



Université du Québec
à Rimouski

Quantification de l'importance du climat dans la rétraction vers le nord de l'aire de distribution du caribou forestier au Québec depuis 1850

Mémoire présenté

dans le cadre du programme de maîtrise en gestion de la faune et de ses habitats

en vue de l'obtention du grade de maître ès sciences

PAR

© CHLOÉ MORINEAU

Avril 2023

Composition du jury :

Guillaume de Lafontaine, président du jury, Université du Québec à Rimouski

Martin-Hugues St-Laurent, directeur de recherche, Université du Québec à Rimouski

Yan Boulanger, codirecteur de recherche, Ressources Naturelles Canada

James Schaefer, examinateur externe, Trent University

Dépôt initial le 12 décembre 2022

Dépôt final le 5 avril 2023

UNIVERSITÉ DU QUÉBEC À RIMOUSKI
Service de la bibliothèque

Avertissement

La diffusion de ce mémoire ou de cette thèse se fait dans le respect des droits de son auteur, qui a signé le formulaire « *Autorisation de reproduire et de diffuser un rapport, un mémoire ou une thèse* ». En signant ce formulaire, l'auteur concède à l'Université du Québec à Rimouski une licence non exclusive d'utilisation et de publication de la totalité ou d'une partie importante de son travail de recherche pour des fins pédagogiques et non commerciales. Plus précisément, l'auteur autorise l'Université du Québec à Rimouski à reproduire, diffuser, prêter, distribuer ou vendre des copies de son travail de recherche à des fins non commerciales sur quelque support que ce soit, y compris l'Internet. Cette licence et cette autorisation n'entraînent pas une renonciation de la part de l'auteur à ses droits moraux ni à ses droits de propriété intellectuelle. Sauf entente contraire, l'auteur conserve la liberté de diffuser et de commercialiser ou non ce travail dont il possède un exemplaire.

REMERCIEMENTS

Je tiens à remercier en premier lieu Martin-Hugues St-Laurent qui accompagne mes premiers pas dans le monde de la recherche depuis 3 ans déjà. Je me plais souvent à raconter à qui me questionne la manière improbable dont j'ai atterri dans ton équipe à l'automne 2019, ne connaissant quasiment rien du Laboratoire de gestion de la faune terrestre, de l'Université du Québec à Rimouski, ni même du Québec. Un genre d'alignement chanceux des astres qui change profondément une trajectoire de vie, assurément. Tes encouragements et ton soutien continu sont pour beaucoup dans l'expérience très positive et au combien enrichissante qu'a été ma maîtrise. Je te suis reconnaissante pour toutes les opportunités auxquelles tu m'as permis d'accéder, à commencer par le projet de doctorat que je débute prochainement avec toi. Merci pour tout, je suis fière de continuer à faire partie de ton équipe.

Puisqu'il est question d'opportunité offerte par MH, je n'aurais pas pu imaginer meilleur codirecteur que Yan Boulanger pour ma maîtrise. Malgré la distance, ce projet n'aurait pas pu être ce qu'il est sans ton implication, tes bonnes idées, mais également ton humour et ta modestie légendaires. Nos rencontres hebdomadaires à trois avaient des allures de réunion de collègues autour d'une bière (mais sans la bière et à 9h30 le matin) et j'ai bien conscience du privilège que cela représente (ou pas, vous êtes quand même un peu bizarres tous les deux des fois...). Je suis vraiment contente que tu continues à faire partie des personnes sur lesquelles je peux compter, à la maîtrise comme au doctorat. Hâte de te voir en vrai !

Je voudrais également remercier mes parents qui m'ont toujours fait confiance et soutenue dans mes prises de décision (et qui s'en mordent peut-être un peu les doigts maintenant que je ne les vois qu'un mois par an...). Je crois que le papa qui faisait faire ses exercices de maths tous les soirs à la Chloé de 16 ans qui n'y comprenait rien n'aurait pas été étonné d'apprendre que je fais maintenant des stats à longueur de journée et que j'aime ça. La maman qui me voyait plus jeune avoir peur de décrocher un téléphone se doutait peut-

être déjà que je finirais par partir toute seule sur un autre continent, dans une petite ville où je ne connaissais personne. Vous avez toujours cru en ma capacité à faire ce que je voulais (souvent bien plus que moi), peu importe l'objectif. Merci, je vous dois plus qu'on ne peut compter. Et oui, vous serez les premiers à lire mon article lorsqu'il sera publié.

Merci à ma cheerwoman personnelle, Evamonster78 (puisque c'est apparemment comme ça que tu veux que je t'appelle dans ce paragraphe). J'ai de la chance de t'avoir. Impatiente de voir ce que tu vas faire dans les prochaines années, ça promet d'être grand ! T'as pas intérêt à m'oublier dans ton propre mémoire de maîtrise.

Je remercie toutes les personnes qui ont participé de près comme de loin à ce projet. Merci à Philippe Gachon et son équipe de l'Université du Québec à Montréal, plus particulièrement Guillaume Dueymes et Clémence Benoit, pour l'accès aux données climatiques essentielles à mes analyses. Votre disponibilité et votre enthousiasme dans la collaboration sont très appréciés. Merci à Daniel Fortin de m'avoir permis de compléter mon jeu de données télémétriques et à Sabrina Plante pour les échanges constructifs et encourageants au cours du projet.

Merci aux étudiants du Laboratoire de gestion de la faune terrestre sans qui faire une maîtrise serait bien moins drôle. Je sais que vous vous ennuierez si vous ne pouvez pas vous moquer de mon accent et de mon vocabulaire bizarre. Vous êtes comme une petite famille (majoritairement) québécoise auprès de laquelle j'apprends de nouvelles choses tous les jours, merci d'être tels que vous êtes. Un grand merci aux professionnelles de notre labo, Kimberly Malcolm, pour la révision linguistique de l'article d'une part, et Jacinthe Gosselin, pour leur aide à toutes les deux dans le domptage d'ArcGIS et l'analyse des données géomatiques. Les discussions à distance et en personne m'ont sauvée bien des fois où je n'étais plus capable de grand-chose à part me rouler en petite boule dans un coin. Merci pour votre disponibilité, votre patience et vos expertises.

Ce projet de maîtrise n'aurait pas pu voir le jour sans le support financier du Ministère des Forêts, de la Faune et des Parcs du Québec et des subventions de recherche à la

Découverte (#2016-05196 et 2022-04307) et d'une subvention Alliance (#566416-21 – projet eFORCE) du Conseil de Recherches en Sciences Naturelles et en Génie du Canada octroyées à Martin-Hugues St-Laurent.

Enfin, je tiens à remercier les membres du jury, les professeurs Guillaume de Lafontaine et James Schaefer, pour le temps pris afin d'évaluer ce mémoire, ainsi que pour leurs commentaires bienveillants qui en ont amélioré la qualité scientifique.

RÉSUMÉ

La perte d'habitat et le réchauffement climatique figurent parmi les grandes menaces pesant sur la biodiversité à échelle globale, avec entre autres des conséquences importantes sur la distribution des espèces de grands mammifères terrestres. Le caribou forestier (*Rangifer tarandus caribou*) a vu la limite méridionale de son aire de distribution québécoise se déplacer radicalement vers le nord depuis 1850. Les causes potentielles de ce déplacement peuvent être multiples et leur identification reste essentielle à la mise en place d'actions de conservation efficaces. Notre hypothèse était que la distribution actuelle du caribou forestier au Québec résulte en partie des effets du réchauffement climatique, ce dernier n'étant pas un facteur majeur dans la contraction vers le nord de l'aire de distribution du caribou forestier. Nous avons modélisé la niche climatique du caribou forestier, puis reconstitué la zone géographique présentant des conditions climatiques propices à sa présence pour plusieurs pas de temps passés. La comparaison entre les positions des limites sud de cette zone et de celle des aires de distribution passées du caribou forestier nous a permis de quantifier la part du réchauffement climatique responsable de la régression vers le nord de la limite sud passée au fil du temps. Les résultats obtenus permettent d'estimer qu'environ 17% de la régression vers le nord observée depuis 1850 semblent liés à l'effet des changements climatiques. Ce chiffre souligne l'effet majoritaire des modifications anthropiques du territoire au cours du XIX^e et XX^e siècles telles l'urbanisation, le développement du réseau routier, mais surtout les coupes forestières qui ont entraîné la perte d'une grande partie des vieilles forêts de conifères, par rapport à celui des changements climatiques. Contrairement à certaines idées reçues sur le sujet du déclin du caribou forestier au Québec, le réchauffement climatique s'avère bien insuffisant comme seul mécanisme pour expliquer la contraction de l'aire de distribution de ce grand mammifère. De ce fait, ce mémoire incite à concentrer les projets de conservation autour de la protection de l'habitat du caribou forestier à travers la province, dont les leviers décisionnels sont directement à notre portée.

Mots clés : Aire de distribution, Caribou forestier, Modèles de niche, Niche climatique, Perte d'habitat, Perturbations anthropiques, Québec, Réchauffement climatique

ABSTRACT

Habitat loss and global warming are among the major threats to biodiversity worldwide, with significant impacts on the distribution of large mammals. The trailing edge of boreal caribou (*Rangifer tarandus caribou*) distribution in Quebec moved northward drastically since 1850. Different factors could be at play in this phenomenon, and identifying them is an essential step towards efficient conservation practices. Our hypothesis stated that the current distribution range of boreal caribou results partially from the influence of climate change, but that the latter is not a major factor in the contemporary northward contraction of caribou range. We modelled the climate niche of boreal caribou and then hindcasted the area where climate conditions were fit for caribou occurrence for several past time steps. Discrepancies between the positions of the southern limit of the hindcasted areas and the southern limit of the past boreal caribou distributions allowed us to quantify the impact of climate change on the northward movement observed in caribou's trailing edge of distribution through time. Our results show that about 17% of this northward trend can be attributed to climate change since 1850. This figure sheds light on the predominant effect of the anthropogenic pressures that transformed the land during the 19th and 20th centuries, such as urbanization, road development, and most importantly forest cuts leading to the loss of old coniferous forests, compared to the effect of climate change. Contrary to popular belief on boreal caribou decline in Quebec, climate change alone appears to be far from enough to explain the contraction of the distribution range of this large mammal species. This thesis will hopefully encourage researchers to conduct more conservation projects focused on the protection of boreal caribou habitat across the province, as this decision-making power is much more available to us than the one needed to act on global warming.

Keywords: Anthropogenic disturbances, Boreal caribou, Climate niche, Distribution range, Global warming, Habitat loss, Niche models, Quebec

TABLE DES MATIÈRES

REMERCIEMENTS.....	vii
RÉSUMÉ	xi
ABSTRACT.....	xii
TABLE DES MATIÈRES.....	xiii
LISTE DES TABLEAUX	xiv
LISTE DES FIGURES	xv
INTRODUCTION GÉNÉRALE	1
CHAPITRE 1 LES CHANGEMENTS CLIMATIQUES NE SUFFISENT PAS À EXPLIQUER LA RÉGRESSION DE L’AIRE DE DISTRIBUTION DU CARIBOU FORESTIER AU QUÉBEC DEPUIS 1850	12
1.1 RÉSUMÉ FRANÇAIS DE L’ARTICLE	12
1.2 CLIMATE CHANGE ALONE CANNOT EXPLAIN BOREAL CARIBOU RANGE RECESSION IN QUEBEC SINCE 1850	14
CONCLUSION GÉNÉRALE.....	65
RÉFÉRENCES BIBLIOGRAPHIQUES.....	71

LISTE DES TABLEAUX

Table 1. List of the climate variables selected to build hindcast models.	23
---	----

LISTE DES FIGURES

- Figure 1.** Schéma intégrateur des concepts et outils principaux abordés dans le mémoire.8
- Figure 2.** Carte de l'aire de distribution actuelle du caribou forestier au Canada. La limite sud de son aire de distribution historique est représentée en ligne pleine rouge (adaptée d'Environnement Canada 2011). 10
- Figure 3.** Historical southern boundaries of boreal caribou distribution across time: ~1850 (solid line); ~1900 (dotdashed); ~1970 (dashed). 19
- Figure 4.** Schematic workflow depicting the different analytical steps used. Hindcasted boreal caribou distributions (maps of probability of occurrence) were produced by climatic niche ensemble modelling for each source of data and time step of interest. Southern boundaries extracted from those distributions are compared to the historical southern boundaries for each time step, by quantifying their respective movements northward, to underline the discrepancies between history and hindcast. These spatial analyses bring forward the impact of climate on the regression of the southern boundary of distribution range through time. The circle represents the ensemble modelling done through BIOMOD2, and the rectangles represent spatial analyses.25
- Figure 5.** Hindcasted probabilities of boreal caribou occurrence over the study area obtained by ensemble modelling for each data source (20CRv3, CERA-20C, ERA5) and each available time step (1850-1900-1970-2010, 1900-1970-2010, and 1970-2010 respectively).27
- Figure 6.** Observed (green) and hindcasted southern range boundaries with the 20CRv3 (red), CERA-20C (blue), and ERA5 (black) reanalysis datasets for each time step of interest (1850, 1900, 1970, 2012).29
- Figure 7.** Boxplot (black line: median value, box: upper and lower quartiles, whiskers: distribution outside of the upper and lower quartiles) of distances between observed southern range boundaries and hindcasted southern range boundaries for each time step

of interest and the three reanalysis datasets available. Distances were measured between points of same longitude on observed and hindcasted southern limits. 30

Figure 8. Latitudinal position of observed and hindcasted southern boundaries through time. Boxes for hindcasted southern boundaries were obtained by combining data from all reanalysis datasets. 31

INTRODUCTION GÉNÉRALE

CHANGEMENTS CLIMATIQUES EN FORÊT BORÉALE

Le réchauffement climatique et ses impacts à échelle globale constituent un sujet majeur de recherche depuis plusieurs décennies (Plass 1956, Lachenbruch & Marshall 1986, Rosenzweig et al. 2008). Si des changements sont visibles sous tous les climats de la planète, leur sévérité et leur vélocité ne sont pas égales partout (Loarie et al. 2009, Settele et al. 2014). En effet, il est maintenant largement reconnu que les régions des hautes latitudes de l'hémisphère nord subissent des transformations plus rigoureuses encore qu'aux plus faibles latitudes (Flato & Boer 2001, Holland & Blitz 2003, Parry et al. 2007). Ce phénomène, appelé amplification arctique, provoque une augmentation des températures arctiques moyennes deux fois plus rapide que pour le reste du globe (Vincent et al. 2015, IPCC 2007).

Dans ce contexte, la forêt boréale et la toundra, notamment en Amérique du Nord, voient leur climat se modifier de manière prononcée (Chapin III et al. 2000, Warszawski et al. 2013, Settele et al. 2014). L'augmentation des températures réduit la période où le couvert nival est présent, lequel fond plus tôt (Stone et al. 2002, Stewart et al. 2004, IPCC 2014). La phénologie printanière est progressivement devancée (Parmesan & Yohe 2003, Parmesan 2007) et les étés sont plus longs (Zhou et al. 2001, Parry et al. 2007, Steltzer & Post 2009), bien que les changements dans la phénologie automnale soient moins documentés. Le régime de feux en forêt boréale se voit également altéré (Weber & Flannigan 1997, Kasischke et al. 2010), résultant en des surfaces brûlées et des fréquences d'incendies recensées parmi les plus élevées des derniers 10 000 ans (Meredith et al. 2019). Ces paramètres entravent la régénération des essences de conifères majoritaires en forêt boréale, favorisant la transition

vers une nouvelle composition forestière (Chapin III et al. 2000, Johnstone et al. 2010, Stralberg et al. 2018).

Une augmentation des précipitations sous forme de pluie et une diminution de celles sous forme de neige contribuent à la réduction de la couverture neigeuse au sol (Brown & Mote 2009, Trenberth 2011), ainsi qu'à une augmentation de la fréquence des événements de pluie sur neige (IPCC 2014, Bieniek et al. 2018). Alors que le réchauffement climatique induit un déplacement des isothermes vers de plus hautes latitudes et altitudes (Parmesan & Yohe 2003, Lenoir et al. 2020), la forêt boréale nord-américaine voit elle aussi sa limite sud progresser vers le nord (Hogg 1994, Goldblum & Rigg 2010).

IMPACTS DIRECTS ET INDIRECTS DU CLIMAT SUR LES ESPÈCES ANIMALES

Ces changements ont des conséquences sur les espèces animales qui composent les écosystèmes sous ces climats (Parmesan & Yohe 2003, Walther 2010). Les liens entre la présence d'une espèce et le climat peuvent être directs ou indirects (Humphries et al. 2004). Les fluctuations du climat peuvent influencer les facteurs biotiques dans l'habitat des espèces et conditionnent donc indirectement leur présence (Humphries et al. 2004, Soberón & Peterson 2005). Une étude à long terme portant sur une communauté de petits mammifères au Yukon a par exemple montré que la composition en espèces s'était modifiée en réponse aux changements climatiques (Krebs et al. 2019). Cette altération s'expliquait potentiellement par une augmentation de la productivité primaire induite par le réchauffement climatique; une augmentation dans l'abondance de certains prédateurs, exerçant une plus forte pression de prédation sur la communauté, serait également mise en cause (Krebs et al. 2019). Ces éléments pourraient suggérer que certaines espèces de petits mammifères auraient augmenté en abondance, profitant d'une plus grande disponibilité de ressources végétales et causant en retour une augmentation de l'abondance de certains prédateurs. Les espèces de proies les plus prédatées ou les moins productives auraient ainsi décliné, modifiant la composition en espèces de la communauté.

Les parasites constituent un autre paramètre biotique susceptible de moduler la relation entre le climat et la distribution des espèces animales (Brooks & Hoberg 2007, Kutz et al. 2009). À titre d'exemple, de nombreux parasites d'ongulés ont un cycle de vie conditionné par les températures estivales et hivernales (Kutz et al. 2012, Kafle et al. 2018, Hoy et al. 2021). Chez le caribou et le renne (*Rangifer tarandus*), une augmentation des températures semblerait entraîner une meilleure survie des parasites (moustiques, *Hypoderma tarandi*, *Cephenemyia trompe*), détériorant ainsi la condition physique et la survie des hôtes, surtout les individus juvéniles (Colman et al. 2003, Weladji et al. 2003, Witter et al. 2012, Raponi et al. 2018).

À ces effets indirects s'ajoutent également les effets directs du climat sur la valeur adaptative des individus (Humphries et al. 2004, Soberón & Peterson 2005, Huey et al. 2012). Ils dépendent de la physiologie de chaque espèce (Huey et al. 2012) et peuvent être résumés par le concept de niche climatique (Thomas et al. 2004, Rinnan & Lawler 2019). La définition de niche climatique utilisée ici est équivalente à la définition de niche écologique d'Hutchinson (1957) appliquée seulement au climat (Thomas et al. 2004), c.-à-d. un hypervolume composé d'autant de dimensions que de variables climatiques nécessaires pour décrire l'environnement dans lequel une espèce peut, en théorie, survivre indéfiniment. L'effet du climat sur la survie des individus a entre autres été étudié chez les endothermes (Angilletta et al. 2010, Cunningham et al. 2021). Ainsi, une étude portant sur la marmotte à ventre jaune (*Marmota flaviventer*) a mis en évidence des influences multiples du climat sur la survie des individus selon la saison et la classe d'âge (Cordes et al. 2020). Par exemple, une longue saison de croissance semblait améliorer la survie estivale des jeunes mais défavoriser la survie hivernale des petits de l'année (Cordes et al. 2020). De plus, la capacité des individus à se reproduire est aussi contrainte par les fluctuations climatiques (Boyles et al. 2011). En effet, Love et al. (2010) soulignent un lien étroit entre les températures printanières et la date de ponte chez l'eider à duvet (*Somateria mollissima*). Selon leur étude, une date de ponte optimale permet une bonne synchronicité entre l'éclosion des poussins et des conditions climatiques favorables à leur développement, ce qui a un impact sur leur survie.

Dans un contexte de changements climatiques, bien que certaines espèces arrivent à maintenir leur distribution actuelle, d'autres doivent se déplacer pour suivre les conditions climatiques auxquelles elles sont adaptées (Tingley et al. 2009, Urban et al. 2013). En effet, ces déplacements sont déjà observables chez certains taxons de l'hémisphère nord lesquels présentent une contraction de leur limite sud, une expansion de leur limite nord et un déplacement vers le nord de leur aire de distribution (Lenoir et al. 2020). Une étude portant sur le lièvre d'Amérique (*Lepus americanus*) a par exemple souligné le rôle des changements climatiques, en particulier de la réduction du couvert neigeux, dans la rétraction vers le nord de la limite sud de son aire de distribution (Sultaire et al. 2016). De plus, Davidson et al. (2017) ont mis en évidence une vélocité des changements climatiques, c'est-à-dire la vitesse à laquelle les organismes devront migrer pour rester sous un climat similaire, de plus de 0,5 km/an chez 40% des mammifères inclus dans leur étude, et de plus de 1 km/an chez 14% d'entre eux.

