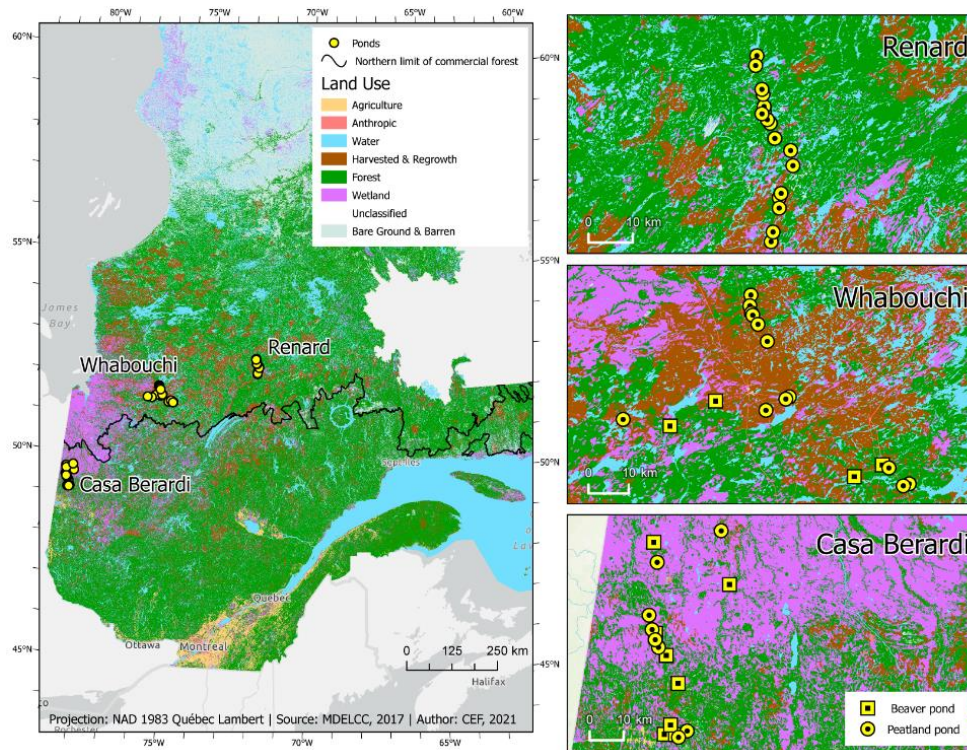


Figure 3.1. Study area with the distribution of ponds sampled in three sectors in 2018 and 2019 in Northern Quebec (Canada) using passive acoustic surveys.

### 3.6.2. Sampling with passive acoustic surveys

We sampled the 50 ponds during the 2018 and 2019 breeding seasons. Each pond was visited during two periods in each year of study: between May 19 and August 12, 2018, and between May 16 and July 21, 2019. Pond visits during a given year were separated by 5–7 weeks. During a given visit, we deployed an autonomous recording unit (ARU). We used a SM4 Song meter (Wildlife Acoustics Incorporation, Concord, Massachusetts, USA) at each pond to record bird and squirrel vocalizations. Certain species such as ducks, herons, and raptor species are underrepresented in our assessment of bird communities because these species rarely vocalize and were

unlikely to be detected by ARUs. At each pond, the ARU was positioned 2–10 m from the water's edge and fastened to a tree or wooden stake at a height of 1.5 m. We removed branches around the unit to reduce wind noise. During a given sampling period, ARUs were set with both microphones facing upward for four consecutive days to record a 5-min sample at 00600 h, at which time most of the singing birds are expected to peak (Robbins, 1981; Wimmer et al., 2013). Previous studies showed that more than 70% of the species can be detected within the first 5-min of recording (Fuller and Langslow, 1984; Sóllymos et al., 2018). Each file was encoded at a sampling rate of 44.1 kHz and a 16-bit resolution.

Each pond was sampled for four consecutive days during two periods in both years, yielding an average of 80 minutes per pond. Due to technical limitations, a total of 92 failures occurred out of 800 (11.5%) planned recording periods, producing a total of 708 five-minute recording fragments. All recording data were analyzed by an ornithologist with extensive field experience in the study region (L. Imbeau) to identify species based on their vocalizations or other aural cue (i.e. wing noise, woodpecker drumming). Species were categorized into four taxonomic guilds based on their requirements for various successional stages of black spruce following Imbeau et al. (2003) and Drapeau et al. (2000): (1) early successional species, associated with open areas of low-vegetation such as young forests or regenerating shrublands; (2) late-successional species preferring older forest stands; (3) generalists, consisting of species that use a wide range of successional stages; and (4) wetland and aquatic species. In addition to birds, we identified the vocalizations of the American red squirrel from recordings, as suggested by Chavel et al. (2017), for use in occupancy analysis.

### 3.6.3. Site and survey covariates

We included four candidate variables as potential predictors of boreal bird occupancy. We used pond type to distinguish between beaver ponds and peatland ponds. To account for a possible effect of predation on bird occupancy, we considered American red squirrel occupancy, because this species is assumed to be a major nest predator of a wide range of birds in both coniferous and adjacent deciduous stands (Darveau et al., 1997; Sieving and Willson, 1998; Willson et al., 2003). We also assessed the proportion of forest cover of all forest types over 2 m (deciduous, mixed, and coniferous forest) within circular buffers of 1000 m centered on acoustic recorder locations (Berger and Leboeuf, 2015; Leboeuf et al., 2012a). Despite potential overlap among buffers, it maintains spatial independence and poses no statistical issue (Zuckerberg et al., 2012). This buffer area roughly corresponded or exceeded the sizes of territories of most bird species expected to occur in the study area (Gauthier and Aubry, 1996). We included latitude to reflect habitat changes given that peatland ponds were more abundant in northern sites and beaver ponds were concentrated in the lower latitudes of the study area.

We considered two parameters that potentially influenced detection probability during acoustic surveys: the quality of the recording and the number of days after snowmelt. Recording quality was classified as bad in cases of high-volume saturation, rain or moderate to strong wind, otherwise quality was classified as good. We used the number of days elapsed since snowmelt to reflect potential differences in the phenology of vocal behaviors of species across our latitudinal gradient (Furnas and Callas, 2015). We defined the date of snowmelt as the first day of a series of 7 consecutive days during which minimum temperatures were above 0 °C.

#### 3.6.4. Data processing and analysis

We investigated occupancy patterns of the American red squirrel, and occupancy of each bird species detected at least once in our recordings. We prepared detection histories for each species at each pond, where we indicated detection (1) or non-detection (0) in each recording of the two periods of four consecutive days in each year. Each pond in each year was considered as an independent site and we included a fixed year effect as well as a site random effect to account for potential differences in occupancy between years (Kéry and Royle, 2020). Thus, detection histories for a given species were arranged in a matrix of 100 rows (50 sites x 2 years) and 8 columns (4 recordings x 2 periods).

We estimated bird occupancy and richness with a multispecies site-occupancy model (Dorazio and Royle, 2005; Royle and Dorazio, 2008, Zipkin et al., 2010). This hierarchical model approach can include rare or discrete species, by sharing information from species that are more common (Zipkin et al., 2009). We adapted a structural equation strategy to our multispecies occupancy model (Cubaynes et al., 2012; Grace et al., 2010; Figure 2). Specifically, one component of our model estimated the occupancy of American red squirrels (a potential nest predator) as a function of different explanatory variables, and then used the latent squirrel occupancy as an explanatory variable in the multispecies occupancy model for individual bird species and richness. This approach allowed us to simultaneously propagate the errors associated with the estimation of the squirrel latent occupancy state directly into the multispecies model. We estimated the occupancy probability of American red squirrel ( $\psi_{\text{Squirrel}, ik}$ ) at site  $i$  in year  $k$  and associated latent occupancy state ( $z_{\text{Squirrel}, ik}$ ):

$$\text{logit}(\psi_{\text{Squirrel}, ik}) = \delta_0 + \delta_{\text{TypeBeaver}} * \text{TypeBeaver}_i + \delta_{\text{Forest}} * \text{Forest}_i +$$

$$\delta_{\text{Year2019}} * \text{Year2019}_{ik} + \delta_{\text{Latitude}} * \text{Latitude}_i$$

$$z_{\text{Squirrel},ik} \sim \text{Bernoulli}(\psi_{\text{Squirrel},ik})$$

where  $\delta_0$  corresponds to the intercept and other  $\delta$  denote the slopes of explanatory variables on squirrel occupancy and where the latent occupancy state  $z_{\text{Squirrel}, ik}$  is drawn from a Bernoulli distribution with probability  $\psi_{\text{Squirrel}, ik}$ . Detection probability of American red squirrel at site  $i$  on visit  $j$  in year  $k$  was estimated as:

$$\text{logit}(p_{\text{Squirrel},ijk}) = \gamma_0 + \gamma_{\text{QualityBad}} * \text{QualityBad}_{ijk} + \gamma_{\text{Thaw}} * \text{Thaw}_{ijk}$$

where  $\gamma$  denotes parameters associated with a given explanatory variable on squirrel detection probability.

The occupancy ( $\psi_{ikl}$ ) of bird species  $l$  at site  $i$  in year  $k$  was modeled with effects of pond type, forest cover, year, latitude, and squirrel latent occupancy state:

$$\text{logit}(\psi_{ikl}) = \phi_{0,l} + \beta_{\text{TypeBeaver},l} * \text{TypeBeaver}_i + \beta_{\text{Forest},l} * \text{Forest}_i +$$

$$\beta_{\text{Year2019},l} * \text{Year2019}_{ik} + \beta_{\text{Latitude},l} * \text{Latitude}_i + \beta_{z_{\text{Squirrel}},l} * z_{\text{Squirrel},ik} + u_i$$

$$z_{ikl} \sim \text{Bernoulli}(\psi_{ikl})$$

where  $\phi_{0,l}$  is the average occupancy of species  $l$ , whereas  $\beta_l$  denotes the slopes of a given explanatory variable for species  $l$ . Because species from the same guild may respond similarly to habitat characteristics, we drew average occupancy as well as the slopes of pond type and forest cover for each species from a normal distribution specific to each guild  $g$ , e.g.,  $\beta_{\text{TypeBeaver},l} \sim N(\mu_{\beta_{\text{TypeBeaver},g}}, \sigma_{\beta_{\text{TypeBeaver},g}}^2)$ . Here,  $\mu_{\beta_{\text{Beaver},g}}$  and

$\sigma_{\beta_{Beaver, g}}^2$  denote the mean slope and variance of  $\beta_{Beaver}$  for guild  $g$ , respectively. In contrast, slopes for year, latitude, and squirrel occupancy state were drawn for each species  $l$  without reference to guild, e.g.,  $\beta_{Year2019, l} \sim N(\mu_{\beta_{Year2019}}, \sigma_{\beta_{Year2019}}^2)$ . The random effect  $v$  of site  $i$  was drawn from  $N(0, \sigma_{Site}^2)$ .

We allowed the detection probability of species  $l$  to vary with the recording quality and the number of days after snowmelt:

$$\text{logit}(p_{ijkl}) = \eta_{0,1} + \theta_{QualityBad, l} * QualityBad_{ijk} + \theta_{Thaw, l} * Thaw_{ijk}$$

Where  $\eta_{0,1}$  corresponds to average detection probability of species  $l$ , and  $\theta_l$  denotes the random slope associated with a given explanatory variable for species  $l$ , drawn from a normal distribution, e.g.,  $\theta_{Thaw, l} \sim N(\mu_{\theta_{Thaw}}, \sigma_{\theta_{Thaw}}^2)$ .

Model parameters were estimated in a Bayesian framework with Markov chain Monte Carlo (MCMC) using five chains in JAGS 4.3.0 within R 4.1.2 using the jagsUI package (Kellner, 2019; Lunn et al., 2013; Plummer et al., 2006; R Core Team, 2021). Each chain consisted of 500 000 iterations with a thinning rate of 25 and we used the first 250 000 iterations as burn-in. We used vague prior distributions for all parameters. Specifically, we considered normal priors with  $N(\mu = 0, \sigma^2 = 100)$  for the  $\beta$  parameters and uniform priors  $U(0, 10)$  for the standard deviation of random intercepts and random slopes. Model structure and priors are reported in Feldman et al. 2022. We used trace plots, posterior density plots, and the Brooks-Gelman-Rubin statistic to assess chain convergence, where values  $< 1.05$  of the latter metric suggested different chains stabilized to similar estimates (Lunn et al., 2013). Model fit was assessed with posterior predictive checks based on a Pearson chi-square aggregated over rows and columns (Kéry and Royle, 2020). We also estimated the area under the receiver operating

characteristic (ROC) curve as a measure of predictive ability (Zipkin et al., 2012). We used the multispecies model to derive the species richness from the posterior distribution of the true occurrence of each species at each site, expressed as the mean of the posterior distribution (Tingley et al., 2020). We investigated the relationship between species richness at site  $i$  in year  $k$  against the explanatory variables pond type, forest cover, latitude, and the posterior mean of the squirrel occupancy state in a linear mixed effect model:

$$\begin{aligned} \mu_{ik} = & \alpha_i + \beta_0 + \beta_{\text{TypeBeaver}} * \text{TypeBeaver}_i + \beta_{\text{Forest}} * \text{Forest}_i + \\ & \beta_{\text{Year2019}} * \text{Year2019}_{ik} + \beta_{\text{Latitude}} * \text{Latitude}_i + \beta_{z\text{Squirrel}} * z_{\text{Squirrel},ik} \\ S_{jk} \sim & N(\mu_{jk}, \sigma_{\text{posterior}}^2) \end{aligned}$$

where  $\alpha_j$  denotes the random deviation of the intercept of site  $i$  with distribution  $N(0, \sigma_{\text{Site}}^2)$  and  $S_{ik}$  is drawn from a normal distribution with mean  $\mu_{ik}$  and variance  $\sigma_{\text{posterior}}^2$ . Here, we used the variance of the posterior distribution ( $\sigma_{\text{posterior}}^2$ ) of the species richness from the multispecies model above to propagate the errors into the linear mixed model (Kéry and Royle, 2020; McCarthy and Masters, 2005). We estimated the parameters using MCMC with five chains each of 75 000 iterations with a thinning rate of 25 and a burn-in of 40 000 iterations. Again, we used vague prior distributions for each parameter (Appendice B, Table B.3). In addition to the posterior diagnostics, we ensured that the normality and homoscedasticity assumptions were met.

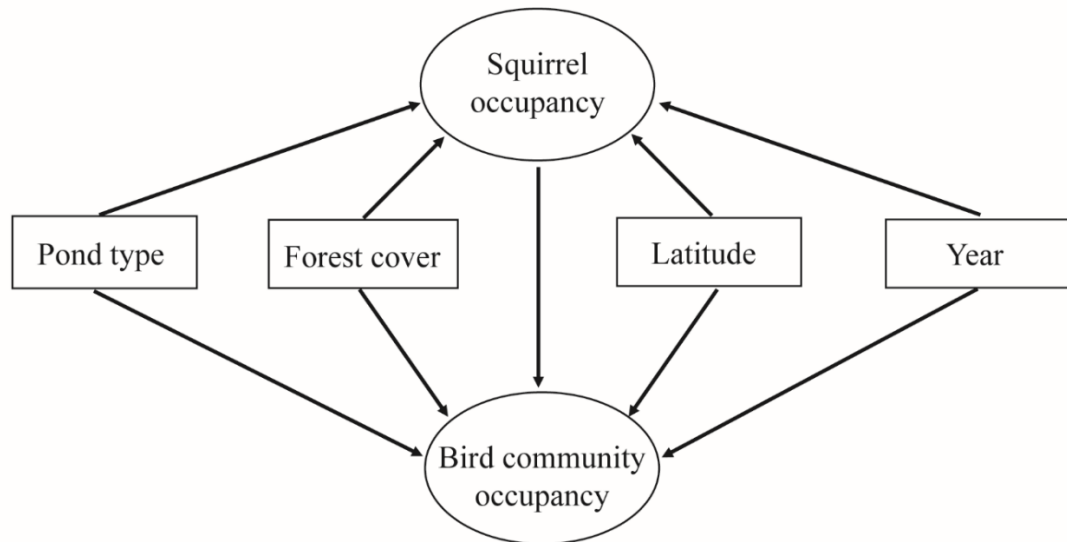


Figure 3.2. Structural equation model showing the hypothesized links between variables and bird community occupancy from the acoustic data recorded at beaver ponds and peatland ponds during the breeding season of 2018 and 2019 in northern Quebec. Explanatory variables are shown in boxes. Arrows link these explanatory variables to the biological parameters of interest (squirrel occupancy, occupancy of different bird species). Note that one component of the model estimates the influence of pond type, forest cover, latitude, and year on the occupancy of American red squirrel. This latent occupancy state for squirrel was then used as a predictor in the final component of the multispecies bird occupancy model, along with the pond type, forest cover, latitude, and year.

### 3.7. Results

A total of 708 five-minute recordings were analyzed and 99.1% of these recordings contained bird vocalizations. We detected a total of 96 bird species from 31 families and 12 orders at beaver and peatland ponds in 2018 and 2019. The most represented families were Parulidae (18 species), Passerellidae (9 species), Picidae (7 species), Fringillidae (6 species), Scolopacidae (5 species), and Tyrannidae (5 species). A total of 88 species were identified in 2018 and 86 species in 2019. Fourteen species were



detected exclusively at each pond type, and 68 species were commonly found in both pond types. The most frequently detected species were the Hermit Thrush (*Catharus guttatus*), White-throated Sparrow (*Zonotrichia albicollis*), and Yellow-rumped Warbler (*Setophaga coronata*). In contrast, 13 species were detected only once. Wetland species were the most encountered (33%) followed by late-successional species (27%), generalists (23%), and early successional species (17%). Among the 96 species detected at our sites with ARUs, only five species do not breed in our study area (Horned Lark, Least Sandpiper, American Pipit, Lapland Longspur, and Semipalmated Plover; Robert 2019).

### 3.7.1. Red squirrel occupancy and bird assemblage response

Trace plots and other diagnostics for the multispecies single-season occupancy model suggested that chains mixed well and were of sufficient length. The posterior predictive check based on the aggregated columns suggested mild lack-of-fit ( $\chi^2_{\text{columns}} = 908.76$ ,  $P = 0.02$ ), whereas the check based on the aggregated rows suggested adequate fit ( $\chi^2_{\text{rows}} = 13170.95$ ,  $P = 0.80$ ). The area under the receiver operating characteristic (ROC) curve was 0.91 (95% CRI: [0.87, 0.93]), suggesting high predictive ability of the model.

The occupancy of American red squirrel did not vary with any of the explanatory variables (Appendix B, Table B.4). However, the detection probability of red squirrels was greater in recordings of good quality and increased with days elapsed since snowmelt (Appendix B, Table B.4). The occupancy of 11 bird species varied with pond type, all with higher occupancy in beaver ponds than in peatland ponds (Fig. 3.3A). This preference was particularly marked among seven early successional

species (Appendice B, Table B.5). Twenty-four species (25%) varied with the presence of American red squirrels (Fig. 3.3B). The occupancy of 20 species was lower in the presence of squirrels, whereas four species responded positively to squirrel presence (Fig. 3.3B). Overall, our analyses revealed that the occupancy of 27 species (28,12%) responded to forest cover within 1000-m surrounding the pond (Fig. 3.3C, Appendice B, Table B.1). For most late-successional species (21 of 26 species, 80.8%), the occupancy probability increased with the proportion of forest cover (Appendice B, Table B.5). Species of the remaining three guilds responded to a lesser degree, with the occupancy of one early successional species and five wetland species decreasing with increasing forest cover (Fig. 3.3C, Appendice B, Table B.1). The occupancy of several species varied with latitude, increasing for 12 species (12.5%), whereas it decreased for 29 species (30.2%; Fig. 3.3D). The occupancy of only eight of the 96 species varied among years (Fig. 3.3E). The occupancy of five species was greater in 2019 than 2018, whereas three species had a lower occupancy in 2019 than 2018 (Appendice B, Table B.1).

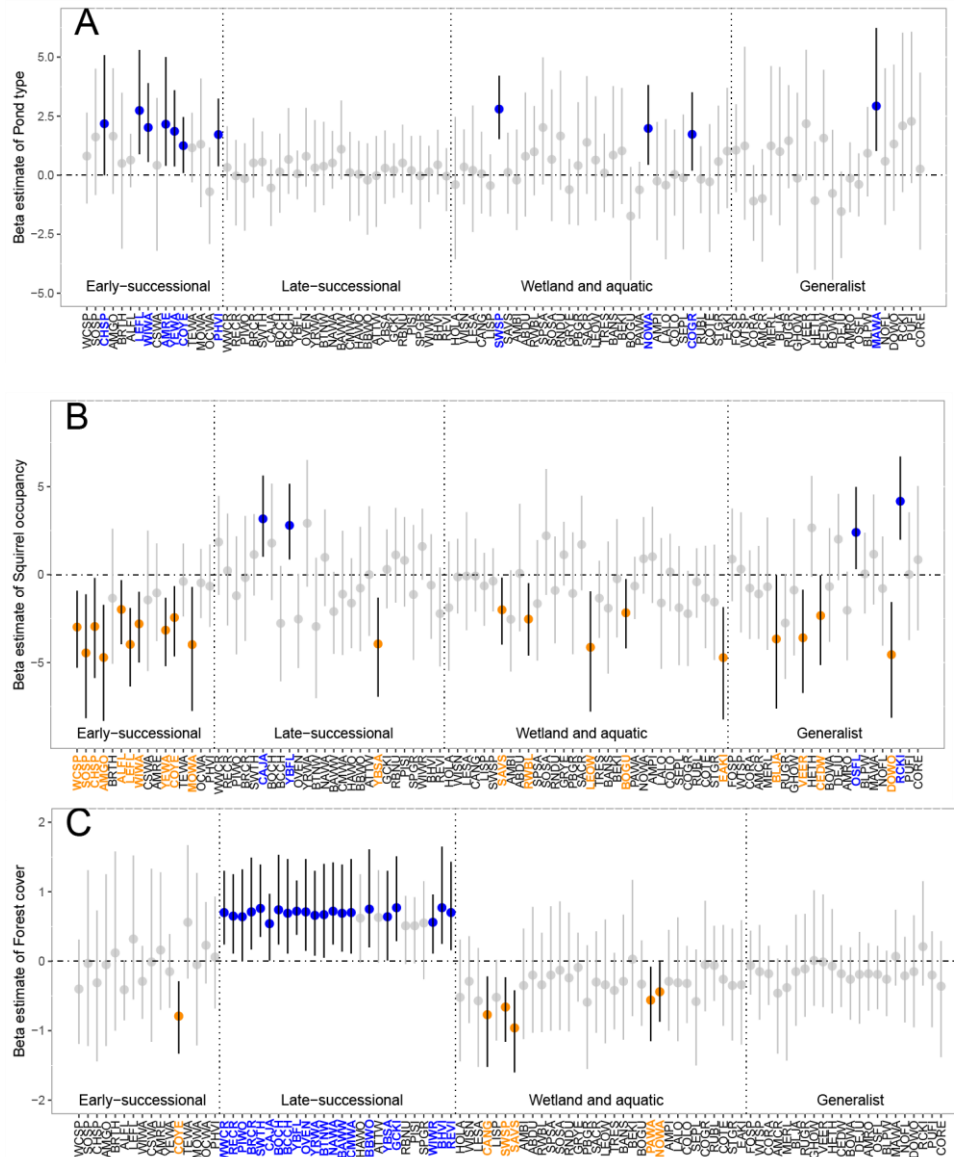
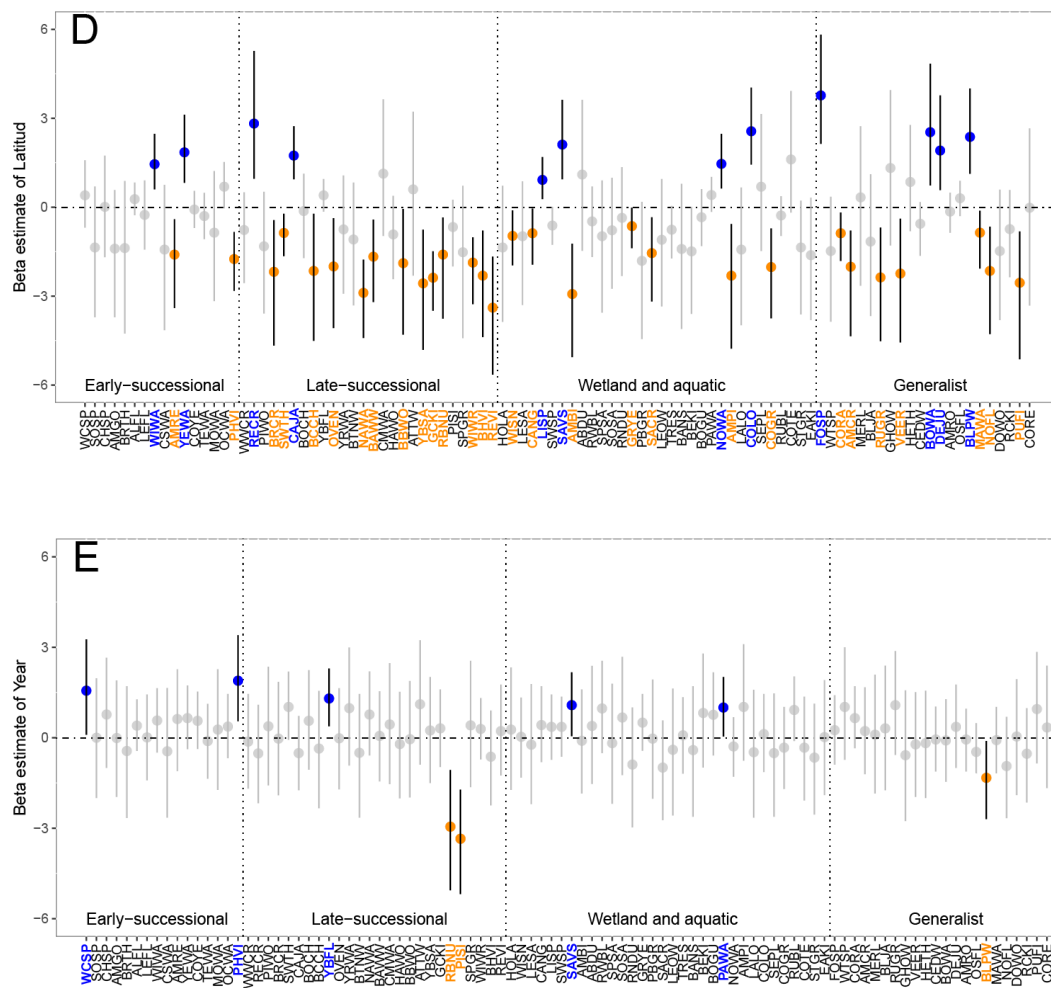


Figure 3.3. Bird community analysis based on acoustic data at beaver and peatland ponds in Northern Quebec in 2018 and 2019 for 96 species. Species-specific beta estimates on occupancy are presented for (A) pond type (beaver as reference level), (B) squirrel latent occupancy state, (C) forest cover, (D) latitude, and (E) year (2019 as reference level). Vertical lines represent the 95% Bayesian credible intervals around estimates obtained from MCMC. Orange points denote species that varied negatively, and blue points denote species that varied positively with a given parameter. Complete species names and species-specific results are presented in Appendix B, Table B.1.

Figure 3.3. Continued



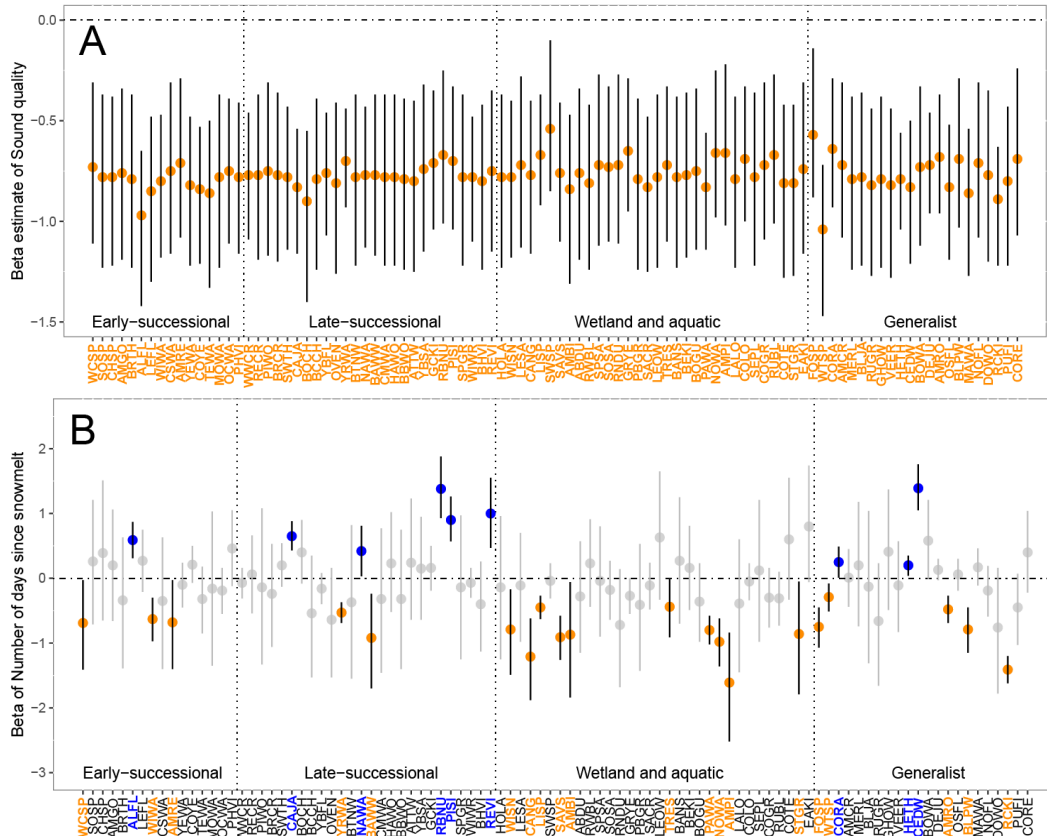


Figure 3.4. Detection probabilities for 5-minute surveys conducted with automated recorders in northern Quebec, 2018–2019. Species level responses to (A) sound quality (bad vs good as reference level), (B) and number of days since snowmelt. Vertical lines represent the 95% CRI around estimates. Orange points denote species that varied negatively, and blue points denote species that varied positively with a given parameter as the estimated coefficients differ significantly from zero. Complete species names and species-specific results are presented in Appendix B, Table B.1.

Detection probability varied among bird species, but all bird species were more likely to be detected in recordings of good quality than those of low quality (Fig. 3.4A). Furthermore, detection probability varied with days elapsed since snowmelt for 29 species among the 96 species (30.2%; Fig. 3.4B). Twenty species were more likely to be detected earlier than later in the season, whereas nine species were more likely to be detected as the season progressed.

### 3.7.2. Species richness and structure of bird assemblages

Trace plots and MCMC diagnostics of the linear mixed model suggested that chains mixed well and that the assumptions of residual normality and homoscedasticity were met. Beaver ponds had an average of 4.9 species (95% CRI: [2.37, 7.46]) greater than peatland ponds (Fig. 3.5A). Bird species richness was lower in the presence of American red squirrel than at sites without this potential predator ( $\beta_{\text{Squirrel}} = -3.97$ , 95% CRI: [-7.52, -0.36]; Fig. 5b, Table S6). Species richness decreased with increasing latitude ( $\beta_{\text{Latitude}} = -3.89$ , 95% CRI: [-5.00, -2.78]), leading to fewer species in the northernmost sites (Fig. 3.5C, Appendice B, Table B.6).

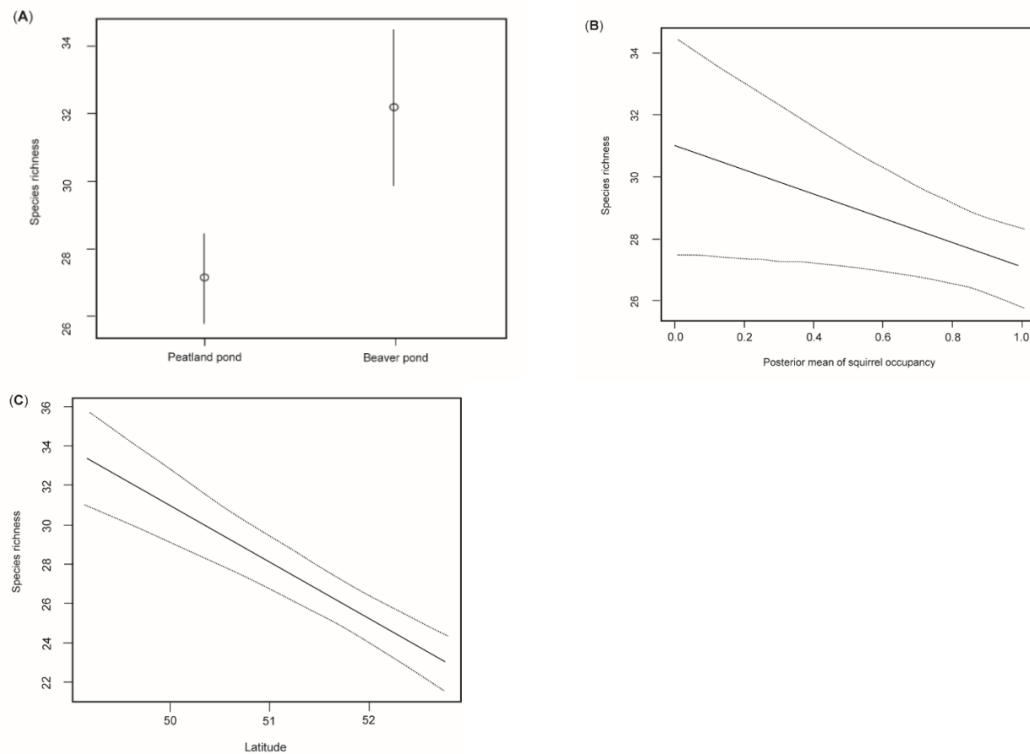


Figure 3.5. Estimated species richness of bird assemblages across A- Pond type, B- Squirrel occupancy state, and C- Latitude in Northern Quebec, Canada. Predictions and

their 95% credible intervals are shown by holding the other explanatory variables at their mean values.