UTILITÉ ET LIMITES DES MODÈLES DE NICHE

Les modèles de niches représentent des outils largement utilisés pour mieux comprendre les mécanismes en jeu dans la répartition géographique des espèces (Figure 1). Ils permettent de projeter ou de reconstituer la distribution d'une espèce dans le temps en créant un lien statistique corrélatif entre la présence de l'espèce en question et des paramètres environnementaux mesurables, comme les composantes du climat ou de la végétation (Elith & Leathwick 2009, Riquelme et al. 2018, Malakoutikhah et al. 2020). Ces modèles sont intéressants entre autres pour leur capacité à produire des résultats utiles malgré le peu d'informations qu'ils nécessitent au préalable, contrairement aux modèles mécanistiques (Robertson et al. 2003, Peterson et al. 2015). Cette méthode a par exemple été employée pour prédire des modifications dans l'aire de distribution de certaines espèces de mammifères d'Amérique du Nord, comme chez le cerf de Virginie (*Odocoileus virginianus*) (Dawe & Boutin 2016) ou chez plusieurs espèces de prédateurs (Pandey & Papeş 2018). Cependant, l'emploi des modèles de niche suppose plusieurs postulats tels que la pertinence des variables

environnementales utilisées pour caractériser l'habitat de l'espèce étudiée, l'exclusion des interactions biotiques, le conservatisme (et donc la transférabilité) de la niche dans le temps et dans l'espace, ou encore la présence de l'espèce dans tous les habitats compatibles avec sa niche, supposant un état d'équilibre entre l'espèce et son environnement (Wiens et al. 2009, Dormann et al. 2012).

L'importance de cette dernière supposition a été soulignée par des études récentes qui comparent les distributions passées des espèces, telles que suggérées par les fossiles, et les distributions passées reconstituées par les modèles de niche (McGuire & Davis 2013, Davis et al. 2014). Ainsi, des modèles de niche construits avec des données de présences récentes peuvent produire des projections biaisées dans les cas où ces données ne sont pas représentatives d'un état à l'équilibre (Williams et al. 2013, Anderson 2013, Davis et al. 2014). Dans le cas fictif d'une population qui se maintient à l'équilibre avec son environnement, la différence entre sa niche climatique réalisée et la niche climatique fondamentale de l'espèce est théoriquement minimale, et le lien écologique entre la présence de l'espèce et les conditions climatiques dans son environnement est maintenu. Si l'aire de distribution de la population venait à se contracter sous l'effet de pressions environnementales, cette différence entre niches réalisée et fondamentale se creuserait, altérant ainsi le lien écologique entre climat et occurrence. Cela dit, de nombreux facteurs peuvent potentiellement limiter la distribution actuelle des espèces (Soberón et Peterson 2005), la réduisant à une fraction de l'éventail complet d'habitats adéquats (Munguía et al. 2008). Un nombre de populations étudiées trop limité pour couvrir l'entièreté de l'aire de distribution de l'espèce, une espèce compétitrice qui occupe une niche similaire, ou encore d'anciennes barrières environnementales qui ont limité la dispersion des individus, déterminant ainsi la distribution actuelle de l'espèce, sont autant de facteurs qui peuvent expliquer que cet état d'équilibre ne soit pas atteint (Munguía et al. 2008, Williams et al. 2013). À cette liste d'éléments pouvant modéliser la distribution des espèces s'ajoutent les perturbations d'origine anthropique des environnements naturels (Wright 1987, Lyons et al. 2004, Boivin et al. 2016). Si les relations entre les activités humaines et la distribution actuelle des espèces sont largement étudiées, le biais de prédiction potentiellement qu'elles

peuvent induire lors de l'utilisation des modèles de niche reste peu documenté chez les grands mammifères en Amérique du Nord. La grande majorité des études utilisant des modèles de niches se concentrent d'ailleurs sur la capacité prédictive des modèles afin de projeter des distributions futures pour les espèces d'intérêt (Sharma et al. 2009, Riquelme et al. 2018). De ce fait, la littérature scientifique est relativement pauvre de cas de reconstitution de distributions passées à l'aide de modèles de niche chez les grands mammifères.

MODIFICATION DES AIRES DE DISTRIBUTION DE GRANDS MAMMIFÈRES EN AMÉRIQUE DU NORD

À une échelle globale, la perte d'habitat et la fragmentation engendrées par les activités humaines figurent parmi les menaces majeures pour la biodiversité, au même titre que la surexploitation des populations naturelles (Pimm et al. 2014, Díaz et al. 2019, Newbold et al. 2015, Tilman et al. 2017). Le risque d'extinction d'une espèce est étroitement lié au niveau de fragmentation de son habitat entre autres chez les mammifères terrestres, et les grands mammifères y semblent particulièrement vulnérables (Bartlett et al. 2016, Crooks et al. 2017, Pardini et al. 2017). En effet, en Amérique du Nord, de nombreuses espèces de grands mammifères ont subi une réduction drastique de leur aire de distribution historique (Laliberté & Ripple 2004, Morrison et al. 2007). Chez le grizzly (*Ursus arctos*), il a été montré que la densité de routes dans son environnement entraînait une augmentation de la mortalité et faisait chuter la densité de population (Lamb et al. 2017). De plus, la fragmentation anthropique de leur habitat réduit dangereusement la taille des populations de grizzlis et les flux génétiques entre elles en les isolant spatialement les unes des autres (Proctor et al. 2005).

Dans bien des cas, l'exploitation des ressources naturelles se fait au détriment de l'intégrité d'habitats de qualité pour plusieurs espèces de grands mammifères (Northrup et al. 2015, Suzuki & Parker 2016, Scanes 2018). Chez le caribou montagnard du sud (*Rangifer tarandus caribou*), en Alberta et en Colombie-Britannique, la perte d'habitat induite par l'aménagement forestier a été identifiée comme une cause majeure de déclin et s'est même accélérée entre 2000 et 2018 (Nagy-Reis et al. 2021). À ces deux pressions s'ajoute la

surexploitation des populations naturelles; en effet, la majorité des grands mammifères d'Amérique du Nord ont connu une période de déclin prononcé de leurs populations induite entre autres par la chasse, avant la mise en place d'efforts de conservation marqués au cours des dernières décennies (Mattson & Merrill 2002, Ray 2010, Venier et al. 2014). Ces diverses causes d'origine humaine n'ont donc rien de récent et se trouvent maintenant couplées aux effets visibles du réchauffement climatique, fragilisant les écosystèmes en forêt boréale (Gauthier et al. 2015).

Toutefois, la distinction claire des effets des changements climatiques de ceux dus aux perturbations et activités anthropiques représente un défi de taille (Figure 1). En effet, depuis les dernières décennies, la magnitude respective de ces effets s'est accrue (IPCC 2019), transformant de concert la composition et la structure des milieux naturels (Parmesan et al. 2022). Les conséquences des changements climatiques peuvent parfois s'avérer similaires à celles des perturbations anthropiques, entre autres des phénomènes de fragmentation (Murray et al. 2017) et de perte d'habitat (Mantyka-Pringle et al. 2012). Elles peuvent également provoquer un déplacement des populations naturelles dans les mêmes directions, souvent vers les plus hautes latitudes et altitudes (Lenoir et al. 2020). Leur importance respective a pu être clarifiée dans certaines études (voir Elmhagen et al. 2015, Dawe & Boutin 2016) mais reste largement méconnue dans de nombreux cas.

ENJEU DU CARIBOU FORESTIER AU QUÉBEC

Partout au Canada, le caribou des bois est reconnu comme une sous-espèce particulièrement sensible aux pressions anthropiques et au dérangement (Vors et al. 2007, Lafontaine et al. 2019, Fryxell et al. 2020). Cette sous-espèce se décline en différents écotypes, dont notamment la population boréale du caribou des bois, aussi appelée caribou forestier au Québec. Le caribou forestier est sédentaire et dépend fortement des forêts matures de conifères pour se nourrir et éviter ses prédateurs (Courtois et al. 2004, Hornseth & Rempel 2016). Il a été désigné comme espèce menacée par le Comité sur la situation des

espèces en péril au Canada (COSEPAC) en 2000, un statut confirmé à l'Annexe 1 de la Loi sur les espèces en péril du Canada (Environnement et Changement climatique Canada 2019). Les perturbations anthropiques, entre autres l'aménagement forestier, résultent en un nombre croissant de chemins forestiers et de parcelles de jeune forêt de feuillus et d'arbustes qui perturbent et fragmentent son habitat essentiel (Courtois et al. 2004, Wittmer et al. 2005, Dickie et al. 2017, Fryxell et al. 2020). Par leurs ressources alimentaires plus appétentes et abondantes, les zones de forêt en régénération sont sélectionnées par l'orignal (*Alces alces americana*) et le cerf de Virginie, et supportent une hausse des densités qui, en retour, induit une augmentation de densité (réponse numérique) et d'efficacité (réponse fonctionnelle) des prédateurs comme le loup (*Canis lupus*) et l'ours noir (*Ursus americanus*) (Wittmer et al. 2005, 2007, Festa-Bianchet et al. 2011). Depuis quelques décennies, ce phénomène de compétition apparente est identifié comme une cause majeure du déclin des populations boréales de caribous des bois (Wittmer et al. 2005, 2007, Festa-Bianchet et al. 2011).

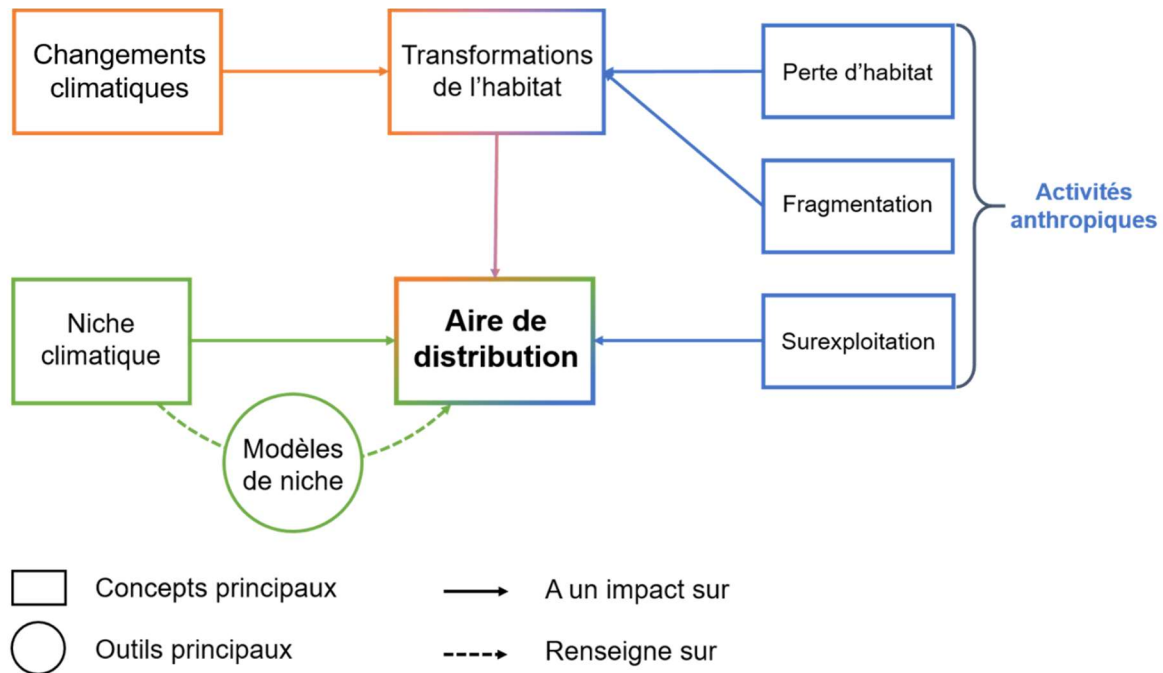


Figure 1. Schéma intégrateur des concepts et outils principaux abordés dans le mémoire.

Ces pressions anthropiques ont fort probablement influencé la distribution de la sous-espèce à travers le temps, au Québec comme ailleurs au Canada (Courtois et al. 2003, Arlt & Manseau 2011, Santomauro et al. 2012). Plusieurs études ont mis en évidence une régression vers le nord de la limite sud de l'aire de distribution du caribou forestier (Schaefer 2003, Vors et al. 2007, Drever et al. 2019). Dans les années 1850, son aire de distribution à l'est du continent s'étendait au sud jusqu'à la frontière actuelle entre le Vermont et le Massachusetts, aux États-Unis (Banfield 1961, Courtois et al. 2003). Cette limite a régressé vers le nord jusqu'à la région du Saguenay-Lac-Saint-Jean, au Québec, et ce, en l'espace d'environ un siècle (Banfield 1961, Courtois et al. 2003) (Figure 2). La tendance est suffisamment marquée pour que certaines études projettent une disparition quasi complète du caribou des bois d'Ontario d'ici à la fin du XXI^e siècle (Schaefer 2003, Masood et al. 2017). Bien que la pression de prédation, exacerbée par l'aménagement forestier, et la conversion d'habitats naturels en secteurs urbanisés ou agricoles demeurent les facteurs principaux de perte d'habitat pour la sous-espèce (Courtois et al. 2007, Vors & Boyce 2009, Serrouya et al. 2019), le réchauffement climatique est maintenant considéré comme une menace non négligeable (Murray et al. 2017, Barber et al. 2018, St-Laurent et al. 2022). Dans ce contexte complexe, où de nombreux paramètres sont entrés en jeu dans la distribution passée du caribou forestier, il est crucial de distinguer les impacts respectifs de l'utilisation humaine de l'espace et du réchauffement climatique.

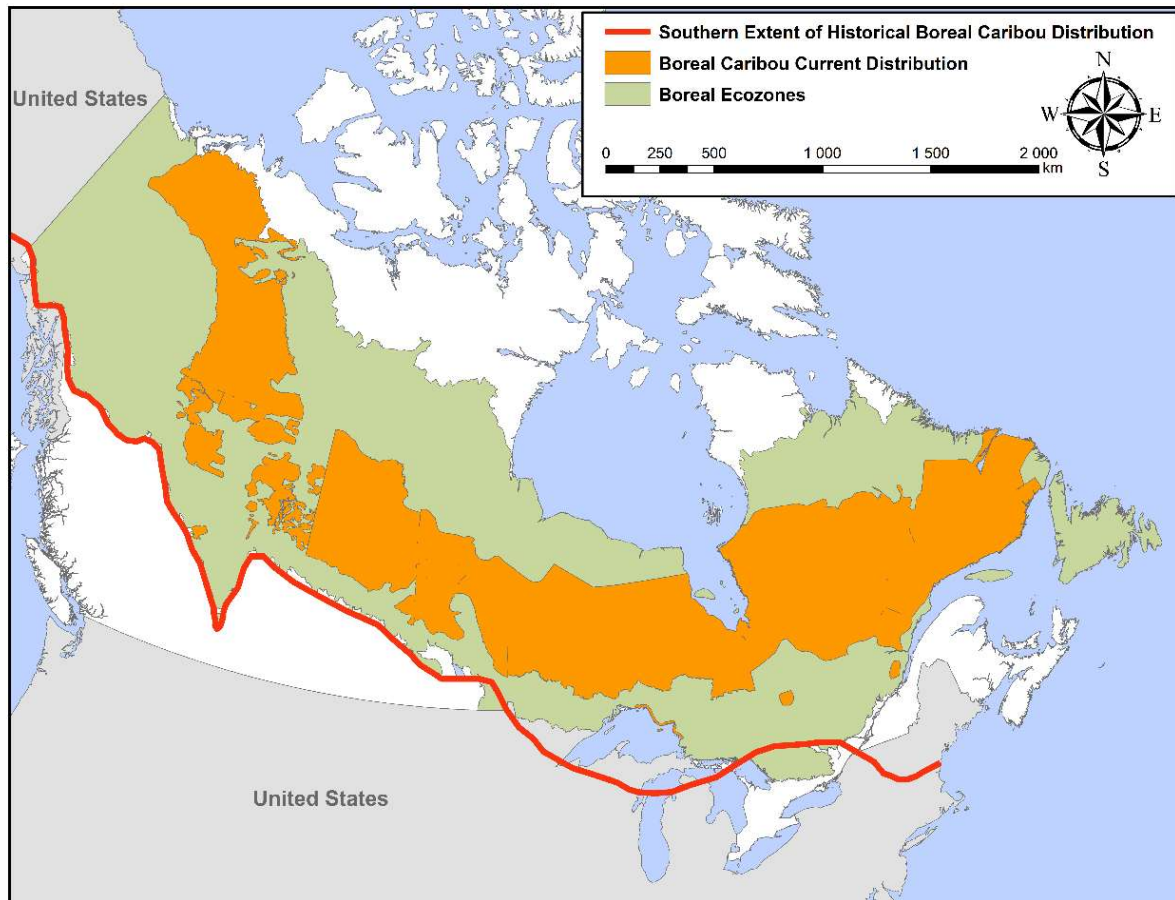


Figure 2. Carte de l’aire de distribution actuelle du caribou forestier au Canada. La limite sud de son aire de distribution historique est représentée en ligne pleine rouge (adaptée d’Environnement Canada 2011).

OBJECTIF, HYPOTHÈSE ET PRINCIPAUX RÉSULTATS

Notre étude visait à mettre en évidence les effets potentiels du réchauffement climatique sur la rétraction vers le nord de l’aire de distribution du caribou forestier au Québec (Canada) depuis 1850. Notre hypothèse stipulait que le réchauffement climatique a participé à la rétraction vers le nord de l’aire de distribution du caribou boréal au Québec, sans en être un facteur majeur.

Pour atteindre cet objectif, nous avons associé des cartes de distribution historique à des réanalyses climatiques de différentes sources. Les modèles de niche climatique construits ont fait ressortir la différence importante entre les positions en latitude des limites sud reconstituées par rapport à celles des limites sud historiques de l'aire de distribution du caribou, situées beaucoup plus au sud. Ces résultats ont ainsi désigné le réchauffement climatique récent comme responsable de seulement ~17% de la régression vers le nord observée pour l'aire de distribution de la sous-espèce depuis 1850. La méthodologie utilisée ici, en particulier la combinaison des différentes sources de données exploitées, est à notre connaissance une première. De telles informations améliorent la compréhension actuelle des interactions caribou forestier – changements climatiques – activités humaines, participant ainsi à l'identification des moteurs de déclin chez les populations de caribou et à la formulation de prédictions plus robustes concernant leurs futures distributions. Compte tenu de la place prépondérante des perturbations anthropiques dans ce déclin, elles apparaissent comme un levier de conservation bien plus efficace que le réchauffement climatique et sur lequel il est possible d'agir rapidement.

CHAPITRE 1

LES CHANGEMENTS CLIMATIQUES NE SUFFISENT PAS À EXPLIQUER LA RÉGRESSION DE L'AIRE DE DISTRIBUTION DU CARIBOU FORESTIER AU QUÉBEC DEPUIS 1850

1.1 RÉSUMÉ FRANÇAIS DE L'ARTICLE

La réduction de l'aire de distribution des espèces est un symptôme majeur de perte de biodiversité à échelle globale. Bien que les activités et la dégradation d'habitat d'origine anthropique soient souvent désignées comme responsables, le changement climatique n'est pas en reste. Chez les espèces menacées, distinguer les effets de la présence humaine des effets du changement climatique sur la transformation des aires de distribution des espèces est un pas supplémentaire vers une conservation plus efficace. En associant des cartes de distributions historiques passées avec les données climatiques de plusieurs réanalyses (ERA5, CERA-20C, 20CRv3), nous avons évalué les effets potentiels des changements climatiques récents sur la rétraction vers le nord de l'aire de distribution du caribou forestier (*Rangifer tarandus caribou*, population boréale) au Québec depuis 1850. Nous avons mis en évidence les différences entre les limites sud d'aires de distribution historiques, prises comme références, et celles reconstituées grâce à des modèles de niche climatique statistiquement robustes. Les limites sud reconstituées présentaient un déplacement vers le nord d'environ 105 km au fil du temps, et ce pour toutes les réanalyses, une tendance radicalement différente de celle observée pour les limites sud historiques depuis 1850 (~620 km). Les tendances différentes de mouvements latitudinaux pour les limites sud historiques et reconstituées suggèrent que le réchauffement climatique récent ne serait responsable que de seulement ~17% du recul vers le nord de la limite sud de l'aire de distribution du caribou forestier depuis 1850. Cet impact limité du climat soutient l'hypothèse qui voudrait que la contraction de l'aire de distribution du caribou forestier soit principalement causée par les pressions anthropiques qui ont modelé la structure et la composition de la forêt québécoise, telles que les coupes, la construction de chemins, l'agriculture ou encore l'urbanisation, ouvrant la voie aux phénomènes de compétition apparente et de surexploitation au cours des 160 dernières années. Nos résultats rappellent également l'importance d'une meilleure prise en compte des aires de distribution passées dans un contexte de projection de futures distributions, en particulier chez les espèces menacées.

Mots-clés : Canada de l'Est; Modèle de niche, Modélisation; Niche climatique; Perturbations anthropiques; *Rangifer tarandus caribou*;

Ce premier article, intitulé « *Climate change alone cannot explain boreal caribou range recession in Quebec since 1850* », a été corédigé par moi-même ainsi que par le professeur Martin-Hugues St-Laurent et le chercheur Yan Boulanger. Cet article sera soumis à la revue avec comité de révision par les pairs *Global Change Biology*. En tant que première auteure, ma contribution à ce travail a été l'essentiel de la recherche, du développement de la méthode, de l'exécution des analyses et de la rédaction de l'article. Le professeur Martin-Hugues St-Laurent et le chercheur Yan Boulanger ont fourni l'idée originale et coordonné l'élaboration du projet, la révision et les commentaires des analyses et du texte de l'article, et Martin-Hugues St-Laurent a assuré son financement.

1.2 CLIMATE CHANGE ALONE CANNOT EXPLAIN BOREAL CARIBOU RANGE RECESSION IN QUEBEC SINCE 1850

ABSTRACT

The contraction of species range is known to be one of the most significant symptoms of biodiversity loss worldwide. While anthropogenic activities and habitat alteration are recognized to be major threats for several species, climate change has not been overlooked either. In the case of species at risk, drawing a distinction between the effects of human disturbances and climate change on past and current range transformations is an important step towards improved conservation strategies. We paired historical range maps with climate reanalyses from different sources (ERA5, CERA-20C, 20CRv3) to assess the potential effects of recent climate change on the observed northward contraction of the distribution of boreal populations of woodland caribou (*Rangifer tarandus caribou*) in Quebec since 1850. We quantified these effects by highlighting the discrepancies between different southern limits of the caribou's distribution range (used as references) observed in the past and reconstitutions obtained through the hindcasting of the climate conditions within which caribou currently range. Southern limits hindcasted through robust ensemble modelling showed a ~105 km movement northward over time under all reanalysis datasets, a trend drastically different from the ~620 km reported for historical southern limits since 1850. The differences in latitudinal shift through time between the observed and hindcasted southern distribution limits suggest that recent climate change could have contributed to only ~17% of caribou range recession since 1850. This limited impact of climate supports the hypothesis that the main causes of caribou range recession are the anthropogenic drivers that have modified the structure and composition of the forest in Quebec through logging, roads, agriculture, and urbanization, paving the way for habitat-mediated apparent competition and overharvesting over the past 160 years. Our results also call for a better consideration of past distribution ranges in models aiming at projecting future distributions, especially for endangered species.

Keywords: anthropogenic disturbances; climate niche; eastern Canada; modelling; *Rangifer tarandus caribou*; species distribution model.

INTRODUCTION

Negative impacts of human activities on ecosystems are not recent news (Plass 1956, Chapin III et al. 2000, Sanderson et al. 2002). The ongoing loss of biodiversity worldwide weakens functioning ecosystems and compromises the benefits human societies gain from them (Chapin III et al. 2000, Díaz et al. 2018, Díaz et al. 2019). Species range contraction happens to be an important symptom of this phenomenon, as it is often linked to population sustainability (Laliberté & Ripple 2004, He 2012, Ceballos et al. 2017). Different mechanisms can lead to range contraction (Yackulic et al. 2011), but anthropogenic habitat alteration stands out as one of the most critical, yielding high extinction risks (Ceballos & Ehrlich 2002, Di Marco et al. 2018, Pacifici et al. 2020). In fact, agriculture, hunting, land-use change and increased human density are some of the factors that caused a significant shrinkage of ranges described in the past decades for many mammals, especially megafaunal species (Karanth et al. 2010; Ripple et al. 2015, Torres-Romeo et al. 2020).

In addition, the impacts of climate change on species distribution range have been growing increasingly visible (Hughes 2000, Parmesan 2006, Colwell et al. 2008). Since the end of the Little Ice Age (ca 1850), a clear accelerating and anthropogenic-driven warming trend is observed at the surface of the globe (Free & Robock 1999, IPCC 2013, IPCC 2021). Resulting in a displacement of isotherms towards higher latitudes and altitudes, it induces a shift in phenology and biome distribution at a global scale (Parmesan & Yohe 2003, Gonzalez et al. 2010, Lenoir et al. 2020). While some species benefit from these changes (e.g. white-tailed deer *Odocoileus virginianus*; Dawe & Boutin 2016), many high-altitude and high-latitude adapted mammals are at risk (Gilg et al. 2012, Pauchard et al. 2016, Freeman et al. 2018). Severe range contraction is observed and predicted for many of them, as global warming is happening at a greater speed at higher latitudes because of Arctic amplification (Parry et al. 2007, Miller et al. 2010, Cai et al. 2021). For instance, temperatures have warmed by 1.7°C on average between 1948 and 2012 in Canada, while average arctic temperatures have been increasing between over two to four times as fast as the rate of the rest of the world (IPCC 2021, Bush & Lemmen 2019, Rantanen et al. 2022). For this reason, the survival of

vulnerable populations may be critical because of the cumulative impacts of anthropogenic and climatic threats (Sultaire et al. 2016, Wan et al. 2019). Although important contractions of distribution range caused by future global warming are projected for many mammal species (La Sorte & Jetz 2010, Zanin et al. 2021), a lot is yet to be understood and quantified regarding the recent effects of climate change on past and current distribution ranges (but see Moritz et al. 2008, McCain et al. 2021). As climate change and human disturbances have occurred simultaneously for the past decades, it is important to be able to disentangle their effects on contraction, expansion or shift of mammal distribution ranges.

Across the northern hemisphere, caribou (*Rangifer tarandus*) is one of the high-profile species that have been suffering from a northward range contraction during the last century (Schaefer 2003, Festa-Bianchet et al. 2011, D'Orangeville et al. 2022). The boreal population (hereafter boreal caribou), an ecotype of the woodland caribou subspecies (*R. t. caribou*) (COSEWIC 2002, Environment Canada 2012), thus represents a great subject to study range contraction as a result of environmental pressures. Though the boreal caribou is listed as Threatened under the federal Species at Risk Act since 2002 (Species at Risk Act 2002, COSEWIC 2002), the southern limit of its distribution range has been shrinking northwards for several decades (Vors et al. 2007, Drever et al. 2019). Boreal caribou rely heavily on mature coniferous forests for foraging and spacing away from predators (Courtois et al. 2004, DeCesare et al. 2012, Hornseth & Rempel 2016). It is thus highly sensitive to anthropogenic disturbances such as intensive logging (e.g., DeCesare et al. 2012, Lafontaine et al. 2019, Fryxell et al. 2020). Human-induced resource extraction activities have converted most of these mature and old-growth stands into a matrix of recent cutblocks, mixed/hardwood regenerating stands, and small remnants of residual older stands, all scattered by a dense network of forest roads (Wittmer et al. 2005, Dickie et al. 2017, Fryxell et al. 2020).

In Canada, the spatial progression of anthropogenic disturbances over time happens to present a rather similar northward trend as the one shown by climate-induced shift in isotherms worldwide (Parmesan & Yohe 2003, Gagné et al. 2016). Anthropogenic disturbances are the most important, well-recognized driver of habitat alteration for boreal

caribou populations (Courtois et al. 2007, Vors & Boyce 2009, Serrouya et al. 2019); for example, Schaefer (2003) identified forestry as the main driver of northward range recession for woodland caribou in Ontario. Nevertheless, the role of recent global warming in the northward displacement of the southern trailing edge of caribou distribution is still poorly known. Though most studies on this topic focus on predicting the impact of climate change on the future distribution of boreal caribou, anthropogenic disturbances are systematically designated as the number-one driver of caribou decline until 2050 (Barber et al. 2018, Leblond et al. 2022, Neilson et al. 2022, St-Laurent et al. 2022). Considering that many factors may have contributed to shape the current distribution range of the subspecies, it is crucial to isolate the specific influence of climate change, as it could orient and constrain our recovery strategies.

Consequently, this study aimed at assessing the potential effects of climate change on the northward contraction of the boreal caribou's distribution in the province of Quebec (eastern Canada) since 1850. More precisely, we modelled and delineated the climate conditions under which boreal caribou occur today and defined them as their realized climate niche. Then we hindcasted where these climate conditions prevailed in the past, from 1970 back to 1850, in order to contrast the past locations of those climate conditions with the observed past ranges of boreal caribou. To do so, we paired historical range maps with historical climate reanalyses from different sources. A lot is still to be done regarding past distribution hindcasting in large mammals but the combined use of such data types in this context is a first, at least to our knowledge. We hypothesized that the current distribution range of boreal caribou results partially from the influence of climate change, but that climate change is not a major factor in the contemporary northward contraction of caribou range. According to previous findings on small mammals and vegetation species (Williams et al. 2013, Davis et al. 2014), we predicted that the distribution hindcasted through climate niche modelling would not accurately match the past observed distribution of boreal caribou because its current realized climate niche is not representative of the actual diversity of climates suitable for its presence.

METHODS

Study area

Our study area covers the whole province of Quebec, and also includes the Maritimes, a part of Labrador and Ontario (Canada), as well as the northeastern region of New England (USA) (63°N to 42°N and 80°W to 56°W; Figure 3). This area was chosen to incorporate the historical southern limits of boreal caribou range in eastern Canada and also its current distribution range in Quebec. Two important ecological gradients exist between ecoregions within the study area, from tundra in the north to eastern temperate forests in the south, and from Hudson plains in the west to Atlantic highlands in the east (Wiken et al. 2011, Berteaux 2014). The climate in the tundra is much colder and drier than that of eastern temperate forests (annual averages of -13°C to -11°C for 100-300 mm of precipitation vs. about 5°C to 9°C for 720-1200 mm of precipitation), while the climate of Atlantic highlands is milder and more humid than the Hudson plains' climate (annual averages of 1°C to 8°C for 850-2000 mm of precipitation vs. -3.5°C to -2°C for 500-800 mm of precipitation) (Wiken et al. 2011). European colonisation and its impacts on natural environments have historically been mostly concentrated in the St. Lawrence River valley between the early 1600s and 1800s (Bélanger & Grenier 2002, Moreau et al. 2007, Terrail et al. 2020). Additional colonization and more intensive forestry activities occurred further north and away from the valley during the 19th century (Boucher et al. 2021). Industrialized forestry became more important in the 20th century, especially after the 1950s (Boucher et al. 2009).

Data acquisition

Caribou data – Current and historical distribution ranges

While raw contours of the current distribution range exist for the province, fine-scale occurrence maps are not common. We thus delineated the current distribution range using telemetry relocations of 253 boreal caribou belonging to 10 different local populations and

monitored from 2004 to 2019 in Quebec: Nottaway, Assinica, Témiscamie, Pipmuacan, Manicouagan, Romaine, Basse-Côte-Nord, Charlevoix, Val-d'Or, and Gaspésie.

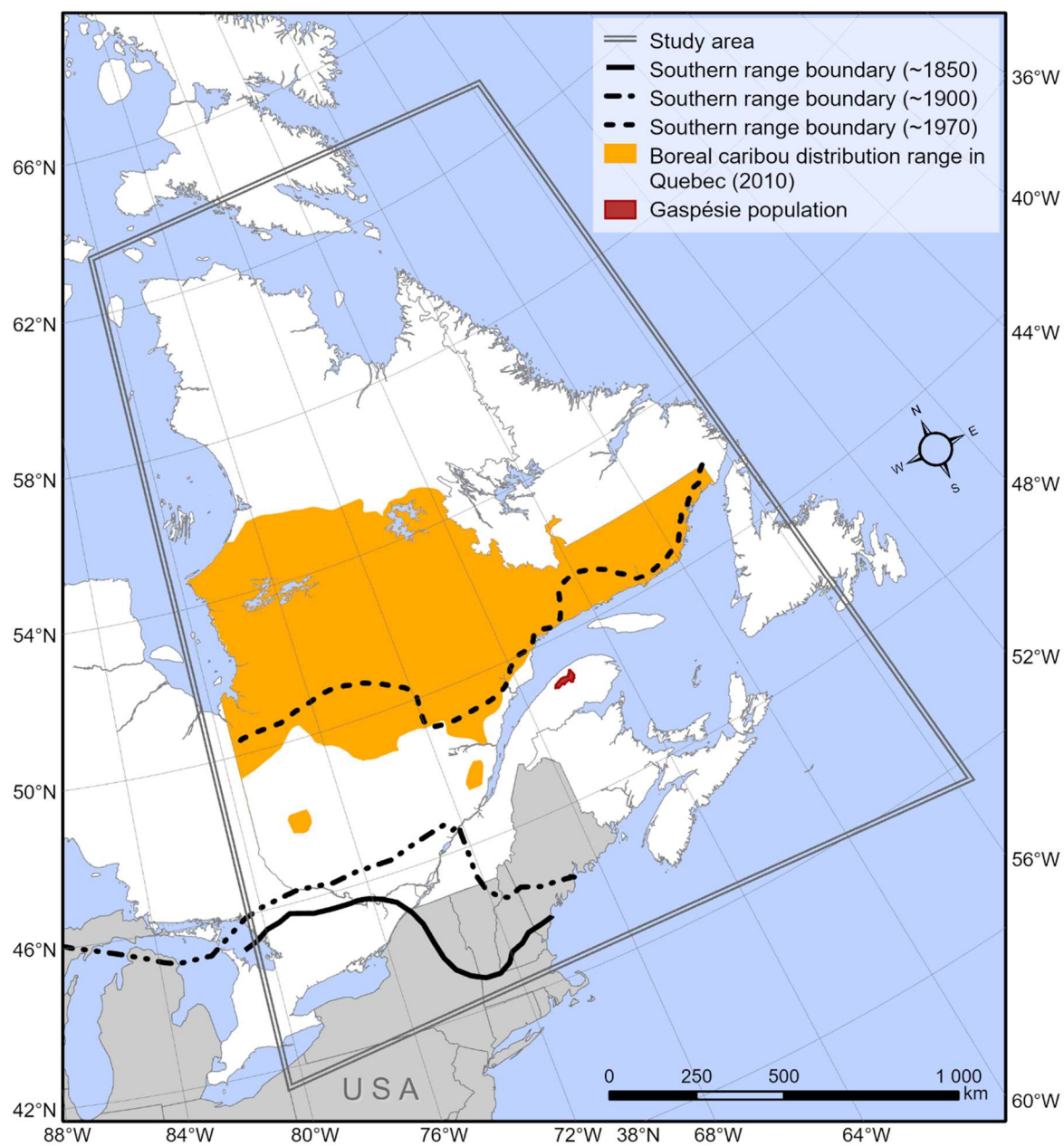


Figure 3. Historical southern boundaries of boreal caribou distribution across time: ~1850 (solid line); ~1900 (dotdashed); ~1970 (dashed).

Adult females were captured and fitted with GPS-collars by field technicians, biologists of the Ministère de l'Environnement, de la Lutte contre les Changements Climatiques, de la Faune et des Parcs du Québec (hereafter referred to as MELCCFP) and their collaborators. Capture and manipulation of study animals were approved by the Animal Welfare Committee (according to the guidelines of the Canadian Council on Animal Care) of the Université du Québec à Rimouski (certificates #36-08-67 and #27-07-53), Université de Laval (certificate #2008026-3), and the MELCCFP (certificates #07-00-02, #04-005, #06-00-27, #07-00-04, #11-03, #12-03, #12-07, #13-09, and #14-05). We created a binary map of the current distribution of boreal caribou in Quebec fitted to the spatial definition of each climate data source (see *Climate data*) by defining every cell with at least one location recorded as 1 and other cells as 0.

We examined archives and other sources to find reliable information on past boreal caribou distributions. We gathered southern boundary clues for three historical time steps: ~1850 (Courtois et al. 2003), ~1900 (Banfield 1961), and ~1970 (Courtois et al. 2003) (see Figure 3). As our sources for past distributions and southern boundaries were digital images from online books and articles, we had to extract the boundaries by tracing them as precisely as possible and georeferencing them using ArcMap 10.6.1 (ESRI 2018). We considered the isolated Atlantic-Gaspésie caribou (hereafter Gaspésie caribou) population as part of the boreal caribou distribution range, despite its current assignation to the montane ecotype, as they used to be included in the broader boreal caribou range back in 1850 and 1900 (Banfield 1961).

Climate data

We extracted the climate data used in this study from three datasets, i.e. ERA5, CERA-20C and 20CRv3, to limit the bias generated by the use of only one data source (Zanin et al. 2021). Data from ERA5 (ECMWF 2022a), CERA-20C (ECMWF 2022b), and 20CRv3 (NOAA 2022) covered 1950–2019, 1901–2010, and 1850–2015 respectively. Spatial

resolution varied between climate datasets with ERA5 having a $0.25^{\circ} \times 0.25^{\circ}$ spatial resolution, while CERA-20C and 20CRv3 had a resolution of $1^{\circ} \times 1^{\circ}$. From these datasets, we built specific climate variables (listed in Table 1) that were further used in our models. We built those variables using the following data: 2-m temperature (i.e. above ground level), precipitation, and ground surface snow depth, in order to fit what was considered most important according to literature when studying a large herbivore such as caribou (Weladji et al. 2002, Masood et al. 2017, Mallory & Boyce 2018) (see Appendix A for detailed variable extraction).

Data analysis

Model building and hindcast

We modelled and hindcasted boreal caribou distributions using different algorithms: Generalized Linear Models (GLM), Generalized Additive Models (GAM), Random Forests (RF) and Boosted Regression Trees (BRT) (Guisan & Zimmermann 2000, Araújo & New 2006, Shabani et al. 2016). This variety of approaches served to minimize the bias produced by the use of only one algorithm to build models (Shabani et al. 2016). We tested for correlation and multicollinearity among climate variables using the Pearson correlation coefficient (r , threshold absolute value of 0.7; Dormann et al. 2013) and the variance inflation factor (VIF, threshold value of 10; Senaviratna & Cooray 2019). Variables presenting indices above threshold values were used in separate models. Out of the entire set of climate variables tested, only a few were eventually used to comply with the thresholds selected for VIF and r values. Different sets of variables were selected to build models for each reanalysis dataset. The variables selected were the mean summer temperature, the total summer rainfall, the total winter rainfall, and the total winter snowfall for models built using the 20CRv3 dataset; the mean summer temperature, the total summer rainfall, the total winter snowfall, and the total number of rain-on-snow events for models built using the CERA-20C dataset; and finally, the mean summer temperature, the total summer rainfall, the total winter rainfall, the

total winter snowfall, the mean snow depth, and the total number of rain-on-snow events for models built using the ERA5 dataset.

A k-fold cross validation was conducted with a 70/30 ratio for calibration and validation of the models respectively, and 20 iterations were produced to minimize sampling bias (as suggested by Berteaux 2014) (generating 80 models total). We assumed that cells with no presence recorded could be considered as true absences, given the coarse spatial scale used here (Lobo et al. 2010) and the robust knowledge of the current distribution range of boreal caribou in Quebec at our disposal, built through several years of telemetry monitoring on an extensive number of individuals in all caribou populations over the province (MFFP 2021a). The models produced were evaluated using the true skill statistic (TSS) performance index and then combined in an ensemble model (Allouche et al. 2006). We used the weighted mean as an ensemble modelling method, according to the TSS values obtained (Berteaux 2014). An ensemble model was produced, from all 80 models generated, for each reanalysis dataset using the 1981–2010 period, hereafter named the “baseline” period. The past distributions of boreal caribou in Quebec were then hindcasted at specific past time steps under each reanalysis dataset by using the ensemble model pertaining to the appropriate reanalysis dataset (Figure 4). Model building and hindcasts were conducted on R 4.1.3 with the BIOMOD2 v.3.5.1 package (Thuiller et al. 2016).

Quantification of spatial discrepancies

We compared the results of hindcasted distributions with the observed distributions of boreal caribou for the four time steps investigated (~1850, ~1900, ~1970, ~2010) to evaluate if there were spatial discrepancies produced by our models (and if so, quantify to what extent) (Figure 4). A threshold of 0.3 probability of occurrence was used to extract southern boundaries from model outputs (i.e. mapped the contours of the distribution range).