### 3.8. Discussion

The aim of the present study was to assess how bird assemblages responded to habitat and landscape factors at the local scale in an understudied boreal region of northern Quebec. By using a multispecies occupancy model, we estimated baseline occupancy for 96 bird species including two species of conservation concern at a national scale (Olive-sided Flycatcher and Rusty Blackbird). Overall, beaver ponds harbored a higher bird species richness and different assemblages than peatland ponds, a pattern driven primarily by early successional species. Another novel aspect of our work was to model squirrel occupancy, as a proxy of potential nest predation risk, and include it as an explanatory variable on bird species occupancy, using a structural equation model approach. We showed that bird species richness and the occupancy of several species in the bird assemblages were lower in the presence of red squirrels.

#### 3.8.1. Beaver activity shaping avian assemblages

We expected that bird assemblages would differ between beaver ponds and peatland ponds. Our study supports this hypothesis and shows that beaver ponds contain a higher bird species richness than peatland ponds. This finding is in general agreement with previous research that has compared bird diversity in beaver ponds to non-flooded wetlands (Aznar and Desrochers, 2008; Longcore et al., 2006). Aznar et Desrochers (2008) found that abandoned beaver ponds supported higher numbers of songbirds

compared to all other adjacent riparian habitats. Although we did not consider beaver ponds along a successional gradient in our study due to a limited number of ponds, various mechanisms may explain the greater species richness we observed in these habitats. For instance, numerous studies documented that beaver-flooded wetlands increase habitat complexity and provide a greater diversity of habitats that favor birds for brood rearing, foraging, and predation avoidance (e.g., Grover and Baldassarre, 1995; Nummi and Holopainen, 2014).

While no species preferred peatland ponds in our study, 11 species increased significantly in beaver ponds, primarily early successional species. This group consisted of sparrows and warblers that usually nest close to the shore and feed on or near the ground in open grassy or shrubby habitats. These species presumably benefit by increased vegetation cover in beaver ponds (Alza, 2014; Stoffyn-Egli and Willison, 2011). Through dam construction, beavers alter water hydrology and create areas of open water with inundated trees and snags. The subsequent denser understories and greater amounts of emergent herbaceous vegetation generated at beaver sites may increase the availability of insects (Reese and Hair, 1976), which is the main diet of these species, and therefore render beaver ponds a more suitable foraging habitat for early successional species (Alza, 2014; Askins et al., 2007; Chandler et al., 2009). The effects of habitat modification through beaver disturbance also influence the stage of vegetation succession. Once beavers abandon the site, beaver ponds drain and form patches with a variety of grasses and shrub species, known as beaver meadows (Naiman et al., 1988). Abandoned beaver ponds limit the progress of forest succession, due to prolonged flooding and anaerobic conditions, and promotes the regrowth of early successional plant species that support many shrubland bird species (Chandler et al., 2009; Terwilliger and Pastor 1999; Wright et al., 2002). As a result, beavers potentially create high quality habitat for early successional species in boreal forest that may



persist in the landscape for many decades after abandonment (Barnes and Dibble, 1988; McMaster and McMaster 2000; Terwilliger and Pastor, 1999).

### 3.8.2. Red Squirrel Presence and possible influence

While the effects of beaver activity on bird assemblages are clearly evident, the effects of red squirrel presence are less clear. The red squirrel may have a direct effect on birds through nest predation (Bayne and Hobson 2002; Reitsma et al., 1990). Our results show that the occupancy of 20 species was lower in the presence of red squirrels, of which early successional species showed the strongest decrease (10 of 16 species, Figure 2A). Several studies have reported a decline in nesting success of bird species in the presence of red squirrels based on artificial nests (Darveau et al. 1997; Jobin and Picman 2002; Sieving and Willson 1998) and natural nests (Martin et al., 2003). Our results are consistent with these patterns. However, our observational study cannot identify the mechanisms behind these patterns or rule out that they were caused by other predators such as corvids, mustelids, or short-tailed shrew (Dyson et al., 2020; Reitsma et al., 1990; Sieving and Willson 1998). We did not find a negative relationship of red squirrels on late successional species. This is in line with reports of late successional species nesting in the upper levels of trees while squirrels prefer to predate bird nests in the understory (Sieving and Willson 1998). However, it is more difficult to explain the positive association between red squirrel presence and four species: Canada Jay, Olive-sided Flycatcher, Yellow-bellied Flycatcher, and Ruby-crowned Kinglet. The Canada Jay is a direct competitor of red squirrel for bird nests, as it can attack as many nests as red squirrels (Boulet et al., 2000). Hence, our data are consistent with Canadian boreal studies that report a high predation pressure and joint dominance of nest predation by red squirrels and Canada Jays (Boulet et al., 2000, 2003;

Sieving and Willson 1998). The Canada Jay and Olive-sided Flycatcher are larger species potentially less vulnerable to nest predation by American red squirrels. Nonetheless, this explanation does not hold for the other two species that had higher occupancy in the presence of squirrels. Because red squirrels are the main source of nest mortality for many bird species (Martin 1993; Rodewald and Yahner 2001), we recommend recording detections of red squirrel when sampling bird occupancy using acoustic methods (Chavel et al., 2017). Acoustic methods for detecting territorial behaviors displayed by squirrels are equally reliable as live trapping, which is more invasive and requires a greater sampling effort (Chavel et al., 2017).

The association between the presence of red squirrels and bird assemblages we observed may also reflect unmeasured variables. For example, an alternative explanation of the association between red squirrel presence and that of early successional species could be related to stand age. Forest stand age plays an important role in driving bird assemblages (Imbeau et al., 2001; Schieck et al., 1995; Stelfox, 1995). Squirrels in the boreal region feed mostly on seeds of black spruce and these trees start producing seeds at about 30 years of age (Viglas et al. 2013). Conifer seed production may be related to the presence of squirrels, as squirrel density decreases with lower seed availability (Gurnell, 1984; Rusch and Reeder 1978). Furthermore, red squirrels typically respond positively to habitat characteristics associated with stand age and cone production that can fluctuate between years (Gurnell, 1983). Addressing the relative importance of red squirrels in structuring boreal avian community will require shedding light on the mechanisms at play among squirrels, nesting bird success, and temporal variations related to cone production and stand age.

### 3.8.3. Amount of forest and latitudinal gradient

The bird assemblages in the boreal wetland landscapes of our study responded differentially to forest cover. The occupancy of late-successional species increased with the forest cover. Our results support the idea that late-successional species are more likely to be negatively affected by habitat loss or fragmentation, mainly because they have large area requirements (e.g., Hutto and Gallo, 2006; Koivula and Schmiegelow, 2007; Venier et al., 2014). This result is not surprising, given that old-growth forest specialists prefer interior forest environments for nesting (Huhta et al., 1999) and because cavity-nesting species included in late-successional guilds generally feed on saproxylic insects (Nappi et al., 2003; Saint-Germain et al., 2007). A reduction in forest cover may lead to decreased availability of insect prey and to the loss of specialized microhabitats for foraging and breeding substrates (Stratford and Stouffer, 2015). Beyond the clear pattern between forest cover and occupancy of species in the late-successional guild, effects of forest cover were inherent to individual species in other guilds. The amount of habitat, measured here as forest cover, is one of the most important landscape determinants of bird biodiversity (Drolet et al., 1999; Harrison et al., 2005; Trzcinski et al., 1999), though other metrics merit investigation. Forest type, forest age, and disturbance type also influence forest bird assemblages (Mitchell et al., 2001; Saab, 1999; Venier et al., 2014), but such variables were not available for our whole study area. These variables could be considered in future investigations of bird assemblages in boreal wetlands.

We believe that the latitudinal patterns detected here are not caused by latitude per se, but rather driven by biotic and abiotic forces (Rohde, 1992). Bird species richness generally decreases moving north (Kouki, 1999). However, latitude in our case reflected that beaver ponds were absent at the northern sites, whereas peatland ponds

were well represented throughout the region. In addition to latitude, another potential bias in our study was the sampling year. We found that occupancy of certain species varied with years, reflecting potential differences in abundance across years. We included latitude and year as explanatory variables on occupancy to reflect potential differences related to these spatial and temporal effects, although they were not the primary focus of our study. These variables allowed us to estimate the effects of the variables of interest, notably pond type, squirrel occupancy, and forest cover.

#### 3.8.4. Detection probability and sampling covariates

Our study highlights the importance of including temporal and sound quality variables when modeling detection probability of birds within wetlands. Species responded differently to the number of days since snowmelt. Of the 96 species studied, 20 species were most active early in the season, whereas 9 species were least active early in the season. Detection probability varied with the breeding song phenology of each species. This result is directly associated with the phase of the reproductive cycle of resident species (Wilson and Bart, 1985) and the timing of arrival or passage of short and long-distance migrants (Furnas and McGrann, 2018). The inclusion of the number of days elapsed since snowmelt also accounted for important differences in locations and spring weather patterns in our study area that spanned 400 000 km<sup>2</sup>. Indeed, using such an approach is beneficial where the expected timing of the breeding season is affected by spatial locations and the timing of surveys (Sólymos et al., 2018).

The detection of birds relied on vocalizations in audio recordings. Unsurprisingly, the quality of the recording was an important predictor of detection probability of all species. Our results concur with previous studies using acoustic surveys (Acevedo and

Villanueva-Rivera, 2006; Celis-Murillo et al., 2009; Swiston and Mennill, 2009). Sound quality decreases with background noise such as rain or wind in passive field recordings. Further refinements of filters to remove background noise or to identify recording quality (several species vocalizing simultaneously) will prove useful in automating species identification.

### 3.9. Conclusion

Overall, we estimated the composition and structure of bird assemblages in boreal wetlands and quantified their relationship with habitat and landscape patterns across a broad geographic region. Our results highlight the benefits of beaver ponds for bird assemblages, in agreement with studies indicating positive effects of beaver activities on boreal communities. These positive impacts should be considered in the context of beaver management practices. Our results suggest drawbacks of red squirrel presence, probably caused by nest predation or through an indirect influence of stand age. We hypothesize that nest predation pressure is high in our study area and is mainly driven by red squirrel. Climate change, by modifying the distribution of these two rodents, has the potential to indirectly impact bird species assemblages found in northern Quebec. These trade-offs could be investigated in further studies which will contribute to prioritize regional wetland conservation in a landscape with increasing rates of wetland loss and degradation.

## Acknowledgment

We wish to thank M. Desrochers for providing valuable assistance to extract spatial data in a georeferenced information system. Special thanks to J. Arsenault and R. Chevalier for their assistance in fieldwork who were instrumental in field deployment and logistical support. We appreciate the insightful comments and feedback on previous drafts by A. Pietrek, and reviewers from *@Corrige-moi* students group including M. Arsenault and N. Chabaud of the Université du Québec en Abitibi-Témiscamingue (UQAT). We thank M. A. Young for identifying Red Crossbill types based on our recordings added to eBird checklists. We thank J. Morarin for the artistic illustrations of the graphical abstract. We thank Hydro-Quebec and FaunENord for providing weather data throughout James Bay region. We also thank Hecla mining (Casa Berardi mine), Nemaska Lithium (Whabouchi mine) and Stornoway Diamonds (Renard mine) for project support and access to study sites. We also thank the associate editor and two anonymous referees for their precious comments on previous versions of this manuscript.

Funding statement: This project was funded by the Natural Sciences and Engineering Research Council (NSERC) of Canada—Université du Québec en Abitibi-Témiscamingue (UQAT) industrial research chair on northern biodiversity in a mining context.

Ethics statement: No animals were handled as part of this research.

Author contributions: L.I conceived the idea; M.J.F. developed, designed, and led the fieldwork supervised by L.I. and M.J.M. L.I. interpreted recordings to identify species through acoustic detection. M.J.M. designed the statistical methods and analyzed the

data. M.J.F. and M.J.M. wrote the paper. All authors contributed to editing the manuscript and approved the submitted version. N.J.F. secured funding.

Data depository: Analyses reported in this article can be reproduced using the data provided by Feldman et al. (2022).

## CHAPITRE IV

### USING CAMERA TRAPS TO ESTIMATE HABITAT PREFERENCES AND OCCUPANCY PATTERNS OF VERTEBRATES IN BOREAL WETLANDS OF NORTHERN QUEBEC

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To be submitted to *Wetlands*



#### 4.1. Abstract

Wetlands are ubiquitous in boreal regions but are suffering from increasing natural and human pressures. These impacts can lead to a reduction in the availability of habitats for boreal mammals and birds that rely on wetlands for breeding, foraging, and resting. Camera traps provide an opportunity to survey mammals and birds for a baseline understanding of their habitat preferences in order to better inform management and conservation actions. We aimed to evaluate how habitat features affect the occupancy of boreal mammals and birds in wetlands. We used a multi-species occupancy model to estimate the habitat associations of 11 mammals and 45 avian species detected at 50 sampling ponds during the summers of 2018 and 2019 in Northern Quebec. We address how each species is influenced by occupancy covariates related to pond type (peatland ponds and beaver ponds), distance to road, forest cover within a 1 km buffer, and latitude, while accounting for detection probability as a function of sampling effort, daily rainfall, and the number of days elapsed since snowmelt. The occupancy of mammals such as Red Fox and River Otters, and birds including the American Pipit, Common Raven, Hooded Merganser, and Greater Yellowlegs were favored by peatland ponds. On the contrary, the Common Grackle showed a positive response to beaver ponds. We found few effects of distance to roads, and no effect of amount of forest cover on species occupancy. The occupancy of 27% of mammals and 24% of birds decreased with increasing latitude. Detection probability increased with the sampling effort for six species and decreased with the snowmelt days for most birds. The observed patterns can inform both habitat conservation and land use planning decisions in boreal Canada in view of ongoing pressures on the habitat of a wide variety of vertebrates. By identifying the preferred pond types for different species, conservation efforts can protect wetlands in northern Quebec while minimizing the impact of infrastructure development such as roads on wildlife habitats.

*Keywords:* camera trap, Bayesian hierarchical model, beaver ponds, northern Quebec, detection probability, multispecies occupancy, peatland ponds.

#### 4.2. Résumé

Les milieux humides sont omniprésents dans les régions boréales, mais ils subissent des pressions naturelles et humaines croissantes. Ces impacts peuvent entraîner une réduction de la disponibilité d'habitats pour les mammifères et les oiseaux boréaux qui dépendent des milieux humides pour se reproduire, se nourrir et se reposer. Les pièges photographiques permettent d'étudier les mammifères et les oiseaux afin d'acquérir une connaissance de base de leurs préférences en matière d'habitat et de mieux orienter les mesures de gestion et de conservation. Nous avons cherché à évaluer comment les caractéristiques de l'habitat affectent l'occupation des mammifères et des oiseaux boréaux dans les milieux humides. Nous avons utilisé un modèle d'occupation multi-espèces pour estimer les associations d'habitat de 11 mammifères et 45 oiseaux détectés dans 50 étangs d'échantillonnage au cours des étés 2018 et 2019 dans le Nord du Québec. Nous abordons la façon dont chaque espèce est influencée par les variables d'occupation liées au type d'étang (étangs de tourbières et étangs à castors), à la distance à une route, à la couverture forestière dans une zone tampon de 1 km et à la latitude, tout en considérant la probabilité de détection en fonction de l'effort d'échantillonnage, des précipitations quotidiennes et du nombre de jours écoulés depuis la fonte des neiges. L'occupation de mammifères tels que le Renard Roux et la Loutre de Rivière, et d'oiseaux tels que le Pipit d'Amérique, le Grand Corbeau, le Harle Couronné et le Grand Chevalier, a été favorisée par les étangs des tourbières. Au contraire, le Quiscale Bronzé a réagi positivement aux étangs de castors. Nous avons trouvé peu d'effets de la distance aux routes, et aucun effet de la quantité de couverture

forestière sur l'occupation des espèces. L'occupation de 27 % des mammifères et de 24 % des oiseaux diminue avec l'augmentation de la latitude. L'effort d'échantillonnage a eu un effet positif sur la détection de six espèces, et la plupart des espèces d'oiseaux ont été mieux détectées en début de saison. Les patrons observés servent de guide peuvent informer à la fois la conservation des habitats et les décisions de planification de l'utilisation des terres dans le Canada boréal, compte tenu des pressions continues sur les habitats d'une grande variété de vertébrés. En identifiant les types d'étangs préférés pour différentes espèces, les efforts de conservation peuvent protéger les milieux humides dans le nord du Québec tout en minimisant l'impact du développement d'infrastructures telles que les routes sur les habitats de la faune.

#### 4.3. Introduction

Wetland ecosystems are experiencing accelerated loss of biodiversity due to natural sources and human pressures (Butchart et al., 2010; Kingsford et al., 2016; Newton et al., 2020). Wetlands provide critical habitat for an array of taxonomic groups (Junk et al., 2006; Keddy et al., 2009). However, many human disturbances affecting wetland ecosystems have been linked to range reduction for several mammal and bird species that depend on these environments (Laliberte and Ripple, 2004; Quesnelle et al., 2013). Medium and large sized mammals (hereafter “mammals”) require large undisturbed areas and many bird species are long-distance migrants that use wetland environments as stopover sites for breeding, foraging, and resting (Bogoni et al., 2020; Niemuth et al., 2006; Skagen et al., 2008). Collectively, mammals and bird species in wetland ecosystems carry out fundamental ecosystem roles as bioindicators, seed consumers and dispersers, as well as predators and prey (Amat and Green, 2010; Green et al., 2002;

Lacher et al., 2019). Unfortunately, habitat preferences are poorly known for most of these groups within regions where wetlands are dominant ecosystems.

In this context, wetlands in Canada's boreal regions are of main importance because they cover a vast area and host many species at their northern range of distribution (Junk et al., 2006; Poulin et al., 2004; Webster et al., 2015). Generally, boreal Canadian regions are largely undeveloped, but anthropic activities related to natural resource exploitation are growing, mainly from forestry, mining, petrochemical industry, and hydroelectric development (Bogdanski, 2008; Brandt et al., 2013; Webster et al., 2015). In addition, dominant pressures from global warming, insect outbreaks, and wildfires are expected to have some of the largest impacts at these latitudes, potentially leading to a reduction in the availability of suitable wildlife habitats as wetlands (Pastro et al., 2014; Stralberg et al., 2015; Venier et al., 2014). With ongoing natural disturbances and industrial development, we know little about these impacts on vertebrates in boreal wetland areas (Fisher and Burton, 2018; Murdoch et al., 2020). Therefore, an understanding of the factors influencing species-habitat relationships of wetland-dwelling species is a first step to inform management and conservation actions (Lehikoinen et al., 2016; Stralberg et al., 2019).

The spatial distribution of mammals and bird communities in boreal areas is also determined by anthropogenic and abiotic factors (Bowman et al., 2010; Speed et al., 2019; Zhang et al., 2013). In northern Canada, road networks are increasingly prevalent to transport natural resources across vast areas (Webster et al., 2015). Roads have been involved in altering the biodiversity with the direction of outcomes being species-specific (Rytwinski and Fahrig, 2013). Some species are negatively affected and tend to avoid roadside areas to minimize predation risk, such as Moose (*Alces alces*), Caribou (*Rangifer tarandus*), Canada Lynx (*Lynx canadensis*), and Red Fox (*Vulpes vulpes*; Bayne et al., 2008; James and Stuart-Smith, 2000; Laurian et al., 2008). In

contrast, other species benefit from roads because they facilitate movement and provide hunting opportunities for carnivorous mammals such as Wolves (*Canis Lupus*), Coyotes (*Canis latrans*), and Black Bears (*Ursus americanus*; Bowman et al., 2010; Lesmeister et al., 2015). Similar to roads, the amount of suitable habitat such as forest cover has also a species-specific influence on mammal and bird occurrence, although the effect can vary depending on their habitat use (Imbeau and Desrochers, 2002a; Lesmerises et al., 2013; Venier et al., 2014). Forest loss typically leads to negative effects on forest specialists and favors open habitat species (Fedrowitz et al., 2014; Vanderwel et al., 2009). Understanding how abiotic and anthropogenic factors determine mammal and bird occupancy is key to address management and conservation actions.

In Northern Quebec, peatlands and beaver ponds form a mosaic of heterogeneous habitats across the landscape. Peatlands dominate the region in the mid-boreal and high boreal regions (Webster et al., 2015). Northern peatlands are often classified as either bogs or fens, with bogs considered to be more acidic and characterized by *Sphagnum* mosses and ericaceous shrubs. Alternatively, fens are often less acidic with a vegetation dominated by sedges (*Carex* spp.) and brown mosses (i.e. the *Amblystegiaceae*). Despite the predominance of peatland ponds in bogs and fens in boreal natural ecosystems, beaver ponds increase the heterogeneity of habitats across the region at the landscape level (Wright et al., 2002). Beavers are ecosystem engineers that typically have a positive impact on plant and animal communities (e.g., Feldman et al., 2023; Jones et al., 1997; Stringer and Gaywood, 2016). At the pond level, some mammal species such as otters (*Lontra canadensis*), minks (*Neogale vison*), and muskrats (*Ondatra zibethicus*) use beaver lodges as shelter or to forage for prey (France, 1997; Müller-Schwarze, 2011; Rosell et al., 2005). For migrating and wetland birds, beaver ponds offer new nesting areas adjacent to the ponds and enhance insects productivity, which provides abundant food sources for breeding pairs and their offspring (Bulluck

and Rowe, 2006; Grover and Baldassarre, 1995). Despite this, we still do not sufficiently understand how many birds and mammals might associate with beaver ponds, dams and lodges in more contiguous northern regions where beaver ponds comprise a small portion of the land area. The distinct environments of peatland and beaver ponds may differently influence the habitat use of these species in northern areas such as Northern Quebec.

In remote regions, camera traps are now a standard method to monitor wildlife (Burton et al., 2015; Gompper et al., 2006; Trolliet et al., 2014). Most camera surveys have primarily focused on medium to large sized mammals and few studies have targeted birds. However, this trend is changing because visual detection of birds provides important ecological information of little-known, discrete and rare species (O'Brien and Kinnaird, 2008; Znidarsic, 2017). Cameras are sensitive enough to detect the movement of small and large birds (Surmacki and Podkova, 2022; Uhe et al., 2020). In a forest-wetland environment, numerous passerines and migratory landbirds depend upon aquatic insects that emerge from the water early in spring (Ewert and Hamas, 1996; Gray, 1993; Nakano and Murakami, 2001). Therefore, motion-triggered camera traps enable researchers to document discrete and non-vocal birds (i.e., waterfowl), as well as insectivorous species, which are both attracted to aquatic wetland habitats.

The goal of our research is to determine how habitat features affect mammals and birds that use boreal wetlands. Specifically, we aim to evaluate how site occupancy of boreal mammals and birds in boreal wetlands varies with habitat type, forest cover, , and anthropogenic linear features. This information will inform conservation and land-use management regarding natural and anthropogenic disturbances on boreal wetland vertebrates. We used camera traps to survey birds and medium- to large- mammals in Northern Quebec and estimated the species-habitat relationships with a community occupancy model. Because beaver activity has positive effects on several mammals and

birds at a local scale, we predicted that occupancy in beaver ponds is higher than in peatland ponds for both groups (Table 1). Among groups, we expected a stronger response of mammals as compared to birds, in relation to distance to roads given that most distant ponds are the least disturbed and therefore more likely to be occupied (Table 1). For both groups, we would expect forest cover to positively affect species that feed and breed in trees, and in contrast, a negative effect of forest cover is predicted for species that prefer open habitats (Table 1).

#### 4.4. Materials and Methods

##### 4.4.1. Study area

The study area spans about 400,000 km<sup>2</sup> in Northern Quebec, Canada, between the latitudes 49° and 53° N. It overlaps the Boreal Shield, Taiga Shield and Hudson Bay Lowlands ecozones, which have different characteristics and degrees of human disturbances. Specifically, the Boreal Shield ecozone covers most of the study area and is dominated by a rolling mosaic of wetlands and thousands of glacially formed lakes of varying size. The Taiga Shield, at the northern portion of the study area, consists of Taiga Forest, lakes and wetland depressions shaped by glaciers. The Hudson Bay Lowlands zone is a coastal plain that consists mainly of poorly drained ombrotrophic bogs and minerotrophic fens along the northern coast. It comprises the largest peatland complex in Canada and among one of the largest in the world (Abraham and Keddy, 2005). A subpolar continental climate characterizes the study area, with mean annual temperatures ranging from -0.05 °C to -4° C and 800 mm of mean annual precipitation (World Weather Online, 2021). The temperature varies throughout the year, with a

mean monthly temperature between 9° C and 17°C from May up to August during our field work (World Weather Online, 2021).

Vegetation composition is characteristic of the northern boreal forest. The plant community is dominated by black spruce (*Picea mariana*) in forest stands of different ages. Mixed wood and deciduous forest also occur (mainly in the southern portion), and the entire landscape is interspersed with an extensive mosaic of wetlands. The understory in the region is primarily composed of ericaceous shrubs (e.g., *Rhododendron groenlandicum*, *Chamaedaphne calyculata*, *Kalmia angustifolia*, *Rhododendron groenlandicum*) and feather mosses (*Pleurozium schreberi*) forming a dense carpet, and *Sphagnum angustifolium*, *S. cuspidatum*, and *S. magellanicum* are abundant in black spruce stands.

Overall, the study area has few human disturbances, with anthropogenic development concentrated in the southern portion and the northern portion remains relatively unaffected. Settlements of local communities include traditional territories of Cree and Abitibiwinni First Nation communities, which practice subsistence activities such as hunting, trapping, and fishing. The landscape in the region has been altered and degraded by mining activities, hydroelectric development, and logging practices. Wildfire and insect outbreaks are common natural disturbances within the study area. The study area supports several larger carnivorous mammals such as Black Bears, Canada Lynx and Gray Wolves, and large herbivores including Woodland Caribou and Moose. Bird species in the study area are estimated at 150-200 species (eBird, 2021), with few year-round residents and most of the avian assemblage are migratory species that breed in boreal forests during summer and migrate southward each year.

Due to scarce information in our study area, we randomly pre-selected potential peatland and beaver ponds from Google Earth. We limited our selection to study sites



< 2 ha. This process yielded an initial sample of approximately 100 potential ponds. From these ponds, we identified those within 1 km from major and logging roads (< 1 km) and with the additional constraint of spacing ponds > 800 m from other sampled ponds to limit potential spatial dependence among sites. This process produced a final set of 50 ponds distributed throughout the study region, including 38 peatland ponds and 12 beaver ponds.

#### 4.4.2. Camera trap survey

We conducted camera trap surveys at the 50 wetlands selected to detect mammal and bird species during the summers of 2018 and 2019. We deployed three cameras at each pond with a detection array in a triangle configuration (Fig 4.1A). All three cameras at a given pond were equally spaced, where the distance depended on the pond size (see Fig. 4.1A). To increase detectability, we installed cameras near signs of animal activity (i.e., apparent game trails, tracks, or feces). We cleared branches or grasses in front of cameras to prevent vegetation from triggering the motion detection sensors. Camera traps were installed at the same points during both years.

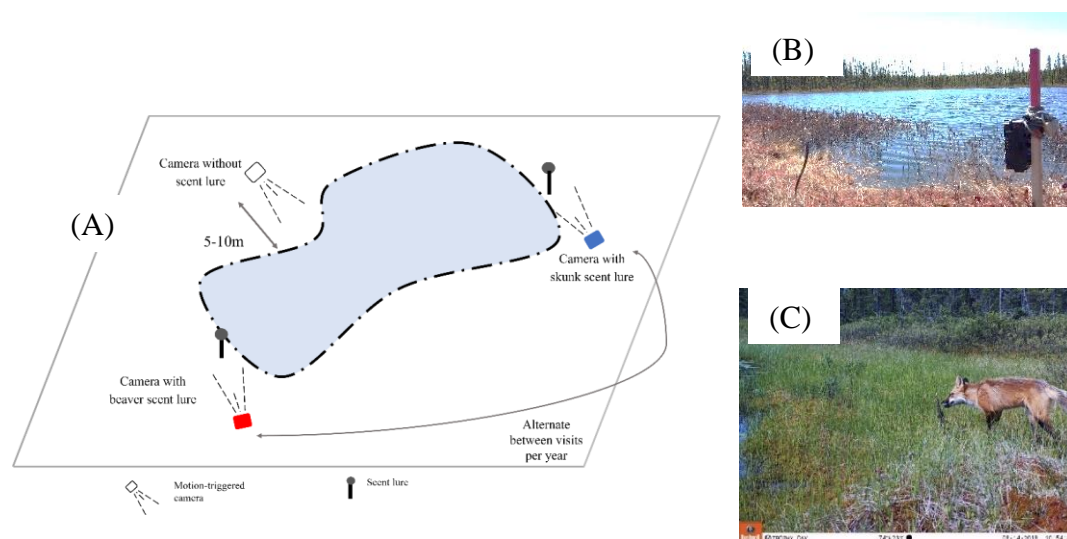


Figure 4.1. (A) Schematic of a three-camera array at a pond. Squares represent camera trap location and colors identify cameras baited with scent lures. (B) A camera placement with a scent lure place on the stick (C) Red fox (*Vulpes vulpes*) detected by a camera baited with a scent lure.

Each camera array consisted of three infrared Bushnell Trophy Cam HD motion-sensing digital cameras set to be active 24 hours/day. Due to limits in the number of cameras available and logistical constraints between sites, cameras were rotated at groups of sites: we sampled 16 or 17 ponds simultaneously. Camera traps were operated during two periods of seven consecutive days (hereafter a “session”) from May to August 2018 and May to July 2019. Consequently, the data collection period lasted 28 days at each pond divided into 2 sessions per year. Cameras were placed at the edge of the pond and secured to a tree or a wooden stake at an average height of 30–60 cm at about 2–5 m from the water (Fig. 4.1B). Cameras were triggered by animal movements and programmed to take 3 photos per trigger event, and a following video of 10-s, with a 1-min interval delay between detections to avoid that a single animal would be the subject of a long event of recording.

We used scent lures as attractants to increase detectability at each pond (Avrin et al., 2021; Ferreras et al., 2018; Fidino et al., 2020). We used beaver-based scent lure (containing beaver *Castor canadensis* castoreum; Mactrap, Richelieu, Quebec, Canada) and skunk-based scent lure (containing skunk *Mephitis mephitis* anal scent gland; Leurre Forget, Sherbrooke, Quebec, Canada). These scents were selected based on Schlexer (2008). We placed scent lure at on a stick at 2 -5 m in front of the camera trap to increase the probability of detecting animals exploring the lure (Fig. 4.1B). The area between the camera and the scent lure was cleared by removing dense vegetation. We randomly assigned scent lures to two of the three cameras. We did not visit cameras or rebait them between the start and the end of the sampling session of seven consecutive days to avoid human disturbance. In the second sampling session of a given year, camera traps were set at the same locations, but we rotated the type of scent lure on baited cameras (Fig. 4.1A).

Before the start of each sampling session of seven consecutive days, lures were refreshed with a new stick (Fig. 4.1B-C). Likewise, all cameras were test-fired to confirm functionality and correctness of angle in the camera placement. In beaver ponds, the unbaited camera was placed on the dam, which are structures frequently used by certain species such as mustelids (Cooke and Zack, 2008; Gauvin, 2017; LeBlanc et al., 2007). For peatland ponds, the unbaited camera was placed randomly along the pond perimeter.

Cameras were checked at the end of the session to collect photos, change batteries, and replace memory cards. During the photo analysis, birds and mammals in the images were identified to species level. We considered photos or videos of the same species at the same pond within the same day as a single record. We combined the information obtained from the three cameras at a given pond on a given day to form one detection event.

#### 4.4.3. Predictors of animal occurrence and detection

We considered covariates expected to influence bird and mammal occupancy and detection probability and that were relevant to our study objectives. We predicted the direction of these effects on each group (Table 4.1).

*Occupancy variables.* We hypothesized that occupancy of birds and mammals is influenced by five local and landscape covariates in our study area (Table 4.1). We considered the binary variables year of sampling to account for annual variation and pond type to compare beaver and peatland ponds. The distribution of the two types of ponds was unbalanced in our study area: peatland ponds were more abundant at the northern sites, whereas beaver ponds were concentrated at the lower latitudes. For these reasons, we included latitude as an explanatory variable in our analysis. Bird and mammal communities in our study area occur in all forest cover types (Imbeau et al. 2001; Venier et al. 2014). Therefore, we determined percent cover of all forest types (deciduous, mixed, and coniferous forest) over 4-m within a buffer of a 1 km radius around each pond (Berger and Leboeuf, 2015; Leboeuf et al., 2012a). We selected a buffer of 1 km as a general descriptor of the habitat surrounding each pond, and although this implies some degree of overlap among buffers, it does not violate the assumption of spatial independence and is therefore not a statistical concern (Zuckerberg et al. 2012). Finally, to incorporate the potential effect of human presence and bird and mammal occupancy, we included the distance of sampling ponds to the nearest road.