Table 1. List of the climate variables selected to build hindcast models.

Name	Unit	Description
Maximum winter temperature	Kelvin (K)	Monthly maximum between December and March
Mean winter temperature	Kelvin (K)	Monthly average between December and March
Minimum winter temperature	Kelvin (K)	Monthly minimum between December and March
Maximum summer temperature	Kelvin (K)	Monthly maximum between June and August
Mean summer temperature	Kelvin (K)	Monthly average between June and August
Minimum summer temperature	Kelvin (K)	Monthly minimum between June and August
Total summer rainfall	Meter (m)	Monthly sum of rainfall between June and August
Total winter rainfall	Meter (m)	Monthly sum of rainfall between December and March
Total winter snowfall	Meter (m)	Monthly sum of snowfall between December and March
Mean snow depth	Meter of water equivalent (mwe)	Monthly average of ground surface snow depth
Total number of rain-on-snow events	Event (number)	Monthly sum of rain-on-snow events
Start of the growing season	Julian Day (JD)	Date of the first day of a series of over 5 consecutive days with an average daily temperature above 5°C
End of the growing season	Julian Day (JD)	Date of the first day of a series of over 5 consecutive days with an average daily temperature under 5°C
Duration of the growing season	Days (number)	Number of days between the date of start and the date of end of the growing season

We selected this value as it presented the best fit of the position of hindcasted southern limits to the position of historical southern limits of distribution for the most recent time step (2010). This step ensured that there was minimal error generated in the inference of southern range boundaries from hindcasted distributions, but also that small southern populations were represented in the tracing of these boundaries. The focus here was on the fit of the southern limit of the range of distribution, and as such we did not use a threshold that would have maximized the value of the TSS (Liu et al. 2005). Indeed, when compared to the 0.1, 0.3 and 0.5 thresholds, the 0.3 threshold presented the shortest median distance between observed and hindcasted southern limits of distribution for 2010, all reanalyses combined (Figure C1). We still tested the sensitivity of our analyses to the choice of such threshold by running them for all considered values (0.1, 0.3, 0.5), yielding similar results and an identical overall trend (Figures C2 and C3).

We evaluated the effect of including the three small, isolated populations found south of the current continuous distribution range (i.e. from west to east: Val-d'Or, Charlevoix and Gaspésie) by hindcasting past distributions with and without those populations in our dataset (see Appendix B for results). Since the contraction of historical caribou range followed a clear south to north pattern, we measured geographical distances between historical and hindcasted southern limits for points of the same longitude, and for each time step of interest, and we compared the latitudes of historical and hindcasted southern limits through time.

NICHE MODELLING

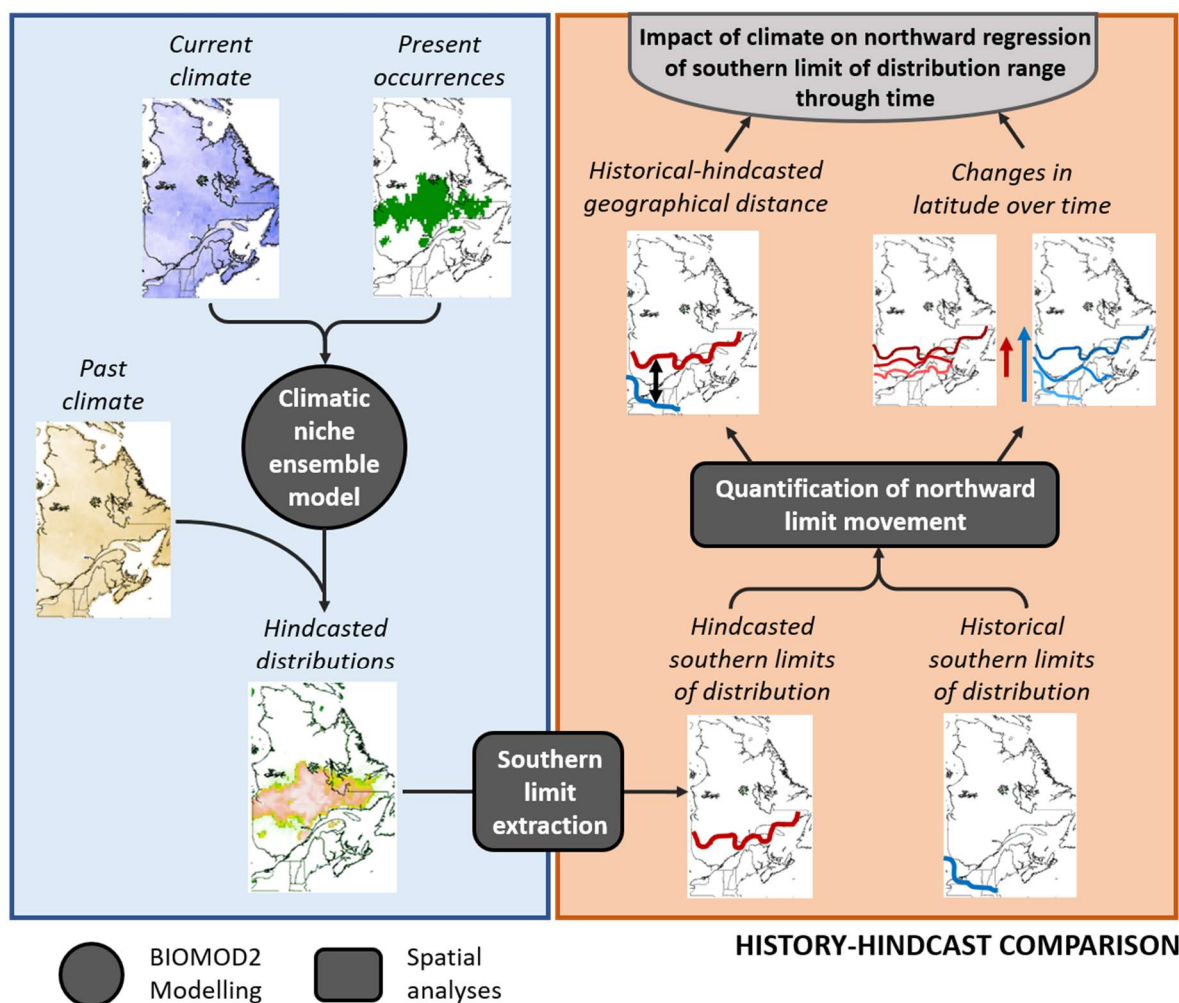


Figure 4. Schematic workflow depicting the different analytical steps used. Hindcasted boreal caribou distributions (maps of probability of occurrence) were produced by climatic niche ensemble modelling for each source of data and time step of interest. Southern boundaries extracted from those distributions are compared to the historical southern boundaries for each time step, by quantifying their respective movements northward, to underline the discrepancies between history and hindcast. These spatial analyses bring forward the impact of climate on the regression of the southern boundary of distribution range through time. The circle represents the ensemble modelling done through BIOMOD2, and the rectangles represent spatial analyses.

RESULTS

Past caribou distributions inferred from climate reanalysis show little effects of climate variation

Ensemble models show very high goodness-of-fit when modelling the current realized climate niche of boreal caribou. Indeed, TSS values of ensemble models with 95% CI were 0.926 [0.918: 0.926], 0.945 [0.945: 0.945], and 0.901 [0.896: 0.901] using 20CRv3, CERA-20C, and ERA5 datasets respectively. The hindcasted locations of the climate conditions fit for caribou occurrence, obtained through ensemble modelling, showed rather similar trends in probability of occurrence through time and space under all reanalyses (Figure 5). These analyses also presented very similar patterns of probabilities of occurrence for a given time step. Probabilities of occurrence over the entire study area and for all data sources were overall higher for recent time steps than for older ones. Furthermore, areas of probable occurrence (>0.3) showed a slight northward trend with time. In other words, hindcasted ranges described here resided at rather consistent longitudes but lightly increasing latitudes, with no visible expansion nor shrinkage, over time and across all reanalysis datasets.

Observed southern boundaries of boreal caribou range presented a clear northward displacement with time (Figure 6). Indeed, limits for all time steps were visually easily distinguishable from each other, and latitudinal positions of limits start around 44–45°N in 1850–1900 to end up around 49–50°N in 1970–2010. However, southern boundaries of the hindcasted locations of climate conditions fit for boreal caribou occurrence showed limited spatial displacement through time, with minimal northward migration between 1850 and 2010 (Figure 6). Boundaries of consecutive time steps from hindcasted climate niche analyses tended to strongly overlap or these boundaries lay just one cell away from each other. The limits used here were generated from a threshold of 0.3 of probability of occurrence applied to the ensemble modelling results, as it best reconstituted observed southern limits of distribution.

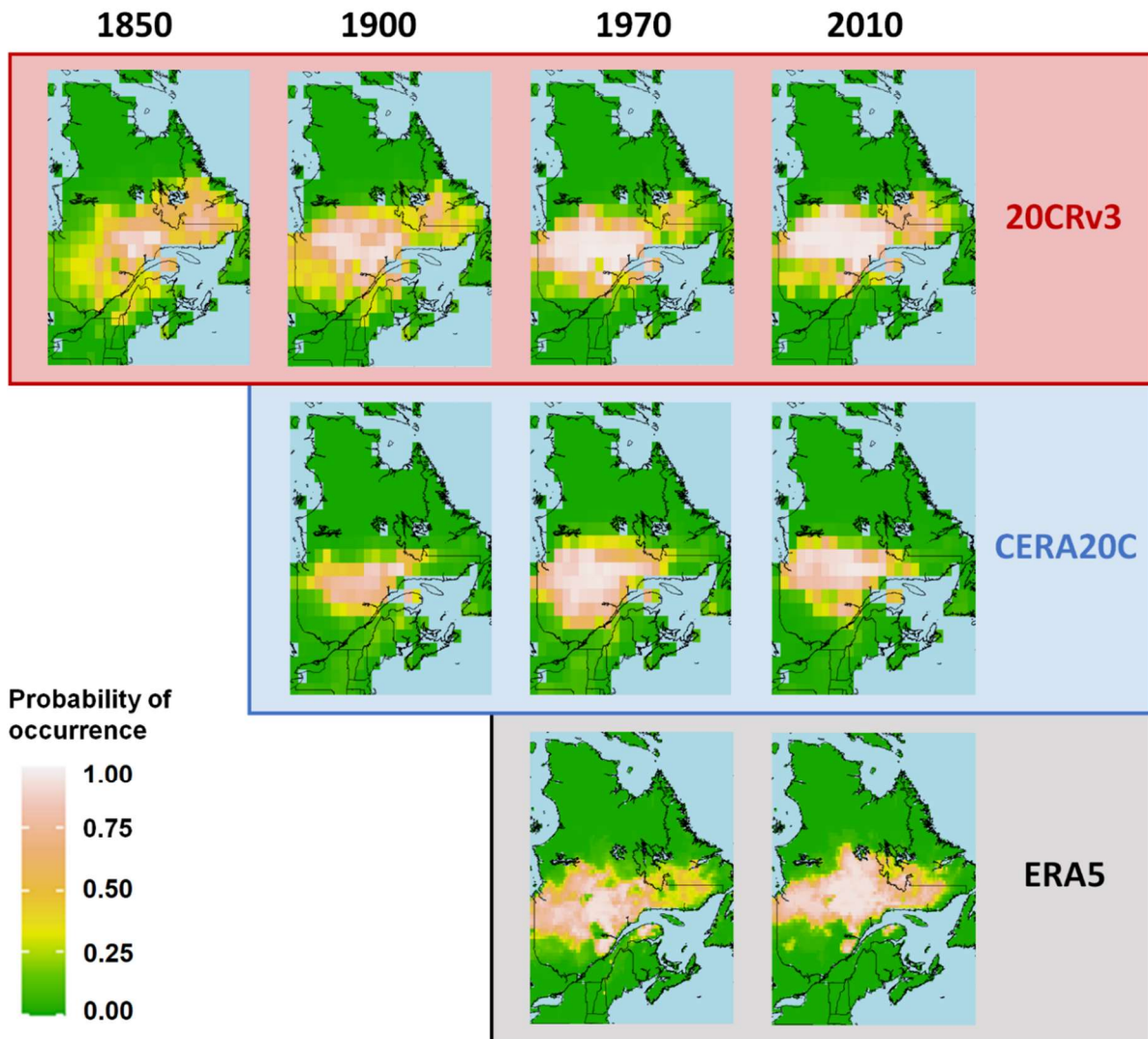


Figure 5. Hindcasted probabilities of boreal caribou occurrence over the study area obtained by ensemble modelling for each data source (20CRv3, CERA-20C, ERA5) and each available time step (1850-1900-1970-2010, 1900-1970-2010, and 1970-2010 respectively).

Discrepancies between observed and hindcasted southern limits across all datasets increase as we go back in time

Distances between southern limits of observed caribou ranges and southern limits of hindcasted locations of climate conditions fit for caribou occurrence largely increased as we go back in time between today and 1850, regardless of the reanalysis dataset used (Figure 7). Indeed, 20CRv3 presented nearly overlapping southern boundaries of past caribou ranges and hindcasted locations of climate conditions suitable for boreal caribou in 2010, the distance between those limits increased over time to reach ~280 km in 1850. Though distributions could be relatively wide for certain time steps, especially 1970, similar trends were observed under CERA-20C and ERA5, for which median distances went from ~100 km in 2010 to ~425 km in 1900, and ~25 km in 2010 to ~90 km in 1970, respectively. These results were similar whether southern boundaries were defined using a probability of occurrence threshold of 0.1, 0.3, or 0.5.

Observed and hindcasted southern limits show distinctly different trends of latitudinal displacement through time

Trends of latitudinal movement through time were markedly different between southern boundaries of observed caribou ranges and southern boundaries of hindcasted locations of climate conditions suitable for boreal caribou (Figure 8).

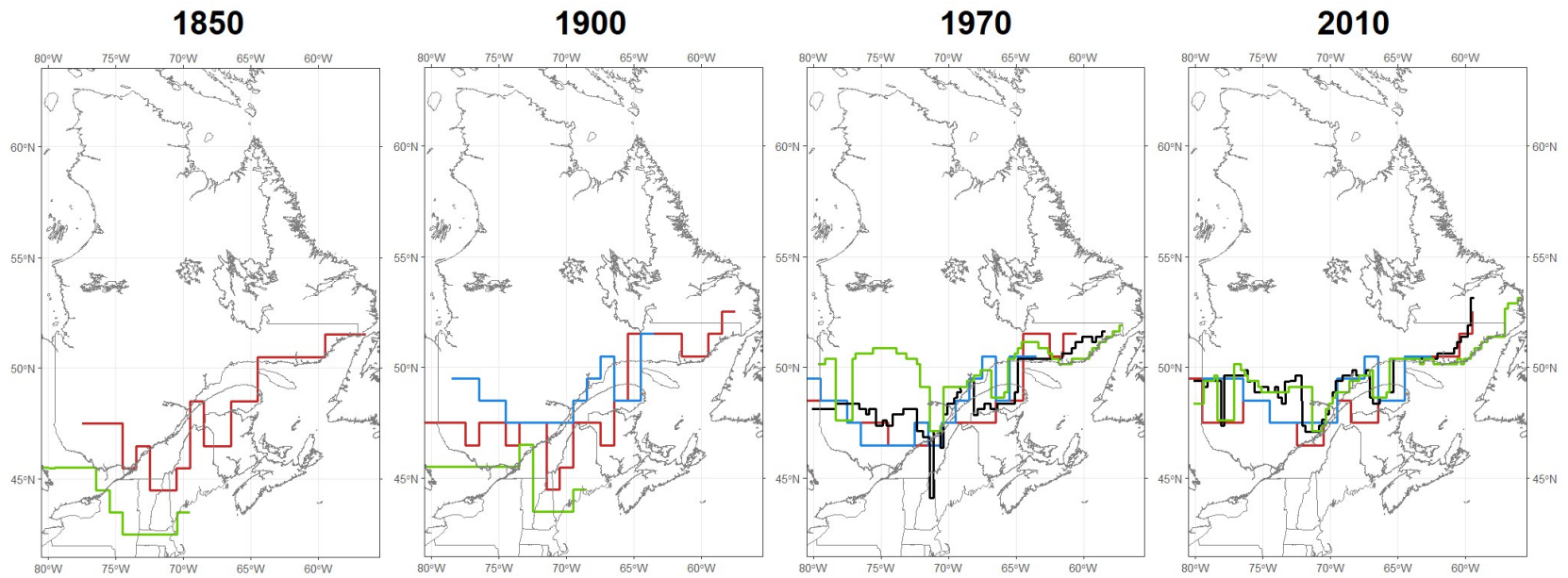


Figure 6. Observed (green) and hindcasted southern range boundaries with the 20CRv3 (red), CERA-20C (blue), and ERA5 (black) reanalysis datasets for each time step of interest (1850, 1900, 1970, 2012).

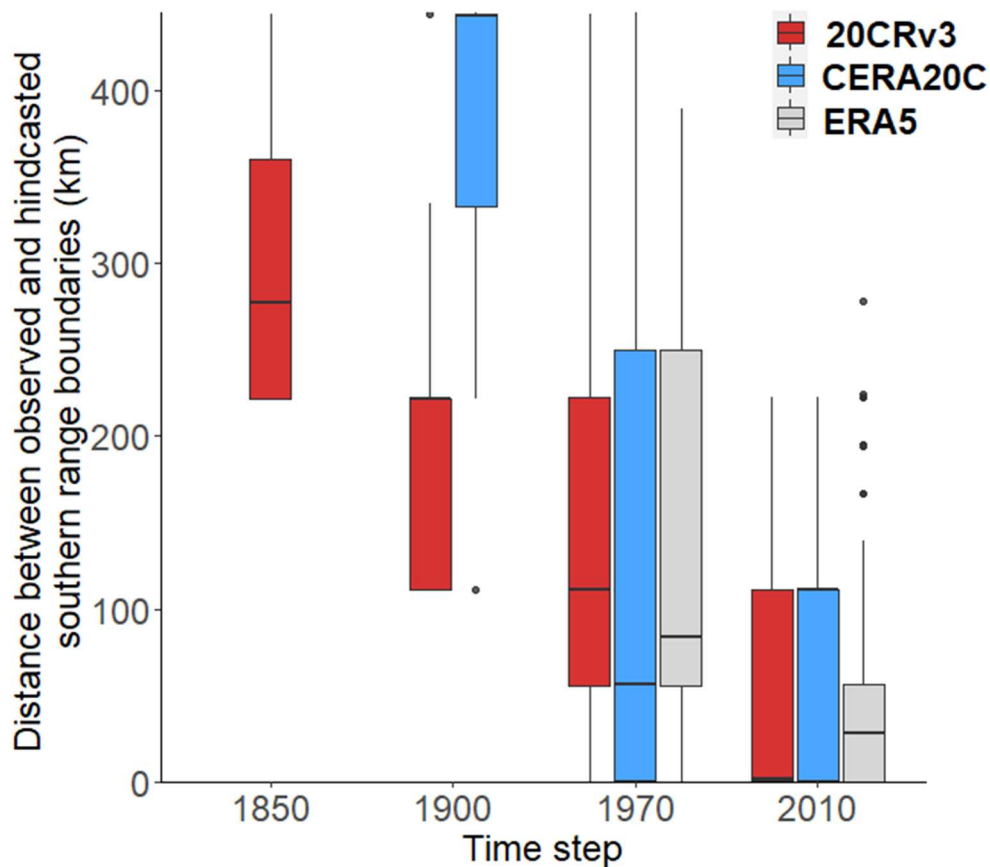


Figure 7. Boxplot (black line: median value, box: upper and lower quartiles, whiskers: distribution outside of the upper and lower quartiles) of distances between observed southern range boundaries and hindcasted southern range boundaries for each time step of interest and the three reanalysis datasets available. Distances were measured between points of same longitude on observed and hindcasted southern limits.

Hindcasted southern boundaries presented a slight northward displacement across time steps, with median latitudes showing a northward range recession of the southern limit from 48° to 49° N. In contrast, the observed past southern boundaries of caribou range showed an important displacement (Figure 8), with a more pronounced northward range recession from 43° to 49° N over time according to median latitude values. The median latitude in 1970 also happens to be higher than the median latitude in 2010. From these results (see Figure 8), we calculated a distance of ~ 105 km between the median positions in latitude of southern limits of hindcasted locations of climate conditions fit for caribou

occurrence in 1850 and the one estimated in 2010. In comparison, the distance between the median positions in latitude of observed southern limits of caribou range in 1850 and the one observed in 2010 is of ~620 km, which equals to a rate of range contraction of approximately 39 km/decade. This trend was similar whether southern boundaries were defined using a probability of occurrence threshold of 0.1, 0.3, or 0.5.