*Detection variables.* We considered three explanatory variables that could potentially affect the detection probability of birds and mammals, mainly through influencing the activity of animals: a) Cumulative rainfall during a given day; b) Number of days

elapsed since snowmelt; and c) Sampling effort as the number of active cameras during a given day (Table 4.1). Rainfall data was extracted from environmental stations at nearby sites. We included the number of days since snowmelt to account for seasonal shifts in species use. Because not all ponds have been surveyed equally, we used the number of active cameras as a measure of sampling effort.

Table 4.1. Potential explanatory variables and associated predictions of the five explanatory variables on occupancy and three variables on detection probability included in the analysis of bird and mammal detection by camera traps in 12 beaver ponds and 38 peatland ponds in Northern Quebec, Canada, in 2018 and 2019.

Covariate	Prediction	Predicted response		Reference
		Birds	Mammals	
<i>Occupancy (<math>\psi</math>)</i>				
Pond type (beaver or peatland pond)	Differences in habitat need will influence species pond use. Beaver ponds promote biodiversity and provide more favorable habitat than peatland ponds.	+	+	(Gauvin, 2017; Rosell et al., 2005; Stringer and Gaywood, 2016)
Distance to the nearest road	As the distance to roads and trails increases, ponds are less disturbed and therefore more likely to be occupied. Yet, some species (i.e., carnivorous) tend to use these openings as an accessible pathway for movement and hunting and thus benefit from the proximity of roads.	+	≠	(Easter et al., 2019; Lesmeister et al., 2015; Rich et al., 2017)
Forest cover surrounding ponds within 1 km	Some species prefer ponds with greater cover of coniferous forests, while early successional or open landscape species might be affected by the opposite pattern.	≠	≠	(Gompper et al., 2016; Hofmeester et al., 2021; Trzcinski et al., 1999)
Table 4.1. Suite				
Latitude	Account for confounding effects of pond type.	≠	≠	(Hofmeester et al., 2019; Hurlbert and Haskell, 2003)
Year	Account for between-years variations	≠	≠	(Avrin et al., 2021)
<i>Detection (<math>p</math>)</i>				
Cumulative rainfall	Rain influences the movement of mammal individuals and affects bird breeding success.	—	—	(Lesmeister et al., 2015; Virkkala et al., 2005)
Number of days since snowmelt	As resources fluctuate throughout the season, the timing of the survey may influence detection depending on species-specific feeding activities and the seasonality of reproduction.	≠	≠	(Hurlbert and Haskell, 2003; Iannarilli et al., 2021; Smith et al., 2018)
Sampling effort	Sampling effort, indicated as the number of active cameras that ranged between 0 and 3, may influence species detection.	+	+	MacKenzie and Royle, 2005; De Solla et al. 2005

(+/-) Positive or negative response for all the species within a group; (≠) Response is variable and species specific within a group.

#### 4.4.4. Data processing and analysis

To increase the detection probability of species on a given day, we pooled detections of species  $l$  across the three camera traps at site  $i$  on a given day. This modification produced a data matrix of 100 rows (50 sites x 2 years) and 14 columns (two 7-day periods) for each species, containing information on whether the species was detected (1) or not (0) on a given day.

We used a multispecies occupancy framework to analyze the combined data of the bird and mammal communities (Dorazio and Royle, 2005; Royle and Dorazio, 2008; Zipkin et al. 2010). The occupancy ( $\psi_{ikl}$ ) of species  $l$  at site  $i$  in year  $k$  was modeled with effects of pond type, forest cover, year, latitude, and distance to the nearest road:

$$\text{logit}(\psi_{ikl}) = \phi_{0,l} + \beta_{\text{TypeBeaver},l} * \text{TypeBeaver}_i + \beta_{\text{Forest}} * \text{Forest}_i + \beta_{\text{Year2019},l} * \text{Year2019}_{ik} + \beta_{\text{Latitude},l} * \text{Latitude}_i + \beta_{\text{DistRoad},l} * \text{DistRoad}_i + v_i$$

$$z_{ikl} \sim \text{Bernoulli}(\psi_{ikl})$$

where  $\phi_{0,l}$  is the average occupancy of species  $l$  and  $\beta_l$  corresponds to the random slope of a given explanatory variable for species  $l$ . We allowed the slopes for pond type, forest cover, year, latitude, and distance to nearest road to differ among species by drawing them from a normal distribution, e.g.,  $\beta_{\text{Forest},l} \sim N(\mu_{\beta_{\text{Forest}}}, \sigma_{\beta_{\text{Forest}}}^2)$ . The random effect  $v$  of site  $i$  was drawn from  $N(0, \sigma_{\text{site}}^2)$ .

We modelled the detection probability of species  $l$  as a function of the total precipitation, days elapsed since snowmelt, and sampling effort:

$$\text{logit}(p_{ijkl}) = \eta_{0,l} + \theta_{\text{Precipitation},l} * \text{Precipitation}_{ijk} + \theta_{\text{Thaw},l} * \text{Thaw}_{ijk} + \theta_{\text{Effort},l} * \text{Effort}_{ijk}$$

where  $\eta_{0,l}$  denotes the average detection probability of species  $l$ , and where  $\theta_l$  gives the random slope associated with a given explanatory variable for species  $l$ , drawn from a normal distribution, e.g.,  $\theta_{\text{Thaw},l} \sim N(\mu_{\theta_{\text{Thaw}}}, \sigma_{\theta_{\text{Thaw}}}^2)$ .

We estimated model parameters using a Bayesian approach based on Markov chain Monte Carlo (MCMC) in JAGS 4.3.0 within R 4.1.2 using the jagsUI package (Plummer et al., 2006; Lunn et al. 2013; Kellner, 2019; R Core Team, 2021). We sampled five chains of 500 000 iterations with a thinning rate of 25, with the first 250 000 iterations used as burn-in. We chose normal priors with  $N(\mu = 0, \sigma^2 = 100)$  for the  $\beta$  parameters and uniform priors  $U(0,10)$  for the standard deviation of random intercepts and random slopes. Complete model structure and priors are shown in Appendice C, Table C.1. We assessed chain convergence based on trace plots, posterior density plots, and the Brooks-Gelman-Rubin statistic. We checked the fit of the model with posterior predictive checks based on a Pearson chi-square aggregated over rows and columns (Kéry and Royle, 2016). We computed the area under the receiver operating characteristic (ROC) curve as an additional measure of predictive ability (Zipkin et al., 2012). Model structure and priors are presented in Table S1.

#### 4.5. Results

Camera traps were operational for 3787 camera days out of a possible total of 4200 (28 days  $\times$  150 camera traps). Our complete data set included 56 species across 200



sessions, 50 pond sites and 150 camera stations. We collected a total of 282 502 images and videos, of which 1313 independent encounters of mammals or birds were included in the study (Table 4.2). A proportion of camera traps malfunctioned (0.09%); thus, we excluded them from our analyses. We excluded small mammals from the analysis because they were only detected in eight instances. We identified 11 species of medium- to large sized mammals and 45 species of birds which were used for further analysis. The species of mammals most detected were beavers (41.9% of the total), Red Fox (16.7%) and the North American River Otter (*Lontra canadensis*; 9.85%), whereas the Greater Yellowlegs (*Tringa melanoleuca*; 27.7%), American Robin (*Turdus migratorius*; 14%), Gray Jay (6.2%), Wood Duck (*Aix sponsa*; 6.1%), and American Black Duck (*Anas rubripes*; 6.1%) ranked highest among bird species detected (Table 4.2). These eight species accounted for 60.9 % of all identified photographs. In contrast, four species of mammals and 18 species of birds were detected less than five times during the study (Table 4.2). Excluding beavers, the Black Bear was the most detected species in beaver ponds, while the Red Fox was the most detected in peatland ponds. The Greater Yellowlegs was the species detected most often in beaver ponds, whereas the American Robin was detected the most often in peatland ponds.

Table 4.2. Total number of detections, proportion of sites with at least one detection per pond type for 56 species of boreal mammals and birds in Northern Quebec. Bird species were grouped into four taxonomic guilds according to their requirements regarding habitat succession: early successional species, late successional species, generalists, and wetland species.

Scientific name	Common name	Guild	Detections	Proportion of sites with detection		
				Total	Beaver ponds	Peatland ponds
<i>Alces americanus</i>	Moose	Mammal	15	0.22	0.16	0.34
<i>Canis lupus</i>	Grey Wolf	Mammal	3	0.04	0.16	0.00
<i>Castor canadensis</i>	Beaver	Mammal	85	0.36	0.83	0.21
<i>Lepus americanus</i>	Snowshoe Hare	Mammal	12	0.14	0.25	0.11
<i>Lontra canadensis</i>	North American River Otter	Mammal	20	0.26	0.00	0.32
<i>Lynx canadensis</i>	Canada Lynx	Mammal	7	0.1	0.25	0.05
<i>Martes americana</i>	American Marten	Mammal	2	0.04	0.00	0.05
<i>Neovison vison</i>	American Mink	Mammal	3	0.04	0.08	0.03
<i>Ondatra zibethicus</i>	Muskrat	Mammal	4	0.06	0.08	0.05
<i>Ursus americanus</i>	Black Bear	Mammal	17	0.26	0.50	0.18
<i>Vulpes vulpes</i>	Red Fox	Mammal	32	0.24	0.00	0.32
<i>Buteo jamaicensis</i>	Red-tailed Hawk	Early	5	0.08	0.25	0.03
<i>Geothlypis trichas</i>	Common Yellowthroat	Early	2	0.04	0.16	0.00
<i>Zonotrichia leucophrys</i>	White-crowned Sparrow	Early	4	0.04	0.00	0.05
<i>Catharus minimus</i>	Gray-cheeked Thrush	Late	1	0.02	0.00	0.03
<i>Catharus ustulatus</i>	Swainson's Thrush	Late	1	0.02	0.00	0.03
<i>Loxia leucoptera</i>	White-winged Crossbill	Late	1	0.02	0.00	0.03
<i>Perisoreus canadensis</i>	Gray Jay	Late	68	0.42	0.42	0.42
<i>Setophaga coronata</i>	Yellow-rumped Warbler	Late	5	0.08	0.08	0.08
<i>Catharus guttatus</i>	Hermit Thrush	Generalist	7	0.06	0.08	0.05
<i>Corvus brachyrhynchos</i>	American Crow	Generalist	1	0.02	0.00	0.03
<i>Corvus corax</i>	Common Raven	Generalist	37	0.30	0.25	0.32
<i>Falco columbarius</i>	Merlin	Generalist	1	0.02	0.08	0.00
<i>Junco hyemalis</i>	Dark-eyed Junco	Generalist	14	0.12	0.00	0.16
<i>Passerella iliaca</i>	Fox Sparrow	Generalist	1	0.02	0.00	0.03
<i>Turdus migratorius</i>	American Robin	Generalist	147	0.58	0.50	0.58
<i>Zonotrichia albicollis</i>	White-throated Sparrow	Generalist	4	0.08	0.08	0.08
<i>Actitis macularius</i>	Spotted Sandpiper	Wetland	13	0.08	0.00	0.11
<i>Agelaius phoeniceus</i>	Red-winged Blackbird	Wetland	5	0.04	0.16	0.00
<i>Aix sponsa</i>	Wood Duck	Wetland	11	0.04	0.08	0.03
<i>Anas crecca</i>	Green-winged Teal	Wetland	9	0.10	0.25	0.05
<i>Anas platyrhynchos</i>	Mallard	Wetland	16	0.14	0.16	0.13
<i>Anas rubripes</i>	American Black Duck	Wetland	67	0.44	0.50	0.42

Table 4.2. Continued

<i>Anthus rubescens</i>	American Pipit	Wetland	15	0.16	0.00	0.21
<i>Antigone canadensis</i>	Sandhill Crane	Wetland	59	0.36	0.33	0.37
<i>Aythya collaris</i>	Ring-necked Duck	Wetland	8	0.08	0.00	0.11
<i>Botaurus lentiginosus</i>	American Bittern	Wetland	3	0.06	0.16	0.03
<i>Branta canadensis</i>	Canada Goose	Wetland	53	0.38	0.25	0.42
<i>Bucephala clangula</i>	Common Goldeneye	Wetland	3	0.04	0.00	0.05
<i>Calidris minutilla</i>	Least Sandpiper	Wetland	1	0.02	0.08	0.00
<i>Canachites canadensis</i>	Spruce Grouse	Wetland	4	0.06	0.08	0.05
<i>Chroicocephalus philadelphia</i>	Bonaparte's Gull	Wetland	32	0.12	0.08	0.13
<i>Euphagus carolinus</i>	Rusty Blackbird	Wetland	56	0.28	0.25	0.29
<i>Gallinago delicata</i>	Wilson's Snipe	Wetland	8	0.08	0.33	0.00
<i>Lophodytes cucullatus</i>	Hooded Merganser	Wetland	21	0.22	0.00	0.29
<i>Anas americana</i>	American Wigeon	Wetland	2	0.02	0.08	0.00
<i>Megaceryle alcyon</i>	Belted Kingfisher	Wetland	2	0.02	0.00	0.03
<i>Melanitta perspicillata</i>	Surf Scoter	Wetland	3	0.06	0.00	0.08
<i>Melospiza georgiana</i>	Swamp Sparrow	Wetland	8	0.10	0.08	0.11
<i>Mergus merganser</i>	Common Merganser	Wetland	6	0.06	0.08	0.05
<i>Parkesia noveboracensis</i>	Northern Waterthrush	Wetland	2	0.02	0.08	0.00
<i>Passerculus sandwichensis</i>	Savannah Sparrow	Wetland	23	0.32	0.16	0.37
<i>Quiscalus quiscula</i>	Common Grackle	Wetland	38	0.12	0.50	0.00
<i>Setophaga palmarum</i>	Palm Warbler	Wetland	4	0.06	0.08	0.05
<i>Tringa melanoleuca</i>	Greater Yellowlegs	Wetland	300	0.60	0.33	0.68
<i>Tringa solitaria</i>	Solitary Sandpiper	Wetland	19	0.20	0.16	0.21

#### 4.5.1. Wildlife responses to occupancy covariates

Trace plots and other diagnostics suggested that the number of iterations and burn-in period were sufficient to allow the chains to stabilize for the parameters of the multispecies model ( $\hat{R} < 1.11$ , MCMC error  $< 2.6\%$  of SD for all parameters). The posterior predictive check based on the aggregated columns and rows suggested adequate fit ( $\chi^2_{\text{columns}} = 760.07$ ,  $P = 0.65$ ), whereas the check based on the aggregated rows suggested adequate fit ( $\chi^2_{\text{rows}} = 10853.57$ ,  $P = 0.37$ ). The area under the receiver operating characteristic (ROC) curve was 0.87 (95% CRI: [0.82, 0.89]), suggesting high predictive ability of the model.

The occupancy of eight species (3 mammals and 5 birds) varied with pond type, of which two species had a higher occupancy in beaver ponds, and five species in peatland ponds (Fig. 4.2A and 4.3A). Although there were no effects of distance to roads on mammals (Fig 4.2B), the occupancy of two bird species decreased with the proximity to roads (Fig. 4.3B). We did not find evidence of an association between forest cover and species occupancy (Fig. 4.2C and 4.3C). The occupancy of three mammal species and 11 bird species decreased with latitude (Fig 4.2D and 4.3D). The occupancy of mammals did not vary with year (Fig. 4.2E). However, four bird species varied with sampling year, with a greater occupancy in 2019 than in 2018 (Fig. 4.3E).

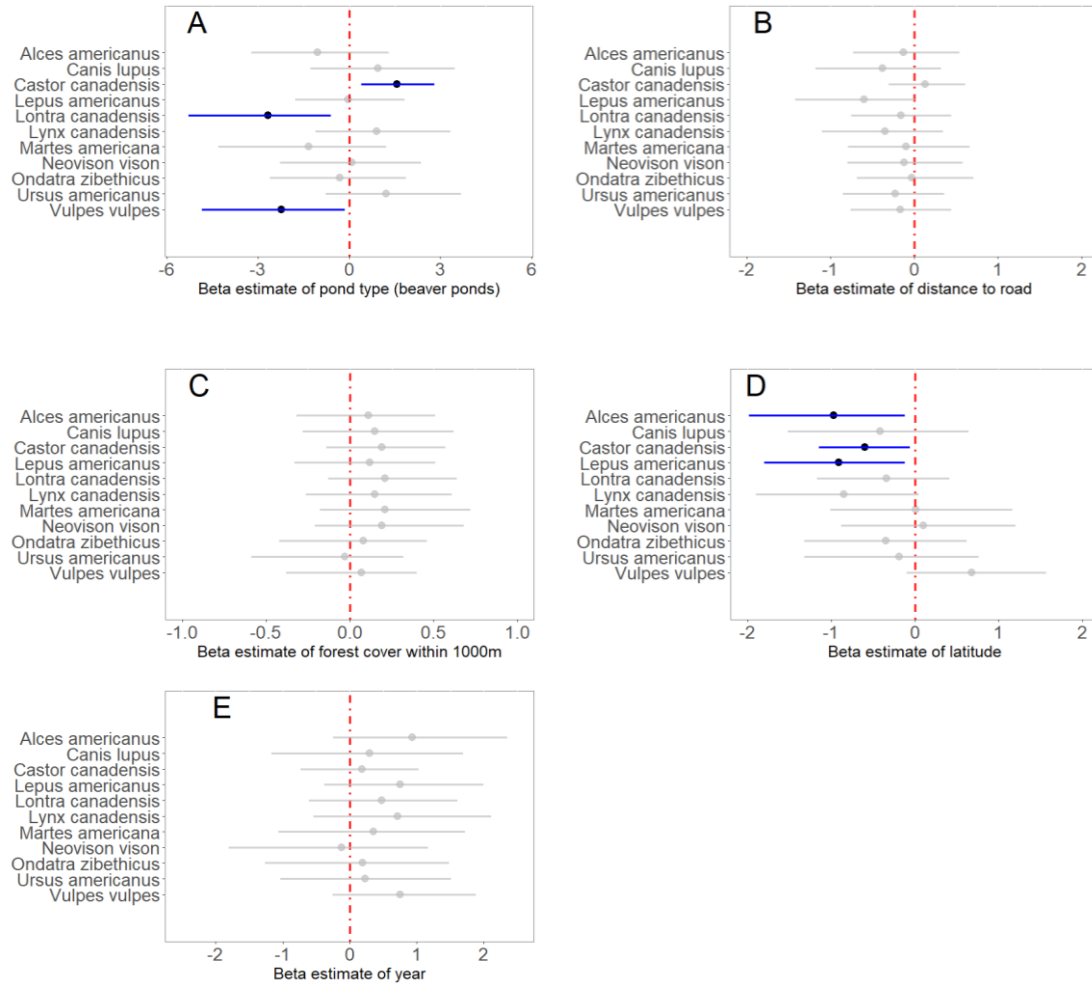


Figure 4.2. Mammal species responses to (A) pond type (beaver as reference level), (B) distance to roads, (C) forest cover, (D) latitude, and (E) sampling year (2019 as reference level). Horizontal lines represent the 95% Bayesian credible intervals. Black dots and bold blue lines indicate that the occupancy of a given species varied with the explanatory variable (parameter estimate differed from zero). Red vertical dashed lines highlight 0, where credible intervals that intersect the red line do not differ from 0.

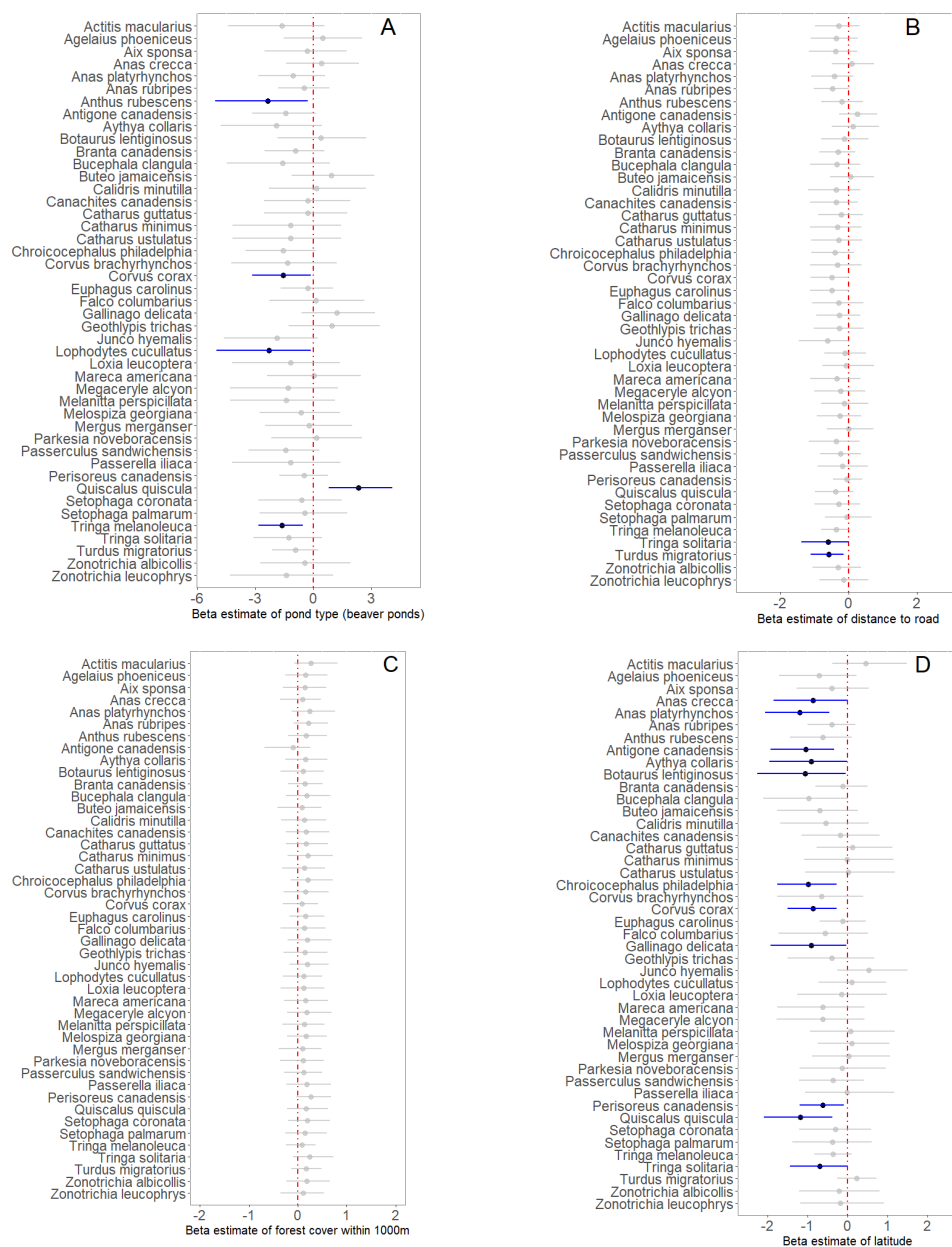
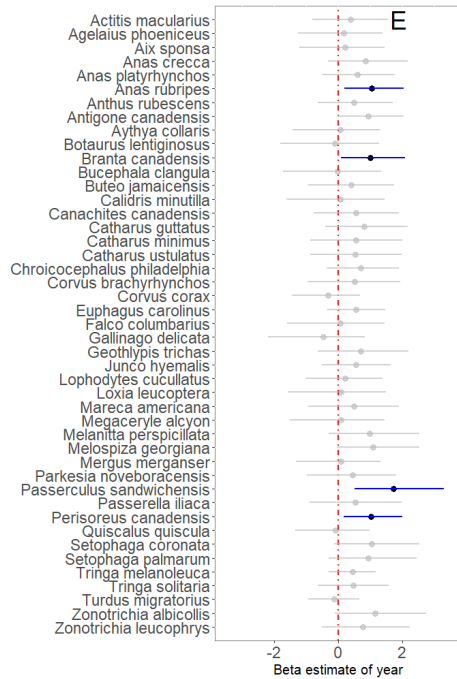


Figure 4.3. Bird species responses to (A) pond type (beaver as reference level), (B) distance to roads, (C) forest cover, (D) latitude, and (E) sampling year (2019 as reference level). Horizontal lines represent the 95% Bayesian credible intervals. Black dots and bold blue lines indicate that the occupancy of a given species varied with the explanatory variable (parameter estimate differed from zero). Red vertical dashed lines highlight 0, where credible intervals that intersect the red line do not differ from 0.

Figure 4.3 Continued



#### 4.5.2. Effect of sampling covariates on detection probabilities

The detection probability of two mammal species and four bird species increased with the sampling effort (number of active cameras per day, Fig. 4.4A, 4.4D). We did not find support for an effect of cumulative rainfall on detection probabilities of any species (Fig. 4.4B and 4.4E). Detection probabilities of one mammal species and 21 bird species decreased as the season progressed (Fig. 4.4C, 4.4F).

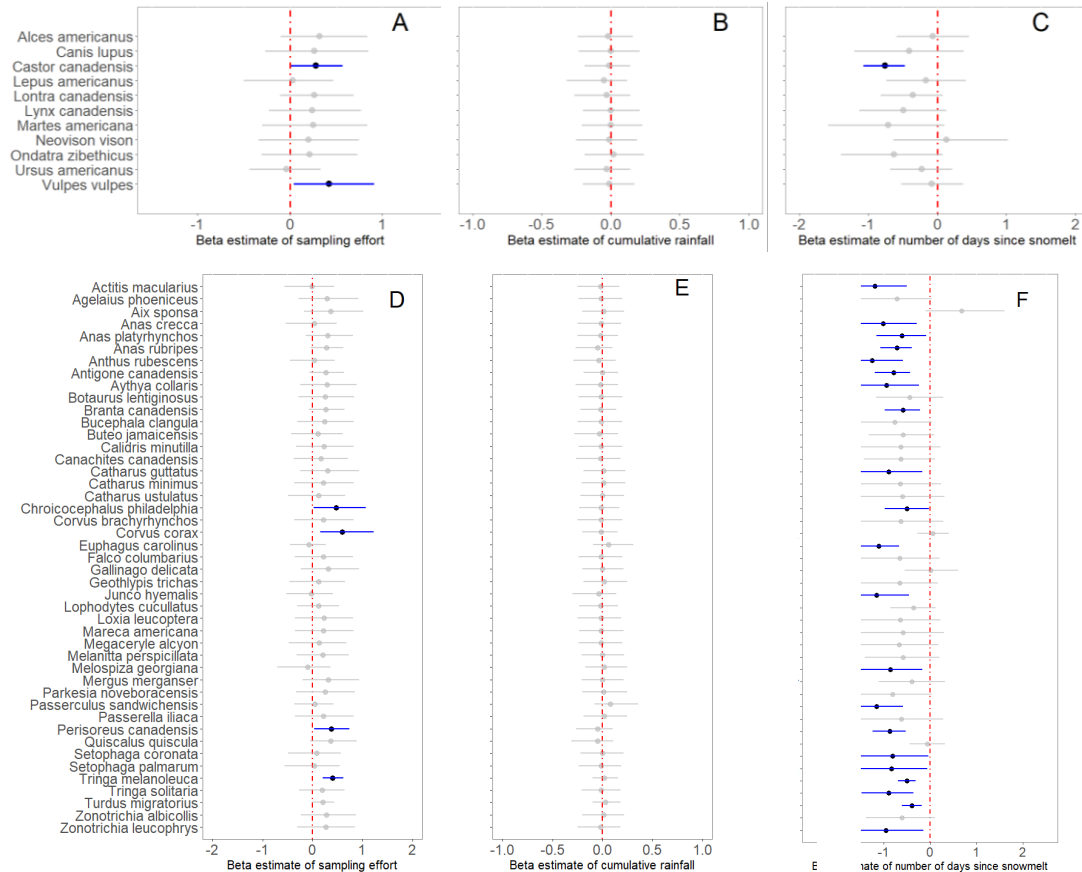


Figure 4.4. Detection probabilities of species using camera trap surveys at wetlands in northern Quebec in 2018–2019. Species responses to sampling effort, cumulative rainfall, and number of days since snowmelt for mammals (A–C) and birds (D–E) in that same order. Horizontal lines represent the 95% Bayesian credible intervals. Black dots and bold blue lines indicate that the detection of a given species varied with the explanatory variable (parameter estimate differed from zero). Red vertical dashed lines highlight 0, where credible intervals that intersect the red line do not differ from 0.

#### 4.6. Discussion

We investigated how habitat and landscape variables influence the occupancy of 11 mammal and 56 bird species while accounting for detection probability, using a



multispecies occupancy model. With a few exceptions, the patterns of habitat response do not lend support to the hypothesis that beaver ponds host higher levels of occupancy of birds and mammals than peatland ponds. Furthermore, in contrast to what we predicted, road proximity did not affect mammal occupancy, but was a relevant predictor for two bird species. Overall, our study shows that camera traps were able to effectively survey not only medium and large-sized mammals (Chen et al., 2022; Rovero et al., 2014), but also wetland bird species that are often overlooked in acoustic or point-count surveys given their discrete or aquatic behaviors (O'Brien and Kinnaird, 2008). We formulate recommendations for species that can be better detected according to an acoustic (Feldman et al., 2023) or a visual method as used here.

*Habitat type*— We expected a higher occupancy of birds and mammals in beaver ponds than in peatland ponds. However, most mammals occurred in both pond types. Only beaver showed a clear and expected preference for beaver ponds, although the species was also detected in peatland ponds (Table 2). However, the North American River Otter and the Red Fox were unexpectedly more likely to occupy peatland ponds rather than beaver ponds. For the North American River Otter, our results contradict the commensal relationship that has previously been described between beavers that create ponds and otters that benefit by obtaining refuges and dens. Dams in beaver ponds tend to increase aquatic food sources that facilitate hunting for prey (Gallant et al., 2009; LeBlanc et al., 2007; Tumilson et al., 1982). A sufficient water level is necessary for otters to dive and catch their prey, which are often slow-swimming fish species (Melquist and Hornocker, 1983; Reid et al., 1994). In our study, peatland ponds were more connected to major streams and had deeper water levels, so this may have favored otter occurrence. The Red Fox is a generalist predator and can inhabit a wide range of habitats (Adkins and Stott, 1998; Jones and Theberge, 1982; Van Etten et al., 2007). However, the species can also be susceptible to intraguild interactions with coyotes and wolves through predation or prey-mediated coexistence (Gosselink et al., 2003;

Lesmeister et al., 2015; Sargeant and Allen, 1989). Therefore, intraguild co-occurrence patterns of red fox should be further investigated to clarify the observed patterns.

For avian species, only the Common Grackle favored beaver ponds over peatland ponds and this pattern was also supported acoustically in the same ponds (Feldman et al., 2023). The Common Grackle feeds mostly on aquatic insects during the nesting season in spring (Homan et al., 1994). In beaver ponds, the amount of dead wood and indirect changes in water temperature and plant growth resulting from beaver flooding activities increase the diversity and abundance of aquatic insects (Mourant et al. 2018; Nummi et al. 2021; Saarenmaa, 1978). The Common Grackle may then benefit from the abundance of these food sources, which in turn are likely to be low in peatland ponds due to conditions associated with water acidity and vegetation structure (Batzer et al. 2016). By contrast, the American Pipit, Common Raven, Hooded Merganser, and Greater Yellowlegs were more likely to occupy peatland ponds rather than beaver ponds. We found no reasons to explain the results for these species. Other factors not addressed here may contribute to explain habitat preference of these four species, including the presence and abundance of fish, water chemistry, and the presence of macrophytes (Longcore et al., 2006; McNicol and Wayland, 1992; Nummi et al., 2016).

*Distance to nearest road*— Our hypothesis that mammal occupancy would be influenced by distance from the nearest road was not supported by our findings. However, for birds, we found negative effects for the Solitary Sandpiper and the American Robin. Previous research indicated that roads impacts on mammal populations occur at distances of up to 5 km from infrastructures, whereas bird populations are most affected at shorter distances of less than 2 km; Benítez-López et al., 2010; Rytwinski and Fahrig, 2015; Wittische. et al., 2021). Lesmeister et al. (2015) found that distance to major roads at 5 km and 10 km around camera locations was a significant predictor of carnivore species occupancy. Carnivorous are known to use

roads as predator paths, which can contribute to movement and provide hunting opportunities (Abrahms et al., 2016, Dickie et al., 2017; Latham et al., 2011). However, our study did not find positive effects on carnivores' occupancy near roads. In our region, human settlements are relatively scarce, and the road network is distant from dense urban centers. Therefore, negative, and positive effects associated with road pressure (i.e., fragmentation) or road traffic (i.e., traffic mortality) are less likely to impact wildlife. Nonetheless, anthropogenic linear features are increasing and may shift northward to new areas. Future associations between road construction and wildlife occurrence warrant further investigation to provide valuable information for the design of effective mitigation strategies.

*Forest cover*— Numerous studies have shown the importance of the amount of suitable habitat to species occurrence (e.g., Chavel et al., 2017; St-Laurent et al., 2009; Urquiza-Haas et al., 2011), but our results were inconsistent with these findings. Mammal occupancy did not vary with forest cover within buffers of 1 km radius. The most plausible explanation may be the spatial scale of our buffer zones, which may be very limited in the case of mammals because most species have a movement area considerably larger than 1 km (e.g., Gosselink et al., 2003). Indeed, earlier studies have found negative responses to the amount of deciduous forest for Red Fox and positive effects of the amount of forest land to Black Bears at buffer scales of 10 or 5 km, rather than smaller scales of 500 m or 3 km (Erb et al., 2012; Long et al., 2011). However, the relationship between the amount of habitat available and species occurrence is rarely linear (Gompper et al. 2016; St-Laurent et al., 2009). Occupancy patterns of large predators are also affected by prey availability and intraguild interference competition (Donadio and Buskirk, 2006; Fuller et al., 2001; Linnell et Strand, 2000). For instance, carnivores that occur sympatrically have a high degree of spatial partitioning as they share the same habitats and food resources (Mukherjee et al. 2009; Thompson and Gese, 2007; Palomares and Caro, 1999). Therefore, assessing the role of interspecific

interactions with the relative importance of landscape factors should be considered to elucidate how these species co-occur in space (Lesmeister et al., 2015; Mazerolle and Villard, 1999; Wisz et al., 2013).