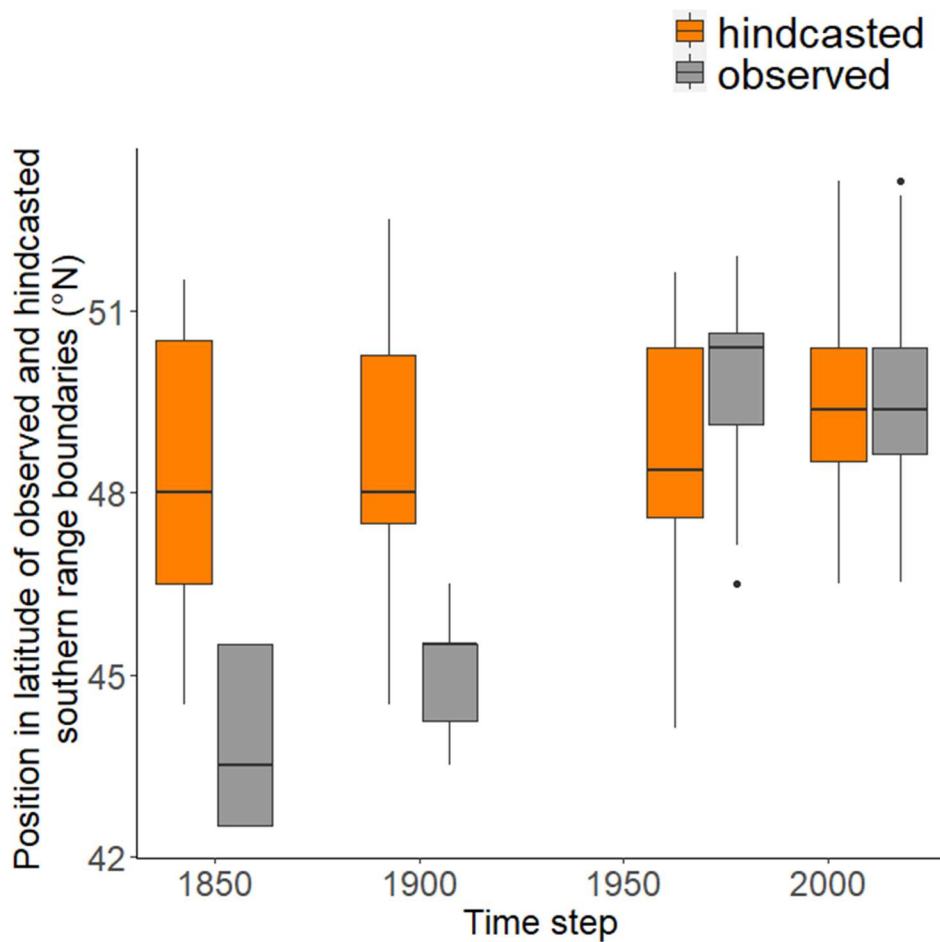


Figure 8. Latitudinal position of observed and hindcasted southern boundaries through time. Boxes for hindcasted southern boundaries were obtained by combining data from all reanalysis datasets.

DISCUSSION

We successfully hindcasted climatic conditions in the boreal caribou's current range (e.g., its current realized climate niche) in the province of Quebec. More interestingly, by comparing the southern limits of occurrence of these climate conditions with the southern boundaries of past boreal caribou range, we highlighted discrepancies between available historical information, used as reference, and reconstitutions through climate niche modelling. Doing so, we showed that climate change appears to have only scarcely contributed to the observed northward recession of the southern limit of boreal caribou range since 1850. We also tested for different thresholds of probability of occurrence when hindcasting southern boundaries and highlighted the robustness of this main result.

Hindcasted-observed southern limit discrepancies: consequences of a truncated realized niche

Hindcasted maps of boreal caribou occurrence based on climate conditions where the species is currently ranging presented a trailing edge of probable distribution moving very slightly northward under all reanalysis datasets, i.e. ~105 km on average for the trailing edge of distribution between 1850 and 2010 (which is equivalent to 6.5 km/decade). As a result, southern limits of the hindcasted locations of climate conditions fit for boreal caribou occurrence under all reanalysis datasets showed minor poleward displacement, while observed southern limits of caribou range presented drastic northward movement through time. Distances between both types of southern limits were also largest in 1850 and decreased over time up to the calibration period (i.e. 2010) (Figures 7,8).

Overall, the reliable ensemble models we built and that account for parameters such as temperature, precipitation, snow cover and phenology cannot reconstitute locations and southern limits of caribou range similar to those observed in the past despite a high statistical robustness and a high quality of both caribou and climate data. Such incoherence, resulting in the inability of these models to recreate past southern distribution limits of caribou range,

suggests that the current distribution range of boreal caribou in Quebec might not be representative of its fundamental climate niche. This situation actually stems from a key condition of niche model building, which is the fact that the species has to be at equilibrium with its environment (Wiens et al. 2009, Dormann et al. 2012). In fact, niche modelling relies on the direct ecological link between environmental clues and a species' presence, and this link has to be intact for niche models to perform. If the species' distribution range is “*an environmentally biased subset of abiotically suitable areas*” (*sensu* Anderson 2013), the predictive power of the niche model can be strongly hindered and projected distributions biased and inaccurate (Williams et al. 2013, Anderson 2013, Davis et al. 2014).

The few studies that hindcasted past ranges of mammal species based on models delineating climate conditions within which the species were found to range showed similar results (Guralnick & Pearman 2010, Davis et al. 2014, McGuire & Davis 2013). As these studies showed partial reconstitutions of observed fossil presence, several of the potential explanations they raised for such mismatches most likely do not apply to our case. In fact, considering the relatively short duration of our study, changes in the climate niche of boreal caribou through time such as niche shifts through evolution or phenotypic plasticity (Guralnick & Pearman 2010, McGuire & Davis 2013) are probably irrelevant. Similarly, climate conditions seem very unlikely to have changed enough since 1850 to produce non-analog climates (Davis et al 2014) that would generate a niche bias as significant as the one presented here. Aside from that, the statistical quality of the models used can obviously be part of the problem. In our case, the ensemble models, suitable algorithms and model calibrations (see the section 2.3.1 Model Building and Hindcast, in Methods), as well as the high scores obtained from a reliable performance index are all elements that indicate that our models have very high goodness-of-fit. For all these reasons, it seems very unlikely that the inability of our reconstitutions to match past boundaries could be due to the poor quality of our data or models.

Differences between the actual distribution range of a species and the area designated by their climate niche are nevertheless expected, as factors such as predation, competition,

or dispersal limitations also weigh into the geographical distribution of species (Colwell & Rangel 2009, McGuire & Davis 2013). That being said, the continuous northward movement for over one and a half centuries and its magnitude exhibited in the case of the range recession of boreal caribou seem unlikely to originate from natural biotic factors. Schaefer (2003) reached the same conclusion in the case of woodland caribou in Ontario, with a similar rate of observed northward range recession during approximately the same period (about 34 km/decade). In addition, the median pace of poleward range shift associated with climate warming is estimated to be about 16.9 km/decade for species globally (Chen et al. 2011), a rate drastically different from the ones observed in Quebec and Ontario, further supporting the limited implication of climate change in caribou range recession.

Thus, we suggest that the distribution of boreal caribou has probably been shaped by anthropogenic drivers (e.g., Laliberte and Ripple 2004, Vors et al. 2007) that have disrupted the state of equilibrium of the species with its climate environment since 1850. This would result in its current distribution being a subset of what it used to be and what it could be in terms of climate conditions. Indeed, there is now growing evidence that anthropogenic activities and space use have affected species range enough to create a significant disconnection between the fundamental climate niche of species and their realized niche (Nogués-Bravo 2009, Veloz et al. 2012, Pineda-Munoz et al. 2021). In mammals, this phenomenon is especially true for large-sized and specialist species whose current distribution ranges are only a portion of what they used to be about 100 years ago (Pineda-Munoz et al. 2021). A major consequence is the great difficulty to rely on current presence data only to calibrate niche models, even though they are usually the most precise available (Faurby & Araújo 2018). Including past distribution ranges and anthropogenic impacts on distribution range alteration in the calibration of climate niche models is, for that reason, often highly recommended (Nogués-Bravo 2009, Faurby & Araújo 2018).

Limited effect of climate change on range shift suggests important impact of anthropogenic land use since 1850

Southern limits of observed past caribou ranges and southern limits of hindcasted areas where climate conditions are suitable for boreal caribou presented two very distinct trajectories of displacement in latitude, with observed limits showing a much more dramatic northward trend. According to our findings, the northward movement of observed southern limits of boreal caribou distribution range between 1850 and 2010 was of ~620 km, whereas it was of only ~105 km for southern limits of the hindcasted locations of climate conditions fit for caribou occurrence. This implies that if climate was solely responsible for current and past caribou distribution range, the latter should have shifted only ~105 km north in the past 160 years. According to our results, only ~17% of the observed recession of caribou range since 1850 would be imputable to the displacement of climate conditions fitting for boreal caribou due to climate change (for a 0.3 threshold of probability of occurrence, see Appendix C for results using 0.1 and 0.5 thresholds). As discussed above, anthropogenic drivers referring to land use (i.e. loss, fragmentation and alteration of caribou habitat induced by natural resource extraction, urbanization or agriculture) or caribou harvest (i.e. traditional Indigenous hunting, poaching or past sport hunting, the latter being prohibited since 2001) are most likely the main cause for the remaining 83%. The importance of habitat loss is consistent with a large body of knowledge on the decline of this species, as reviewed by Festa-Bianchet et al. (2011).

As in many other places in the world, the human footprint has grown rapidly in the province of Quebec since 1850 (Boucher et al. 2014). Lumber as well as pulp and paper were some of the province's biggest industries in the 19th century (Minville 1946, Natural Resources Canada 2014). Forest harvesting developed as an important economic activity in regions surrounding the St. Lawrence River and in most of southern Quebec (Girard 1989), gaining in intensity by the 1920s (Blais & Boucher 2008, Flamand-Hubert 2016). At the same time, a dense network of roads and railways progressively covered the southern part of the province, eastwards to the Gaspé Peninsula in the 1850s, but also northward to the region of Lac-St-Jean by the beginning of the 20th century, and further northwest to the region of

Abitibi by the 1930s (Rinfret & Taché 1907, Editions Forest 1935, Letarte 1971). The population of the province increased from ~890,000 to ~2 million inhabitants between 1850 and 1911 (Department of the Interior Canada & Chalifour 1915), inducing a rapid conversion of forests (i.e., caribou habitat) into agricultural lands around the valley of the St-Lawrence River (Dick & Taylor 2015, Behiels 2020).

By the beginning of the 20th century, cities, concentrated mostly in the southern part of Quebec, began growing in size and population (Letarte 1971, Department of the Interior Canada & Chalifour 1915), furthering the transformation of landscapes south of the province. In addition to this increasing anthropogenic land use, boreal caribou was commonly hunted by non-Indigenous populations (Minville 1946, Government of Quebec 2022), until endangered species laws started protecting it under federal and provincial jurisdiction in the 2000s (Environment Canada 2012, MFFP 2021a). For all these reasons, we suggest that anthropogenic land use and activities have probably been an important driver of the historical local extirpation of boreal caribou from the southern part of the province, exceeding climate change in terms of impact and leading to the northward range recession recorded since 1850. Indeed, in Quebec there is close correspondence between the southern range limits of boreal caribou and the northern limits of forest fragmentation (Schindler & Lee 2010).

The literature is rich regarding studies focusing on the negative impacts of various types of anthropogenic disturbances on boreal caribou in Quebec and other Canadian provinces, such as forest harvesting (Vors et al. 2007, Lafontaine et al. 2019, Fryxell et al. 2020, Lochhead et al. 2022), railways, paved and forest roads (Whittington et al. 2011, Leblond et al. 2013, Newton et al. 2017, Lochhead et al. 2022), and other industrial exploitations of natural resources (Dyer et al. 2001, Stewart et al. 2020, MacNearney et al. 2021). Whether they affect their movement capacities (Dyer et al. 2001, Beauchesne et al. 2013), survival rates (Courtois et al. 2007, Losier et al. 2015, Fryxell et al. 2020), or reproductive outputs (Pinard et al. 2012, Leclerc et al. 2014), potential anthropogenic drivers of caribou decline are numerous. Many of these disturbances lead to apparent competition with other deer species, which may serve as alternative prey for wolves or coyotes (Wittmer

et al. 2005, DeCesare et al. 2012, Frenette et al. 2020). The increase in early regeneration stands resulting from forest harvesting in the habitat of caribou induces a rise in moose and white-tailed deer populations attracted by abundant and palatable early-seral vegetation, which in turn generates growing wolf or coyote populations that also travel more easily, increasing predation pressure on caribou populations (Wittmer et al. 2005, DeCesare et al. 2012, Frenette et al. 2020). All those elements further support the hypothesis of post-industrial human-driven land-use change and anthropogenic activities in caribou range recession, which have been exerting their detrimental effects on boreal caribou populations in Quebec for over 150 years. Though several factors, such as diseases (Environment and Climate Change Canada 2019, MFFP 2021b), nutrition and access to key resources (Bergerud & Mercier 1989, MFFP 2021b), and dispersion (Bergerud & Mercier 1989), have been put forward over the last few decades to explain caribou decline, the major direct or indirect implications of anthropogenic land use are now clearly identified (Schaefer 2003, COSEWIC 2002). Moreover, predation and fires, both historical drivers that have shaped the boreal ecosystem, now represent threats to caribou population sustainability because of their link with human land use activities (Environment and Climate Change Canada 2019). In a landscape historically modelled by forest fires, the deep modifications done by human presence reduce even further the area of available suitable habitat (Racey & Armstrong 1998, Environment and Climate Change Canada 2019). In addition, high predation rates are inherent to the apparent competition phenomenon identified as a considerable factor of caribou decline across Canada and a result of anthropogenic habitat alteration (DeCesare et al. 2012, Frenette et al. 2020). Hence, the limited impacts of climate change in the past boreal caribou range recession tend to align with those assertions.

LIMITS

As climate niche modelling relies on climate data, any default in the reconstitution of past climates by the reanalysis data used here definitely affects the quality of hindcasted distributions. Despite scarce literature on the local performances of ERA5, CERA-20C and

20CRv3 over the province specifically, some studies indicate that these data are sufficient for analyses on a broader geographic scale and for various uses (Alves et al. 2020, Crossett et al. 2020, Tarek et al. 2020, Slivinski et al. 2021).

An important assumption made in this study is that the historical southern boundaries are actually representative of the situation for the time steps they describe and can therefore be used to test the predictive capacity of our models. Considering the different methods and sources most likely used to trace those boundaries through time (archive descriptions, aerial surveys, etc.), their quality can obviously be questioned, as for any historical source of information. Because they describe the past, sometimes in a biased or imprecise manner, they still bring a new perspective into the topic of boreal caribou conservation and hold unique information that could not be accessed otherwise. For that reason, we chose to use these sources and deemed them reliable enough to include in analyses designed to understand the mechanisms that lead to the current situation regarding boreal caribou distribution. That being said, the fact that our results produced the median latitude of the 1970 southern range boundary north of the one for 2010 is most likely due to the difference in precision between the methods used to define those limits. The southern boundary observed in 1970 was based on aerial survey data, whereas the 2010 observed southern boundary was obtained using telemetry data, which is more spatiotemporally precise and more geographically extensive. The boundaries observed in 1850 and 1900 could also be imprecise, but they were both described by at least two different sources, ensuring a relative reliability to the information. Furthermore, the observed recession described in our results presents a distance that is much greater than the potential imprecision held by each archival boundary used in our analyses.

CONCLUSION

By highlighting the limited role of climate change in the northward recession of the southern boundaries of boreal caribou range since 1850, our study suggests that anthropogenic land use (i.e. timber harvesting, agriculture, development of cities, villages

and road networks) and caribou harvest (hunting and poaching) were the most important drivers at play during the last 160 years. This implies that management measures aiming at limiting the detrimental impacts of human activities on boreal caribou habitat are far from irrelevant. Moreover, our results do not align with the ideas that the caribou's northward range recession in Quebec is mainly driven by climate change and that land-use practices (mainly timber harvesting and oil and gas extraction) have nothing to do with this major, pan-Canadian decline, though this argument is commonly raised by opponents to caribou conservation (e.g. Alliance Forêt Boréale 2019, St-Gelais & Gilbert 2021). Such denial campaigns can have detrimental effects on decision-maker commitment and on stakeholder involvement toward caribou recovery actions (Boan et al. 2018), especially when caribou conservation threatens socioeconomic development (Hebblewhite 2017). Whereas the evidence for climate-driven range contraction is scant, the evidence for habitat loss is immense (Schaefer 2003, Festa-Bianchet et al. 2011, Courtois et al. 2007, Vors & Boyce 2009, Serrouya et al. 2019, D'Orangeville et al. 2023).

Although climate change is an unavoidable concern for the future (Leblond et al. 2022, St-Laurent et al. 2022), our results call for the upholding and strengthening of conservation actions to protect boreal caribou populations in Quebec, especially in relation to forest management. The combined negative effect of anthropogenic pressures and global warming has been identified as an important threat to endangered species, with climate change growing in magnitude and aggravating the decline of species made vulnerable by human activities (Carroll 2007, García-Valdés et al. 2015, Penjor et al. 2021). In the case of the boreal caribou, expected changes in fire regimes in the boreal forest (Boulanger et al. 2014, Barber et al. 2018), in parasite transmission (Pickles et al. 2013), or in temperature (Racey et al. 2005, Masood et al. 2017) due to climate change are main factors of uncertainty that could become particularly detrimental to caribou if cumulated over an already deteriorated habitat resulting from anthropogenic activities (St-Laurent et al. 2022).

In conclusion, and from a theoretical perspective, our results suggest that future distribution range predictions should be made with caution when using species distribution models based on climate, notably for species currently recognized as threatened or endangered, as they are not necessarily in equilibrium with their environment. If using recent, high-quality presence data is a benefit, accurate predictions will have to take into account such non-equilibrium states, notably by considering information from past distributions.

LITERATURE CITED

- Alliance Forêt Boréale (2019). *Caribou forestier : mythes et réalités*. Accessed September 20th, 2022. <https://allianceforetboreale.org/caribou-forestier--mythes-et-realites>
- Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, 43(6), 1223-1232.
- Alves, M., Nadeau, D. F., Music, B., Anctil, F., & Parajuli, A. (2020). On the performance of the Canadian Land Surface Scheme driven by the ERA5 reanalysis over the Canadian boreal forest. *Journal of Hydrometeorology*, 21(6), 1383-1404.
- Anderson, R. P. (2013). A framework for using niche models to estimate impacts of climate change on species distributions. *Annals of the New York Academy of Sciences*, 1297(1), 8-28.
- Araújo, M. B., & New, M. (2006). Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*, 22(1), 42-47.
- Banfield, A. W. F. (1961). *A revision of the reindeer and caribou, genus Rangifer* (No. 66). Queen's Printer.
- Barber, Q. E., Parisien, M. A., Whitman, E., Stralberg, D., Johnson, C. J., St-Laurent, M. H., Delancey, E. R., Price, D. T., Arseneault, D., Wang, X., & Flannigan, M. D. (2018). Potential impacts of climate change on the habitat of boreal woodland caribou. *Ecosphere*, 9(10), e02472.
- Beauchesne, D., Jaeger, J. A., & St-Laurent, M. H. (2013). Disentangling woodland caribou movements in response to clearcuts and roads across temporal scales. *PLoS One*, 8(11), e77514.
- Behiels, M. D. (2020, May 15). *Quebec*. Encyclopedia Britannica. Accessed August 1st, 2022. <https://www.britannica.com/place/Quebec-province>
- Bélanger, L., & Grenier, M. (2002). Agriculture intensification and forest fragmentation in the St. Lawrence valley, Québec, Canada. *Landscape Ecology*, 17(6), 495-507.
- Bergerud, A. T., & Mercer, W. E. (1989). Caribou introductions in eastern North America. *Wildlife Society Bulletin (1973-2006)*, 17(2), 111-120.
- Berteaux, D. (2014). *Changements climatiques et biodiversité du Québec : vers un nouveau patrimoine naturel*. Presses de l'Université du Québec. <https://books.google.co.jp/books?id=N1snDwAAQBAJ>

- Blais, R., & Boucher, J.L. (2008). *Les Régimes forestiers québécois. Régimes d'accumulation, structures d'acteurs et modèles de développement*. Cahiers de recherche du CRISES, coll. « Études théoriques », Montréal.
- Boan, J. J., Malcolm, J. R., Vanier, M. D., Euler, D. L., & Moola, F. M. (2018). From climate to caribou: How manufactured uncertainty is affecting wildlife management. *Wildlife Society Bulletin*, 42(2), 366-381.
- Boucher, Y., Arseneault, D., Sirois, L., & Blais, L. (2009). Logging pattern and landscape changes over the last century at the boreal and deciduous forest transition in Eastern Canada. *Landscape Ecology*, 24(2), 171-184.
- Boucher, Y., Grondin, P., & Auger, I. (2014). Land use history (1840–2005) and physiography as determinants of southern boreal forests. *Landscape Ecology*, 29(3), 437-450.
- Boucher, Y., Auger, I., Arseneault, D., Elzein, T., & Sirois, L. (2021). Long-term (1925–2015) forest structure reorganization in an actively managed temperate-boreal forest region of eastern North America. *Forest Ecology and Management*, 481, 118744.
- Boulanger, Y., Gauthier, S., & Burton, P. J. (2014). A refinement of models projecting future Canadian fire regimes using homogeneous fire regime zones. *Canadian Journal of Forest Research*, 44(4), 365-376.
- Bush, E. and Lemmen, D.S., editors (2019): Canada's Changing Climate Report; Government of Canada, Ottawa, ON. 444 p
- Cai, Q., Wang, J., Beletsky, D., Overland, J., Ikeda, M., & Wan, L. (2021). Accelerated decline of summer Arctic sea ice during 1850–2017 and the amplified Arctic warming during the recent decades. *Environmental Research Letters*, 16(3), 034015.
- Carroll, C. (2007). Interacting effects of climate change, landscape conversion, and harvest on carnivore populations at the range margin: marten and lynx in the northern Appalachians. *Conservation Biology*, 21(4), 1092-1104.
- Ceballos, G., & Ehrlich, P. R. (2002). Mammal population losses and the extinction crisis. *Science*, 296(5569), 904-907.
- Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*, 114(30), E6089-E6096.
- Chapin III, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., Hobbie, S. E., Mack, M. C. & Díaz, S. (2000). Consequences of changing biodiversity. *Nature*, 405(6783), 234-242.

- Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333(6045), 1024-1026.
- Colwell, R. K., Brehm, G., Cardelús, C. L., Gilman, A. C., & Longino, J. T. (2008). Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science*, 322(5899), 258-261.
- Colwell, R. K., & Rangel, T. F. (2009). Hutchinson's duality: The once and future niche. *Proceedings of the National Academy of Sciences*, 106(supplement 2), 19651-19658.
- COSEWIC. (2002). COSEWIC assessment and update status report on the woodland caribou *Rangifer tarandus caribou* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xi + 98 pp.
- Courtois, R., Ouellet, J. P., Gingras, A., Dussault, C., Breton, L., & Maltais, J. (2003). Historical changes and current distribution of caribou, *Rangifer tarandus*, in Quebec. *The Canadian Field-Naturalist*, 117(3), 399-414.
- Courtois, R., Ouellet, J. P., Dussault, C., & Gingras, A. (2004). Forest management guidelines for forest-dwelling caribou in Québec. *The Forestry Chronicle*, 80(5), 598-607.
- Courtois, R., Ouellet, J. P., Breton, L., Gingras, A., & Dussault, C. (2007). Effects of forest disturbance on density, space use, and mortality of woodland caribou. *Ecoscience*, 14(4), 491-498.
- Crossett, C. C., Betts, A. K., Dupigny-Giroux, L. A. L., & Bombliès, A. (2020). Evaluation of daily precipitation from the ERA5 global reanalysis against GHCN observations in the northeastern United States. *Climate*, 8(12), 148.
- D'Orangeville, L., M.-H. St-Laurent, L. Boisvert-Marsh, X. Zhang, G. Bastille-Rousseau, and M. Itter. 2023. Current Symptoms of Climate Change in Boreal Forest Trees and Wildlife. Pp. 747-771, Ch. 30, *In: Boreal Forests in the Face of Climate Change: Sustainable Management*. Girona, M.M., H. Morin, S. Gauthier, Y. Bergeron (Editors). *Advances in Global Change Research 74*, Springer, Switzerland, 837 p.
- Davis, E. B., McGuire, J. L., & Orcutt, J. D. (2014). Ecological niche models of mammalian glacial refugia show consistent bias. *Ecography*, 37(11), 1133-1138.
- Dawe, K. L., & Boutin, S. (2016). Climate change is the primary driver of white-tailed deer (*Odocoileus virginianus*) range expansion at the northern extent of its range; land use is secondary. *Ecology and Evolution*, 6(18), 6435-6451.
- DeCesare, N. J., Hebblewhite, M., Schmiegelow, F., Hervieux, D., McDermid, G. J., Neufeld, L., Bradley, M., Whittington, J., Smith, K. G., Morgantini, L. E., Wheatley,

M., & Musiani, M. (2012). Transcending scale dependence in identifying habitat with resource selection functions. *Ecological Applications*, 22(4), 1068-1083.

Department of the Interior Canada (publisher) & Chalifour, J. E. (printer) (1915). Population: Province of Quebec; Province of Nova Scotia; Province of New Brunswick; Province of Prince Edward Island. (on upper margin). Atlas of Canada. (to accompany) Department of the Interior Canada. Atlas Of Canada [statistical diagram]. Retrieved from

<https://www.davidrumsey.com/luna/servlet/detail/RUMSEY~8~1~251936~5517820:Population?qvq=w4s:/what%2FPopulation%2Fwhere%2FQuebec%2F;lc:RUMSEY~8~1&mi=6&trs=9>

Di Marco, M., Venter, O., Possingham, H. P., & Watson, J. E. (2018). Changes in human footprint drive changes in species extinction risk. *Nature communications*, 9(1), 1-9.

Díaz, S., Pascual, U., Stenseke, M., Martín-López, B., Watson, R. T., Molnár, Z., Hill, R., Chan, K. M. A., Baste, I. A., Brauman, K. A., Polasky, S., Church, A., Lonsdale, M., Larigauderie, A., Leadley, P. W., van Oudenhoven, A. P. E., van der Plaats, F., Schröter, M., Lavorel, S., Aumeeruddy-Thomas, Y., Bukvareva, E., Davies, K., Demissew, S., Erpul, G., Failler, P., Guerra, C. A., Hewitt, C. L., Keune, H., Lindley, S. & Shirayama, Y. (2018). Assessing nature's contributions to people. *Science*, 359(6373), 270-272.

Díaz, S., Settele, J., Brondízio, E. S., Ngo, H. T., Agard, J., Arneth, A., Balvanera, P., Brauman, K. A., Butchart, S. H. M., Chan, K. M. A., Garibaldi, L. A., Ichii, K., Liu, J. Subramanian, S. M., Midgley, G. F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, S., Purvis, A., Razzaque, J., Reyers, B., Chowdhury, R. R., Shin, Y.-J., Visseren-Hamakers, I., Willis, K. J., & Zayas, C. N. (2019). Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science*, 366(6471), eaax3100.

Dick, L., & Taylor, J. (May 1st, 2015). Histoire de l'agriculture jusqu'à la Deuxième Guerre mondiale. *L'Encyclopédie Canadienne*. Accessed 29 Nov. 2022. <https://www.thecanadianencyclopedia.ca/fr/article/histoire-de-lagriculture>.

Dickie, M., Serrouya, R., DeMars, C., Cranston, J., & Boutin, S. (2017). Evaluating functional recovery of habitat for threatened woodland caribou. *Ecosphere*, 8(9), e01936.

Dormann, C. F., Schymanski, S. J., Cabral, J., Chuine, I., Graham, C., Hartig, F., Kearney, M., Morin, X., Römermann, C., Schröder, B., & Singer, A. (2012). Correlation and process in species distribution models: bridging a dichotomy. *Journal of Biogeography*, 39(12), 2119-2131.

- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., García Marquéz, J. R., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36(1), 27-46.
- Drever, C. R., Hutchison, C., Drever, M. C., Fortin, D., Johnson, C. A., & Wiersma, Y. F. (2019). Conservation through co-occurrence: Woodland caribou as a focal species for boreal biodiversity. *Biological Conservation*, 232, 238-252.
- Dyer, S. J., O'Neill, J. P., Wasel, S. M., & Boutin, S. (2001). Avoidance of industrial development by woodland caribou. *The Journal of Wildlife Management*, 531-542.
- ECMWF. (July 7th, 2022)a. *ERA5. ECMWF (European Centre for Medium-Range Weather Forecasts)*. Accessed 8 Jul. 2022. <https://www.ecmwf.int/en/forecasts/datasets/reanalysis-datasets/era5>
- ECMWF. (July 1st, 2022)b. *CERA-20C. ECMWF (European Centre for Medium-Range Weather Forecasts)*. Accessed 8 Jul. 2022. <https://www.ecmwf.int/en/forecasts/datasets/reanalysis-datasets/cera-20c>
- Editions Forest (Text author). (1935). Carte de la province de Québec (Canada) dressée d'après les cartes de géographie du Québec et publiée par la Maison Forest [map]. Girard et Barrère. Retrieved from <https://gallica.bnf.fr/ark:/12148/btv1b53060676x/f1.item>
- Environment Canada. (2012). Recovery Strategy for the Woodland Caribou (*Rangifer tarandus caribou*), Boreal population, in Canada. Species at Risk Act Recovery Strategy Series. Environment Canada, Ottawa. xi + 138 pp.
- Environment and Climate Change Canada. (2019). Amended Recovery Strategy for the Woodland Caribou (*Rangifer tarandus caribou*), Boreal population, in Canada [Proposed]. Species at Risk Act Recovery Strategy Series. Environment and Climate Change Canada, Ottawa. xiii + 143pp.
- Environmental Systems Research Institute (ESRI). (2018). *ArcMap Release 10.6.1*. Redlands, CA.
- Faurby, S., & Araújo, M. B. (2018). Anthropogenic range contractions bias species climate change forecasts. *Nature Climate Change*, 8(3), 252-256.
- Festa-Bianchet, M., Ray, J. C., Boutin, S., Côté, S. D., & Gunn, A. (2011). Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. *Canadian Journal of Zoology*, 89(5), 419-434.

- Flamand-Hubert, M. (2016). Les premiers pas de l'aménagement forestier au Québec. Vers une régularisation de la marche des coupes. *Histoires forestières du Québec*, n.d.(n.d.), 23-28.
- Free, M., & Robock, A. (1999). Global warming in the context of the Little Ice Age. *Journal of Geophysical Research: Atmospheres*, 104(D16), 19057-19070.
- Freeman, B. G., Lee-Yaw, J. A., Sunday, J. M., & Hargreaves, A. L. (2018). Expanding, shifting and shrinking: The impact of global warming on species' elevational distributions. *Global Ecology and Biogeography*, 27(11), 1268-1276.
- Frenette, J., Pelletier, F., & St-Laurent, M. H. (2020). Linking habitat, predators and alternative prey to explain recruitment variations of an endangered caribou population. *Global Ecology and Conservation*, 22, e00920.
- Fryxell, J. M., Avgar, T., Liu, B., Baker, J. A., Rodgers, A. R., Shuter, J., Thompson, I. D., Reid, D. E. B., Kittle, A. M., Mosser, A., Newmaster, S. G., Nudds, T. D., Street, G. M., Brown, G. S. & Patterson, B. (2020). Anthropogenic disturbance and population viability of woodland caribou in Ontario. *The Journal of Wildlife Management*, 84(4), 636-650.
- Gagné, C., Mainguy, J., & Fortin, D. (2016). The impact of forest harvesting on caribou–moose–wolf interactions decreases along a latitudinal gradient. *Biological Conservation*, 197, 215-222.
- García-Valdés, R., Svenning, J. C., Zavala, M. A., Purves, D. W., & Araújo, M. B. (2015). Evaluating the combined effects of climate and land-use change on tree species distributions. *Journal of Applied Ecology*, 52(4), 902-912.
- Girard, C. (1989). Histoire et région : L'industrie forestière du nord-est québécois 1850-1930. *Histoire sociale/Social History*, 22(43).
- Gilg, O., Kovacs, K. M., Aars, J., Fort, J., Gauthier, G., Grémillet, D., Ims, R. A., Meltofte, H., Moreau, J., Post, E., Schmidt, N. M., Yannic, G., & Bollache, L. (2012). Climate change and the ecology and evolution of Arctic vertebrates. *Annals of the New York Academy of Sciences*, 1249(1), 166-190.
- Gonzalez, P., Neilson, R. P., Lenihan, J. M., & Drapek, R. J. (2010). Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. *Global Ecology and Biogeography*, 19(6), 755-768.
- Government of Quebec. (June 20th, 2022). *La situation du caribou au Québec*. Accessed August 2nd, 2022. <https://www.quebec.ca/agriculture-environnement-et-ressources-naturelles/faune/gestion-faune-habitats-fauniques/situation-caribou>.
- Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, 135(2-3), 147-186.

- Guralnick, R., & Pearman, P. B. (2010). Using species occurrence databases to determine niche dynamics of montane and lowland species since the Last Glacial Maximum. *Data Mining for Global Trends in Mountain Biodiversity*, 125-134.
- He, F. (2012). Area-based assessment of extinction risk. *Ecology*, 93(5), 974-980.
- Hebblewhite, M. (2017). Billion dollar boreal woodland caribou and the biodiversity impacts of the global oil and gas industry. *Biological Conservation*, 206: 102-111
- Hornseth, M. L., & Rempel, R. S. (2016). Seasonal resource selection of woodland caribou (*Rangifer tarandus caribou*) across a gradient of anthropogenic disturbance. *Canadian Journal of Zoology*, 94(2), 79-93.
- Hughes, L. (2000). Biological consequences of global warming: is the signal already apparent? *Trends in Ecology & Evolution*, 15(2), 56-61.
- IPCC, 2007: Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 996 pp.
- IPCC, 2013: Summary for Policymakers. In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- IPCC, 2021: Summary for Policymakers. In: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Masson-Delmotte, V., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (eds.)]. In Press.
- Karanth, K. K., Nichols, J. D., Karanth, K. U., Hines, J. E., & Christensen Jr, N. L. (2010). The shrinking ark: patterns of large mammal extinctions in India. *Proceedings of the Royal Society B: Biological Sciences*, 277(1690), 1971-1979.
- La Sorte, F. A., & Jetz, W. (2010). Projected range contractions of montane biodiversity under global warming. *Proceedings of the Royal Society B: Biological Sciences*, 277(1699), 3401-3410.

- Lafontaine, A., Drapeau, P., Fortin, D., Gauthier, S., Boulanger, Y., & St-Laurent, M. H. (2019). Exposure to historical burn rates shapes the response of boreal caribou to timber harvesting. *Ecosphere*, *10*(5), e02739.
- Laliberté, A. S., & Ripple, W. J. (2004). Range contractions of North American carnivores and ungulates. *BioScience*, *54*(2), 123-138.
- Leblond, M., Dussault, C., & Ouellet, J. P. (2013). Impacts of human disturbance on large prey species: do behavioral reactions translate to fitness consequences?. *PLoS One*, *8*(9), e73695.
- Leblond, M., Boulanger, Y., Puigdevall, J.P., St-Laurent, M.-H. (2022). There is still time to reconcile forest management with climate-driven declines in habitat suitability for boreal caribou. *Global Ecology and Conservation* *39*: e02294.
- Leclerc, M., Dussault, C., & St-Laurent, M. H. (2014). Behavioural strategies towards human disturbances explain individual performance in woodland caribou. *Oecologia*, *176*(1), 297-306.
- Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J., & Grenouillet, G. (2020). Species better track climate warming in the oceans than on land. *Nature Ecology & Evolution*, *4*, 1-16.
- Letarte, J. (1971). *Atlas d'histoire économique et sociale du Québec 1851-1901*. Editions Fides.
- Lochhead, K. D., Kleynhans, E. J., & Muhly, T. B. (2022). Linking woodland caribou abundance to forestry disturbance in southern British Columbia, Canada. *The Journal of Wildlife Management*, *86*(1), e22149.
- Lobo, J. M., Jiménez-Valverde, A., & Hortal, J. (2010). The uncertain nature of absences and their importance in species distribution modelling. *Ecography*, *33*(1), 103-114.
- Losier, C. L., Couturier, S., St-Laurent, M. H., Drapeau, P., Dussault, C., Rudolph, T., Brodeur, V., Merkle, J. A., & Fortin, D. (2015). Adjustments in habitat selection to changing availability induce fitness costs for a threatened ungulate. *Journal of Applied Ecology*, *52*(2), 496-504.
- MacNearney, D., Nobert, B., & Finnegan, L. (2021). Woodland caribou (*Rangifer tarandus*) avoid wellsite activity during winter. *Global Ecology and Conservation*, *29*, e01737.
- Mallory, C. D., & Boyce, M. S. (2018) Observed and predicted effects of climate change on Arctic caribou and reindeer. *Environmental Reviews*, *26*(1), 13-25.

- Masood, S., Van Zuiden, T. M., Rodgers, A. R., & Sharma, S. (2017). An uncertain future for woodland caribou (*Rangifer tarandus caribou*): the impact of climate change on winter distribution in Ontario. *Rangifer*, 37(1), 11-30.
- McCain, C. M., King, S. R., & Szewczyk, T. M. (2021). Unusually large upward shifts in cold-adapted, montane mammals as temperature warms. *Ecology*, 102(4), e03300.
- McGuire, J. L., & Davis, E. B. (2013). Using the palaeontological record of *Microtus* to test species distribution models and reveal responses to climate change. *Journal of Biogeography*, 40(8), 1490-1500.
- Miller, G. H., Alley, R. B., Brigham-Grette, J., Fitzpatrick, J. J., Polyak, L., Serreze, M. C., & White, J. W. (2010). Arctic amplification: can the past constrain the future? *Quaternary Science Reviews*, 29(15-16), 1779-1790.
- Minville, E. (1946). Notre Milieu : Aperçu général sur la province de Québec. (Études sur Notre Milieu, Collection dirigée par Esdras Minville.) Montréal : Editions Fides ; École des Hautes Études Commerciales. Pp. 443.
- MFFP. (2021a). *Liste des espèces fauniques menacées ou vulnérables au Québec – Caribou des bois, écotype forestier*. Accessed March 17th, 2022. https://www3.mffp.gouv.qc.ca/faune/especes/menacees/fiche.asp?noEsp=53&_ga=2.205379029.431219693.1647537695-1554414406.1647361964&_gl=1*11qxr19*_ga*MTU1NDQxNDQwNi4xNjQ3MzYxOTY0*_ga_7KG0CGH2EY*MTY0NzUzNzY5NC4yLjAuMTY0NzUzNzY5NC4w
- MFFP. (2021b). *Revue de littérature sur les facteurs impliqués dans le déclin des populations de caribous forestiers au Québec et de caribous montagnards de la Gaspésie*. Accessed September 20th, 2022. https://consultation.quebec.ca/uploads/decidim/attachment/file/122/RevueLitterature_CaribouVF.pdf
- Moreau, C., Vézina, H., & Labuda, D. (2007). Effets fondateurs et variabilité génétique au Québec. *Médecine/Sciences*, 23(11), 1008-1013.
- Moritz, C., Patton, J. L., Conroy, C. J., Parra, J. L., White, G. C., & Beissinger, S. R. (2008). Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science*, 322(5899), 261-264.
- Natural Resources Canada (February 21st, 2014). *Canadian forest sector history (Article 3): The great transformation (1891–1929)—Capitalization of the forest industry and sawmilling evolution*. Accessed July 28th, 2022. <https://scf.rncan.gc.ca/selective-cuttings/70>

- Neilson, E. W., Castillo-Ayala, C., Beckers, J. F., Johnson, C. A., St-Laurent, M. H., Mansuy, N., Price, D., Kelly, A., & Parisien, M. A. (2022). The direct and habitat-mediated influence of climate on the biogeography of boreal caribou in Canada. *Climate Change Ecology*, 3, 100052.
- Newton, E. J., Patterson, B. R., Anderson, M. L., Rodgers, A. R., Vander Vennen, L. M., & Fryxell, J. M. (2017). Compensatory selection for roads over natural linear features by wolves in northern Ontario: Implications for caribou conservation. *PloS one*, 12(11), e0186525.
- NOAA (May 11th, 2022). *NOAA/CIRES/DOE 20th Century Reanalysis (V3)*. NOAA Physical Sciences Laboratory. Accessed July 8th, 2022. https://www.psl.noaa.gov/data/gridded/data.20thC_ReanV3.html
- Nogués-Bravo, D. (2009). Predicting the past distribution of species climatic niches. *Global Ecology and Biogeography*, 18(5), 521-531.
- Pacifici, M., Rondinini, C., Rhodes, J. R., Burbidge, A. A., Cristiano, A., Watson, J. E., Woinarski, J. C. Z. & Di Marco, M. (2020). Global correlates of range contractions and expansions in terrestrial mammals. *Nature Communications*, 11(1), 1-9.
- Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, 37, 637-669.
- Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918), 37-42.
- Parry, M., Parry, M. L., Canziani, O., Palutikof, J., Van der Linden, P., & Hanson, C. (Eds.). (2007). *Climate change 2007-impacts, adaptation and vulnerability: Working group II contribution to the fourth assessment report of the IPCC* (Vol. 4). Cambridge University Press.
- Pauchard, A., Milbau, A., Albiñ, A., Alexander, J., Burgess, T., Daehler, C., Englund, G., Essl, F., Evengard, B., Greenwood, G. B., Haider, S., Lenoir, J., McDougall, K., Muths, E., Nunez, M. A., Olofsson, J., Pellissier, L., Rabitsch, W., Rew, L. J., Robertson, M., Sanders, N., & Kueffer, C. (2016). Non-native and native organisms moving into high elevation and high latitude ecosystems in an era of climate change: new challenges for ecology and conservation. *Biological Invasions*, 18(2), 345-353.
- Penjor, U., Wangdi, S., Tandin, T., & Macdonald, D. W. (2021). Vulnerability of mammal communities to the combined impacts of anthropic land-use and climate change in the Himalayan conservation landscape of Bhutan. *Ecological Indicators*, 121, 107085.