In the case of birds, we expected contrasting landscape effects between early and late successional forest species in response to the amount of forest cover (Drolet et al., 1999; St-Laurent et al., 2009; Trzcinski et al., 1999). Yet, no bird species varied with the amount of forest cover. A similar pattern was observed for marsh birds in buffers within 500 m from the wetland edge (Smith and Chow-Fraser, 2010). Nonetheless, the lack of effects of forest cover found here was surprising because it disagrees with patterns identified for 10 of 35 species using acoustic recorders (Feldman et al., 2023). These discrepancies could be due to differences in sampling methods: camera traps detect individuals within a smaller area than acoustic recorders (Darras et al., 2018; Shonfield and Bayne, 2017). Previous efforts combining both technologies highlighted the complementarity of both methods, rather than using them independently, to expand the diversity of species monitored and to improve detectability (Buxton et al., 2018; Cruncheon et al., 2020; Rich et al., 2019).

*Detection variables*— Factors affecting the sampling design included a quantitative factor, such as the number of cameras used per site, and a temporal variable of timing of sampling during the season. Increasing the number of camera traps (sampling effort) deployed at a study site had a positive effect on the probability of detection of two species of mammals (Beaver and Red Fox) and four bird species (Bonaparte's Gull, Common Raven, Gray Jay, and Greater Yellowlegs). This is in line with previous research (Dennis et al., 2010; Evans et al., 2019; Tyre et al., 2003). This suggests that it may be preferable to increase the intensity of sampling by adding more cameras in a site unit, which would increase the chances of detection (Shannon et al., 2014). On the other hand, beaver and 21 bird species were negatively affected by the number of days

since snowmelt, meaning that detectability is higher at the beginning of the season rather than later in the season. The same pattern was detected in our acoustic approach (Feldman et al., 2023), where 18 out of 35 bird species showed the same response, mainly aquatic species. Species detection was not affected by precipitation. The lack of effect of cumulative precipitation contrasts with previous studies that found precipitation reduced movement of carnivores and birds (Avrin et al., 2021; Nagy-Reis et al., 2017; Robbins, 1981). Our results suggest that rainy days over short periods may not reduce movement and activity levels, possibly because movement in response to precipitation is subject to individual variation (Madsen et al., 2020).

The sampling design used in our study may have impacted species detectability, and it is important to consider potential sources of bias. By placing cameras near signs of animal activity and using olfactory lures, we may have inadvertently favored certain species over others. This approach can result in an underestimation of species present in the area, particularly those that are less active or use different routes. Additionally, using scent lures can attract some species at the expense of others, potentially resulting in an overestimation of the attracted species. The placement of the unbaited camera on the beaver dam may have introduced bias towards certain species that are known to frequent these structures. To mitigate these biases, we recommend employing a randomized sampling design that covers a broad range of areas and using a variety of lures that can attract a diverse range of species or even no lures. This information is essential for future studies utilizing camera traps to monitor mammal species.

*Conclusion*— This study holds significant implications for wetland conservation as it sheds light on the intricate relationships between species and their preferred habitats in wetlands. We provide an overview of how two distinct boreal wetlands, as well as natural and anthropogenic features, influence the occurrence of birds and mammals in relatively little impacted boreal landscapes. Our findings demonstrate that certain

wetland characteristics and anthropogenic factors influence the patterns of species association and their habitat preferences. Specifically, the study highlights that peatland ponds were the preferred habitat for certain mammals, including the Red Fox and River Otters, as well as various bird species such as the American Pipit, Common Raven, Hooded Merganser, and Greater Yellowlegs. Conversely, the Common Grackle was observed to have a positive association with beaver ponds, suggesting a positive correlation between the species and this type of wetland environment. These findings provide valuable insight for wetland conservation efforts, enabling conservationists to make informed decisions about the management of wetland habitats and the protection of their associated species. The new information gained from this study should encourage future efforts to better understand the response of mammals and birds to various disturbance factors in boreal regions. Time of sampling and the number of cameras emphasize the importance of including detectability and suggest that multiple cameras and early sampling in the season would increase detectability. In addition to being widely used for mammals, we also recommend camera traps for monitoring wetland birds, especially waterfowl.

#### Acknowledgment

Special thanks to R. Chevallier and J. Arsenault for their assistance with fieldwork and M. Desrochers for providing valuable assistance to extract spatial data in a georeferenced information system. P. Fournier provided help with identification for mammal species. We thank Hydro-Quebec and FaunENord for providing weather data throughout James Bay region. We also thank Hecla mining (Casa Berardi mine), Nemaska Lithium (Whabouchi mine) and Stornoway Diamonds (Renard mine) for

project support and access to study sites. Funding was provided by the Natural Sciences and Engineering Research Council (NSERC) of Canada—Université du Québec en Abitibi-Témiscamingue (UQAT) industrial research chair on northern biodiversity in a mining context. Analyses were run on the Narval high performance computing cluster of Calcul Québec and Calcul Canada.

## **CHAPITRE V**

### **CONCLUSION GÉNÉRALE**

#### 5.1. Sommaire

L'objectif général de cette thèse était de comprendre l'utilisation de l'habitat de trois groupes de vertébrés et de relier les modèles d'occupation à des caractéristiques du site de l'étang et aux interactions biotiques dans une zone boréale relativement peu étudiée du nord du Canada. Nous avons recueilli des données à 50 étangs et collecté des données pour 120 espèces dans la région d'Eeyou Istchee Baie James sur une superficie équivalente à près de 400 km<sup>2</sup> pendant 2 ans (2018 – 2019). Nos résultats sont articulés en trois chapitres qui portent sur trois groupes de vertébrés : les amphibiens (chapitre II), les oiseaux (chapitres III et IV) et les mammifères (chapitre IV). Cette thèse représente des contributions scientifiques au domaine de l'écologie et de la biologie de ces groupes en abordant des questions écologiques sur les préférences et les exigences en matière d'habitat, et les interactions biotiques entre différents taxons à différentes échelles. Ce chapitre présente une synthèse des contributions scientifiques et perspective des recherches.

Pour les amphibiens (chapitre II), les patrons d'occupation des sites ont démontré que les étangs de tourbières sont autant utilisés que les étangs à castors par les individus après métamorphose (juvéniles et adultes, et mâles chanteurs), pour lesquels nous avons mesuré l'abondance chez deux espèces (grenouille du Nord et grenouille des bois). Cependant, nous avons constaté que les grenouilles des bois avaient des masses d'œufs plus abondantes dans les étangs de castors, ce qui est aussi soutenu par des travaux indiquant les effets positifs des castors sur les anoues dans les étangs en



Amérique du Nord. Il semble que certaines conditions dans les étangs de castors, comme la profondeur, la température de l'eau, la végétation aquatique et l'absence de poissons prédateurs, pourraient correspondre aux conditions favorables à la grenouille des bois pendant la ponte (Naiman et Melillo, 1984; Rosell et al., 2005; Smith et al., 1991). Il n'y avait pas d'effets des caractéristiques de l'étang et du paysage sur l'occupation et l'abondance de ces deux espèces aux stades juvéniles et adultes. Cela suggère que les anoues dans ces latitudes sont des espèces généralistes, non restreintes à des conditions d'habitat spécifiques. Pour la grenouille du Nord, nous avons observé des effets au niveau de l'étang sur l'abondance des juvéniles et adultes, ce qui suggère que les petits étangs moins acides représentent un habitat plus approprié pour les individus métamorphosés.

En combinant les chapitres III et IV, nous avons estimé l'occupation pour 61 espèces des oiseaux détectées acoustiquement, 10 espèces détectées visuellement et 35 espèces détectées par les deux méthodes (Fig. 5.1). Les étangs de castors abritaient une plus grande richesse en espèces d'oiseaux que celle des étangs de tourbières. Ce résultat est principalement dû aux espèces de débuts de succession (chapitre III). En présence d'un important prédateur des nids d'oiseaux, l'écureuil roux, l'occupation de 25 % des espèces était plus faible et cet effet était également évident au niveau de la richesse en espèces (chapitre III). Nos résultats soulignent donc l'importance des ingénieurs écologiques et l'influence des prédateurs sur les assemblages d'oiseaux.

L'importance de l'habitat (couverture forestière) sur l'occupation des espèces était variable selon les deux méthodes d'échantillonnage et devrait être clarifiée par des études supplémentaires pour chaque espèce. Cependant, il convient de noter que la méthode de suivi acoustique présente certaines limites. Par conséquent, afin de tirer des conclusions solides sur les réponses des espèces aux caractéristiques du paysage en utilisant ces techniques, il est essentiel de prendre en compte d'autres facteurs

spécifiques à chaque espèce. Par exemple, tenant en compte de la distance de chant, le couvert latéral, la densité d'arbres et les environnements contenus dans cette distance (Darras et al., 2018). Le couvert forestier mesuré dans cette étude ne peut être considéré comme le seul déterminant de la présence ou de l'absence de certaines espèces dans un habitat donné. D'autres facteurs peuvent également jouer un rôle important dans la détection des oiseaux chanteurs. Par conséquent, une évaluation plus approfondie des habitats des espèces devrait être menée en utilisant des méthodes complémentaires, comme les pièges photographiques, pour obtenir une compréhension plus complète de leur réponse aux caractéristiques du paysage.

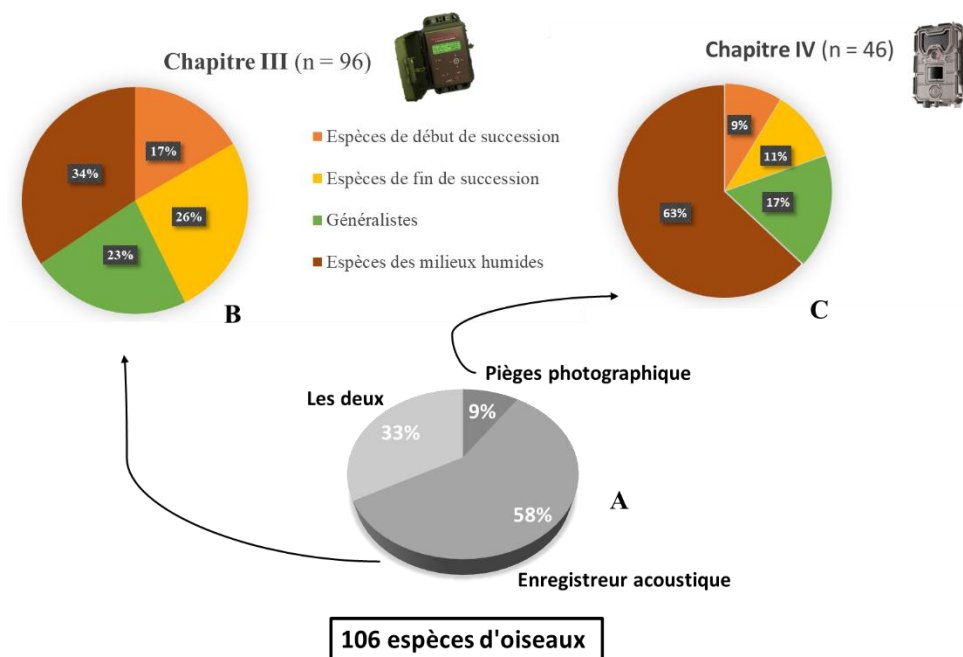


Figure 5.1. A- Proportion d'espèces d'oiseaux détectées par des méthodes acoustiques et visuelles combinées (A). Proportion par guildes en fonction de la succession forestière pour la détection par enregistreur acoustique (B) et par les pièges photographiques (C).

En tant que contributions méthodologiques, le chapitre IV en utilisant de pièges photographiques a démontré que cette méthode est efficace pour étudier les oiseaux qui se trouvent dans les milieux humides (Fig. 5.1), en particulier la sauvagine, un groupe discret d'oiseaux important pour les habitats des milieux humides qui n'est généralement pas ciblé par une approche acoustique. Les mammifères de taille moyenne et grande étaient également susceptibles d'être présents dans les deux habitats, avec une préférence inattendue du renard roux et de la loutre de rivière pour les étangs de tourbières (chapitre IV). Nous avons constaté une absence générale d'effets du paysage (couverture forestière et distance à la route).

Les variables associées aux conditions d'échantillonnage ont eu peu d'effets significatifs sur les anoues (chapitre II), avec seulement un effet positif de la température de l'air sur l'activité des chorales de rainette crucifère. Les variables de l'échantillonnage ont eu des effets significatifs sur la détection des oiseaux vocalisant, avec 30% des espèces affectées par le moment de la session d'échantillonnage (chapitres III et IV) et l'ensemble des espèces affectées par la qualité de l'enregistrement (chapitre III). Cela suggère que la qualité des enregistrements est cruciale pour la détection des oiseaux et que les oiseaux des milieux humides sont plus sensibles aux variations des conditions de la période d'échantillonnage que les autres groupes de cette étude. L'effort d'échantillonnage favorise certaines espèces (2 mammifères et 4 oiseaux), ce qui signifie qu'il serait nécessaire d'utiliser plus d'une caméra par site, et que l'utilisation de leurres pourrait améliorer l'échantillonnage (chapitre IV).

## 5.2. La richesse des étangs de tourbières et des étangs de castors

La persistance à long terme d'une population dépend de l'intégrité des habitats utilisés tout au long de son cycle de vie. Les castors sont des créateurs de milieux humides et ont une influence directe sur le maintien des écosystèmes de ces milieux. En tant qu'ingénieurs écologiques, les castors modifient les propriétés physico-chimiques des milieux humides en construisant des barrages et peuvent donc influencer un large spectre d'espèces grâce à ces modifications. Au chapitre II, les résultats de l'échantillonnage acoustique suggèrent que les étangs à castor peuvent augmenter les populations de grenouilles des bois en créant un habitat de reproduction. Dans le chapitre III, les résultats de l'échantillonnage acoustique ont montré que les oiseaux avaient une plus grande richesse dans les étangs à castors. Ces sites semblent offrir de meilleures conditions pour l'élevage des couvées, la recherche de nourriture et la prévention des prédateurs (Alza, 2014; Askins et al., 2007; Chandler et al., 2009; Grover et Baldassarre, 1995; Nummi et Holopainen, 2014). Les castors sont susceptibles d'étendre leur aire de répartition nordique et de coloniser les écosystèmes de la toundra en raison de changement climatique et de la croissance accrue des arbustes (Jarema et al., 2009; Jones et al., 2020; Tape et al., 2018). Par conséquent, le fait que les castors constituent un habitat de reproduction important pour les amphibiens et qu'ils favorisent les espèces en début de succession suggère que certains étangs de castors peuvent être des sources de population dans la région (Gill, 1978). Cette hypothèse devrait être étudiée plus en profondeur, par exemple en faisant des inventaires des masses d'œufs, des larves et des têtards sur le long terme et à différents stades de la succession des étangs à castor.

Par rapport aux environnements modifiés par les castors, nous avons montré que les étangs de tourbières sont des environnements moins propices à la ponte des anoues,

bien qu'une seule espèce n'ait été mesurée dans cette étude, et contiennent une plus faible richesse en oiseaux. Néanmoins, les anoues juvéniles et adultes n'évitent pas les substrats des tourbières et utilisent les étangs de tourbières dans la même mesure que les étangs de castors. Quant aux exigences spécifiques aux espèces, certaines espèces semblent même préférer ces environnements pour des raisons inconnues. Cette préférence pour les étangs de tourbières se retrouve également pour deux espèces de mammifères, contrairement à ce que nous attendions (loutre de rivière et renard roux). Par conséquent, les tourbières ne semblent pas être des habitats aussi pauvres en vertébrés comme décrit précédemment (Desrochers et Duinen, 2006; Junk et al., 2006; Warner et Asada, 2006). Cette thèse tend à soutenir que la méconnaissance de la présence des vertébrés est peut-être ce qui a conduit à cette affirmation. En effet, les étangs de tourbières sont des milieux acides qui sont censés être exempts de poissons, connus pour être des prédateurs d'amphibiens et des prédateurs d'insectes qui compétitionnent avec les oiseaux des milieux humides. Par conséquent, les tourbières sont peut-être des milieux moins productifs, mais elles sont utilisées comme endroits de refuge et comme source de nourriture, ce qui leur confère une pertinence similaire à celle des étangs de castors.

### 5.3. Limitations

L'une des forces de cette étude est la taille de notre échantillon de 50 étangs, qui, considérée indépendamment chaque année, permet d'obtenir un total de 100 sites. Nous avons choisi d'augmenter la taille de l'échantillon en échantillonnant les mêmes endroits deux années consécutives au lieu d'ajouter des étangs d'échantillonnage supplémentaires. Cela représente une grande taille d'échantillon pour des zones boréales relativement peu étudiées. Cependant, les comparaisons entre les types

d'étangs sont difficiles à interpréter étant donné que les étangs de tourbières échantillonnés étaient trois fois plus nombreux que les étangs de castors (38 contre 12). L'augmentation du nombre d'étangs a été un défi en raison de problèmes logistiques tels que la disponibilité de l'équipement, les endroits éloignés et les distances entre les trois secteurs de notre zone d'étude.

Une autre limite est que nous n'avons pas pu comparer différents types d'habitats au sein des deux principaux types d'habitats, c'est-à-dire différents types d'étangs de tourbières (minérotrophe et ombrotrophe) et d'étangs de castors (actifs et abandonnés). Bien que nous ayons fait une première tentative, celle-ci n'a pas pu être réalisée. Nous pouvons l'expliquer pour deux raisons. La première était que, dans certains cas, il était difficile d'identifier s'il s'agissait d'une tourbière minérotrophe ou d'une tourbière ombrotrophe, car malgré leurs caractéristiques différentes (par exemple, le pH, la source d'eau), la plupart des tourbières ne sont pas exclusivement ombrotrophe ou minérotrophe. Il existe un long gradient de tourbières entre ces deux principaux types (par exemple, les tourbières minérotrophes pauvres) d'où la difficulté de faire cette distinction sur le terrain (Bourgeau-Chavez et al., 2017). Deuxièmement, en se déplaçant vers le nord, les tourbières sont beaucoup plus abondantes que les étangs de castors, qui sont rarement détectés et sont éloignés des routes, de sorte que malgré les efforts, nous avons obtenu un faible nombre d'étangs de castors actifs et abandonnés pour la comparaison. En fait, il est possible que nous n'ayons pas été en mesure de détecter un effet important des étangs de castors abandonnés sur les habitats de reproduction des anoues, comme cela a été suggéré précédemment (Cunningham et al., 2007; Stevens et al., 2006). Un nombre plus important d'étangs de tourbières et d'étangs à castor aurait pu permettre de faire des comparaisons entre différents types d'étangs, notamment dans les chapitres III et IV.

Nous avons analysé les données de 120 espèces de trois groupes de vertébrés (en outre, 4 amphibiens et 6 poissons ont été détectés, mais non analysés dans le chapitre II, Appendice A). Cependant, nous avons eu quelques limites dans la détection d'un assemblage plus complet, car certaines espèces n'étaient pas documentées. Nous avons omis les amphibiens non-chanteurs (par exemple, les urodèles) et quelques anoues en raison du faible taux de détection (chapitre II, Appendice A), les oiseaux nocturnes (par exemple, les hiboux, les engoulevents) et surtout, certaines espèces de mammifères non détectées dans nos pièges photographiques en raison du faible effort d'échantillonnage dans une vaste zone d'étude. Les milieux humides ne constituent pas un habitat exclusif pour des mammifères qui ne sont pas contraints de résider dans les milieux humides (c'est-à-dire le castor, la loutre de rivière, le rat musqué). La plupart des espèces se déplacent sur de longues distances et utilisent ces habitats de manière opportuniste. Des efforts supplémentaires sont donc nécessaires pour décrire de manière plus adéquate les assemblages de mammifères et mieux saisir les modèles d'occurrence d'habitat en utilisant plus de caméras sur une plus longue période, pendant toute la période de fin de printemps et d'été si possible. Une période d'échantillonnage d'un mois minimum et 3 500 jours de piégeage sont normalement utilisés pour obtenir de meilleures estimations des espèces rares ou insaisissables pour les études d'occupation multi-espèces (Burton et al., 2015; Chatterjee et al., 2021). Malgré ces limitations, nous pensons que nos résultats fournissent des informations de base précieuses dans cette région boréale.

### 5.3. Perspectives de recherche

Nos résultats sont limités aux effets à court terme des petits étangs. D'autres études sont nécessaires pour évaluer l'utilisation des tourbières et des étangs de castors sur des

échelles de temps plus longues afin de comprendre les effets de l'hétérogénéité naturelle et anthropique de l'habitat. Par exemple, les résultats du chapitre II pourraient être complétés par plusieurs années d'analyse des patrons d'abondance des masses d'œufs, des juvéniles et des adultes afin de mieux définir la distribution démographique sur une plus longue échelle de temps. La surveillance à long terme est importante pour s'assurer que les petits étangs sont résilients aux perturbations et continuent de fournir un habitat d'importance pour les vertébrés. Le suivi des petits étangs sur plusieurs années est idéal pour examiner l'impact des changements d'utilisation des terres sur des habitats encore peu affectés dans les systèmes boréaux. Une documentation à long terme des modèles de colonisation et d'extinction sur les mêmes habitats permettrait de tirer des conclusions plus claires sur les organismes qui fréquentent ces sites.

Nous nous sommes limités à l'étude des vertébrés dans deux types d'étangs principaux du paysage, mais notre zone d'étude est parsemée d'autres types d'habitats qui contribuent à l'hétérogénéité du paysage. Il serait intéressant d'étudier davantage la contribution de ces habitats à la diversité des vertébrés et leur utilisation tout au long du cycle de vie des espèces. Par exemple, l'utilisation d'autres habitats et les mouvements après la reproduction des amphibiens dans la région, notamment les étangs vernaux, rivages de cours d'eau, ruisseaux, rivières, marais, marécages, les grands étangs, les lacs, et les cours d'eau bordés de rochers (Fortin et al., 2012; Karraker et Gibbs, 2009). Les habitats d'hibernation aquatiques ou terrestres restent largement sous-étudiés, et il serait intéressant d'étudier l'utilisation des environnements naturels par rapport aux environnements perturbés (par exemple, les parcs à résidus miniers, les étangs artificiels) afin de guider la planification durable future et de soutenir la priorisation des amphibiens qui sont les taxons de vertébrés les plus menacés. Des questions concernant les habitats utilisés par les oiseaux migrateurs des milieux humides et les routes de migration au-dessus de ces habitats sont



nécessaires pour compléter la compréhension des impacts du changement climatique dans ces latitudes.

Dans le cadre des travaux des chapitres III et IV, nous avons obtenu une réponse différente à une variable du paysage en utilisant différentes méthodes passives pour les oiseaux (Fig. 1). Une démarche possible est d'approfondir les raisons de ces résultats afin de mieux interpréter les facteurs du paysage sur l'occupation des espèces. Avec l'augmentation de la popularité de la surveillance acoustique, les progrès technologiques ont mené vers des équipements moins encombrants, très efficaces et durables (Toenies et Rich, 2021), et plus récemment, des reconnaisseurs automatiques qui diminuent drastiquement le temps d'écoute (Marchal et al., 2022; Priyadarshani et al., 2018; Stowell et al., 2019; Venier et al., 2017). Cependant, une grande masse de données générées reste difficile à traiter pour l'analyse, et de nouveaux développements devraient aller dans ce sens pour débloquer ce goulot d'étranglement.

Nous n'avons pas abordé la succession des étangs de castors, ni comparé les étangs actifs et les étangs abandonnés. Toutefois, il faudrait approfondir cette question concernant l'influence de l'activité des castors sur les vertébrés. La valeur relative des milieux humides influencés par le castor devrait être étudiée, par exemple, pour déterminer si le succès de la reproduction des amphibiens ou un habitat de reproduction plus approprié diffère entre différents étangs de castors ayant des caractéristiques différentes qui fluctuent dans le temps et qui dépendent de l'activité des castors (absence de poissons, niveau d'eau, température de l'eau, hydropériode, couverture végétale).

Dans le chapitre III, nous avons utilisé la présence de l'écureuil roux comme prédicteur de l'occupation des oiseaux. Les résultats montrent que ce rongeur influence les assemblages d'oiseaux et peut même jouer un rôle important dans la dynamique des

populations. Cependant, nous encourageons une exploration plus approfondie de la manière dont la présence ou l'absence de l'écureuil, ainsi que différents niveaux de densité de population d'écureuils, peuvent affecter la détection des espèces. Pour ce faire, l'utilisation d'un modèle de cooccurrence plus complexe, prenant en compte les espèces concernées et les écureuils, en combinaison avec l'inclusion d'autres facteurs tels que le type et la densité de la forêt environnante, sera utile pour mieux comprendre cette association. En outre, le rôle des interactions interspécifiques entre les mammifères (par exemple, la prédation, la compétition, l'association spatiale positive) devrait être pris en compte pour élucider si les espèces sympatriques (par exemple, le coyote, le lynx, le renard roux, le loup gris) sont influencées dans l'utilisation de l'habitat lorsqu'il y a des compétiteurs potentiels ou des prédateurs dominants (Gese et al., 1996; Henke et Bryant, 1999; Lesmeister et al., 2015).

La perturbation des habitats qui sont importants pour la persistance des populations se produit en partie parce que les connaissances sur les besoins en habitat des espèces des régions boréales sont insuffisantes. Le Nord-du-Québec comprend un grand nombre de milieux humides qui seront potentiellement affectés par les activités naturelles et anthropiques dans un avenir proche. Les espèces moins sensibles aux perturbations, en tant que généralistes de l'habitat, peuvent être plus résistantes à ces changements, tandis que les espèces ayant des exigences spécifiques en matière d'habitat peuvent avoir des difficultés en raison des pressions exercées par des caractéristiques d'habitat inadaptées. Les recherches futures devraient élargir les connaissances en vue de déterminer la relation entre les espèces des milieux humides et les pressions croissantes, en mettant l'accent sur les perturbations humaines. Le suivi des petits étangs avant et après les projets de développement peut être intégré aux évaluations afin d'estimer les impacts que les projets d'exploitation minière, et de développement ont sur eux. En outre, l'étude d'autres assemblages biologiques que les vertébrés (par exemple, les invertébrés, les plantes) dans les étangs naturels par rapport aux étangs

touchés pourrait aider à mieux orienter l'atténuation des impacts de la perte des milieux humides.

Le projet réalisé dans le cadre de cette thèse pourrait être complété en améliorant l'identification des différents types de petits milieux humides par des études de télédétection. Par exemple, les informations de télédétection peuvent aider à détecter rapidement les étangs à castors, qui sont des habitats de reproduction privilégiés pour les amphibiens. De même, de meilleures informations sur les étangs de tourbières devraient être disponibles, puisque, selon cette étude, ils sont également pertinents pour une grande variété d'organismes. Par conséquent, nous recommandons de mieux intégrer les étangs de castors et les étangs de tourbières dans les systèmes de cartographie et de classification écologiques des milieux humides afin de fournir ces informations aux gestionnaires. Cela aidera à identifier les sites existants et potentiels pour la modélisation spatiale prédictive dans un contexte de perte croissante de milieux humides.

L'absence de données sur l'occupation des espèces limite notre capacité à faire des inférences sur des populations relativement peu étudiées. Dans le nord du Québec, les données de recherche sont rares et, à certains égards, constituent des trous noirs de données fauniques. Bien que ce ne soit pas le sujet principal de cette thèse, nous avons souligné la pertinence et la nécessité d'utiliser et de promouvoir la science citoyenne (Annexe I). Ce type d'information, ainsi que la combinaison de données provenant de différentes sources, sont particulièrement importantes dans les régions peu étudiées (Fletcher et al., 2019; Isaac et al., 2020; Miller et al., 2019), comme celle de la baie James de l'Eeyou Istchee dans le nord du Québec. Par conséquent, nous recommandons que les recherches futures dans la région puissent utiliser, promouvoir et mettre en œuvre l'utilisation de ces données dans les communautés locales, telles que les Premières Nations Crie et Abitibiwinni.

Puisque les milieux humides boréaux s'étendent sur une grande partie du nord du Canada, les résultats et les recommandations de notre étude peuvent logiquement être appliqués à d'autres régions du Québec et du Canada où l'on trouve des assemblages d'espèces similaires et des petits étangs semblables. D'autres études sont nécessaires pour établir pleinement toutes les fonctions d'habitat de ces petits étangs pour les vertébrés locaux et d'autres espèces animales. Leur réponse aux activités anthropiques multiples et complexes qui sont susceptibles de se produire, ainsi qu'aux perturbations naturelles et aux impacts des changements climatiques dans différentes parties de la forêt boréale, permettra de générer des connaissances plus efficaces en matière de conservation et de gestion afin de mieux protéger les petits milieux humides et les populations fauniques.

### 5.3. Conclusion

Cette thèse a produit de nouvelles informations sur les relations habitat-espèces des amphibiens, oiseaux et mammifères dans l'est du Canada boréal. Le Nord-du-Québec est susceptible d'être perturbé par des activités anthropiques futures qui pourraient avoir des impacts à la fois locaux et à plus grande échelle, avec le développement d'infrastructures qui pourraient éliminer ou affecter les milieux humides de faible surface. Notre travail aura permis de mieux comprendre comment l'hétérogénéité de l'habitat, les interactions biotiques et les caractéristiques des milieux humides influencent l'occupation des espèces dans le Nord-du-Québec, en fournissant une base de connaissance pour des études à plus large échelle dans le Canada boréal. Les nouvelles questions soulevées par notre recherche devraient nous rapprocher de la compréhension des mécanismes qui régissent les préférences et les exigences des vertébrés boréaux en matière d'habitat des vertébrés boréaux. Ce travail de recherche

pourrait aussi servir de point de départ à l'élaboration de stratégies de conservation et de gestion durable visant à éviter les impacts potentiels sur les milieux humides naturels du Canada au bénéfice de la faune qui dépend de ces environnements.

Plus précisément, les gestionnaires des milieux humides devraient tenir compte des préférences des espèces en matière d'habitat lorsqu'ils planifient des stratégies de gestion des milieux humides. Les milieux humides de faible superficie tels que les étangs de tourbières et les étangs de castors devraient être conservés en tant qu'habitats essentiels pour les amphibiens, les oiseaux et les mammifères. Les résultats de la thèse pourraient être intégrés dans les projets de développement des ressources naturelles pour minimiser les impacts sur les milieux humides et les espèces associées. En prenant en compte les préférences des espèces en matière d'habitat et en travaillant en étroite collaboration avec les communautés locales et autochtones, il est possible de planifier des stratégies de gestion des milieux humides qui minimisent les impacts négatifs des activités anthropiques futures tout en préservant les habitats vitaux pour la faune dépendante.

La contribution théorique de cette thèse se situe dans l'approfondissement de notre compréhension de l'écologie des milieux humides boréaux et de l'influence des facteurs biotiques et abiotiques sur les espèces vertébrées qui y habitent. En particulier, cette thèse contribue à notre connaissance de la manière dont les amphibiens, les oiseaux et les mammifères utilisent les étangs de tourbières et les étangs de castors, ainsi que des facteurs qui caractérisent ces habitats et les interactions biotiques qui les affectent. Les résultats de cette recherche ont des implications importantes pour la gestion des milieux humides nordiques, notamment en ce qui concerne la préservation de l'habitat pour les espèces qui dépendent de ces écosystèmes. En définitive, cette thèse contribue à notre compréhension globale de la manière dont les écosystèmes fonctionnent et des interactions complexes entre les espèces et leur environnement.

## APPENDICE A

### SUPPLEMENTARY INFORMATION CHAPTER II

Table A.1. Candidate set of models and associated ecological hypotheses to explain pond habitat use and abundance by anuran species. We considered the effect of 11 different candidate models on single-season occupancy and abundance for each anuran species sampled in 2018 and 2019 in 50 small ponds in Northern Quebec, Canada. To explain detection probability, occupancy models considered three variables (quality, weather and, days elapsed since snowmelt), and N-mixture models considered four detection variables for wood frog and mink frog adults (observer, weather, and days elapsed since snowmelt) and include three variables for wood frog egg masses (observer, days elapsed since snowmelt and the combinations of these two).

Variables on each parameter	Model category	Ecological hypotheses
<i>Occupancy probability or abundance</i>		
Year	Null model	Occupancy and abundance vary with the years (Berven, 1990)
Habitat type + Year	Type	Beaver ponds favor occupancy and abundance as they are most used by pond-breeding amphibians (Cunningham et al., 2007; Karraker and Gibbs, 2009; Stevens et al., 2007)
% Deciduous and mixed forest + coniferous forest + Year *	Habitat heterogeneity	Vegetation cover creates complex microhabitats that provide sites for oviposition and refuges for developing larvae, provide shade, moderate temperature, and retain moisture (Guerry and Hunter, 2002; Herrmann et al., 2005; Seale, 1982). Positive correlation of anuran abundance and deciduous and mixed vegetation (Browne et al., 2009; Eigenbrod et al., 2008;).
Table A.1. Suite		
% Open wetlands	Wetland*	Occupancy and abundance increase with surrounding wetlands (Mazerolle et al., 2005; Scherer et al., 2012).
% Deciduous and mixed forest + coniferous forest + % open wetlands + Year	Landscape *	Occupancy and abundance vary with surrounding forests (Mazerolle et al., 2005; Scherer et al., 2012).

Table A.1. Continued

Fish presence + Year	Predator	Predatory fish affect amphibian survival and reduce anuran abundance (Hecnar and M'Closkey, 1997; Hopey and Petranka, 1994).
pH + water depth + pond area + Year	Water and pond characteristics	Acidic ponds reduce survival of juveniles and adults (Cummins, 1986; Freda and Dunson, 1984; Vatnick et al., 1999). Occupancy increases with pond size (Hecnar, 2004). Frog occurrence and egg mass abundance increase with pond depth (Laan and Verboom, 1990; Skidde et al., 2007).
Fish presence + pH + water depth + pond area + Year	Predator + Water conditions	Occupancy decreases with predator occurrence and varies with water conditions (Babbitt and Tanner, 2000; Babbitt, 2005).
<i>Detection probability (p)</i>		
Sound Quality (good, not good)	Quality	Sound quality due to background noise from wind, rain, or traffic and calling distance influence detection probability (Koehler et al., 2017).
Air temperature (°C) + humidity (HR)	Weather	Detection increases with air temperature (Heyer et al., 2014; Oseen and Wassersug, 2002). Calling activity and local movements are positively affected by relative humidity (Bellis, 1962; Green, 1997).
Snowmelt (number of days)	Snowmelt	Detection decreases for explosive breeders with increasing days since thaw and increases with prolonged breeders thaw (Schmidt, 2005).
Observer	Observer	Detection probabilities vary with observer (Alldredge et al., 2006).
Snowmelt + Observer	Snowmelt + Observer	See above.

\* These models were fitted for buffer areas of 300 m and 1000 m.

Table A.2. Number of ponds with detections of fish species using three Silver Creek galvanized minnow traps (6.25 mm mesh size with openings of 2 cm) randomly positioned and equally spaced from one another in each pond at 1 - 2 m from the shore in northern Quebec in 2018-2019.

Fish species	Peatland pond (n = 38)	Beaver pond (n = 12)
Brook Stickleback ( <i>Culaea inconstans</i> )	6	7
White Sucker ( <i>Catostomus commersoni</i> )	1	1
Yellow Perch ( <i>Perca flavescens</i> )	1	0
Fatty Minnow ( <i>Pimephales promelas</i> )	0	2
Pearl Dace ( <i>Margariscus margarita</i> )	3	1
Daces ( <i>Chrosomus</i> sp)	2	6



Table A.3. Number of ponds where a species was present is followed in parentheses by the maximum calling index (CI) in acoustic surveys (at 21h00), and range of individuals observed in visual surveys by walking along the shore of the ponds in Northern Quebec in 2018-2019.

	Peatland ponds (n = 38)	Beaver ponds (n = 12)
<b>Acoustic surveys</b>		
American toad ( <i>Anaxyrus americanus</i> )	1 (CI 1)	1 (CI 1)
Mink frog ( <i>Lithobates septentrionalis</i> )	25 (CI 2)	9 (CI 1- 2)
Green frog ( <i>Lithobates clamitans</i> )	1 (CI 1)	0
Northern leopard frog ( <i>Lithobates pipiens</i> )	0	1 (CI 1)
Spring peeper ( <i>Pseudacris crucifer</i> )	36 (CI 3)	11 (CI 3)
Wood frog ( <i>Lithobates sylvaticus</i> )	22 (CI 3)	9 (CI 3)
<b>Visual surveys</b>		
American toad metamorphosed individuals	5 (0-6)	6 (0-6)
American toad egg masses	0	1 (0-1)
Mink frog metamorphosed individuals	19 (0-97)	11 (0-34)
Wood frog metamorphosed individuals	27 (0-37)	8 (0-7)
Wood frog egg masses	13 (0-84)	8 (0-275)
Salamander egg masses ( <i>Ambystoma sp.</i> )	4 (0-12)	0

Table A.4. Parameter estimates ( $\beta$ ) and 95% confidence intervals for covariates considered to explain the probability of occupancy of three anuran species in beaver and peatland ponds in Northern Quebec (Canada) in 2018 and 2019. Estimates and confidence intervals were obtained from multimodel inference with correction for overdispersion ( $\hat{c}$ ). The  $\hat{c}$  of each species was estimated from the most parsimonious model. See Table 2.2 for a complete description of the covariates.

Species	Covariates	$\beta \pm (SE)$	95% confidence	
			lower	upper
Wood frog ( $\hat{c} = 1.39$ )	Year	$-1.59 \pm 0.88$	-3.31	0.13
	Habitat type	$-0.1 \pm 0.44$	-0.97	0.76
	DECMIX300	$0.27 \pm 2.98$	-5.58	6.12
	DECMIX1000	$0.15 \pm 0.34$	-0.51	0.81
	CONIF300	$-0.13 \pm 0.29$	-0.69	0.44
	CONIF1000	$-0.15 \pm 0.31$	-0.75	0.45
	WET300	$0.01 \pm 0.12$	-0.22	0.25
	WET1000	$-0.002 \pm 0.11$	-0.22	0.22
	Fish	$0.09 \pm 0.37$	-0.63	0.81
	pH	$0.06 \pm 0.21$	-0.36	0.47
	Pond area	$-0.03 \pm 0.15$	-0.32	0.26
	Water depth	$0.0006 \pm 0.1$	-0.2	0.2
Spring Peeper chorus ( $\hat{c} = 1.52$ )	Year	$-2.6 \pm 1$	-4.56	-0.65
	Habitat type	$-0.3 \pm 0.75$	-1.78	1.18
	DECMIX300	$0.02 \pm 0.05$	-0.1	0.11
	DECMIX1000	$0.01 \pm 0.08$	-0.15	0.17
	CONIF300	$-0.001 \pm 0.05$	-0.1	0.1
	CONIF1000	$0.01 \pm 0.07$	-0.14	0.15
	WET300	$-0.001 \pm 0.08$	-0.16	0.16
	WET1000	$-0.06 \pm 0.2$	-0.44	0.33
	Fish	$0.67 \pm 0.98$	-1.26	2.6
	pH	$-0.005 \pm 0.1$	-0.2	0.2
	Pond area	$-0.01 \pm 0.11$	-0.23	0.21
	Water depth	$-0.04 \pm 0.19$	-0.42	0.33
Mink frog ( $\hat{c} = 1.77$ )	Year	$0.06 \pm 0.84$	-1.59	1.71
	Habitat type	$-0.01 \pm 0.32$	-0.64	0.61
	DECMIX300	$0.03 \pm 0.18$	-0.33	0.39
	DECMIX1000	$0.06 \pm 0.7$	-1.32	1.44

Table A.4. Continued

CONIF300	-0.04 ± 0.18	-0.39	0.32
CONIF1000	-0.03 ± 0.16	-0.35	0.29
WET300	-0.05 ± 0.21	-0.46	0.36
WET1000	-0.01 ± 0.16	-0.33	0.31
Fish	0.02 ± 0.3	-0.57	0.6
pH	0.01 ± 0.07	-0.13	0.14
Pond area	-0.002 ± 0.06	-0.12	0.11
Water depth	0.003 ± 0.06	-0.12	0.13

DECMIX300: Deciduous and mixed forest (%) within 300 m; DECMIX1000: Deciduous and mixed forest (%) within 1000 m; CONIF300: Coniferous Forest (%) within 300 m; CONIF1000: Coniferous Forest (%) within 1000 m.

Table A.5. Parameter estimates ( $\beta$ ) and 95% confidence intervals for covariates considered to explain the probability of detection of three anuran species in beaver and peatland ponds in Northern Quebec (Canada) in 2018 and 2019. Estimates and confidence intervals were obtained from multimodel inference with correction for overdispersion ( $\hat{c}$ ). The  $\hat{c}$  of each species was estimated from the most parsimonious model. See Table 2.2 for a complete description of the covariates.

Species	Covariates	$\beta \pm (SE)$	95% lower	confidence upper
<i>Wood frog</i> ( $\hat{c} = 1.39$ )	Quality	-0.73 ± 0.49	-1.69	0.23
	Temp	0.02 ± 0.09	-0.16	0.2
	Hum	-0.01 ± 0.08	-0.16	0.13
	Snowmelt	0.003 ± 0.16	-0.31	0.31
<i>Spring Peeper chorus</i> ( $\hat{c} = 1.52$ )	Quality	-2.9e-06 ± 0.002	-0.003	0.003
	Temp	1.08 ± 0.22	0.66	1.51
	Hum	0.24 ± 0.15	-0.06	0.55
	Snowmelt	8.9e-08 ± 0.003	-0.0005	0.000
<i>Mink frog</i> ( $\hat{c} = 1.77$ )	Quality	-0.02 ± 0.21	-0.43	0.38
	Temp	0.02 ± 0.24	-0.45	0.5
	Hum	-0.41 ± 0.31	-1.01	0.19
	Snowmelt	-0.03 ± 0.23	-0.48	0.42

Quality: Sound quality; Temp: Temperature; Hum: Humidity; Snowmelt: Number of days after snowmelt.

Table A.6. Parameter estimates ( $\beta$ ) and 95% confidence intervals for covariates considered to explain the abundance of Wood Frog egg masses, Wood Frog and Mink Frog metamorphosed individuals in beaver and peatland ponds in Northern Quebec (Canada) in 2018 and 2019. Estimates and confidence intervals were obtained from multimodel inference with correction for over-dispersion ( $\hat{c}$ ). The  $\hat{c}$  of each species was estimated from the most parsimonious model. See Table 2.2 for a description of the covariates.

Species	Covariates	$\beta \pm (\text{SE})$	95% lower	confidence upper
Wood Frog egg masses ( $\hat{c} =$	Year	$0.1 \pm 0.13$	-0.15	0.36
	Habitat type	$-1.86 \pm 0.31$	-2.46	-1.27
	DECMIX300	$2.6\text{e-}08 \pm 0.0001$	-0.0002	0.0002
	DECMIX1000	$0.01 \pm 0.07$	-0.13	0.15
	CONIF300	$1.32\text{e-}08 \pm 6.3\text{e-}05$	-0.0001	0.0001
	CONIF1000	$-0.0007 \pm 0.01$	-0.03	0.03
	WET300	$-1.8\text{e-}08 \pm 0.0001$	-0.0002	0.0002
	WET1000	$-0.02 \pm 0.15$	-0.32	0.28
	Fish	$7.23\text{e-}08 \pm 0.0002$	-0.0004	0.0004
	pH	$5.89\text{e-}08 \pm 0.0001$	-0.0003	0.0003
	Pond area	$-6.71\text{e-}08 \pm 0.0002$	-0.0004	0.0003
	Water depth	$-7.4\text{e-}08 \pm 0.0002$	-0.0004	0.0004
Wood Frog metamorphosed individuals ( $\hat{c} = 2.27$ )	Year	$-0.07 \pm 0.31$	-0.68	0.53
	Habitat type	$0.05 \pm 0.21$	-0.37	0.47
	DECMIX300	$-0.02 \pm 0.09$	-0.21	0.16
	DECMIX1000	$-0.01 \pm 0.06$	-0.13	0.11
	CONIF300	$0.03 \pm 0.09$	-0.14	0.2
	CONIF1000	$0.01 \pm 0.04$	-0.08	0.09
	WET300	$-0.004 \pm 0.04$	-0.08	0.07
	WET1000	$-0.02 \pm 0.07$	-0.15	0.12
	Fish	$-0.26 \pm 0.44$	-1.12	0.6
	pH	$-0.05 \pm 0.13$	-0.31	0.21
	Pond area	$-0.03 \pm 0.09$	-0.2	0.14
	Water depth	$-0.03 \pm 0.1$	-0.23	0.17

Table A.6. Continued

Mink frog metamorphosed individuals ( $\hat{c} = 3.06$ )	Year	$-0.12 \pm 0.21$	-0.53	0.29
	Habitat type	$2.18\text{e-}10 \pm 1.9\text{e-}05$	$-3.7\text{e-}05$	$3.7\text{e-}05$
	DECMIX300	$-8.4\text{e-}05 \pm 0.005$	-0.009	0.009
	DECMIX1000	$0.0002 \pm 0.01$	-0.01	0.01
	CONIF300	$-0.0002 \pm 0.01$	-0.02	0.02
	CONIF1000	$-0.001 \pm 0.03$	-0.06	0.05
	WET300	$-0.0001 \pm 0.01$	-0.02	0.02
	WET1000	$-0.0008 \pm 0.02$	-0.04	0.04
	Fish	$-0.01 \pm 0.1$	-0.21	0.19
	pH	$0.54 \pm 0.12$	0.31	0.77
	Pond area	$-0.28 \pm 0.09$	-0.46	-0.11
	Water depth	$-0.02 \pm 0.11$	-0.25	0.2

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DECMIX300: Deciduous and mixed forest (%) within 300 m; DECMIX1000: Deciduous and mixed forest (%) within 1000 m; CONIF300: Coniferous Forest (%) within 300 m; CONIF1000: Coniferous Forest (%) within 1000 m.

Table A.7. Parameter estimates ( $\beta$ ) and 95% confidence intervals for covariates considered to explain the detection probability of Wood Frog egg masses, Wood Frog and Mink Frog metamorphosed individuals in beaver and peatland ponds in Northern Quebec (Canada) in 2018 and 2019. Estimates and confidence intervals were obtained from multimodel inference with correction for over-dispersion ( $\hat{c}$ ). The  $\hat{c}$  of each species was estimated from the most parsimonious model. See Table 2.2 for a description of the covariates.

Species	Covariates	$\beta \pm (\text{SE})$	95% lower	confidence upper
Wood Frog egg masses ( $\hat{c} = 3.62$ )	Observer	$-0.28 \pm 0.17$	-0.61	0.05
	Snowmelt	$0.59 \pm 0.54$	-0.46	1.64
Wood Frog metamorphosed individuals ( $\hat{c} = 2.27$ )	Observer	$-0.01 \pm 0.08$	-0.17	0.15
	Temp	$-0.37 \pm 0.31$	-0.97	0.24
	Hum	$-0.95 \pm 0.52$	-1.96	0.06
	Snowmelt	$0.03 \pm 0.14$	-0.24	0.3
Mink frog metamorphosed individuals ( $\hat{c} = 3.06$ )	Observer	$-4.14\text{e-}10 \pm 5.03\text{e-}05$	$-9.8\text{e-}05$	$9.8\text{e-}05$
	Temp	$0.2 \pm 0.31$	-0.39	0.8
	Hum	$0.01 \pm 0.08$	-0.16	0.17
	Snowmelt	$0.36 \pm 0.26$	-0.16	0.87

Temp: Temperature; Hum: Humidity; Snowmelt: Number of days after snowmelt

## APPENDICE B

### SUPPLEMENTARY INFORMATION CHAPTER III

Table B.1. Summary of results for individual species from the multispecies occupancy model based on bird surveys conducted in ponds of northern Quebec in 2018 and 2019. Guilds were based on forest successional status according to Drapeau et al. (2000) and Imbeau et al. (2003). Results indicate variations of species occupancy with predator latent occupancy, pond type, forest cover, latitude, and year. Positive (+) and negative (-) signs reflect the relationship of species occupancy with a given explanatory variable, when the 95% credible interval excludes 0. Species codes for the 96 birds are used in Figures 3.2 and 3.3.

Code	Common Name	Scientific name	Guild	Predator occupancy	Pond type (beaver)	Forest cover	Latitude	Year (2019)
WIWA	Wilson's Warbler	<i>Cardellina pusilla</i>	Early	—	+		+	
ALFL	Alder Flycatcher	<i>Empidonax alnorum</i>	Early	—				
LEFL	Least Flycatcher	<i>Empidonax minimus</i>	Early	—	+			
MOWA	Mourning Warbler	<i>Geothlypis philadelphia</i>	Early	—				
COYE	Common Yellowthroat	<i>Geothlypis trichas</i>	Early	—	+	—		
OCWA	Orange-crowned Warbler	<i>Leiothlypis celata</i>	Early					
TEWA	Tennessee Warbler	<i>Leiothlypis peregrina</i>	Early					
SOSP	Song Sparrow	<i>Melospiza melodia</i>	Early	—				
CSWA	Chestnut-sided Warbler	<i>Setophaga pensylvanica</i>	Early					
YEWA	Yellow Warbler	<i>Setophaga petechia</i>	Early	—	+		+	
AMRE	American Redstart	<i>Setophaga ruticilla</i>	Early		+		—	
AMGO	American Goldfinch	<i>Spinus tristis</i>	Early	—				
CHSP	Chipping Sparrow	<i>Spizella passerina</i>	Early	—	+			
BRTH	Brown Thrasher	<i>Toxostoma rufum</i>	Early					
PHVI	Philadelphia Vireo	<i>Vireo philadelphicus</i>	Early		+		—	+

Table B.1. Continued

WCSP	White-crowned Sparrow	<i>Zonotrichia leucophrys</i>	Early	—			+
SWTH	Swainson's Thrush	<i>Catharus ustulatus</i>	Late			+	—
BRCR	Brown Creeper	<i>Certhia americana</i>	Late			+	—
PIWO	Pileated Woodpecker	<i>Dryocopus pileatus</i>	Late			+	
YBFL	Yellow-bellied Flycatcher	<i>Empidonax flaviventris</i>	Late	+		+	+
NAWA	Nashville Warbler	<i>Leiothlypis ruficapilla</i>	Late			+	—
HAWO	Hairy Woodpecker	<i>Dryobates villosus</i>	Late				
RECR	Red Crossbill	<i>Loxia curvirostra</i>	Late			+	+
WWCR	White-winged Crossbill	<i>Loxia leucoptera</i>	Late			+	
BAWW	Black-and-white Warbler	<i>Mniotilta varia</i>	Late			+	—
CAJA	Canada Jay	<i>Perisoreus canadensis</i>	Late	+		+	+
BBWO	Black-backed Woodpecker	<i>Picoides arcticus</i>	Late			+	—
ATTW	American Three-toed Woodpecker	<i>Picoides dorsalis</i>	Late				
BCCH	Black-capped Chickadee	<i>Poecile atricapillus</i>	Late			+	—
BOCH	Boreal Chickadee	<i>Poecile hudsonicus</i>	Late			+	
GCKI	Golden-crowned Kinglet	<i>Regulus satrapa</i>	Late			+	—
OVEN	Ovenbird	<i>Seiurus aurocapilla</i>	Late			+	—
YRWA	Yellow-rumped Warbler	<i>Setophaga coronata</i>	Late			+	
CMWA	Cape May Warbler	<i>Setophaga tigrina</i>	Late			+	
BTNW	Black-throated Green Warbler	<i>Setophaga virens</i>	Late			+	
RBNU	Red-breasted Nuthatch	<i>Sitta canadensis</i>	Late				—
YBSA	Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	Late	—		+	—
PISI	Pine Siskin	<i>Spinus pinus</i>	Late				—
WIWR	Winter Wren	<i>Troglodytes hiemalis</i>	Late			+	—
REVI	Red-eyed Vireo	<i>Vireo olivaceus</i>	Late			+	—
BHVI	Blue-headed Vireo	<i>Vireo solitarius</i>	Late			+	—



Table B.1. Continued

CORE	Common Redpoll	<i>Acanthis flammea</i> <i>Bombycilla</i>	Genera list			
CEDW	Cedar Waxwing	<i>cedrorum</i>	Genera list	—		
BOWA	Bohemian Waxwing	<i>Bombycilla garrulus</i>	Genera list			+
RUGR	Ruffed Grouse	<i>Bonasa umbellus</i>	Genera list			—
GHOW	Great Horned Owl	<i>Bubo virginianus</i>	Genera list			
VEER	Veery	<i>Catharus fuscescens</i>	Genera list	—		—
HETH	Hermit Thrush	<i>Catharus guttatus</i>	Genera list			
NOFL	Northern Flicker	<i>Colaptes auratus</i>	Genera list			—
OSFL	Olive-sided Flycatcher	<i>Contopus cooperi</i>	Genera list	+		
AMCR	American Crow	<i>Corvus brachyrhynchos</i>	Genera list			—
CORA	Common Raven	<i>Corvus corax</i>	Genera list			—
BLJA	Blue Jay	<i>Cyanocitta cristata</i>	Genera list	—		
DOWO	Downy Woodpecker	<i>Dryobates pubescens</i>	Genera list	—		
MERL	Merlin	<i>Falco columbarius</i>	Genera list			
PUFI	Purple Finch	<i>Haemorhous purpureus</i>	Genera list			—
DEJU	Dark-eyed Junco	<i>Junco hyemalis</i>	Genera list			+
FOSP	Fox Sparrow	<i>Passerella iliaca</i>	Genera list			+
RCKI	Ruby-crowned Kinglet	<i>Corthylio calendula</i>	Genera list	+		
MAWA	Magnolia Warbler	<i>Setophaga magnolia</i>	Genera list		+	—
BLPW	Blackpoll Warbler	<i>Setophaga striata</i>	Genera list			+
AMRO	American Robin	<i>Turdus migratorius</i>	Genera list			—
WTSP	White-throated Sparrow	<i>Zonotrichia albicollis</i>	Genera list			
SPSA	Spotted Sandpiper	<i>Actitis macularius</i>	Wetland			
RWBL	Red-winged Blackbird	<i>Agelaius phoeniceus</i>	Wetland	—		
ABDU	American Black Duck	<i>Anas rubripes</i>	Wetland			

Table B.1. Continued

AMPI	American Pipit	<i>Anthus rubescens</i>	Wetland						
			d						—
SACR	Sandhill Crane	<i>Antigone canadensis</i>	Wetland						
			d						—
			Wetland						
LEOW	Long-eared Owl	<i>Asio otus</i>	d	—					
	Ring-necked	<i>Aythya</i>	Wetland						
RNDU	Duck	<i>collaris</i>	d						
	American	<i>Botaurus</i>	Wetland						
AMBI	Bittern	<i>lentiginosus</i>	d						—
		<i>Branta</i>	Wetland						
		<i>canadensis</i>	d			—			—
CANG	Canada Goose	<i>Calcarius</i>	Wetland						
	Lapland	<i>lapponicus</i>	d						
LALO	Longspur	<i>Calidris</i>	Wetland						
		<i>minutilla</i>	d						
LESA	Least Sandpiper	<i>Canachites</i>	Wetland						
		<i>canadensis</i>	d						
SPGR	Spruce Grouse	<i>Charadrius</i>	Wetland						
	Semipalmated	<i>semipalmatus</i>	d						
SEPL	Plover	<i>Chroicocephalus</i>	Wetland						
		<i>philadelphia</i>	d						
BOGU	Bonaparte's Gull	<i>Eremophila</i>	Wetland	—					
		<i>alpestris</i>	d						
HOLA	Horned Lark	<i>Euphagus</i>	Wetland						
		<i>carolinus</i>	d						
RUBL	Rusty Blackbird	<i>Gallinago</i>	Wetland						
		<i>delicata</i>	d						—
WISN	Wilson's Snipe		Wetland						
		<i>Gavia immer</i>	d						+
COLO	Common Loon	<i>Megaceryle</i>	Wetland						
	Belted	<i>alcyon</i>	d						
BEKI	Kingfisher	<i>Melospiza</i>	Wetland						
		<i>georgiana</i>	d			+		—	
SWSP	Swamp Sparrow	<i>Melospiza</i>	Wetland						
	Lincoln's	<i>lincolnii</i>	d						+
LISP	Sparrow	<i>Parkesia</i>	Wetland						
		<i>noveboracensis</i>	d						
NOWA	Northern Waterthrush	<i>Passerculus</i>	Wetland			+		—	+
	Savannah	<i>sandwichensis</i>	d						
SAVS	Sparrow	<i>Podilymbus</i>	Wetland	—				—	+
	Pied-billed	<i>podiceps</i>	d						
PBGR	Grebe	<i>Quiscalus</i>	Wetland						
	Common	<i>quiscula</i>	d						
COGR	Grackle	<i>Riparia</i>	Wetland			+			—
		<i>riparia</i>	d						
BANS	Bank Swallow	<i>Setophaga</i>	Wetland						
		<i>palmarum</i>	d					—	
PAWA	Palm Warbler	<i>Sterna</i>	Wetland						+
		<i>hirundo</i>	d						
COTE	Common Tern		d						

Table B.1. Continued

		<i>Tachycineta</i>	Wetlan	
TRES	Tree Swallow	<i>bicolor</i>	d	
	Greater	<i>Tringa</i>	Wetlan	
GRYE	Yellowlegs	<i>melanoleuca</i>	d	—
	Solitary	<i>Tringa</i>	Wetlan	
SOSA	Sandpiper	<i>solitaria</i>	d	
	Sharp-tailed	<i>Tympanuchus</i>	Wetlan	
STGR	Grouse	<i>phasianellus</i>	d	
	Eastern	<i>Tyrannus</i>	Wetlan	
EAKI	Kingbird	<i>tyrannus</i>	d	—

Forest successional guilds include Early: early-successional; Late: late-successional; Generalist, and Wetland: wetland and aquatic species.

Table B.2. Multispecies single-season occupancy model structure implemented in JAGS for the bird community data collected with passive acoustic recorders in 2018 and 2019 in ponds of northern Quebec, Canada. The model involves a first component to estimate the latent occupancy state of American red squirrels using explanatory variables. Using a structural equation strategy, this latent occupancy state is later used as an explanatory variable for the occupancy of the bird species, along with the other explanatory variables.

Model statement
<pre> ## Define model ## each of the 50 ponds appears twice in the data (1 row in 2018, 1 row in 2019 ## data set has 100 rows (50 sites x 2 years)  model{  ##squirrel occupancy - single-season single-species model with ##random site effect ##priors on psi beta0.squ ~ dnorm(0, 0.01) beta.a1.squ ~ dnorm(0, 0.01) #type beta.a2.squ ~ dnorm(0, 0.01) #forest beta.a3.squ ~ dnorm(0, 0.01) #year beta.a4.squ ~ dnorm(0, 0.01) #latitude  ##priors of on p alpha0.squ ~ dnorm(0, 0.01) alpha.b1.squ ~ dnorm(0, 0.01) #bad sound quality alpha.b2.squ ~ dnorm(0, 0.01) #days since thaw  ##likelihood ##first loop over nsites (site-year combinations) for (i in 1:J) {   ##True occupancy z at site i (biological process)   z.squ[i] ~ dbern(psi.squ[i])    ##linear predictor of psi   logit(psi.squ[i]) &lt;- beta0.squ + beta.a1.squ * type.beaver[i] + beta.a2.squ * forest[i] + beta.a3.squ * year.2019[i] + beta.a4.squ * lat[i]    ##second loop over nvisits   for (j in 1:K) {      ##linear predictor of p </pre>

```

logit(p.squ[i, j]) <- alpha0.squ + alpha.b1.squ * bad[i, j] + alpha.b2.squ *
thaw[i, j]
##p = 0 if site not occupied
eff.p.squ[i, j] <- z.squ[i] * p.squ[i, j]

##detection at i j (observation process)
y.squ[i, j] ~ dbern(eff.p.squ[i, j])
}
}

#####
##multispecies occupancy model

##prior distribution of average occupancy of species in the
##community for each guild
for(g in 1:n.guild) {
  ##mean for each guild
  psi.mean[g] ~ dunif(0, 1)
  beta0[g] <- log(psi.mean[g]) - log(1 - psi.mean[g])

  ##prior distribution of beta on occupancy
  mua1[g] ~ dnorm(0, 0.001) #random slope of type.beaver
  mua2[g] ~ dnorm(0, 0.001) #random slope of forest

  ##prior distribution of SD of average occupancy
  sigma.u[g] ~ dunif(0, 10)
  tau.u[g] <- pow(sigma.u[g], -2)

  ##variance of beta parameters on occupancy
  sigma.a1[g] ~ dunif(0, 10) #variance of type.beaver
  tau.a1[g] <- pow(sigma.a1[g], -2)

  sigma.a2[g] ~ dunif(0, 10) #variance of forest
  tau.a2[g] <- pow(sigma.a2[g], -2)
}

##random slopes of year drawn from common distribution for
##all species (no guild)
mua3 ~ dnorm(0, 0.001) #random slope of year2019
sigma.a3 ~ dunif(0, 10) #variance of year2019
tau.a3 <- pow(sigma.a3, -2)

```

```

##random slopes of latitude drawn from common distribution
##for all species (no guild)
mua4 ~ dnorm(0, 0.001) #random slope of latitude
sigma.a4 ~ dunif(0, 10) #variance of latitude
tau.a4 <- pow(sigma.a4, -2)

##random slopes of squirrel occupancy (latent state z.squ)
##drawn from common distribution for all species (no guild)
mua5 ~ dnorm(0, 0.001) #random slope of squirrel occupancy
sigma.a5 ~ dunif(0, 10) #variance of squirrel occupancy
tau.a5 <- pow(sigma.a5, -2)

##prior distribution of average detection over all species
##in the community
p.mean ~ dunif(0, 1)
alpha0 <- log(p.mean) - log(1 - p.mean)

##prior distribution of beta parameters for covariates on
##detection
nub1 ~ dnorm(0, 0.001) #random slope of bad sound quality
nub2 ~ dnorm(0, 0.001) #random slope of days since thaw
#nub3 ~ dnorm(0, 0.001)

##prior distribution of SD of average detection
sigma.v ~ dunif(0, 10)
##precision (1/variance) of parameters
tau.v <- pow(sigma.v, -2)

##variance of beta parameters on detection
sigma.b1 ~ dunif(0, 10) #bad sound quality
sigma.b2 ~ dunif(0, 10) #days since thaw
tau.b1 <- pow(sigma.b1, -2)
tau.b2 <- pow(sigma.b2, -2)

##random effect of site on psi (50 unique sites)
sigma.psi.site ~ dunif(0, 150)
tau.psi.site <- pow(sigma.psi.site, -2)

for (b in 1:nsiteID){ #50 unique sites
  alpha.site[b] ~ dnorm(0, tau.psi.site)
}

```

```

}

for (i in 1:n.species) {
  ##priors for species i from the community level
  ##parameters on occupancy
#intercept on occupancy - different distribution for each guild
  phi0[i] ~ dnorm(beta0[guild[i]], tau.u[guild[i]])
#beta for type.beaver - different distribution for each guild
  a1[i] ~ dnorm(mua1[guild[i]], tau.a1[guild[i]])
#beta for forest - different distribution for each guild
  a2[i] ~ dnorm(mua2[guild[i]], tau.a2[guild[i]])
  a3[i] ~ dnorm(mua3, tau.a3) #beta for year2019
  a4[i] ~ dnorm(mua4, tau.a4) #beta for latitude
  a5[i] ~ dnorm(mua5, tau.a5) #beta for squirrel occupancy

  ##parameters on detectability
  eta0[i] ~ dnorm(alpha0, tau.v) #intercept on detection
  b1[i] ~ dnorm(nub1, tau.b1) #beta for bad sound quality
  b2[i] ~ dnorm(nub2, tau.b2) #beta for days since thaw

  ##Loop to estimate the Z matrix (true occurrence for
  ##species i at site j (site-year combination)
  for (j in 1:J) {
    logit(psi[j, i]) <- phi0[i] + a1[i] * type.beaver[j] + a2[i] * forest[j] + a3[i] *
year.2019[j] + a4[i] * lat[j] + a5[i] * z.squ[j] + alpha.site[SiteNum[i]]

    Z[j, i] ~ dbern(psi[j, i]) #prior distribution for
    ##latent variable for occurrence of species i in site j

    ##Loop to estimate detection for species i at site j
    ##during sampling period k.
    for (k in 1:K) {
      logit(p[j, k, i]) <- eta0[i] + b1[i] * bad[j, k] + b2[i] * thaw[j, k]

      ##if species not present (Z = 0), then p = 0
      mu.p[j,k,i] <- p[j, k, i]*Z[j, i]
      X[j,k,i] ~ dbern(mu.p[j, k, i])
    }
  }
}

```

```

##compute derived parameters
##species richness at each pond-year combination
for(j in 1:J){
  sp.rich[j] <- sum(Z[j,]) # Number of species
}

##derived parameters - sums of columns, rows, and AUC

##compute predicted observations at species i, site j, visit k
for(i in 1:n.species) {#i species
  for(j in 1:J){ #j sites
    for(k in 1:K){#k visits
      ##remove values that are NA by multiplying by 0
      yCor[j, k, i] <- X[j, k, i] * yNA[j, k, i]
      predY[j, k, i] <- psi[j, i] * p[j, k, i] * yNA[j, k, i]
      ySim[j, k, i] ~ dbern(mu.p[j, k, i])
      ##remove values that are NA by multiplying by 0
      ySimCor[j, k, i] <- ySim[j, k, i] * yNA[j, k, i]
    }
  }
}

##compute sum of detections and predictions across ponds
for (i in 1:n.species){
  for(k in 1:K){
    diffColObsVisits[i, k] <- pow(sum(yCor[, k, i]) - sum(predY[, k, i]),
2)/(sum(predY[, k, i]) + 0.0001)
    diffColSimVisits[i, k] <- pow(sum(ySimCor[, k, i]) - sum(predY[, k, i]),
2)/(sum(predY[, k, i]) + 0.0001)
  }
}

##compute sum of detections and predictions across visits
for (i in 1:n.species){
  for(j in 1:J){
    diffRowObsVisits[i, j] <- pow(sum(yCor[j, , i]) - sum(predY[j, , i]),
2)/(sum(predY[j, , i]) + 0.0001)
    diffRowSimVisits[i, j] <- pow(sum(ySimCor[j, , i]) - sum(predY[j, , i]),
2)/(sum(predY[j, , i]) + 0.0001)
  }
}

```



```

##sum of values
chiColObs <- sum(diffColObsVisits[,])
chiColSim <- sum(diffColSimVisits[,])
chiRowObs <- sum(diffRowObsVisits[,])
chiRowSim <- sum(diffRowSimVisits[,])
##end of model statement
}

```

Table B.3. Linear mixed model structure implemented in JAGS for the species richness derived from the multispecies single-season site occupancy model on data collected with passive acoustic recorders in 2018 and 2019 in ponds of northern Quebec, Canada. Note that both the mean and the variance of the posterior distribution of species richness informed the linear mixed model to propagate the errors from the multispecies occupancy model.