- Pickles, R. S., Thornton, D., Feldman, R., Marques, A., & Murray, D. L. (2013). Predicting shifts in parasite distribution with climate change: a multitrophic level approach. *Global Change Biology*, *19*(9), 2645-2654.
- Pinard, V., Dussault, C., Ouellet, J. P., Fortin, D., & Courtois, R. (2012). Calving rate, calf survival rate, and habitat selection of forest-dwelling caribou in a highly managed landscape. *The Journal of Wildlife Management*, *76*(1), 189-199.
- Pineda-Munoz, S., Wang, Y., Lyons, S. K., Tóth, A. B., & McGuire, J. L. (2021). Mammal species occupy different climates following the expansion of human impacts. *Proceedings of the National Academy of Sciences*, *118*(2), e1922859118.
- Plass, G. N. (1956). The carbon dioxide theory of climatic change. *Tellus*, *8*(2), 140-154.
- Racey, G. D. (2005). Climate change and woodland caribou in Northwestern Ontario: a risk analysis. *Rangifer*, *25*(4), 123–136.
- Racey, G., & Armstrong, T. (2000). Woodland caribou range occupancy in northwestern Ontario: past and present. *Rangifer*, *20*(5), 173–184.
- Rantanen, M., Karpechko, A. Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T., & Laaksonen, A. (2022). The Arctic has warmed nearly four times faster than the globe since 1979. *Communications Earth & Environment*, *3*(1), 168.
- Rinfret, G., (Draftsman) & Taché, E.-E. (Cartographer) (1907). Carte de la province de Québec, indiquant ses frontières nord, nord-ouest et nord-est telles que reconnues par les statuts du Canada, 61 Victoria, cap. 3. [map]. Réduite et dessinée par Gustave Rinfret ; d'après la carte de la province de Québec par E.-E. Taché. Département des terres et forêts (Québec). Retrieved from <https://gallica.bnf.fr/ark:/12148/btv1b84457731/f1.item#>
- Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., Hayward, M. W., Kerley, G. I. H., Levi, T., Lindsey, T. A., Macdonald, D. W., Malhi, Y., Painter, L. E., Sandom, C. J., Terborgh, J., & Van Valkenburgh, B. (2015). Collapse of the world's largest herbivores. *Science Advances*, *1*(4), e1400103.
- Species at Risk Act, S.C. 2002, c. 29, List of Wildlife Species at Risk (2002). <https://www.laws-lois.justice.gc.ca/eng/acts/S-15.3/page-10.html#h-435647>
- Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. V., & Woolmer, G. (2002). The human footprint and the last of the wild: the human footprint is a global map of human influence on the land surface, which suggests that human beings are stewards of nature, whether we like it or not. *BioScience*, *52*(10), 891-904.
- Schaefer, J. A. (2003). Long-term range recession and the persistence of caribou in the taiga. *Conservation Biology*, *17*(5), 1435-1439.

- Schindler D. W. & P. G. Lee. 2010. Comprehensive conservation planning to protect biodiversity and ecosystem services in Canadian boreal regions under a warming climate and increasing exploitation. *Biological Conservation*, 143:1571-1586.
- Senaviratna, N. A. M. R., & Cooray, T. M. J. A. (2019). Diagnosing multicollinearity of logistic regression model. *Asian Journal of Probability and Statistics*, 5(2), 1-9.
- Serrouya, R., Seip, D. R., Hervieux, D., McLellan, B. N., McNay, R. S., Steenweg, R., Heard, D. C., Hebblewhite, M., Gillingham, M., & Boutin, S. (2019). Saving endangered species using adaptive management. *Proceedings of the National Academy of Sciences*, 116(13), 6181-6186.
- Shabani, F., Kumar, L., & Ahmadi, M. (2016). A comparison of absolute performance of different correlative and mechanistic species distribution models in an independent area. *Ecology and Evolution*, 6(16), 5973-5986.
- Slivinski, L. C., Compo, G. P., Sardeshmukh, P. D., Whitaker, J. S., McColl, C., Allan, R. J., Brohan, P., Yin, X., Smith, C. A., Spencer, L. J., Vose, R. S., Rohrer, M., Conroy, R. P., Schuster, D. C., Kennedy, J. J., Ashcroft, L., Brönnimann, S., Brunet, M., Camuffo, D., Cornes, R., Cram, T. A., Domínguez-Castro, F., Freeman, J. E., Gergis, J., Hawkins, E., Jones, P. D., Kubota, H., Lee, T. C., Lorrey, A. M., Luterbacher, J., Mock, C. J., Przybylak, R. K., Pudmenzky, C., Slonosky, V. C., Tinz, B., Trewin, B., Wang, X. L., Wilkinson, C., Wood, K., Wyszyński, P. (2021). An Evaluation of the Performance of the Twentieth Century Reanalysis Version 3. *Journal of Climate*, 34(4), 1417–1438.
- St-Gelais, S., & Gilbert, A. (Novembre 30, 2021). Le caribou forestier : le cœur et la raison. Retrieved from https://boisaco.com/wp-content/uploads/2021/11/Le-caribou-forestier-le-coeur-et-la-raison_30-11-2021.pdf
- St-Laurent, M. H., Boulanger, Y., Cyr, D., Manka, F., Drapeau, P., & Gauthier, S. (2022). Lowering the rate of timber harvesting to mitigate impacts of climate change on boreal caribou habitat quality in eastern Canada. *Science of The Total Environment*, 156244.
- Stewart, F. E., Nowak, J. J., Micheletti, T., McIntire, E. J., Schmiegelow, F. K., & Cumming, S. G. (2020). Boreal caribou can coexist with natural but not industrial disturbances. *The Journal of Wildlife Management*, 84(8), 1435-1444.
- Sultaire, S. M., Pauli, J. N., Martin, K. J., Meyer, M. W., Notaro, M., & Zuckerberg, B. (2016). Climate change surpasses land-use change in the contracting range boundary of a winter-adapted mammal. *Proceedings of the Royal Society B: Biological Sciences*, 283(1827), 20153104.

- Tarek, M., Brissette, F. P., & Arsenault, R. (2020). Evaluation of the ERA5 reanalysis as a potential reference dataset for hydrological modelling over North America. *Hydrology and Earth System Sciences*, *24*(5), 2527-2544.
- Terrail, R., Morin-Rivat, J., de Lafontaine, G., Fortin, M. J., & Arsenault, D. (2020). Effects of 20th-century settlement fires on landscape structure and forest composition in eastern Quebec, Canada. *Journal of Vegetation Science*, *31*(1), 40-52.
- Thuiller, W., Georges, D., Engler, R., Breiner, F., Georges, M. D., & Thuiller, C. W. (2016). Package 'biomod2'. *Species distribution modeling within an ensemble forecasting framework*.
- Torres-Romero, E. J., Giordano, A. J., Ceballos, G., & López-Bao, J. V. (2020). Reducing the sixth mass extinction: Understanding the value of human-altered landscapes to the conservation of the world's largest terrestrial mammals. *Biological Conservation*, *249*, 108706.
- Veloz, S. D., Williams, J. W., Blois, J. L., He, F., Otto-Bliesner, B., & Liu, Z. (2012). No-analog climates and shifting realized niches during the late quaternary: implications for 21st-century predictions by species distribution models. *Global Change Biology*, *18*(5), 1698-1713.
- Vors, L. S., Schaefer, J. A., Pond, B. A., Rodgers, A. R., & Patterson, B. R. (2007). Woodland caribou extirpation and anthropogenic landscape disturbance in Ontario. *The Journal of Wildlife Management*, *71*(4), 1249-1256.
- Vors, L. S., & Boyce, M. S. (2009). Global declines of caribou and reindeer. *Global Change Biology*, *15*(11), 2626-2633.
- Wan, X., Jiang, G., Yan, C., He, F., Wen, R., Gu, J., Lia, X., Mac, J., Stenseth, N. C., & Zhang, Z. (2019). Historical records reveal the distinctive associations of human disturbance and extreme climate change with local extinction of mammals. *Proceedings of the National Academy of Sciences*, *116*(38), 19001-19008.
- Weladji, R. B., Klein, D. R., Holand, Ø., & Myrsterud, A. (2002). Comparative response of *Rangifer tarandus* and other northern ungulates to climatic variability. *Rangifer*, *22*(1), 33-50.
- Whittington, J., Hebblewhite, M., DeCesare, N. J., Neufeld, L., Bradley, M., Wilmshurst, J., & Musiani, M. (2011). Caribou encounters with wolves increase near roads and trails: a time-to-event approach. *Journal of Applied Ecology*, *48*(6), 1535-1542.
- Wiens, J. A., Stralberg, D., Jongsomjit, D., Howell, C. A., & Snyder, M. A. (2009). Niches, models, and climate change: assessing the assumptions and

uncertainties. *Proceedings of the National Academy of Sciences*, 106(supplement 2), 19729-19736.

- Wiken, E., Nava, F. J., & Griffith, G. (2011). North American Terrestrial Ecoregions - Level III. Commission for Environmental Cooperation, Montreal, Canada.
- Williams, J. W., Kharouba, H. M., Veloz, S., Vellend, M., McLachlan, J., Liu, Z., Otto-Bliesner, B., & He, F. (2013). The ice age ecologist: testing methods for reserve prioritization during the last global warming. *Global Ecology and Biogeography*, 22(3), 289-301.
- Wittmer, H. U., Sinclair, A. R., & McLellan, B. N. (2005). The role of predation in the decline and extirpation of woodland caribou. *Oecologia*, 144(2), 257-267.
- Yackulic, C. B., Sanderson, E. W., & Uriarte, M. (2011). Anthropogenic and environmental drivers of modern range loss in large mammals. *Proceedings of the National Academy of Sciences*, 108(10), 4024-4029.
- Zanin, M., Palomares, F., & Mangabeira Albernaz, A. L. (2021). Effects of climate change on the distribution of felids: mapping biogeographic patterns and establishing conservation priorities. *Biodiversity and Conservation*, 30(5), 1375-1394.

APPENDIX A. DETAILS ON CLIMATE VARIABLE EXTRACTION METHODS

Table A1. Name, description, and step-by-step summary of the extraction method for each climate variable used in this study.

Name	Description	Extraction method
Maximum winter temperature	Monthly maximum between December and March	<ul style="list-style-type: none"> • Determination of minimum, average and maximum temperature for each month between December and March, from 2-meter temperature data from reanalyses and projection datasets
Mean winter temperature	Monthly average between December and March	<ul style="list-style-type: none"> • Averaging of the monthly values over 30 years to generate climate variable input in BIOMOD2
Minimum winter temperature	Monthly minimum between December and March	
Maximum summer temperature	Monthly maximum between June and August	<ul style="list-style-type: none"> • Determination of minimum, average and maximum temperature for each month between June and August, from 2-meter temperature data from reanalyses and projection datasets
Mean summer temperature	Monthly average between June and August	<ul style="list-style-type: none"> • Averaging of the monthly values over 30 years to generate climate variable input in BIOMOD2
Minimum summer temperature	Monthly minimum between June and August	

Total summer rainfall	Monthly sum of rainfall between June and August	<ul style="list-style-type: none"> • Splitting of daily precipitation data as either rainfall or snowfall for each day between December and March and then between June and August included, from 2-meter temperature (273.15K tipping point) and precipitation data from reanalyses and projection datasets.
Total winter rainfall	Monthly sum of rainfall between December and March	<ul style="list-style-type: none"> • Sum of monthly rainfall and snowfall separately between December and March and then between June and August included.
Total winter snowfall	Monthly sum of snowfall between December and March	<ul style="list-style-type: none"> • Averaging of the monthly sum values over 30 years to generate climate variable input in BIOMOD2
Mean snow depth	Monthly average of ground surface snow depth	<ul style="list-style-type: none"> • Determination of average ground surface snow depth for each month from ground surface snow depth (in water equivalent) data from reanalyses and projection datasets • Averaging of the monthly mean values over 30 years to generate climate variable input in BIOMOD2
Total number of rain-on-snow events	Monthly sum of rain-on-snow events	<ul style="list-style-type: none"> • Determination of daily rain-on-snow events (0 or 1) from 2-meter temperature (273.15K tipping point), precipitation (over 0 mm), and ground surface snow depth (over 0 mm) data from reanalyses and projection datasets. • Sum of monthly rain-on-snow events (maximum as the number of days of each month). • Averaging of the monthly sum values over 30 years to generate climate variable input in BIOMOD2
Start of the growing season	Date of the first day of a series of over 5 consecutive days with an average	<ul style="list-style-type: none"> • Determination of the date of yearly first day of a series of at least 6 consecutive days with an average daily temperature above 5°C (Frich et al. 2002, Peichl et al. 2014) between January 1st and

	daily temperature above 5°C	<p>August 31st (see Figure), from 2-meter temperature data from reanalyses and projection datasets.</p> <ul style="list-style-type: none"> • Averaging of the yearly values over 30 years to generate climate variable input in BIOMOD2
End of the growing season	Date of the first day of a series of over 5 consecutive days with an average daily temperature under 5°C	<ul style="list-style-type: none"> • Determination of the date of yearly first day of a series of at least 6 consecutive days with an average daily temperature under 5°C (Frich et al. 2002, Peichl et al. 2014) between August 15th and March 31st (see Figure), from 2-meter temperature data from reanalyses and projection datasets • Averaging of the yearly values over 30 years to generate climate variable input in BIOMOD2
Duration of the growing season	Number of days between the date of start and the date of end of the growing season	<ul style="list-style-type: none"> • Determination of the duration between the dates of start and end of growing season for each year. If the date of start is detected after the date of end of growing season (overlap of detection periods between August 15th and 31st), duration is considered having a null value. • Averaging of the yearly values over 30 years to generate climate variable input in BIOMOD2

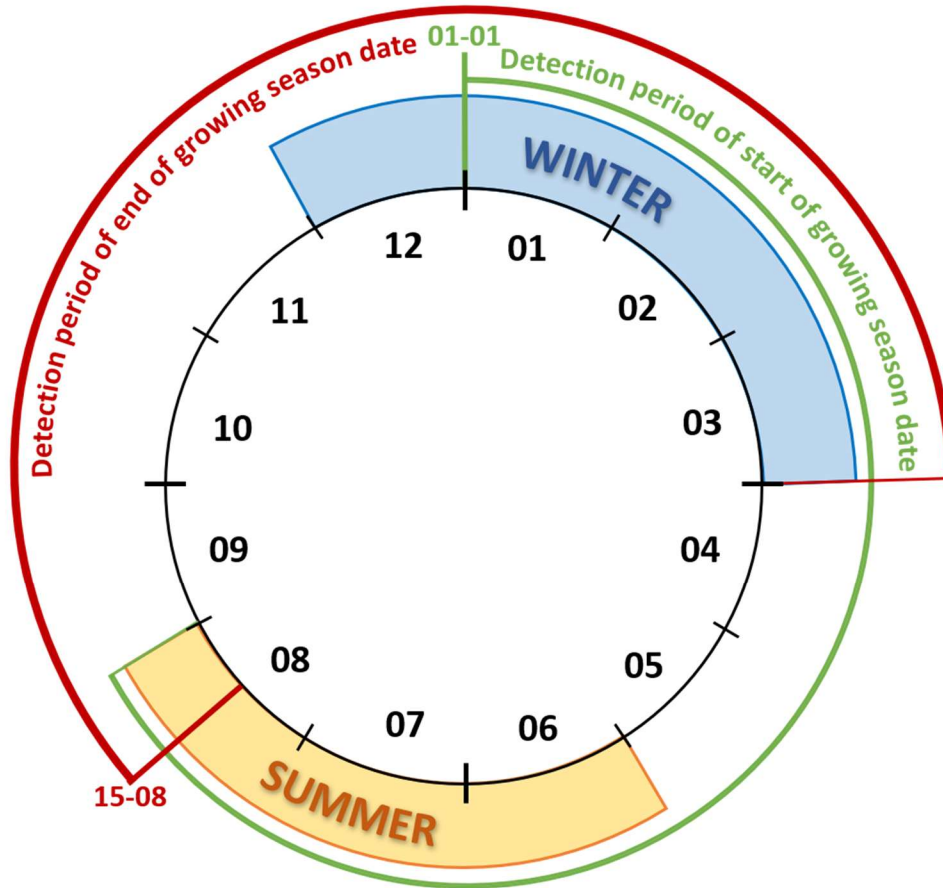


Figure A1. Diagram of detection periods of dates for phenological variable extraction. Dates of the start and end of growing season (dates of the beginning of spring and fall respectively) can be detected until the end of the next season (for example, if by the end of summer, no beginning date of spring has been detected, it is concluded that no growing season has occurred, according to the detection criteria defined here for starting date of growing season).

APPENDIX B: BIOMOD2 ENSEMBLE MODELLING RESULTS WITHOUT INCLUDING SMALL, ISOLATED POPULATIONS IN PRESENCE INPUT DATASET

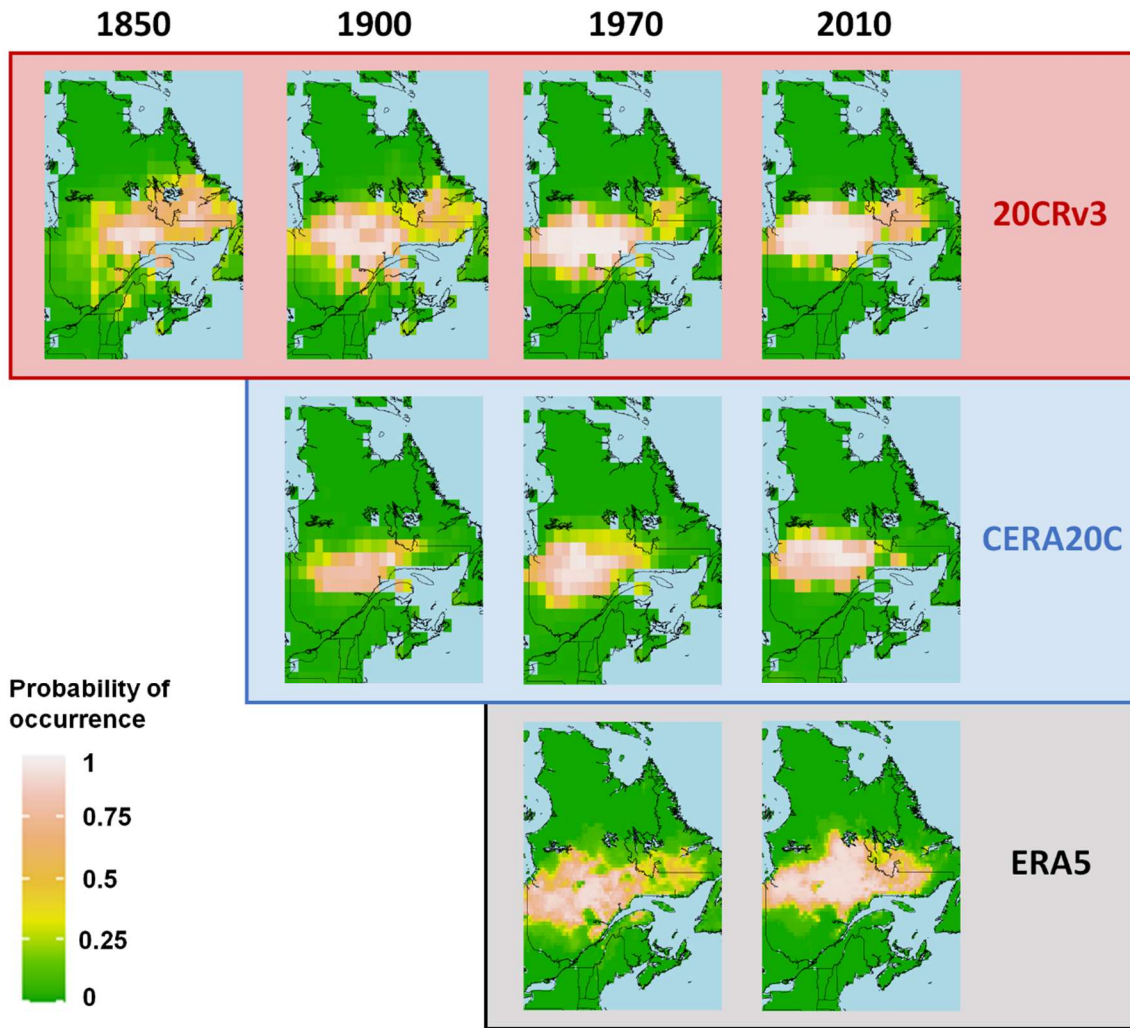


Figure B1: Hindcasted probability of boreal caribou occurrence over the study area obtained by ensemble modelling for each data source (20CRv3, CERA-20C, ERA5) and each available time step (1850-1900-1970-2010, 1900-1970-2010, and 1970-2010 respectively) without considering the three southern, isolated populations.