Model statement

```

## Define model
model{

  ##Priors for linear mixed model
  ##fixed effects
  beta0 ~ dnorm(0, 0.001)
  beta.beaver ~ dnorm(0, 0.001)
  beta.forest ~ dnorm(0, 0.001)
  beta.year ~ dnorm(0, 0.001)
  beta.lat ~ dnorm(0, 0.001)
  beta.squirrel ~ dnorm(0, 0.001)

  ##site random effects (50 unique sites)
  sigma.site ~ dunif(0, 150)
  tau.site <- pow(sigma.site, -2)

  ##random deviations of intercepts relative to beta0
  for (b in 1:nsiteID){ #50 unique sites
    alpha.site[b] ~ dnorm(0, tau.site)
  }

  ## Likelihood – including variance of posterior distribution

```

```

## based on McCarthy and Masters 2005 and Kéry and Royle 2016
##(pp. 679--682)
for (i in 1:J) { #100 site-year combinations
  sp.rich[i] ~ dnorm(mu[i], tau.psd[i])
  ##sigma.psd is posterior SD of sp.rich from multispecies
  ##model to include directly in analysis
  tau.psd[i] <- pow(sigma.psd[i], -2)

  mu[i] <- alpha.site[SiteNum[i]] + beta0 + beta.beaver * type.beaver[i] +
beta.forest * forest[i] + beta.year * year.2019[i] + beta.lat * lat[i] + beta.squirrel *
squirrel[i]
}

## Derived values
for (i in 1:J) {
  ##residuals
  res[i] <- sp.rich[i] - mu[i]
  ##predictions
  pred[i] <- mu[i]
}
}

```

Table B.4. Summary of posterior distribution of the estimates of explanatory variables on the occupancy ( $\psi$ ) and detection probability ( $p$ ) of American red squirrel at ponds sampled in 2018 and 2019 in northern Quebec. The American red squirrel component was included as an explanatory variable in the multispecies single-season model of the bird community. Effects that differ from 0 are in bold.

Parameter group	Parameter	Mean	SD	95% Credible interval
$\psi$	$\beta_0$ , Squirrel	2.77	0.69	[1.57, 4.28]
$\psi$	$\beta_{\text{PondBeaver}}$ , Squirrel	-0.21	1.03	[-2.17, 1.88]
$\psi$	$\beta_{\text{Forest}}$ , Squirrel	-0.47	0.55	[-1.68, 0.49]
$\psi$	$\beta_{\text{Year2019}}$ , Squirrel	0.55	0.87	[-1.12, 2.30]
$\psi$	$\beta_{\text{Latitude}}$ , Squirrel	0.36	0.46	[-0.55, 1.28]
$p$	$\alpha_0$ , Squirrel	-0.54	-0.11	[-0.75, -0.33]
$p$	$\alpha_{\text{SoundQualityBad}}$ , Squirrel	<b>-1.09</b>	<b>0.20</b>	<b>[-1.49, -0.70]</b>
$p$	$\alpha_{\text{Thaw}}$ , Squirrel	<b>0.36</b>	<b>0.09</b>	<b>[0.19, 0.54]</b>

Table B.5. Summary of posterior distribution of guild and community hyperparameters from the multispecies single-season site occupancy model of bird communities at beaver and peatland ponds sampled in 2018 and 2019 in northern Quebec. Parameters that varied with guilds are presented with the guild between brackets. For example,  $\beta_{0[\text{Early}]}$  is the mean intercept for the occupancy of early-successional species, where the intercept of each species  $i$  of that guild is drawn from a normal distribution,  $\beta_{0i} \sim N(\beta_{0[\text{Early}]}, \sigma_{\mu[\text{Early}]})$ . Effects that differ from 0 are in bold.

Parameter group	Parameter	Mean	SD	95% Bayesian credible interval
$\Psi$	$\beta_{0[\text{Early}]}$	-1.17	0.70	[-2.58, 0.20]
$\Psi$	$\beta_{0[\text{Late}]}$	<b>-2.31</b>	<b>0.62</b>	<b>[-3.57, -1.12]</b>
$\Psi$	$\beta_{0[\text{Wetland}]}$	<b>-1.42</b>	<b>0.48</b>	<b>[-2.39, -0.49]</b>
$\Psi$	$\beta_{0[\text{Generalist}]}$	-0.32	0.69	[-1.69, 1.03]
$\Psi$	$\mu_{\text{PondBeaver}[\text{Early}]}$	<b>1.34</b>	<b>0.54</b>	<b>[0.31, 2.46]</b>
$\Psi$	$\mu_{\text{PondBeaver}[\text{Late}]}$	0.24	0.33	[-0.40, 0.89]
$\Psi$	$\mu_{\text{PondBeaver}[\text{Wetland}]}$	0.44	0.39	[-0.33, 1.24]
$\Psi$	$\mu_{\text{PondBeaver}[\text{Generalist}]}$	0.64	0.59	[-0.45, 1.91]
$\Psi$	$\mu_{\text{Forest}[\text{Early}]}$	-0.07	0.24	[-0.49, 0.45]
$\Psi$	$\mu_{\text{Forest}[\text{Late}]}$	<b>0.67</b>	<b>0.15</b>	<b>[0.40, 0.99]</b>
$\Psi$	$\mu_{\text{Forest}[\text{Wetland}]}$	-0.36	-0.14	[-0.62, -0.08]
$\Psi$	$\mu_{\text{Forest}[\text{Generalist}]}$	-0.16	0.14	[-0.44, 0.12]
$\Psi$	$\mu_{\text{Year}2019}$	0.11	0.17	[-0.23, 0.44]
$\Psi$	$\mu_{\text{Latitude}}$	<b>-0.59</b>	<b>0.21</b>	<b>[-1.02, -0.19]</b>
$\Psi$	$\sigma_{\mu[\text{Early}]}$	<b>1.99</b>	<b>0.83</b>	<b>[0.44, 3.81]</b>
$\Psi$	$\sigma_{\mu[\text{Late}]}$	<b>2.09</b>	<b>0.72</b>	<b>[0.68, 3.61]</b>
$\Psi$	$\sigma_{\mu[\text{Wetland}]}$	<b>1.33</b>	<b>0.61</b>	<b>[0.13, 2.54]</b>
$\Psi$	$\sigma_{\mu[\text{Generalist}]}$	<b>2.71</b>	<b>0.83</b>	<b>[1.23, 4.52]</b>
$\Psi$	$\sigma_{\text{PondBeaver}[\text{Early}]}$	<b>1.40</b>	<b>0.66</b>	<b>[0.31, 2.92]</b>
$\Psi$	$\sigma_{\text{PondBeaver}[\text{Late}]}$	<b>0.75</b>	<b>0.46</b>	<b>[0.05, 1.81]</b>
$\Psi$	$\sigma_{\text{PondBeaver}[\text{Wetland}]}$	<b>1.48</b>	<b>0.42</b>	<b>[0.81, 2.45]</b>
$\Psi$	$\sigma_{\text{PondBeaver}[\text{Generalist}]}$	<b>1.90</b>	<b>0.67</b>	<b>[0.88, 3.50]</b>
$\Psi$	$\sigma_{\text{Forest}[\text{Early}]}$	<b>0.58</b>	<b>0.25</b>	<b>[0.19, 1.17]</b>
$\Psi$	$\sigma_{\text{Forest}[\text{Late}]}$	<b>0.24</b>	<b>0.18</b>	<b>[0.01, 0.66]</b>
$\Psi$	$\sigma_{\text{Forest}[\text{Wetland}]}$	<b>0.41</b>	<b>0.17</b>	<b>[0.11, 0.78]</b>
$\Psi$	$\sigma_{\text{Forest}[\text{Generalist}]}$	<b>0.31</b>	<b>0.21</b>	<b>[0.01, 0.80]</b>
$\Psi$	$\sigma_{\text{Year}2019}$	<b>1.12</b>	<b>0.19</b>	<b>[0.78, 1.53]</b>
$\Psi$	$\sigma_{\text{Latitude}}$	<b>1.71</b>	<b>0.21</b>	<b>[1.34, 2.17]</b>
$\Psi$	$\sigma_{\text{SquirrelOccupancy}}$	<b>2.45</b>	<b>0.31</b>	<b>[1.89, 3.11]</b>
$\Psi$	$\sigma_{\text{Site}}$	<b>1.00</b>	<b>0.52</b>	<b>[0.08, 1.99]</b>
$p$	$\sigma_v$	<b>1.42</b>	<b>0.15</b>	<b>[1.14, 1.74]</b>
$p$	$\mu_{\text{SoundQualityBad}}$	<b>-0.77</b>	<b>0.05</b>	<b>[-0.87, -0.67]</b>
$p$	$\mu_{\text{Thaw}}$	-0.13	0.08	[-0.28, 0.03]
$p$	$\sigma_{\text{SoundQualityBad}}$	<b>0.18</b>	<b>0.08</b>	<b>[0.02, 0.34]</b>
$p$	$\sigma_{\text{Thaw}}$	<b>0.65</b>	<b>0.07</b>	<b>[0.53, 0.80]</b>

Table B.6. Summary of the posterior distribution of parameter estimates from the linear mixed model of bird species richness at beaver and peatland ponds sampled in 2018 and 2019 in northern Quebec. Effects that differ from 0 are in bold.

Parameter	Mean	SD	95% Bayesian credible interval
$\beta_0$	<b>30.98</b>	<b>1.75</b>	<b>[27.46, 34.41]</b>
$\beta_{\text{PondBeaver}}$	<b>4.90</b>	<b>1.29</b>	<b>[2.37, 7.46]</b>
$\beta_{\text{SquirrelOccupancy}}$	<b>-3.97</b>	<b>1.79</b>	<b>[-7.52, -0.36]</b>
$\beta_{\text{Forest}}$	-0.16	0.46	[-1.05, 0.74]
$\beta_{\text{Latitude}}$	<b>-3.89</b>	<b>0.56</b>	<b>[-5.00, -2.78]</b>
$\beta_{\text{Year2019}}$	0.87	0.50	[-0.11, 1.83]
$\sigma_{\text{Site}}$	<b>2.72</b>	<b>0.45</b>	<b>[1.93, 3.68]</b>

## APPENDICE C

### SUPPLEMENTARY INFORMATION CHAPTER IV

Table C.1. Multispecies single-season occupancy model structure implemented in JAGS for the bird and mammal community data collected with camera traps in 2018 and 2019 in 50 ponds of northern Quebec, Canada.

Model statement
<pre>## Define model model{ ##prior distribution of average occupancy over all species in the community psi.mean ~ dunif(0, 1) beta0 &lt;- log(psi.mean) - log(1 - psi.mean)  ##prior distribution of average detection over all species in the community p.mean ~ dunif(0, 1) alpha0 &lt;- log(p.mean) - log(1 - p.mean)  ##prior distribution of beta parameters for covariates on occupancy mua1 ~ dnorm(0, 0.001) #hyperparameter defining mean of random slope of type.beaver mua2 ~ dnorm(0, 0.001) #hyperparameter defining mean of random slope of forest mua3 ~ dnorm(0, 0.001) #hyperparameter defining mean of random slope of latitude mua4 ~ dnorm(0, 0.001) #hyperparameter defining mean of random slope of year mua5 ~ dnorm(0, 0.001) #hyperparameter defining mean of random slope of dist.road  ##prior distribution of beta parameters for covariates on detection nub1 ~ dnorm(0, 0.001) #hyperparameter defining mean of random slope of days since thaw nub2 ~ dnorm(0, 0.001) #hyperparameter defining mean of random slope of prec nub3 ~ dnorm(0, 0.001) #hyperparameter defining mean of random slope of effort  ##prior distribution of SD of average occupancy sigma.u ~ dunif(0, 10) ##prior distribution of SD of average detection</pre>

```

sigma.v ~ dunif(0, 10)
##precision (1/variance) of parameters
tau.u <- pow(sigma.u, -2)
tau.v <- pow(sigma.v, -2)

##variance of beta parameters on occupancy
sigma.a1 ~ dunif(0, 10) #hyperparameter defining variance of random slope of
type
tau.a1 <- pow(sigma.a1, -2)
sigma.a2 ~ dunif(0, 10) #hyperparameter defining variance of random slope of
forest
tau.a2 <- pow(sigma.a2, -2)
sigma.a3 ~ dunif(0, 10) #hyperparameter defining variance of random slope of
latitude
tau.a3 <- pow(sigma.a3, -2)
sigma.a4 ~ dunif(0, 10) #hyperparameter defining variance of random slope of
year
tau.a4 <- pow(sigma.a4, -2)
sigma.a5 ~ dunif(0, 10) #hyperparameter defining variance of random slope of
dist.road
tau.a5 <- pow(sigma.a5, -2)

##variance of beta parameters on detection
sigma.b1 ~ dunif(0, 10) #hyperparameter defining variance of random slope of
prec
sigma.b2 ~ dunif(0, 10) #hyperparameter defining variance of random slope of
days since thaw
sigma.b3 ~ dunif(0, 10) #hyperparameter defining variance of random slope of
effort

tau.b1 <- pow(sigma.b1, -2)
tau.b2 <- pow(sigma.b2, -2)
tau.b3 <- pow(sigma.b3, -2)

##random effect of site on psi
sigma.psi.site ~ dunif(0, 150)
tau.psi.site <- pow(sigma.psi.site, -2)

for (b in 1:nsiteID){
  alpha.site[b] ~ dnorm(0, tau.psi.site)
}

```

```

}

for (i in 1:n.species) {

  ##Create priors for species i from the community level prior distributions
  ##parameters on occupancy
  phi0[i] ~ dnorm(beta0, tau.u) #intercept on occupancy
  a1[i] ~ dnorm(mua1, tau.a1) #beta for type.beaver
  a2[i] ~ dnorm(mua2, tau.a2) #beta for forest
  a3[i] ~ dnorm(mua3, tau.a3) #beta for latitude
  a4[i] ~ dnorm(mua4, tau.a4) #beta for year
  a5[i] ~ dnorm(mua5, tau.a5) #beta for dist.road

  ##parameters on detectability
  eta0[i] ~ dnorm(alpha0, tau.v) #intercept on detection
  b1[i] ~ dnorm(nub1, tau.b1) #beta for prec
  b2[i] ~ dnorm(nub2, tau.b2) #beta for days since thaw
  b3[i] ~ dnorm(nub3, tau.b3) #beta for effort

  #Loop to estimate the Z matrix (true occurrence for species i at site j
  for (j in 1:J) {
    logit(psi[j, i]) <- phi0[i] + a1[i] * type.beaver[j] + a2[i] * forest[j] + a3[i] *
latitude[j] + a4[i] * year2019[j] + a5[i] * dist.road[j] + alpha.site[SiteNum[i]]
  }

  #prior distribution for latent variable for occurrence of species i in site j
  Z[j, i] ~ dbern(psi[j, i])

  ##Loop to estimate detection for species i at site j during sampling period k.
  for (k in 1:K) {
    logit(p[j, k, i]) <- eta0[i] + b1[i] * thaw[j, k] + b2[i] * prec[j, k] + b3[i] *
effort[j, k]

    ##if species not present (Z = 0), then p = 0 for species (species cannot be
detected)
    mu.p[j,k,i] <- p[j, k, i]*Z[j, i]
    X[j,k,i] ~ dbern(mu.p[j, k, i])
  }
}
}
}

```

```

##compute derived parameters
##species richness at each quadrat
for(j in 1:J){
  sp.rich[j] <- sum(Z[j,]) # Number of species
}

##derived parameters - sums of columns, rows, and AUC

##compute predicted observations at species i, site j, visit k
for(i in 1:n.species) {#i species
  for(j in 1:J){ #j sites
    for(k in 1:K){#k visits
      ##remove values that are NA by multiplying by 0
      yCor[j, k, i] <- X[j, k, i] * yNA[j, k, i]
      predY[j, k, i] <- psi[j, i] * p[j, k, i] * yNA[j, k, i]
      ySim[j, k, i] ~ dbern(mu.p[j, k, i])
      ##remove values that are NA by multiplying by 0
      ySimCor[j, k, i] <- ySim[j, k, i] * yNA[j, k, i]
    }
  }
}

##compute sum of detections and predictions across sites
for (i in 1:n.species){
  for(k in 1:K){
    diffColObsVisits[i, k] <- pow((sum(yCor[, k, i]) - sum(predY[, k, i]),
2)/(sum(predY[, k, i]) + 0.0001)
    diffColSimVisits[i, k] <- pow((sum(ySimCor[, k, i]) - sum(predY[, k, i]),
2)/(sum(predY[, k, i]) + 0.0001)
  }
}

##compute sum of detections and predictions across visits
for (i in 1:n.species){
  for(j in 1:J){
    diffRowObsVisits[i, j] <- pow((sum(yCor[j, , i]) - sum(predY[j, , i]),
2)/(sum(predY[j, , i]) + 0.0001)
    diffRowSimVisits[i, j] <- pow((sum(ySimCor[j, , i]) - sum(predY[j, , i]),
2)/(sum(predY[j, , i]) + 0.0001)
  }
}

```



```
}  
  
##sum of values  
chiColObs <- sum(diffColObsVisits[,])  
chiColSim <- sum(diffColSimVisits[,])  
chiRowObs <- sum(diffRowObsVisits[,])  
chiRowSim <- sum(diffRowSimVisits[,])  
  
##end of model statement  
}
```

## ANNEXE A

### TRENDS AND GAPS IN THE USE OF CITIZEN SCIENCE DERIVED DATA AS INPUT FOR SPECIES DISTRIBUTION MODELS: A QUANTITATIVE REVIEW

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Published in *PLoS ONE*, 16(3): e0234587.

### A1.1. Abstract

Citizen science (CS) currently refers to some level of volunteer participation in any discipline of scientific research. Over the last two decades, nature-based CS has flourished due to innovative technology, novel devices, and widespread digital platforms used to collect and classify species occurrence data. For scientists, CS offers a low-cost approach of collecting species occurrence information at large spatial scales that otherwise would be prohibitively expensive. We examined the trends and gaps linked to the use of CS as a source of data for species distribution models (SDMs), in order to propose guidelines and highlight solutions. We conducted a quantitative literature review of 224 peer-reviewed articles to measure how the representation of different taxa, regions, and data types have changed in SDM publications since the 2010s. Our review shows that the number of papers using CS for SDMs has increased at approximately double the rate of the overall number of SDM papers. However, disparities in taxonomic and geographic coverage remain in studies using CS. Western Europe and North America were the regions with the most coverage (71.2%). Papers on birds (51.2%) and mammals (26.2%) outnumbered other taxa. Among invertebrates, flying insects including Lepidoptera and Odonata received the most attention. Compared to studies on animal taxa, papers on plants using CS data remain rare. Although the aims and scope of SDM papers are diverse, conservation remained the central theme of SDM using CS data. We present examples of the use of CS and highlight recommendations to motivate further research, such as combining multiple data sources and promoting local and traditional knowledge. We hope our findings will strengthen citizen-researchers partnerships to better inform SDMs, especially for less-studied taxa and regions. Researchers stand to benefit from the large quantity of data available from CS sources to improve global predictions of species distributions.

*Keywords:* databases, biodiversity, crowdsourcing, volunteer, sampling bias, quantitative review

## A1.2. Introduction

Species distribution models have become a widely used tool in ecology in recent years [1-3]. Understanding the association between the occurrence of species and environmental conditions is a first step in addressing questions about species distributions, abundances and habitat preferences [4, 5]. Current global-scale issues such as climate and land-use changes have increased the need to understand and predict the distribution of migratory or invasive species across a landscape. In fact, knowledge on species distribution is paramount to develop biodiversity conservation and management strategies [6]. The fundamental theory behind species distribution models (SDMs, hereafter) assumes that the presence of a species in a given location strongly depends on the environment, which implies that ecologists are able to estimate future species distributions based on the environment of current locations [7]. Specifically, SDMs use empirical data to link information about the presence of a species to the environmental variables of their known locations, and apply statistical models to predict the spatial distribution of species [4, 5, 8]. Consequently, we can identify three major components in any framework for SDMs: species presence data, landscape or environmental data, and a statistical model that links the first two components.

Species distribution models have been used to tackle a wide range of scientific issues at different spatial and temporal scales. SDMs are used in both fundamental science and applied sciences in biogeography, evolution, dispersal, migration, species invasion, meta-population, conservation, and climate change [3]. For example, SDMs have

shown their value, for example, in characterizing the current distribution range of a species [9, 10], predicting variables measured in the field [11], assessing species invasions [12], or evaluating the impact of land-use changes [13]. Species distribution models have multiple uses, including predicting spatial changes in response to climate change [14, 15], assessing the suitability of possible conservation areas [16, 17], or suggesting areas to improve survey efforts for rare species [18].

Modelling the spatiotemporal distribution of species usually requires a large amount of information collected over multiple years of standardized fieldwork. However, the long-term collection of broad-scale information on a wide range of species is prohibitively expensive. Yet, for some taxa, an impressive volume of data collected using non-standardized protocols is currently available in museum collections, distribution atlases and online portals, through efforts collectively labelled as citizen science (CS, hereafter). Globally, a huge variety of CS programs are currently being implemented involving a wide range of taxa [19]. Nevertheless, CS data are still challenging to analyze due to the intrinsic issues of non-standardized protocols that can affect the credibility and quality of the data.

Issues within CS datasets arise from the large number of observers that collect species data. Previous studies have tackled the different sources of variation in CS data [20-22]. Firstly, CS datasets are typically biased towards human population centers, areas that are easy to access, protected areas, or regions frequented by active observers. These problems lead to disparities in effort between over-sampled and under-sampled areas [22-27]. Secondly, geographical coverage of CS data can be biased towards well-financed and more industrialized countries, mainly in North America and Europe [28-30]. These two regions contribute substantially more data than any other region in the Global Biodiversity Information Facility (GBIF) database [31-35]. Consequently, a large proportion of samples occur in a restricted geographical extent, controlled by

administrative borders. This results in a non-representative sample of species' distribution. Thirdly, over time, the observation and reporting protocols can change. For example, the Audubon Christmas Bird Count at its start in 1900 aimed at offering an alternative to hunting on Christmas Day morning, with a loose survey protocol. The count day became flexible over years. For example, it was from December 22-29 in 1940-41 [36] and December 21 to January 2 in 1966-67 [37]. In 1966-67, the goal became to collect a snapshot of wintering birds around Christmas time: the survey protocol was standardized [38]. In 2000, the survey period expanded again, this time to 23 days as the count should now be completed on a day between December 14 and January 5 [39]. Unfortunately, changes in survey protocols are often poorly documented. Fourthly, among biological groups, CS observations can be taxonomically biased because volunteers are usually attracted to large and common species, to species that are brightly colored and easy to detect, and to more charismatic groups [21, 34, 40, 41]. This taxonomical disparity results in more information on relatively well-known groups than for under-reported groups. Finally, another source of variation in CS programs includes the variation in skill and expertise among observers, primarily due to the participation of a wide range of volunteers. As the quality of observations depends on the ability of observers to correctly identify species, this introduces a qualitative bias that can lead to misinterpretation of results. Indeed, this inter-observer sampling variation increases for species that are harder to detect [42-44]. Bias inherent to each of these five sources of variation may influence predictions of future trends. A major challenge is to account for these issues in species distribution models [45, 46].

Despite these issues regarding data quality, the use of CS has increased in recent years in different fields of study [47, 48]. For instance, CS is used in astronomy to classify galaxy images or to search for signals in radio data, and in atmospheric sciences to record the quality of air, soil, and water [47, 49, 50]. However, the main application of

CS is in conservation and ecology to monitor species occurrence [33, 51]. Several reviews have focused on how CS contributes to biodiversity monitoring [33], global change [52], and conservation biology [53]. Considering the increasing prevalence of CS in ecological studies, there is a need to synthesize the application of CS in SDMs. Accordingly, the main objective of this review was to quantify the variation over time in the use of CS data as an input for modelling species distribution. To achieve this objective, we assessed the current strengths in the use of CS in SDMs and identified partiality and gaps relative to taxa, regions, and data acquisition methods. Our main questions were: (1) What is the trend in the use of CS data for SDMs over the last decade? (2) Is there variation across regions, taxa, and types of data used? (3) What are the information gaps and how can we meet research needs in the near future?

Given the increasing use of citizen science in different field studies, we expected an increasing use of CS in SDMs. We also anticipated that because volunteers behave differently according to the region and group of interest, the set of papers would reflect clear preferences towards regions that are easy to access and groups that are apparently visually appealing to volunteers. However, we expected that these preferences would change over time due to the growing diversification of initiatives and platforms worldwide over the last decade.

### A1.3. Materials and Methods

#### A1.3.1. Paper selection

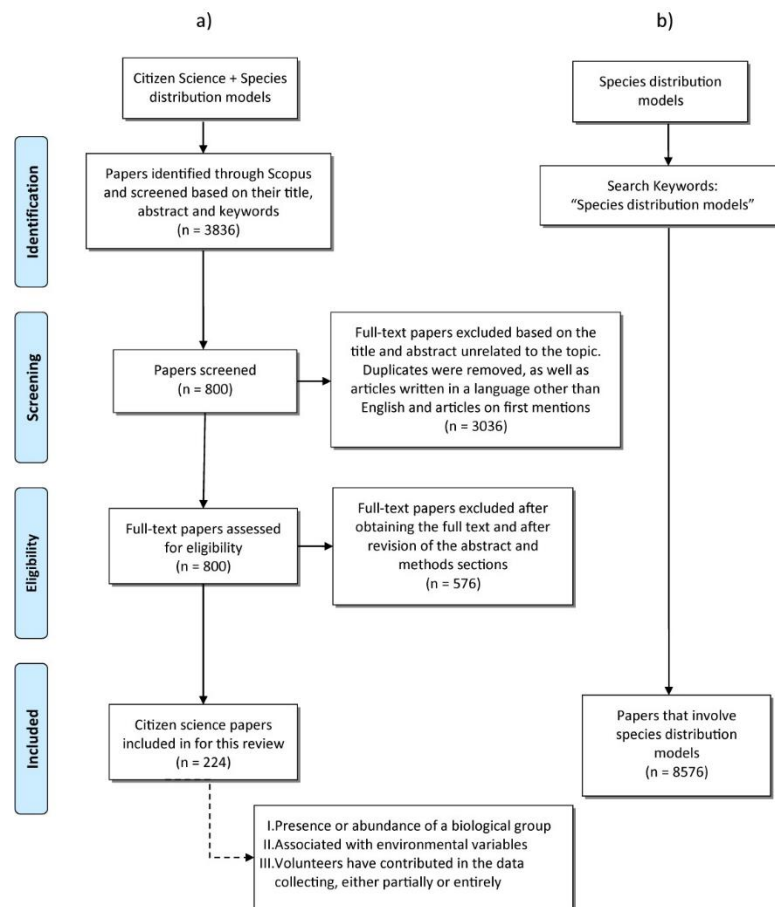
We used the Scopus search engine to conduct a literature review of peer-reviewed papers focusing on species distribution models that used citizen science. Our search

spanned a period of 10 years, considering papers from 2010, when the “citizen science” term was widely accepted by several authors [50, 54, 55], until 17 October 2019. We searched for papers using the following combination of keywords: (“citizen science” OR “public participation” OR “community monitoring program” OR “participatory monitoring”) AND (“species distribution model” OR “predictive model” OR “distribution map” OR “invasive species” OR “occupancy model” OR “occurrence” OR “migration” OR “climate change”).

#### A1.3.2. Data collection

From the first Scopus search, we screened a total of 3,836 papers based on their title, abstract and keywords (Fig. 1a). We dismissed those not related with either CS or SDMs. The remaining 800 papers were reduced after a further revision of abstracts and methodologies. We excluded papers written in languages other than English (n=4), all review papers, and also papers using data gathered by volunteers but without applications of SDMs (e.g., first report of a species or new occurrence data). To consider a given paper as relevant for our review, each of the following three conditions had to be met: the data included the presence or abundance of a biological group, the data were collected by volunteers (either partially or entirely), and a statistical method was applied to assess relationships with environmental data (Fig. 1a). We ended up with 224 papers in peer-reviewed journals that formed the basis of the analyses presented herein. Details and extracted information about all papers included in our review are listed in Supporting information (A.S1 Table). We believe this list does not reflect the total influence of CS programs in SDMs, but only their contribution to published articles.





From: Moher D, Liberati A, Tetzlaff J, Altman DG, The PRISMA Group (2009). Preferred Reporting Items for Systematic Reviews and Meta-Analyses: The PRISMA Statement. PLoS Med 6(7): e1000097. doi:10.1371/journal.pmed1000097

For more information, visit [www.prisma-statement.org](http://www.prisma-statement.org).

Figure A.1. Flow chart of papers selection for a) the CS papers set and b) for the entire SDMs field set. All 224 papers in a) are listed in S1 Table.

From each paper we extracted the following information: (1) year of publication; (2) focal taxa; (3) source of data or platform used (if any); (4) country and region where the data was taken; (5) scope of the SDM paper — when appearing in the title, abstract, or keywords; (6) data type used (presence-only, presence-absence, or abundance); (7)

statistical approach used, and 8) the method of collecting CS data (opportunistic data, count data, community-based monitoring, historical records, local knowledge, or trained volunteers). In order to assess the contribution of CS to SDMs over the last decade, we first compiled papers within Scopus by using the keyword “species distribution models” to obtain the number of papers in this field (Fig. 1b). This search resulted in 8576 papers.

### A1.3.3. Data analyses

*Contribution of CS to the SDMs.* We consider these papers to be the number of papers published within the SDM field in the last decade. We tested for differences in the number of CS-SDM papers and the overall number of SDM papers using linear models (with the number of papers on a log scale) that included an interaction term between the year and type of paper (CS-SDM and SDMs). We expected papers using CS data to have increased at a faster rate than the SDM field as a whole.

*Taxonomic groups.* In order to assess the representation of CS within the biological groups, we categorized each paper within the following taxonomic groups: invertebrates, plants and fungi (including bryophytes and lichens), fish, reptiles, amphibians, mammals, and birds. We used a chi-square test to compare the number of CS papers with data on each group observed to the numbers expected based on the proportion of species in each group according to the Catalogue of Life [56] (accession date April 2020). To compare the observed (CS) and expected proportions for each of the five taxonomic groups, we constructed a logistic regression model excluding the intercept to estimate the logit of the probability that a taxa  $t$  appears in a CS study:

$$\text{logit}(p_t) = \beta_t \quad (1)$$

We then calculated a Z-score from the difference between  $\beta_t$  and the logit of  $E_t$ , the expected proportion for that taxa, scaled by the standard error of  $\beta_t$ :

$$Z_t = \frac{\beta_t - \text{logit}(E_t)}{SE \beta_t} \quad (2)$$

We obtained a two-tailed p-value for the null hypothesis that the observed proportion was equal to the expected proportion by comparing  $Z_t$  to the standard normal distribution. We excluded papers that focused on more than one taxonomic group to meet assumptions of statistical independence of observations. For invertebrates, we only analyzed the taxonomic orders represented in our CS set of papers (Lepidoptera, Odonata, Hymenoptera, Coleoptera and Mollusca).

*Geographic regions.* Papers were individually classified into country and continent of origin of the CS data, including Africa, Asia, Eastern Europe, Western Europe, Oceania, North America, Central America, and South America. To assess if these regions were over or under-sampled in the CS papers set, we used a one-sample chi-square test to compare the number of CS papers in each region to the number expected based on the proportion of the Earth's land area covered by each region (from <http://www.worlddata.info>; accessed 29.11.19). Then, we compared these observed and expected proportions for each of these geographic regions. Using the same strategy as above, we constructed a logistic regression model that excluded the intercept to estimate the logit of the probability that the region  $y$  appears in a CS study:

$$\text{logit}(p_y) = \beta_y \quad (3)$$

We then calculated a  $Z$ -score from the difference between  $\beta_y$  and the logit of  $E_y$ , the expected proportion for that region, scaled by the standard error of  $\beta_y$ :

$$Z_y = \frac{\beta_y - \text{logit } E_y}{SE \beta_y} \quad (4)$$

We compared the  $Z_y$  against the standard normal distribution. We excluded papers that focused on more than one region to meet assumptions of statistical independence of the observations.

#### A1.4. Results and discussion

*Year of publication.* Our analysis indicates that the use of CS data in the peer-reviewed SDM literature has increased in frequency over the past 10 years (Fig A.2a). Numerous authors have indicated the increase in publications using different types of CS data [47, 48, 52, 57, 58], but also the growing rate of SDMs in publications [59, 60]. In our analysis, however, the use of CS in SDMs is growing approximately twice as fast as the number of papers using SDMs in general (Fig A.2b). In addition, given its peak in 2019 with 75 papers (Fig A.2a), the next few years may extend the exponential growth of the use of CS in SDMs.

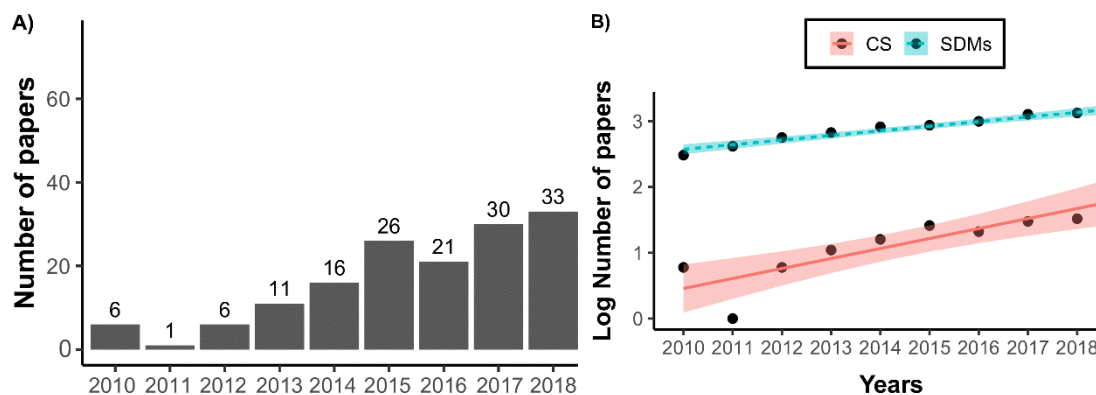


Figure A.2. (a) Annual number of papers that have used species distribution models (SDMs) with citizen science (CS) data; (b) Linear regression of the log of total papers using SDMs (blue) and the papers using CS data (red) across the 10-year period covered by our review (difference in slopes:  $-0.08$ , std. error:  $0.03$   $p=0.01$ ).

*Taxonomic groups.* As we predicted, there were marked variations among taxonomic groups, with birds ( $n = 87$ ), invertebrates ( $n = 49$ ), and mammals ( $n = 43$ ) being the main taxa studied. Reptiles ( $n = 12$ ), fish ( $n = 11$ ) and amphibians ( $n = 11$ ) received less attention (Figure A.3.a). This taxonomic preference towards bird species was previously noted by other authors [33, 47, 52].

Compared to their global richness, vertebrate groups were unequally represented in the CS papers ( $\chi^2 = 280.14$ ,  $df = 4$ ,  $p < 0.05$ ). Specifically, birds ( $Z_{birds} = 11.8$ ;  $p < 0.05$ ) and mammals ( $Z_{mammals} = 7.3$ ;  $p < 0.05$ ) were over-sampled, whereas amphibians ( $Z_{amphibians} = -2.3$ ;  $p < 0.05$ ), reptiles ( $Z_{reptiles} = -8.9$ ;  $p < 0.05$ ) and fish ( $Z_{fish} = -8$ ;  $p < 0.05$ ) were under-represented in CS papers compared to their estimated global richness in the Catalogue of Life database (Fig. 3A). We also found differences between the observed proportion of invertebrates in our CS data set and the proportion expected based on global richness ( $\chi^2 = 326.9$ ,  $df = 11$ ,  $p < 0.005$ ). Lepidoptera ( $Z_{lepidoptera} = 3.5$ ;  $p < 0.05$ ) and Odonata ( $Z_{odonata} = 5.8$ ;  $p < 0.05$ ) were over-

sampled relative to their global richness (Fig. 3B). Only Coleoptera ( $Z_{coleoptera} = -4.2$ ;  $p < 0.05$ ) were under-sampled. However, the proportion of papers on Mollusca ( $Z_{mollusca} = 0.9$ ;  $p = 0.39$ ) and Hymenoptera ( $Z_{hymenoptera} = 0.7$ ;  $p = 0.44$ ) did not differ from the proportion expected from global species richness. The remaining invertebrates orders in the Catalogue of Life database did not occur in the set of CS papers studied (Fig. 3B).

The plant and fungi group included papers involving vascular plants ( $n = 18$ ), fungi ( $n = 3$ ), lichens ( $n = 1$ ), and bryophytes ( $n = 1$ ; S1 Table). Considering the known number of species in each group according to the Catalogue of Life database (vascular plants: 348,000 species; fungus: 140,000 species; bryophytes 16,000 species), plant taxonomic groups were remarkably under-represented in CS papers. The major obstacle could be that identifying plants up to species level in the field is sometimes complex, even for expert botanists [61, 62]. Plant identification is time consuming for several families, requires significant botanical skills, and can be frustrating for non-expert volunteers [62]. In addition, there is not as strong a tradition for botanists in sharing observations using online portals, compared to animal databases. Nonetheless, plant initiatives seem to be highly attractive to the general public. Millions of observations are produced and stored in broad databases such as GBIF, iNaturalist, and in particular botanic platforms such as Pl@ntNet [63], Project Bud Burst [64], or Plant Watch Canada [65]. Several authors recommend using this information collected from volunteers for the early detection and control of invasive species [66, 67], or to improve the performance of models [67-69]. Nevertheless, our review confirms a notable under-use of plant, fungi, lichen and bryophyte public databases in the last decade in papers that model the distribution of species (10% of the total).

*Geographic coverage.* Our review identified strong geographic biases in CS sampling efforts ( $\chi^2 = 1424.5$ ,  $df = 7$ ,  $p < 0.05$ ). While Western Europe ( $Z_{Western\ Europe} = 21$ ;  $p < 0.05$ ) and North America ( $Z_{North\ America} = 8.1$ ;  $p < 0.05$ ) were over-sampled relative to their fraction of the planet's land area, Africa ( $Z_{Africa} = -4.5$ ;  $p < 0.05$ ), Asia ( $Z_{Asia} = -6.3$ ;  $p < 0.05$ ), South America ( $Z_{South\ America} = -3.6$ ;  $p < 0.05$ ) and Eastern Europe ( $Z_{Eastern\ Europe} = -3.9$ ;  $p < 0.05$ ) were under-sampled (Fig. 3C). Oceania ( $Z_{Oceania} = 1.5$ ;  $p = 0.11$ ) and Central America ( $Z_{Central\ America} = 0.1$ ;  $p = 0.89$ ) were sampled proportionally to their area. At the country level, most of the papers using CS data were from USA ( $n = 42$ ), the UK ( $n = 16$ ), Australia ( $n = 15$ ), France ( $n = 9$ ), and South Africa ( $n = 8$ ; Fig. 3D).

Such a strong geographic inclination toward Europe and North America has already been indicated by several authors [33, 35, 70]. Others also revealed the same pattern of CS being predominantly conducted in Europe and North America, but with a greater number of studies in South and Central America [17, 30] than reported in our study. This large disparity of CS-based papers is likely influenced by three factors. First, North America and Europe host more developed countries, which have more funding available for research [40], and consequently tend to publish more. Some of these countries have traditional national platforms such as the National Biodiversity Gateway (NBN) in the United Kingdom (containing around 127 million records), the Atlas of Living Australia (ALA; containing 87,179,824 records on 19<sup>th</sup> April 2020), or the Sweden Species Gateway (containing around 60,000 species). Individual country platforms share characteristics associated with successful CS programs that contributed more to global biodiversity monitoring. These platforms receive important support by national governments and are linked to well-funded institutions with active involvement of academic researchers [33]. These factors explain why the expansion of CS platforms in developing countries might be limited by the availability of necessary

infrastructures [33]. Secondly, this geographic pattern is consistent with the tradition of CS, which emerged in North America and then spread globally, primarily driven by some iconic platforms and surveys such as the Christmas Bird Count, *eBird*, and Project BudBurst [64]. Lastly, in regions with fewer papers using CS data, sharing of biodiversity data remains difficult due to a lack of an open-access culture and language barriers [33, 71]. Papers in languages other than English were not included in our review, which may introduce a bias in our coverage of geographical areas in Arab countries, Latin America, or Asia [70]. In addition to language barriers and geographic location, national security concerns and economy also fosters spatial variations in the coverage of global databases [70].



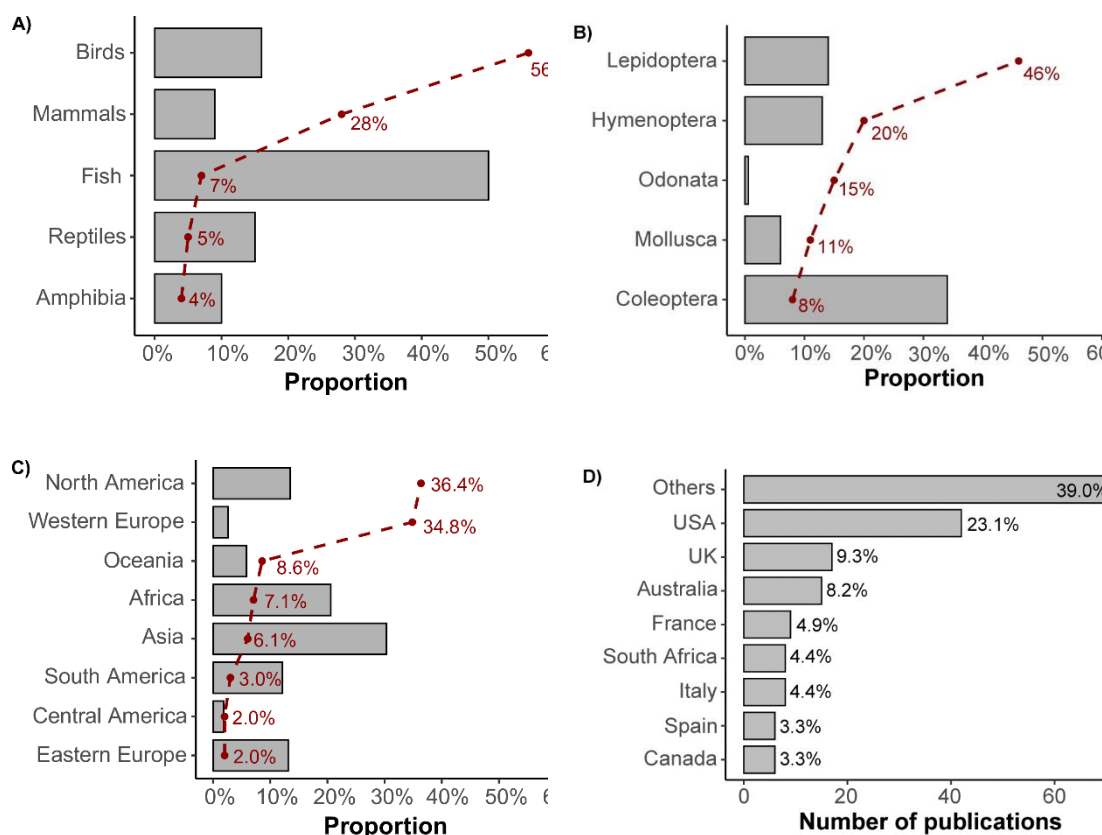


Figure A.3. Proportion of citizen science (CS) papers from this review (red dotted line) relative to the proportion of global richness in the Catalogue of Life (grey bars) by taxa, for (a) Vertebrates ( $n = 151$ ) and (b) Invertebrates ( $n = 41$ ); (c) Proportion of CS papers by data collection region (red dotted lines) relative to each region's fraction of the Earth's land area (grey bars); and (d) Proportion of CS papers by country.

*Source of data.* The main reason for the predominance of bird CS papers was the significant use of three global networks of birders: the *eBird* project, the Breeding Bird Survey (BBS), and the Southern African Bird Atlas Project (SABAP, Fig A.4). For insects, the Butterfly Monitoring Scheme (BMS) was widely used and proved to be a powerful tool to detect population trends [72]. Even if GBIF was the second most used source of information, this portal aggregates global biodiversity information from a variety of sources [33], including other CS portals listed in Fig A.4. Indeed, the major

GBIF contributor is *eBird* [33, 70]. For that reason, we cannot dissociate the GBIF database from other sources of CS in Fig 4.

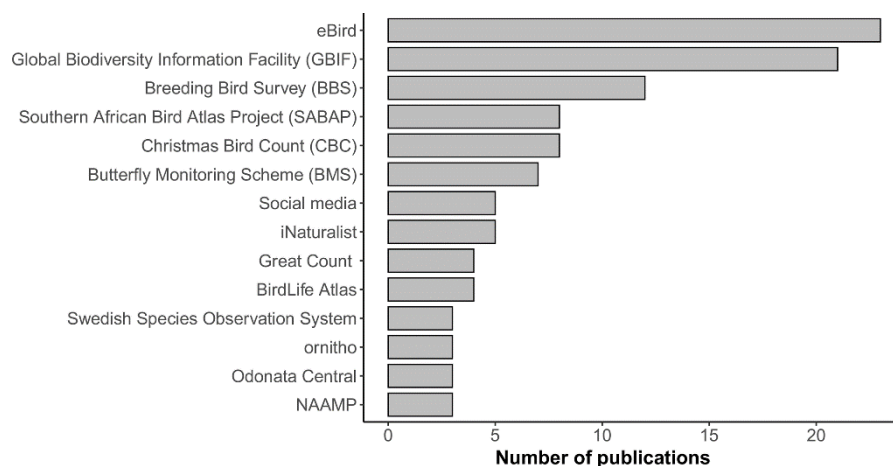


Figure A.4. Sources of information used in the papers included in the literature review ( $n = 224$ ). Only databases with three or more papers are shown. Great Count: worldwide surveys targeting birds and mammals.

*Study scope.* Although the scope and geographical coverage varied greatly among SDM papers using CS data (Figure A.5), most papers addressed issues related to conservation ( $n = 104$ ), followed by population trends ( $n = 69$ ), habitat suitability ( $n = 61$ ), and climate change ( $n = 57$ ; Figure A.5.a). Furthermore, conservation remains the central aim of these studies (Fig A.5b). The same pattern was observed for SDMs in tropical regions [1]. Most conservation papers using CS documented species of conservation concern, rare species, or poorly-studied regions [25, 73].

*Method of collecting CS data.* A number of methods of collecting CS data were reported in the set of papers we reviewed. Opportunistic data collection accounted for 38.4% of the papers (Figure A.5.c). With the growing popularity of online databases compiling occurrence data, the predominance of opportunistic data collection is not surprising [74]. Opportunistic data can be collected in many forms, including

crowdsourcing databases or historical records from museums or papers (7.4%; Figure A.5.c). The second most often used method of collection consisted of count surveys (34.3%). In contrast to opportunistic data collection, count surveys differ in the structure of the methodology used, and may involve transect counts, point counts, or censuses. Among other methods of collection, CS with trained volunteers only comprised a small proportion (11%) of the papers we reviewed, highlighting that training volunteers is not a barrier to publish. Nevertheless, projects with trained volunteers are more likely to be published than projects without training [52]. Data collection based on local knowledge (7.7%) and community-based monitoring (CBM) (2%) were rarely used (Figure A.5.c). Including local and traditional knowledge of indigenous communities in SDMs may increase the value of the data collected, the number of taxa covered and the level of engagement by participants [75, 76]. However, to fully benefit from this data collection method, researchers must be familiar with social science methods. Researchers may encounter difficulties in cross-cultural interactions, including language communication barriers and the reticence of the communities to share information about their environment (93). Despite such difficulties, both scientist and communities can benefit from building on the interest and concerns of local community members when applying local knowledge and CBM (82). Usually, the full potential of CBM programs is expressed when local communities participate actively during the entire scientific program, from the conceptual design and interpretation of results to the formulation of conclusions [75, 77]. Such cases have rarely occurred in the last decade for SDMs, probably because these programs are typically designed to monitor environmental factors rather than to collect species occurrence.

*Data type.* CS data usually include presence-only (PO) data, which are easy to collect with minimum effort. In our literature review, 118 out of 224 papers used PO data, 41 used presence-absence (PA) data, and 41 used abundance (AB) data (Figure A.5.d).

Twenty-four papers used two types of data (see A.S1 Table) and one paper used all three data types [78]. Several authors have highlighted the limitations of PO data, which confound information about habitat preferences and availability, have a strong spatial bias (more effort in sampling certain areas than others), and ignore environmental conditions associated with species occurrence [20, 26, 79]. If the probability of presence cannot be calculated, as in PO data (but see [80, 81]), the questions that can be addressed become limited and predictions are hindered [20, 82]. This issue with PO data explains the unexpectedly high proportion of PA and AB in the SDM papers we reviewed (47% in total; Figure A.5.d). Presence-absence (PA) allows the comparison of a species' occupancy between different areas or time periods [20], but PA is generally less common in CS data. The recent development of statistical techniques to estimate occupancy, especially those that account for imperfect detection, has contributed to the increasing use of PA data to infer the spatial distribution of species [79, 83, 84]. Hence, this development would explain the increasing use of PA data obtained from CS databases. Abundance (AB) data occurred in similar proportions to PA in the set of studies reviewed. Information on the number of individuals (AB) is essential to detect changes in population sizes [20]. Presence-absence (PA) and AB data can both be obtained from checklists, point-counts, or transect surveys by volunteers [79]. The large number of studies that use PA and AB data is also highlighted by the high proportions of papers that used count-surveys data (34%, Figure A.5.c), and of papers that used occupancy models, generalized linear models or Bayesian hierarchical models (37.5% of the total; Figure A.5.e).

*Statistical approach.* The statistical approaches used in the papers we reviewed were diverse, including linear regression approaches (LR, 12.7%), maximum entropy (MaxEnt, 13.3%), generalized linear models (GLM, 18.3%), occupancy models (11.2%), and generalized additive models (GAM; 10.1%; Figure A.5.e). Presence-only (PO) data were most frequently analyzed with MaxEnt ( $n = 42$ ), whereas PA data were

most frequently analyzed with occupancy models and GLM ( $n = 14$  and  $13$ , respectively). Abundance (AB) data were most often analyzed with GLM ( $n = 14$ ). The proportion of use of the statistical approaches in CS papers that we reviewed did not seem to change over time between 2010 and 2019, with the exception of Bayesian hierarchical models (BHM) and GAMs appearing in papers from 2013 onward (Figure A.5.f).

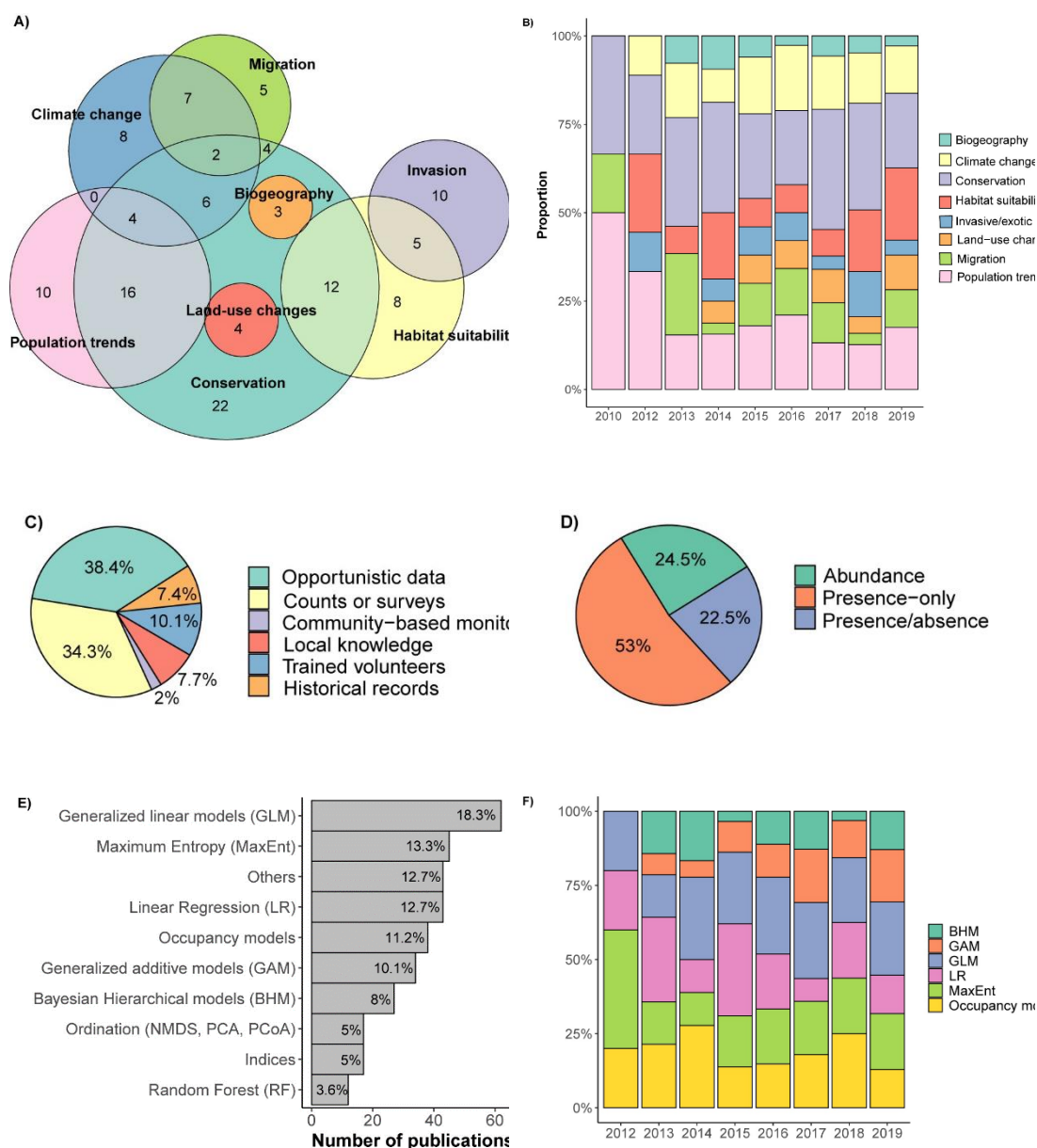


Figure A.5. Papers that have analyzed species distribution models (SDMs) using citizen science (CS) data in our literature review illustrating (a) study scope illustrated by a Venn diagram (intersections containing a single study not shown); (b) study scope per year; (c) method of collecting citizen science data; (d) data type used; (e) statistical approach and (f) statistical approach per year. All details for the 224 papers are cited in Supplementary Information S1 Table.

*Multiple data sources.* Of the 224 articles reviewed, 88 (39.7%) used multiple sources of data, merging CS with professional data. In 29 of these cases, volunteers and professional data were compared and only three studies revealed mismatches, particularly for species abundance [43, 85, 86]. The integration of CS and professional data has been a growing trend in recent years [87-89] and shows promise to improve inferences and the predictive ability of models, as well as to fill knowledge gaps for under-studied areas or poorly studied species [87-90]. This approach of combining data benefits from robust survey schemes and expands the geographic and taxonomic coverage using complementary unstructured opportunistic schemes. However, integrating highly heterogeneous data types such as large unstructured presence-only data and standardized abundance surveys, is still challenging for modelling purposes. Similar concerns exist when contemporary data are combined with historical datasets obtained from museums, grey literature or paleontological information to extend the temporal scale of a given study.

#### A1.5. Conclusion

In this review, we examined the trends and information gaps in the use of citizen science (CS) data for species distribution models (SDMs) in peer-reviewed papers over the last decade. Citizen science already makes substantial contributions to the field of SDMs, particularly for online occurrence databases. Indeed, the use of CS in SDMs increased exponentially during the last decade. However, taxonomic and geographic unevenness of CS projects for SDMs still remain [33, 40, 91]. This geographical disparity of data-sharing networks reduces the ability of researchers to assess national and international trends, particularly for mobile organisms [92].

The reviewed citizen science papers considered a wide range of taxa, regions, and countries, from numerous biomes and landscape types. This variability is mostly driven by the interest of the volunteers who collect data, which results in over and under-represented groups and regions. Volunteers favor certain charismatic taxa or habitats [93]. Thus, the challenge is to increase information for lesser-known locations and taxa. Filling this information gap may require reducing structured sampling efforts in areas already well-covered by volunteers, and enhancing the use of local knowledge or of community-based monitoring approaches.

We presented examples of the use of CS and highlighted recommendations to motivate further research, such as combining multiple data sources and promoting local and traditional knowledge. Accounting for the disparities in CS is crucial to adequately cover spatial and temporal scales, and strategically deploying formal surveys in areas or for species not covered by volunteers can be a key to better predict species distribution. Finally, researchers should not dismiss the impact they might have by contributing to citizen science projects. We strongly suggest researchers consider contributing to citizen science. The active participation of researchers in citizen science platforms (e.g., validating species identifications in iNaturalist) can increase the interest of participants in countries where we currently have little information on the distribution of certain species.

#### A1.6. Acknowledgement

This project was made possible with funding provided by the Natural Sciences and Engineering Research Council (NSERC) of Canada – Université du Québec en Abitibi-Témiscamingue (UQAT) industrial research chair on northern biodiversity in a mining



context. Earlier versions of the manuscript benefited from comments by Alexandre Nolin.

#### A1.7. Author contributions

Paper selection and data collection was completed by M. Feldman. All authors made substantial contributions to all stages including the conception, research, analysis, writing and revision of this review.

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## A1.9. Supporting information

Methodologies of 207 papers published from 2010 to 17 October 2019 that used citizen science data to model species distribution resulting from the above described search protocol in the Scopus database.

Table A.S1. Summary of methodologies of 224 articles published from 2010 to 17 October 2019 that have used citizen science data to model species distribution.

Reference	Year	Taxa	Country	Region	Scope	Method of collecting CS data	Data type	Statistical approach	Multiple data sources
Aizpurua <i>et al</i> (1)	2015	bird	Belgium	W-Eur	bio	OP	PO	MaxEnt	no
Allen <i>et al</i> (2)	2019	bird	Netherlands	W-Eur	mig, pop	OP	PO	CMR	yes
Allen <i>et al</i> (3)	2019	bird	Netherlands	W-Eur	mig, pop	OP	PO	CMR	no
Allen <i>et al</i> (4)	2019	fish	USA	N-Ame	cli, hab, pop	TR	PO	GLMM, LM	no
Alves <i>et al</i> (5)	2019	bird	Iceland	W-Eur	cli, mig, pop	OP	PO	GLMM	no
Andrew <i>et al</i> (6)	2019	fungus	NA	Europe	cli, lan	OP, HI	PO	GAMM	yes
Arthur <i>et al</i> (7)	2014	mammal	France	W-Eur	hab	TR	PO	GLM, GAM	no
Ashcroft <i>et al</i> (8)	2012	hymenoptera	Australia	Ocean	hab, inv	OP, TR	PO	MaxEnt	yes
Baker <i>et al</i> (9)	2019	bird	Australia	Ocean	cli, con, pop	CO	AB	Occupancy	no
Balestrieri <i>et al</i> (10)	2019	mam	Italy	W-Eur	lan	OP, HI	PO	Other	yes
Barrows <i>et al.</i> (11)	2016	reptile	NA	N-Ame	cli	TR	AB	Ordin	yes
Bauer <i>et al</i> (12)	2019	insect	Germany, Ecuador	W-Eur, S-Ame	inv	OP, HI	PO	Ordin, MaxEnt	yes
Beale <i>et al</i> (13)	2019	fish	Indonesia	Asia	con, cli	OP, LEK	AB	CMR	no
Belt & Krausman (14)	2012	mammal	USA	N-Ame	pop	TR	AB	N-mixt	yes
Blanc <i>et al.</i> (15)	2014	mammal	France	W-Eur	con, pop	CO	PA, AB	CMR, BHM, Occupancy	yes
Bled <i>et al.</i> (16)	2013	bird	S-Africa	Africa	bio, cli	CO	PA	BHM, GAM	no
Bonnet-Lebrun <i>et al</i> (17)	2019	mammal	Greece	W-Eur	con, hab	OP	PO	GAM	no

Table A. S1 Continued

Botella <i>et al.</i> (18)	2018	plant	France	W-Eur	inv	OP	PO	MaxEnt	no
Boyle & Sigel (19)	2015	bird	Costa Rica	C-Ame	con, cli, hab, pop	CO	PA	GLM, indices	no
Bradsworth <i>et al.</i> (20)	2017	bird	Australia	Ocean	con, hab	OP	PO	MaxEnt, indices	no
Bradter <i>et al.</i> (21)	2018	bird	Sweden	W-Eur	con, cli, hab, inv	OP	PO	MaxEnt, BHM, LR	yes
Breining <i>et al.</i> (22)	2019	reptile	USA	N-Ame	con, hab	CO	AB	BHM, N-mixt, occupancy	no
Bried & Siepielski (23)	2018	odonata	USA	N-Ame	bio	OP, CO	PO, PA	Ordin	no
Brommer <i>et al.</i> (24)	2017	mammal	Finland	W-Eur	bio, inv, pop	LEK	AB	N-mixt, BHM	no
Broms <i>et al.</i> (25)	2014	bird	S-Africa	Africa	hab	OP	PA	BHM, occupancy	no
Buldrini <i>et al.</i> (26)	2015	plant	Italy	W-Eur	con, inv, pop	OP	PO	indices	no
Bulleri & Benedetti-Cecchi (27)	2014	fish	Italy	W-Eur	con	CO	PA, AB	Ordin, occupancy	yes
Burke <i>et al.</i> (28)	2019	mammal	Mexico, USA	N-Ame	con, mig	OP, HI	PO	MaxEnt	yes
Burley <i>et al.</i> (29)	2019	plant	Australia	Ocean	cli, hab	OP	PO	MaxEnt, GAM	no
Butler <i>et al.</i> (30)	2016	reptile	USA, Mexico	N-Ame	cli	OP	PO	MaxEnt	yes
Camacho (31)	2016	bird	Chile, Peru	S-Ame	con, pop	OP	PO	GLM	no
Campbell & Engelbrecht (32)	2018	spider	S-Africa	Africa	con	OP, HI	PO	BRT	yes
Cantú-Salazar & Gaston (33)	2013	amphibian, bird, mammal	NA	America	con	CO	PO	MaxEnt	yes
Casey <i>et al.</i> (34)	2015	hymenoptera	UK, Ireland	W-Eur	cli, hab, inv, pop	OP, HI	PO	MaxEnt, ordin, LR	yes
Cerrano <i>et al.</i> (35)	2017	mollusca	NA	Europe	con, cli	CO, TR	PA, AB	Other	no
César de Sá <i>et al.</i> (36)	2019	plant	Portugal	W-Eur	inv, hab	OP	PO	GLM, GAM, RF, MaxEnt	yes
Chamberlain <i>et al.</i> (37)	2019	bird	S-Africa	Africa	lan, pop	CO	PA	Occupancy, LM	no
Champion <i>et al.</i> (38)	2018	fish	Australia	Ocean	cli, hab	LEK	PO	GAMM	no
Clare <i>et al.</i> (39)	2019	mammal	USA	N-Ame	NA	TR	PO	GLM, BHM	no

Table A. S1 Continued

Colino-Rabanal & Peris (40)	2016	mammal	Spain	W-Eur	NA	OP	PO	LR		yes
Collins <i>et al.</i> (41)	2017	odonata, lepidoptera	USA	N-Ame	hab	CO, HI	PA	MaxEnt		no
Coxen <i>et al.</i> (42)	2017	bird	USA	N-Ame	cli, mig	CO	PO	MaxEnt		yes
Crall <i>et al.</i> (43)	2015	plant	USA	N-Ame	hab, inv	TR	PO	MaxEnt		yes
Crewe <i>et al.</i> (44)	2019	lepidoptera	Canada	N-Ame	lan, mig, pop	OP, CO, CBM,	AB, PO	LM		yes
Croft <i>et al.</i> (45)	2019	mammal	UK	W-Eur	con	OP	PO	BHM		no
Crone <i>et al.</i> (46)	2019	lepidoptera	NA	N-Ame	con, cli, hab, lan, pop	CO	AB	LM		no
Crum <i>et al.</i> (47)	2017	mammal	USA	N-Ame	con, lan	CO, LEK	PA, AB	Occupancy		no
Davis <i>et al.</i> (48)	2014	bird	USA	N-Ame	hab	CO	PO	RF		no
De Coster <i>et al.</i> (49)	2015	bird	Belgium	W-Eur	lan, pop	CO	AB	GLM, LR		no
de Medeiros <i>et al.</i> (50)	2018	hymenoptera	Iberian peninsula	W-Eur	inv	OP	PO	MaxEnt		yes
De Rock <i>et al.</i> (51)	2019	mammal	Namibia	Africa	con, hab	OP	PO	MaxEnt		yes
de Sá Dechoum <i>et al.</i> (52)	2019	plant	Brazil	S-Ame	hab, inv	CO	PA	RF, BRT, GLM		no
De Solan <i>et al.</i> (53)	2018	reptile	France	W-Eur	bio, lan	OP	PO	Ordin, LR		yes
Dennhardt <i>et al.</i> (54)	2015	bird	USA	N-Ame	con, mig	CO	PO	CMR		yes
Dennis <i>et al.</i> (55)	2019	lepidoptera	Scotland	W-Eur	hab, land, pop	OP, CO	AB, PO	Occupancy, GLM		no
Dennis <i>et al.</i> (56)	2017	lepidoptera	UK	W-Eur	pop	CO	AB	GLM		yes
Derville <i>et al.</i> (57)	2018	mammal	New Caledonia	Ocean	con, hab	OP, TR	PO	BRT, GLM, MaxEnt, GAM		yes
Desaegher <i>et al.</i> (58)	2019	plant	France	W-Eur	land	CO	PA	LM, GLMM		no
Deutsch <i>et al.</i> (59)	2017	amphibian	Argentina	S-Ame	con	CO, LEK	PO	Other		yes
Dilts <i>et al.</i> (60)	2019	insect, plant	USA	N-Ame	cli, con, hab, mig, pop	OP, HI	PO	MaxEnt		yes
Dissanayake <i>et al.</i> (61)	2019	mammal	Australia	Ocean	land, pop	OP	PO	Other		no
Dörler <i>et al.</i> (62)	2018	mollusca	Spain	W-Eur	inv	TR	AB, PO	GLM		no



Table A. S1 Continued

Droz <i>et al.</i> (63)	2019	bird	Switzerland	W-Eur	con, hab, lan	OP	PO	GLM, ordin, GAM,	yes
Dunn (64)	2019	bird	NA	N-Ame	mig, pop	CO	AB	GAM, GLM	yes
Dyderski <i>et al.</i> (65)	2018	plant	NA	Europe	con, cli, mig, hab, inv	OP	PO	MaxEnt, ordin-PCA	yes
Edgar <i>et al.</i> (66)	2018	fish	Australia	Ocean	cli, pop	CO, LEK	AB	GLM	yes
Evangelista <i>et al.</i> (67)	2018	mammal	Somaliland	Africa	con, hab	LEK	PO	BRT, MaxEnt	no
Evans <i>et al.</i> (68)	2019	coleptera	NA	N-Ame	cli	CO, HI	AB	LR	no
Fabrizio (69)	2019	mammal	Italy	W-Eur	con, hab	OP	PO	MaxEnt	no
Fink <i>et al.</i> (70)	2010	bird	USA	N-Ame	mig	CO	PA	STEM	no
Flaherty (71)	2019	mammal	Ireland	W-Eur	inv, lan	OP	PO	Other	yes
Flesch & Belt (72)	2017	mammal	USA	N-Ame	NA	TR	PO	Occupancy	yes
Fournier <i>et al.</i> (73)	2017	bird	NA	N-Ame	con, mig	LEK	PO	Other	no
Gange (74)	2019	fungus	UK, Switzerland	W-Eur	bio, con, hab, pop	OP	AB	GAM, indices	yes
Girado-Beltrán <i>et al.</i> (75)	2015	plant	Spain	W-Eur	inv	OP, HI	PO	GLMM, LR	yes
Girardello (76)	2019	lepidoptera	NA	Global	con	OP	PO	BHM, GLM	no
Giroux <i>et al.</i> (77)	2016	bird	Canada	N-Ame	cli, mig, pop	CO	PA	LR	no
Goodenough (78)	2014	bird	UK	W-Eur	con, hab, mig	TR	PO	LR	no
Goodwin <i>et al.</i> (79)	2017	mammal	UK	W-Eur	con, pop	CO, TR, CBM	PO, AB	GAM, GLM	no
Gorta (80)	2019	bird	Australia	Ocean	con, cli, pop	CO	AB, PA	GAM, GLM	no
Goswami <i>et al.</i> (81)	2015	mammal	India	Asia	lan	TR	PO	Occupancy,	no
Grüss <i>et al.</i> (82)	2019	fish	NA	Gulf of Mexico	NA	CO	PO	GLM, GAM	yes
Hackworth (83)	2019	bird	USA	N-Ame	hab, lan, pop	OP, HI	PO	Other	yes
Hahn <i>et al.</i> (84)	2016	hemiptera	USA	N-Ame	NA	OP	PO	LR	no
Hallworth <i>et al.</i> (85)	2015	bird	NA		bio, con, mig	CO	AB	N-mixt	no

Table A. S1 Continued

Hansen <i>et al.</i> (86)	2015	bird	Australia	Ocean	mig, pop	CO	AB	LR	no
Hart <i>et al.</i> (87)	2018	hymenoptera	UK	W-Eur	bio	OP	PO	GLMM	no
Hertzog <i>et al.</i> (88)	2014	coleoptera	France, Iberian peninsula	W-Eur	lan, pop	OP, HI	PO	BRT, MaxEnt	no
Hieb <i>et al.</i> (89)	2017	mammal	NA	Gulf of Mexico	con, lan	OP, LEK	PO	LR	no
Higa <i>et al.</i> (90)	2015	bird	Japan	Asia	NA	OP	PO, PA	LR, occupancy	yes
Hill et Lloyd (91)	2017	bird	USA, Canada	N-Ame	con, cli, pop	CO	AB	N-mixt	no
Horns <i>et al.</i> (92)	2018	bird	NA	N-Ame	con, pop	OP, CO	PA	LR	no
Horton (93)	2019	bird	NA	Gulf of Mexico	cli, mig	CO	AB	RF, STEM, GAMM, GAM	no
Hosseini (94)	2019	mammal	Iran, Turmekistan, Afganistan	Asia	con, hab	OP, LEK	PO	MaxEnt	yes
Howes (95)	2019	bird	NA	Africa	hab, mig, pop	CO, HI	AB	GLMM	yes
Hugo & Altwegg (96)	2017	bird	S-Africa, Lesotho, Swaziland	Africa	NA	OP, TR	PO	LR, ordin, GLMM	no
Humphreys (97)	2019	bird	USA	N-Ame	bio, con, hab, mig	CO	PA, AB	BHM	no
Ivanova (98)	2019	bird	S-Africa	Africa	inv, hab, pop	CO	PO, AB	GLM	no
Jackson <i>et al.</i> (99)	2015	bird	Canada	N-Ame	cli, con, hab	OP, CO, LEK	PO	RF, BRT, GLM, MaxEnt, GAM	yes
Jiguet <i>et al.</i> (100)	2012	bird	NA	Europe	cli, con, pop	CO, TR, CBM	AB	CMR, LR	no
Jiménez-Valverde (101)	2019	spider	Spain	W-Eur	con	OP	PO	GAM, LR	yes
Johnston <i>et al.</i> (102)	2018	bird	NA	NA	pop	CO	PA	GAM, Occupancy	no
Jones <i>et al.</i> (103)	2013	mammal	NA	Europe	NA	OP	PO	MaxEnt	no
Kalle <i>et al.</i> (104)	2018	bird	S-Africa	Africa	con, cli, lan	CO	PA	Occupancy	no
Kamp <i>et al.</i> (105)	2016	bird	Denmark	E-Eur	con, pop	CO, HI	AB	Occupancy, GLMM	yes
Kasahara & Koyama(106)	2010	bird	Japan	Asia	pop	CO, CBM	AB	GLM, indices	no
Kery <i>et al.</i> (107)	2010	odonata	Switzerland	W-Eur	NA	CO	PA	GLM, Occupancy	no

Table A. S1 Continued

Kery <i>et al.</i> (108)	2010	bird	Switzerland	W-Eur	pop	OP	PA	Occupancy	yes
Khwaja (109)	2019	mammal	NA	Africa, Asia	con	OP	PO	Occupancy	yes
Koparde (110)	2019	bird	NA	Eurasia	con, bio, cli, hab	OP	PO	MaxEnt	yes
Kreling (111)	2019	mammal	USA	N-Ame	lan	OP	PO	LR	no
Krolikowska <i>et al.</i> (112)	2018	bird	Poland	W-Eur	con, hab, pop	TR	PA	RF	yes
La Sorte <i>et al.</i> (113)	2017	bird	NA	C-Ame	cli, lan, mig, pop	CO	PA	BRT, STEM, GAMM	no
La Sorte <i>et al.</i> (114)	2019	bird	NA	N-Ame	cli, mig	CO	AB	GAMM, STEM, GLM	no
La Sorte <i>et al.</i> (115)	2015	bird	USA	N-Ame	con, mig, cli	CO	PA	STEM, GAMM	no
La Sorte <i>et al.</i> (116)	2016	bird	NA	N-Ame	cli, mig	CO	PA	NA	no
Laughlin <i>et al.</i> (117)	2016	bird	USA	N-Ame	mig	CO	PA	STEM, GAM, LR	yes
Laughlin <i>et al.</i> (118)	2013	bird	NA	N-Ame	hab, mig	CO	PA	LR	yes
Lees & Martin (119)	2015	bird	Brazil	S-Ame	bio, con, lan	OP, HI	PO	LR	yes
Lin <i>et al.</i> (120)	2015	lepidoptera	Taiwan	Asia	NA	OP	PO	MaxEnt	yes
Long (121)	2019	bird	USA	N-Ame	con, hab, mig	CO	PO	Other	no
Looney (122)	2019	hymenoptera	NA	N-Ame	hab	OP	PO	MaxEnt	no
Louvrier <i>et al.</i> (123)	2018	mammal	France	W-Eur	con	OP, CO, TR	PO	Occupancy	yes
Louvrier <i>et al.</i> (124)	2019	mammal	NA	W-Eur	con	OP, LEK	PO	Occupancy	yes
Luigi Nimis <i>et al.</i> (125)	2018	plant	Italy	W-Eur	inv, lan, mig	OP	PO	Ordin	yes
Luizza <i>et al.</i> (126)	2016	plant	USA	N-Ame	cli, hab, inv	OP, LEK	PO	MARS, RF, GLM, MaxEnt	no
Luizza <i>et al.</i> (127)	2016	plant	Ethiopia	Africa	hab, inv	CBM	PO	MaxEnt, indices	yes
Lyon (128)	2019	fish	Australia	Ocean	hab, pop	LEK	AB	CMR, BHM	yes
MacPhail (129)	2019	hymenoptera	Canada	N-Ame	con, pop	OP, CO, HI	PO, AB	LR	yes
Mair <i>et al.</i> (130)	2017	fungus	Sweden	W-Eur	con, lan	OP, TR	PO	GLM, MaxEnt, Occupancy	no

Table A. S1 Continued

Marsh <i>et al.</i> (131)	2019	amph	NA	N-Ame	NA	CO	PA	LR	no
Marsh <i>et al.</i> (132)	2017	amph	USA	N-Ame	bio, con, lan	CO	PA	GLM, Occupancy	no
Martin (133)	2019	bird	Iberian Peninsula	W-Eur	mig, pop	CO, TR	PA, AB	LR	yes
Martin (134)	2019	plant	France	W-Eur	cli, hab	CO, CBM	PA, AB	BHM	no
Marx & Quillfeldt (135)	2018	bird	Germany	W-Eur	con, hab	CO, OP	PO, PA	BioClim, RF, CART, GLM	no
Mason <i>et al.</i> (136)	2018	lepidotpera	UK	W-Eur	bio, con	CO, OP	AB	LR, indices	no
Massimino <i>et al.</i> (137)	2018	mammal	UK	W-Eur	con, pop	OP	AB	GAM	no
McCoshum <i>et al.</i> (138)	2016	lepidotpera	USA	N-Ame	con, mig	OP	PO	MaxEnt	no
McDuffie (139)	2019	bird	USA	N-Ame	pop	OP	PO, AB	GLMM	no
Meehan (140)	2019	bird	NA	N-Ame	pop	CO	AB	BHM	no
Melero <i>et al.</i> (141)	2016	lepidotpera	Spain	W-Eur	pop	CO	AB	BHM, GAMM, GLMM, GLM	no
Miller <i>et al.</i> (142)	2016	bird	USA	N-Ame	con, hab, lan, pop	CO, TR	AB	N-mixt, Occupancy	no
Mims <i>et al.</i> (143)	2018	amphibian, reptile, fish	USA	N-Ame	cli, con	OP, HI	PO	RF, ordin, CART, indices	yes
Mingozzi <i>et al.</i> (144)	2013	bird	Italy	W-Eur	cli, mig	OP	AB	LR	no
Mohanty & Measey (145)	2018	amphibian	India	Asia	inv	CO, LEK	PA	Occupancy	no
Mohanty <i>et al.</i> (146)	2018	bird, mollusca	India	Asia	inv	LEK	PA	Occupancy	no
Molinari-Jobin <i>et al.</i> (147)	2018	mammal	NA	W-Eur	con	OP, TR	PO	Occupancy	no
Monsarrat <i>et al.</i> (148)	2018	mammal	S-Africa	Africa	con	HI	PO	Indices	no
Morii & Nakano (149)	2017	mollusca	Japan	Asia	inv	OP, LEK	PO	NA	no
Mosnier (150)	2019	reptile	Canada	N-Ame	cli, hab	OP, CO, LEK	PO	GAM	yes
Musilová <i>et al.</i> (151)	2018	bird	Czech Rep	E-Eur	cli, hab, pop	CO	AB	LR	no
Musilová <i>et al.</i> (152)	2018	bird	Czech Rep	E-Eur	con, hab, pop	CO	AB	LR, GLMM	no
Nagy <i>et al.</i> (153)	2012	bird	USA	N-Ame	hab	CO, TR	PA	Occupancy	yes

Table A. S1 Continued

Newson <i>et al.</i> (154)	2016	bird	UK	W-Eur	con, cli, pop	CO	PA, AB	GAM	yes
Ortega-Álvarez <i>et al.</i> (155)	2018	bird	Mexico	N-Ame	lan	CO, LEK, CBM	PO	Occupancy	no
Pace (156)	2019	mammal	Italy	W-Eur	con, hab	OP, CO	PO	MaxEnt, GLM	yes
Pacifici (157)	2019	bird	USA	N-Ame	NA	CO	PA	Occupancy	yes
Pagel <i>et al.</i> (158)	2014	lepidoptera	UK	W-Eur	bio, con, pop	OP, CO	PO, PA, AB	BHM	no
Paukkunen <i>et al.</i> (159)	2018	hymenoptera	Finland	W-Eur	con, hab, pop	OP, HI	PO, AB	Other	yes
Peach <i>et al.</i> (160)	2017	bird	USA	N-Ame	con, pop	OP	PO	Occupancy, BHM	no
Penã-Aguilera (161)	2019	spider	Iberian peninsula	W-Eur	cli	OP	PO	Ordin	yes
Péron & Altwegg (162)	2015	bird	S-Africa	Africa	NA	CO	PA	Occupancy, ordin	no
Péron & Altwegg (163)	2015	bird	S-Africa, Lesotho, Swaziland	Africa	cli, con, land, pop	CO	PA	Occupancy	no
Pescott <i>et al.</i> (164)	2015	lichen, bryophyte, lepidoptera	UK	W-Eur	NA	OP	PO	LR	no
Phillips <i>et al.</i> (165)	2017	fish	NA	Global	bio, con, hab, mig	OP	PO	MARS, RF, CART, GLM, GAM	no
Pillay <i>et al.</i> (166)	2014	mammal, bird, reptile	India	Asia	bio, con	LEK	PA	Occupancy	yes
Plummer <i>et al.</i> (167)	2015	bird	UK	W-Eur	cli, con, mig	CO	PA	GLMM	no
Prodon <i>et al.</i> (168)	2017	reptile, amphibian	France	W-Eur	cli, mig	OP	PO	GLM, GAM	no
Puan (169)	2019	bird	Malasya	Asia	lan	CO	AB	GLMM	no
Purves (170)	2019	bird	NA	N-Ame	con, lan, pop	CO, TR	PO	Occupancy	no
Ralston <i>et al.</i> (171)	2015	bird	USA	N-Ame	con, pop	CO	PA	LR	no
Rapacciuolo <i>et al.</i> (172)	2017	odonata	USA	N-Ame	con, pop	OP, HI	PO	BHM	yes
Reed <i>et al.</i> (173)	2017	mammal	USA	N-Ame	hab	OP	PA	GLM, LR	yes
Ribeiro (174)	2019	bird	Portugal	W-Eur	NA	OP	PO	GLM	no
Richardson <i>et al.</i> (175)	2015	plant	New Zealand	Ocean	con	OP	PO	Ordin, GLM	yes
Robinson <i>et al.</i> (176)	2018	bird	USA	N-Ame	con	CO	PO	RF, CART	no
Robinson <i>et al.</i> (177)	2014	bird	UK	W-Eur	con, pop	CO	AB	GLM	no

Table A. S1 Continued

Rodewald (178)	2019	bird	Colombia, Ecuador, Peru	S-Ame	con, mig, pop	CO	AB	STEM	no
Rodhouse <i>et al.</i> (179)	2015	mammal	USA	N-Ame	con, pop	OP, CO	PO	BHM	yes
Ruete <i>et al.</i> (180)	2017	bird	Sweden	W-Eur	mig	OP	PO	BHM	no
Ruiz-Gutierrez <i>et al.</i> (181)	2016	amphibian	NA	N-Ame	NA	CO	PA	BHM	no
Rutten (182)	2019	mammal	Belgium	W-Eur	hab	OP, LEK	PO	MaxEnt	no
Sadoti <i>et al.</i> (183)	2013	bird	USA	N-Ame	NA	OP	PO	Occupancy, LR	no
Santika <i>et al.</i> (184)	2014	mammal	Australia	Ocean	cli, con, lan	OP	PO	Occupancy	no
Sardà-Palomera <i>et al.</i> (185)	2012	bird	Spain	W-Eur	con	OP, CO	PO, PA	MaxEnt	no
Sequeira <i>et al.</i> (186)	2014	mammal	Australia	Ocean	cli, con, hab	CO	PA	GLMM, GLM	no
Sewell <i>et al.</i> (187)	2010	amphibian	UK	W-Eur	con	CO, TR	PA	Occupancy	yes
Sillero <i>et al.</i> (188)	2014	amphibian, reptile	NA	Europe	bio, con, cli	OP	PO	Indices	yes
Silva <i>et al.</i> (189)	2016	coleoptera	Brazil	S-Ame	bio, con	OP	PO	MaxEnt, ordin	yes
Smale (190)	2019	plant	UK	W-Eur	con, hab	TR, CO	PA, AB	GLMM, Ordin	no
Snäll <i>et al.</i> (191)	2011	bird	Sweden	W-Eur	NA	CO	PO	BHM, indices	yes
Soroye <i>et al.</i> (192)	2018	lepidoptera	Canada	N-Ame	cli	OP	PO	LR	yes
Soykan <i>et al.</i> (193)	2016	bird	NA	N-Ame	cli, con, lan, pop	CO	AB	GLM, BHM	yes
Stefanescu <i>et al.</i> (194)	2013	lepidoptera	NA	Western Paleoartic	mig	CO	AB	GLM	yes
Summer (195)	2019	hymenoptera	UK	W-Eur	NA	OP, TR	PO	GLM, GAM	yes
Sun (196)	2019	mam	USA	N-Ame	con	OP	PA	Occupancy, CMR	yes
Supp <i>et al.</i> (197)	2015	bird	NA	N-Ame	cli, mig	CO	PO	GAMM	no
Sweet (198)	2019	plant	USA	N-Ame	cli, con	CO	PO	MaxEnt	yes
Szabo <i>et al.</i> (199)	2010	bird	Australia	Ocean	con, pop	CO, HI	PO	LR	no
Termaat (200)	2019	odonata	NA	W-Eur	cli	OP	PO	Occupancy	no
Thorson <i>et al.</i> (201)	2014	fish	USA	N-Ame	hab, pop	OP, LEK	AB	GLMM	no
Tiago <i>et al.</i> (202)	2017	amphibian, reptile	Portugal	W-Eur	cli	OP	PO	GLMM, GAM	yes

Table A. S1 Continued

Titeux <i>et al.</i> (203)	2017	lepidoptera	NA	Europe	cli, con	OP	PO	GAM	no
Todd <i>et al.</i> (204)	2016	amphibian, reptile	USA	N-Ame	con, lan	OP	PO	Other	no
Tonachella <i>et al.</i> (205)	2012	mammal	USA	N-Ame	pop	CO	AB	GLMM	no
Tulloch <i>et al.</i> (206)	2013	bird	Australia	Ocean	con	CO	PO	GLM, LR	yes
Tye <i>et al.</i> (207)	2017	mammal	USA	N-Ame	con	OP	PO	MaxEnt	yes
van Strien <i>et al.</i> (208)	2013	odonata	NA	Europe	con, pop	OP	PA	Occupancy, BHM	yes
van Strien <i>et al.</i> (209)	2013	odonata, lepidoptera	Netherlands	W-Eur	con, pop	OP	PA	Occupancy	no
van Strien <i>et al.</i> (210)	2019	lepidoptera	Netherlands	W-Eur	hab, pop	OP, HI, CO	PO	LR	yes
Vantieghem <i>et al.</i> (211)	2017	lepidoptera	Belgium	W-Eur	con	OP	PO	GLM, MaxEnt, GAM	yes
Veran <i>et al.</i> (212)	2016	coleoptera	France	W-Eur	inv	OP	PA	BRT, Occupancy	no
Villeneuve (213)	2019	mollusca	Dominica Rep	C-Ame	mig	TR	PO	CMR, LR	no
Wang (214)	2019	plant	China	Asia	cli, inv	OP	PO	MaxEnt	no
White <i>et al.</i> (215)	2015	fish	Costa Rica	C-Ame	pop	CO	AB	GLMM	no
Widenfalk <i>et al.</i> (216)	2014	lepidoptera, hemiptera	Sweden	W-Eur	con, inv	OP	PO, AB	MaxEnt, indices	no
Williams <i>et al.</i> (217)	2016	bird	Australia	Ocean	con, pop	CO	AB	LR, GLM	no
Wilson <i>et al.</i> (218)	2015	lepidoptera	UK	W-Eur	cli	CO, TR	AB	LR	no
Wine <i>et al.</i> (219)	2015	mammal	USA	N-Ame	inv	OP	PO	LR	no
Yue <i>et al.</i> (220)	2019	reptile	Taiwan	Asia	con, hab	OP	PO	MaxEnt	no
Zapponi <i>et al.</i> (221)	2017	coleoptera	Italy	W-Eur	cli, con	CBM, OP	PO	Other	yes
Zeng <i>et al.</i> (222)	2018	bird	China	Asia	con	TR	PA	RF	no
Zhang & Vincent (223)	2017	fish	China	Asia	con	LEK	PO	MaxEnt	yes
Zub <i>et al.</i> (224)	2018	mammal	NA	Europe	cli, con, hab	OP	PA	GLMM	no

Regions

*W-Eur*: Western Europe; *E-Eur*: Eastern Europe; *N-Ame*: North America; *S-Ame*: South America; *C-Ame*: Central America.

Scope

*Con*: conservation; *cli*: climate change, *hab*: habitat suitability; *inv*: invasion; *lan*: land-use changes; *pop*: population trends, *mig*: migration; *bio*: biogeography.

Method of collecting CS data

*CO*: counts or surveys; *OP*: opportunistic data; *LEK*: local knowledge; *TR*: trained volunteers; *CBM*: community-based monitoring; *HIS*: historical records.

Data type

*PO*: presence-only; *PA*: presence-absence; *AB*: abundance.

Statistical approach

*Indices*: Indices of richness, abundance and others; *LR*: Multiple regression approaches; *GLM*: Generalized linear models; *MaxEnt*: maximum-entropy; *Ordin*: Ordination (NMDS, PCA, PCoA, PERMANOVA); *GAM*: Generalized Additive Models; *BHM*: Bayesian Hierarchical models; *RF*: Random Forest; *GLMM*: Generalized Linear mixed models; *BRT*: Boosted Regression trees; *N-mix*: N-mixture models; *GAMM*: Generalized additive mixed modelling; *CART*: classification and regression trees; *CMR*: Capture-mark-recapture models; *STEM*: The spatiotemporal exploratory model; *MARS*: Multivariate adaptive regression splines; *NN*: Neural networks; *MET*: mixed-effects



trees; *GWR*; Geographically-weighted regression; *BioClim*: bioclimate analysis and prediction system.

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## ANNEXE B

### EATING FROGS IN THE NORTH: ATTEMPTED PREDATION OF *TRINGA* *MELANOLEUCA* ON BOREAL LITHOBATES ADULT FROGS

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Published in *Herpetology Notes*, volume 15: 399-402 (2022)

*Keywords:* Greater Yellowlegs, Anurophagy, shorebirds, feeding behaviour, Northern Quebec, camera trap.

Trophic interactions between birds and amphibians are frequent (Cook, 1987; Toledo et al., 2007; Wells, 2010), but rarely observed in the wild and are therefore poorly documented in the literature. Given this challenge, field observations made indirectly by passive monitoring equipment such as camera traps can provide valuable complementary information on elusive animal behaviours including foraging and predation events (e.g., da Silva et al., 2019; Galetti et al., 2016; Luciano et al., 2020). Predation by omnivorous and carnivorous birds on anurans generally occurs on eggs, larvae, and tadpoles rather than on adults (González-Salazar et al., 2014; Toledo et al., 2007; Wells, 2010).

Among birds, one plausible but uncommon predator of anurans is the Greater Yellowlegs (*Tringa melanoleuca*, Gmelin, 1789). The Greater Yellowlegs is a medium-sized shorebird with a wide geographic distribution. It breeds in northern latitudes, in central Canada and southern Alaska, and migrates south during the winter to non-breeding areas across Central and South America (Swarth, 1988; Elphick and Tibbitts, 2020). Despite the widespread distribution of Greater Yellowlegs, general knowledge on the diet is based on the stomach contents of a limited number of individuals and anecdotal observations (Brooks, 1967b; Hicklin and Spaans, 1993; Elphick and Tibbitts, 2020). Greater Yellowlegs are mostly generalists and their diet may vary among regions, but includes aquatic insects, small fish, crustaceans, worms, and a variety of terrestrial invertebrates (Brooks, 1967a; Swarth, 1988; Elphick and Tibbitts, 2020). There are also infrequent observations of the species feeding on dragonflies (Anderson and Holmes, 2019; Brooks, 1967b), crabs (Garcia and Paterlini, 2009), juvenile toads (Hickling and Spaans, 1993), and plant material such as seeds or

berries (Brooks, 1967a; Elphick and Tibbitts, 2020). However, most of this dietary information excludes the feeding ecology of the species in their northern breeding latitudes. Thus, new records of unusual feeding events may improve our understanding of their role in the food web.

In this note, we report two events of predation on frogs by the Greater Yellowlegs recorded with camera traps. On the 1st of July 2018, a camera trap in a peatland pond in the James Bay region of Northern Quebec, Canada (52.6468 °N, 72.1903 °W) recorded a Greater Yellowlegs biting a frog and grabbing it with its beak (Fig. B.1a). The second event occurred on the 24th of May 2019 (49.6038 °N, 79.2913 °W), when a frog was caught by a Greater Yellowlegs in a different peatland pond (Fig. B.1b). The bird showed a dunking behaviour, holding the frog and then dipping it repeatedly into the water at the edge of the pond (Fig. B.2). We acknowledge that pictures and videos recorded only show birds with frogs held in their beaks – they do not show the whole process up to ingestion. Even if firm evidence of the birds swallowing the frogs is lacking, these observations strongly suggest that predation on adult frogs by Greater Yellowlegs is possible.

Anurans are preyed upon by a wide variety of vertebrates including birds (Lopes et al. 2005; Poulin et al. 2001; Toledo, 2003). Among birds, larger species such as herons, bitterns, and storks are reported most frequently as anuran predators (Wells, 2010; Menkhorst, 2012; Andrade et al., 2013). To the best of our knowledge, there are no written published reports of shorebirds capturing adult frogs, so these attempted predation events are unusual according to the known biology of the species. We report what is one of the first documented evidence of the Greater Yellowlegs as an apparently opportunistic predator upon adult anurans in their breeding sites in the James Bay region of Northern Quebec, Canada.

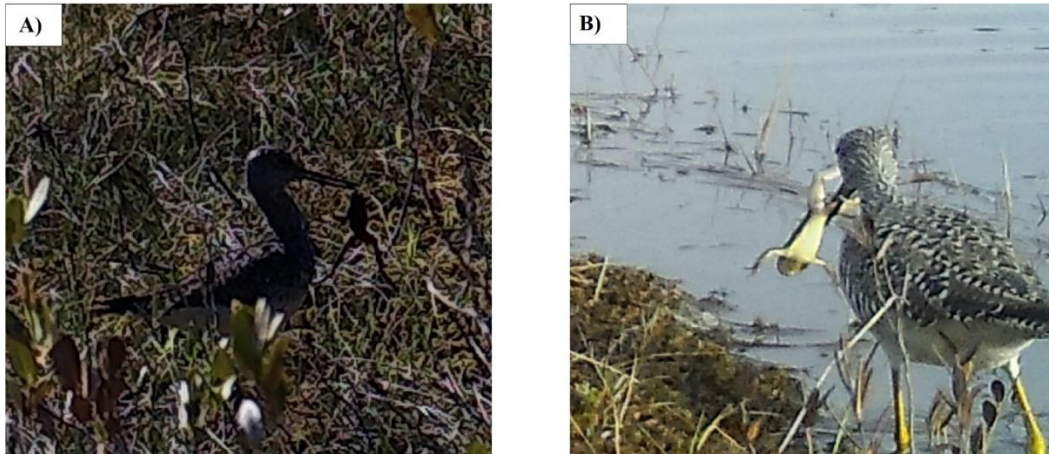


Figure B.1. Records of attempted predation of Greater Yellowlegs (*Tringa melanoleuca*) on *Lithobates* spp. A) *T. melanoleuca* holding a frog, probably a wood frog (*Lithobates sylvaticus*), green frog (*L. clamitans*), or mink frog (*L. septentrionalis*). B) Probable predation on green frog (*L. clamitans*) or mink frog (*L. septentrionalis*). Both events were recorded in the James Bay region of Northern Quebec, Canada surrounding a peatland pond.

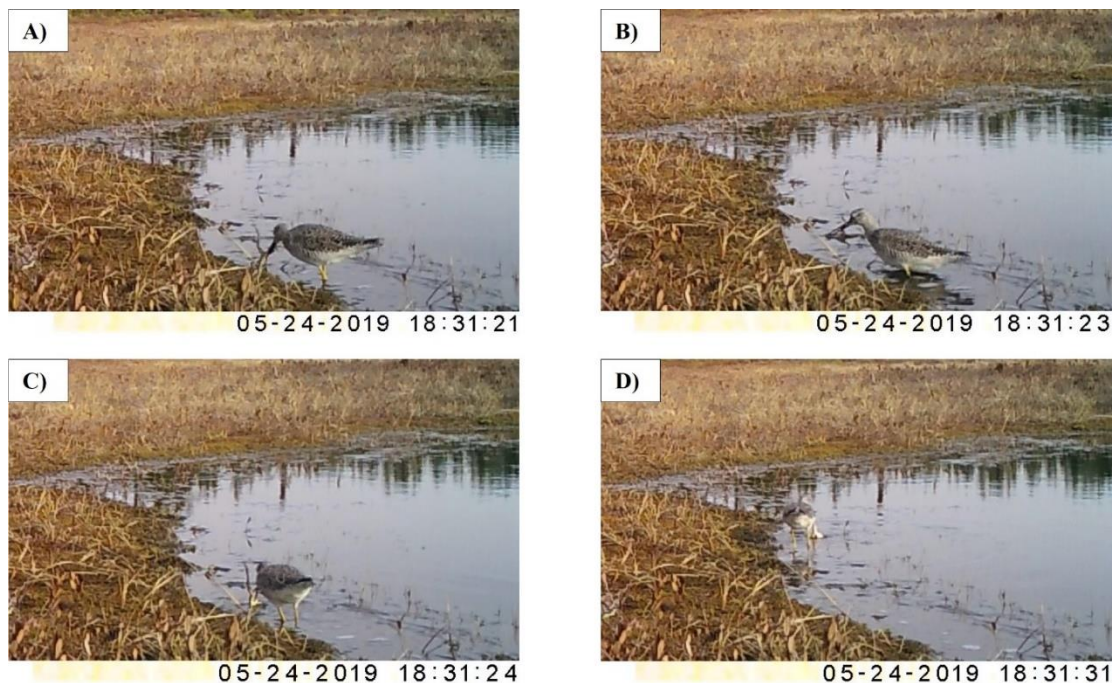


Figure B.2. A sequence of dunking behaviour and presumed predation by a Greater Yellowlegs (*Tringa melanoleuca*) on a green frog (*Lithobates clamitans*) or mink frog (*L. septentrionalis*) in a peatland pond on 24 May 2019 in the James Bay region of Northern Quebec, Canada. The video recording was deposited at <https://doi.org/10.6084/m9.figshare.17912462>.

The difficulty of monitoring unusual trophic interactions in the wild makes our observations noteworthy for two reasons. First, there are no published observations of shorebirds eating adult frogs. Secondly, it is only the second report of a Greater Yellowlegs showing dunking behaviour. The dunking behaviour consists of complete submersion of food under water before ingestion. Dunking enables birds to swallow food picked up in mud, as well as unpalatable or toxic prey (Drinkwater et al., 2017). Although this behaviour has been reported for at least 25 species (Morand-Ferron et al., 2004), dunking was thought to occur relatively infrequently in shorebirds (Morand-Ferron et al., 2004; Nol et al., 2014). However, a similar dunking observation was



already reported for a relative of the Greater Yellowlegs, the Redshank (*Tringa totanus*) feeding on young edible frogs (*Pelophylax kl. esculentus*) of less than 2 cm (Henry et al., 1998). Given a previous observation of dunking behaviour on crickets also involving the Greater Yellowlegs (Jordheim 1965), as well as a report of dunking food items collected in mud involving the Common Sandpiper (*Tringa hypoleucos*), our additional report suggests that dunking behaviour may be more common than expected among *Tringa* shorebird species.

Documentation of novel predation events such as these can help understand the interactions between different species occurring in boreal peatlands. Such acidic habitats may be poor in invertebrates (Batzer et al., 2016). If the density of the preferred prey becomes scarce, shorebirds may feed more intensively on other organisms (Davis and Smith, 2001). Our data reinforce that *T. melanoleuca* exhibit an uncommon diet flexibility and feeding behaviour such that frogs potentially represent a seasonal component of their diet during the breeding season in this northern region.

Although both observations are the result of an opportunistic event, the potential for shorebird-frog interaction will only be confirmed with additional data on their diet. We hope these records provide insights into the natural history of *T. melanoleuca* and *Lithobates* frogs, highlighting the existence of potentially important trophic connections between shorebirds and boreal frogs.

Acknowledgment. We thank anonymous reviewers from @*Corrige-moi* UQAT students' group for critical revision and suggestions on the manuscript. We acknowledge the financial assistance by the Natural Sciences and Engineering Research Council (NSERC) of Canada—Université du Québec en Abitibi-Témiscamingue (UQAT) industrial research chair on northern biodiversity in a mining context.

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