The effect of including or not the three small, isolated populations (i.e. Gaspésie, Charlevoix and Val-d'Or) on hindcasted probabilities of occurrence was negligible, as maps of probability of occurrence produced when discarding these three populations showed little variation from the ones obtained when including them (Figures 5 and B1). Areas described

with and without isolated populations were similar in trends of geographical position, size, and probability of occurrence change through time. Ensemble models show very high goodness-of-fit. Indeed, TSS values of the ensemble models were 0.957 [0.950; 0.958], 0.993 [0.989; 0.993], and 0.914 [0.913; 0.914] using 20CRv3, CERA-20C, and ERA5 datasets respectively. Maps obtained through ensemble modelling without the three isolated populations showed rather similar trends in probability of occurrence through time and space under all reanalyses (Figure B1). They also presented very similar patterns for a given time step. Probabilities of occurrence over the entire study area and for all data sources were overall higher for recent time steps than for older ones. Furthermore, areas of probable occurrence (>0.3) showed a slight northward trend with time. In other words, hindcasted ranges described here resided at rather consistent longitudes but lightly increasing latitudes, with no visible expansion nor shrinkage, over time and across all reanalysis datasets.

APPENDIX C: SELECTION OF THE THRESHOLD OF PROBABILITY OF OCCURRENCE AND SENSITIVITY OF OUR ANALYSES TO ITS VALUE

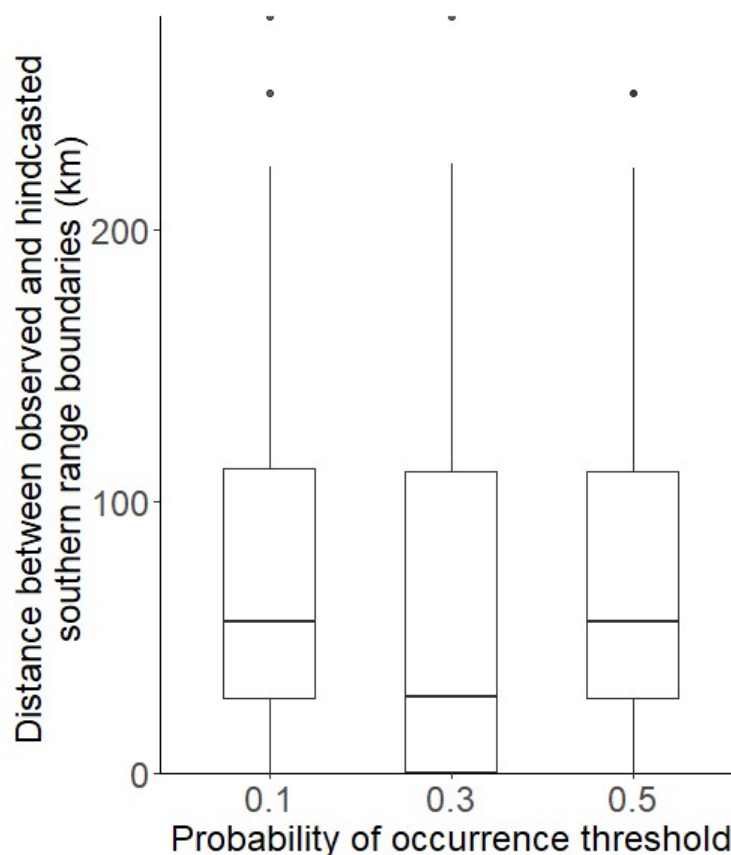


Figure C1: Boxplot (black line: median value, box: upper and lower quartiles, whiskers: distribution outside of the upper and lower quartiles) of the distance between observed and hindcasted southern limits of distribution for 2010 for each considered threshold (0.1, 0.3 and 0.5 of probability of occurrence). Distance measurements from all reanalyses were combined to obtain each box.

The threshold value presenting the shortest median distance between observed and hindcasted southern range boundaries for 2010 is 0.3 (Figure C1). All figures obtained from the same analysis showed similar results, independently of the threshold selected (Figure C2a, b and c, and Figure C3a, b and c, respectively). We calculated a distance of ~291 km between the median latitude of southern limits of hindcasted locations of climate conditions fit for caribou occurrence in 1850 and the one estimated in 2010 when using a threshold value

of 0.1, ~104 km for a threshold of 0.3, and ~14 km for a threshold of 0.5. In comparison, the distance between the median positions in latitude of observed southern limits of caribou range in 1850 and the one observed in 2010 is of ~620 km. These results allow us to estimate that, for thresholds of 0.1, 0.3 and 0.5 of probability of occurrence, ~47%, ~17% and ~2% respectively of the observed recession of caribou range since 1850 would be imputable to the displacement of climate conditions fitting for boreal caribou, due to climate change. No matter what threshold value was considered, trends and conclusions from these results are also identical to what has been described in the body of the article, underlining the relatively low sensitivity of our analyses to the choice of said threshold and the robustness of the trend in our results.

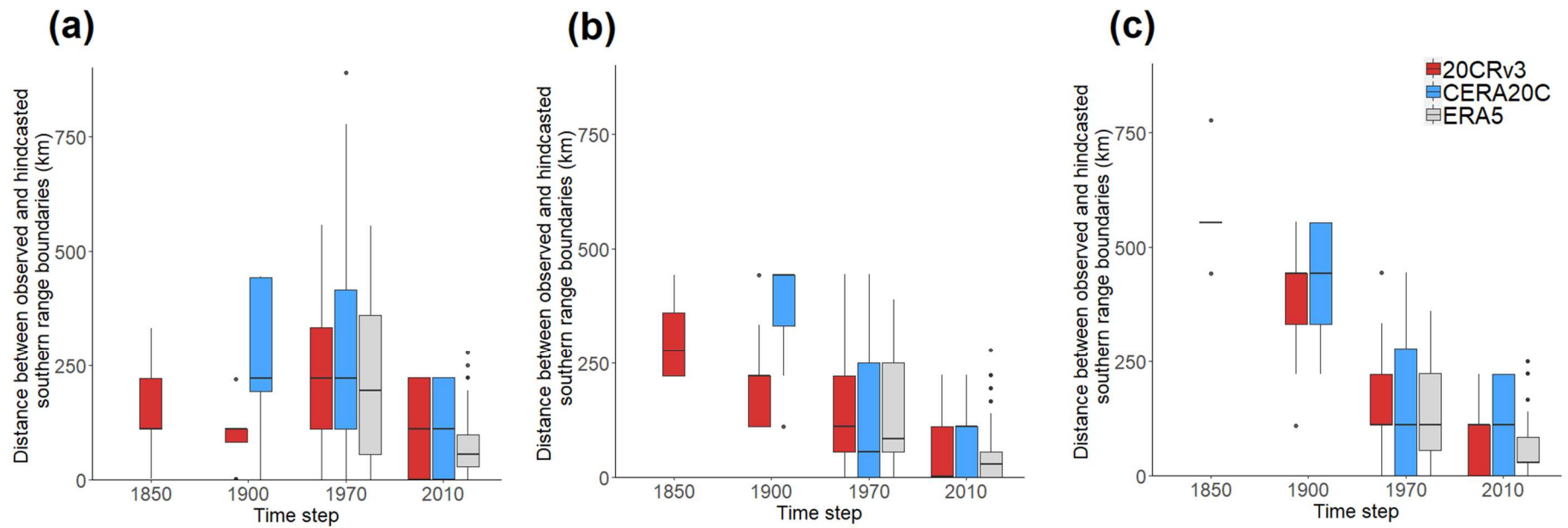


Figure C2: Boxplots of distances between historical southern range boundaries and hindcasted southern range boundaries for each time step of interest and the three reanalysis datasets available, for each considered threshold of probability of occurrence: (a) 0.1, (b) 0.3 and (c) 0.5. Distances were measured between points of same longitude on observed and hindcasted southern limits.

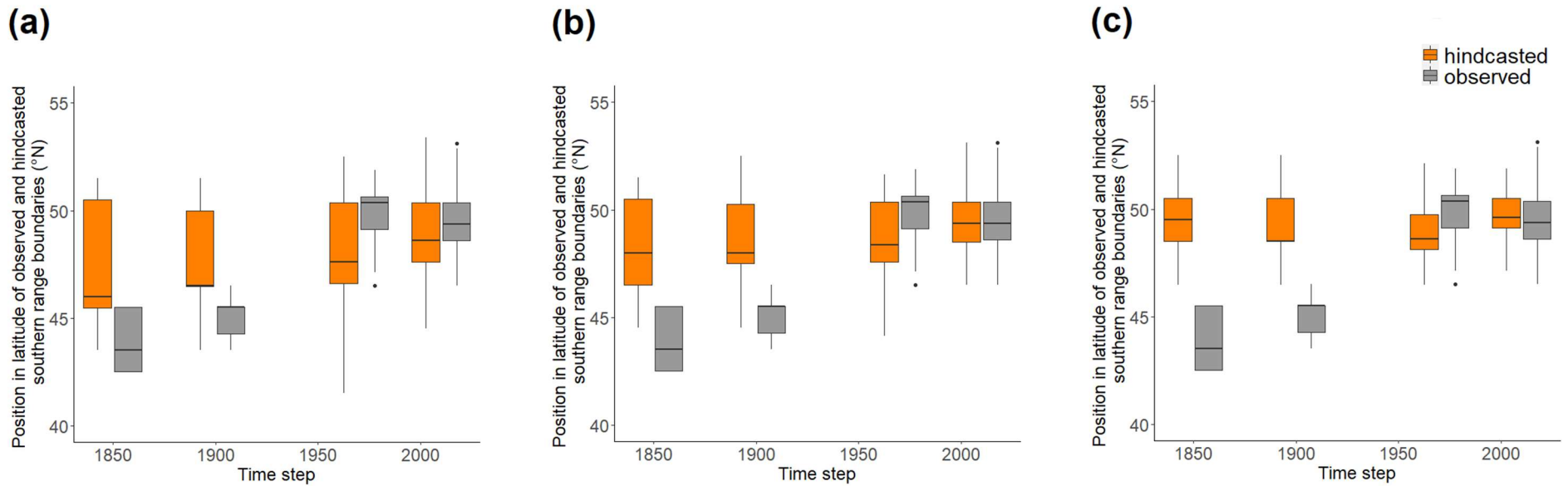


Figure C3: Latitudinal position of observed and hindcasted southern boundaries through time, for each considered threshold of probability of occurrence: (a) 0.1, (b) 0.3 and (c) 0.5. Boxes for hindcasted southern boundaries were obtained by combining data from all reanalysis datasets.

CONCLUSION GÉNÉRALE

Retour sur les objectifs et les principaux résultats

Notre objectif était de quantifier la part du climat ayant pu jouer un rôle dans la régression vers le nord de la limite sud de l'aire de distribution du caribou forestier (*Rangifer tarandus caribou*) au Québec depuis 1850. Grâce à l'utilisation de données historiques d'archives comparées aux reconstitutions de nos modèles de niche, nous avons pu contraster la position dans l'espace des conditions climatiques représentatives de celles rencontrées dans l'aire de distribution actuelle du caribou (c.-à-d. 2010). Ces résultats ont mis en évidence que les changements du climat n'étaient responsables que de ~17% du recul de la marge sud de l'aire de distribution continue de l'espèce depuis 160 ans. Ainsi, le développement des activités anthropiques (c.-à-d. aménagement forestier, agriculture, construction de routes et de villes) dans le sud de la province depuis 1850 apparaît comme un facteur important, bien supérieur aux effets des changements climatiques, pouvant expliquer la majeure partie de cette contraction historique.

Contributions théoriques

Notre étude a permis de mettre en évidence que la niche climatique est un outil particulièrement utile pour mieux comprendre les mécanismes régissant à la distribution géographique des grands mammifères. Par le fait même, elle souligne la potentielle perte de l'état d'équilibre entre une espèce et son environnement et le biais de modélisation généré par une telle situation. Cet élément a déjà été mis en évidence par le passé par d'autres études s'intéressant à l'utilisation des modèles de niche (*hindcast*) chez d'autres mammifères (McGuire & Davis 2013, Davis et al 2014) quoique jamais, à notre connaissance, pour des

espèces de grands mammifères et, *a fortiori*, pour le caribou forestier. La quantification du biais de modélisation mise en avant dans notre étude permet de mieux appréhender l'étendue de la niche climatique du caribou, qui a jusqu'ici été documentée dans un cadre prédictif seulement. En effet, ces études utilisaient des données de distribution récentes (caribou forestier : Neilson et al. 2022 ; caribou des bois : Deb et al. 2020), donc susceptibles d'avoir été fortement influencées par l'occupation anthropique du territoire, et ne faisait pas particulièrement de cas de la présence de ce biais dans les données.

D'autre part, la présente étude souligne la pertinence des données climatiques de réanalyses de qualité, pour leurs importantes couvertures temporelle et spatiale (ECMWF 2022a, ECMWF 2022b, NOAA 2022), dans un contexte de reconstitution à une échelle spatiale aussi large. De plus, l'utilisation de ces données en combinaison avec des sources historiques pour compléter les informations récentes concernant les aires de distribution des espèces est une approche novatrice dans le cas du caribou forestier. L'utilisation de ces données d'archives permet une prise de recul face aux résultats des modèles de niche, dans un but de reconstitution ou de projection (Guralnick & Pearman 2010, Davis et al 2014, McGuire & Davis 2013). Cette vérification s'avère même cruciale, comme le montre notre étude, dans les cas où l'espèce à l'étude est rendue vulnérable par les activités anthropiques, ce qui, ironiquement, constitue une part importante des cas présentant un besoin de prédictions, entre autres pour guider les actions de conservation (Schwartz 2012, Zhu et al. 2021). La littérature est malheureusement pauvre en études ayant recours à une telle vérification par données historiques (mais voir Davis et al. 2014). Aussi, notre étude supporte la prise en compte de données historiques lorsqu'elles sont disponibles, comme moyen efficace de s'assurer du respect des conditions d'application des modèles de niche et pour mettre en perspective les résultats de modélisation.

Contributions appliquées au cas du caribou forestier

La littérature abonde d'études mettant en évidence les divers impacts délétères des activités anthropiques sur le caribou forestier et son habitat (p. ex. Newton et al. 2017, Lafontaine et al. 2019, Fryxell et al. 2020, Stewart et al. 2020, MacNearney et al. 2021, Lochhead et al. 2022). Cependant, l'impact du réchauffement climatique reste à bien des égards une source de questionnement scientifique. Notre étude apporte de nouvelles informations qui confirment non seulement le rôle potentiellement limité des changements climatiques récents dans le déclin passé du caribou forestier (Neilson et al. 2022) mais renseignent aussi davantage sur l'historique de ce déclin, probablement en lien avec l'utilisation anthropique du territoire depuis 1850. Nos résultats ne vont pas dans le sens d'une rétraction vers le nord de la limite méridionale d'aire de distribution du caribou forestier causée par le réchauffement climatique des 160 dernières années. Les activités anthropiques telles que les coupes, les chemins forestiers et la conversion de forêts en territoires agricoles et urbains, ainsi que leurs impacts indirects comme l'augmentation de la pression de prédation, de même que la chasse et le braconnage, ont été mises en évidence comme les facteurs majeurs de déclin pour le caribou forestier, incitant à des modifications profondes de ces activités et des actions rapides de conservation. Cependant, l'incertitude (toutefois décroissante) reliée aux impacts des changements climatiques sur cette espèce tend à être disproportionnellement prise en compte, au sein du corpus de connaissances actuelles sur ce déclin, et peut parfois même être détournée par certains lobbys pour justifier l'immobilisme à des fins économiques (Alliance Forêt Boréale 2019). La présente étude vient, pour la première fois, chiffrer cet impact sur le recul de son aire de distribution et ainsi apporter un élément factuel central dans la problématique du caribou forestier au Québec. Elle soutient l'hypothèse qui désigne l'exploitation anthropique du territoire, et en particulier de la forêt mature de conifères, comme principale responsable du recul vers le nord des populations de caribou. Si les conséquences néfastes des activités anthropiques ont été largement explorées dans la littérature, le manque de mise en perspective par rapport à celles des changements climatiques alimentait des spéculations (p. ex. Alliance Forêt Boréale 2019, St-Gelais & Gilbert 2021). Notre analyse soutient ainsi l'importance des actions de

conservation centrées autour de ces mécanismes anthropiques, en particulier l'aménagement forestier. En montrant les conséquences limitées du réchauffement climatique depuis 1850, elle invite à concentrer les efforts de conservation sur les solutions les plus efficaces à notre portée, à savoir la protection et la restauration des habitats, des leviers qui sont complètement sous notre contrôle (St-Laurent et al. 2022).

Nos résultats soulignent également l'utilité des modèles de niche, malgré leurs limites, pour la compréhension des changements dans la distribution géographique des aires présentant un climat propice à la présence du caribou forestier. De tels outils peuvent profiter à des projets de conservation des populations en offrant des informations spatiales qui permettent de cibler des zones géographiques critiques au maintien des populations et donc potentiellement d'améliorer l'efficacité des actions menées. Plusieurs études ont déjà employé de tels modèles dans un but d'identification de zones propices à l'instauration d'aires protégées (Bernardo-Silva et al. 2012, Zhu et al. 2021).

Limites

Les limites sud d'aires de distribution historiques ont été extraites de sources fiables (cartes et archives) mais restent limitées dans leur précision spatiale par la nature de leur tracé, surtout pour les sources les plus anciennes. De plus, les méthodes qui ont servi à générer ces tracés ayant changé avec le temps, les positions relatives de ces limites sud peuvent parfois sembler manquer de cohérence, comme c'est le cas de la limite sud de 1970 par rapport à celle de 2010.

Nos modèles ont été calibrés spécifiquement pour notre aire d'étude et peuvent donc difficilement être exportables dans d'autres aires d'étude sans ajustements, faute de quoi ils pourraient générer des erreurs de projection. L'emploi de la même méthode pour une autre espèce ou dans une autre aire d'étude nécessiterait ainsi de produire de nouveaux modèles, bien que les variables d'intérêt risquent d'être sensiblement les mêmes s'il est de nouveau question de caribous forestiers. L'ajout de composantes mécanistiques (p. ex. un modèle de

thermorégulation) à nos modèles corrélatifs pourrait probablement améliorer cet enjeu de transférabilité dans l'espace (Peterson et al. 2015).

D'autre part, bien que les données climatiques de réanalyses utilisées ici soient d'une grande qualité, elles restent issues de modélisations et ont donc une certaine marge d'erreur, proportionnelle à l'horizon de reconstitution. Ainsi, nos modélisations présentent-elles également une marge d'erreur plus importante pour 1850 que pour 1970, bien qu'elle reste globalement faible. De plus, nos analyses ont été réalisées à une échelle spatiale relativement grossière (1°x1°). Bien que les tendances lourdes persisteraient très certainement, l'utilisation de données climatiques à une résolution spatiale plus fine améliorerait la précision géographique de nos résultats. Dans un contexte prédictif, un tel ajustement permettrait la visualisation de zones de climats actuelles et futures à échelle locale, ce qui faciliterait la protection anticipée de régions « refuges » pour le caribou forestier au Québec.

Conclusion et pistes de recherche futures

La perte actuelle massive de biodiversité à l'échelle planétaire pousse les scientifiques à s'interroger sur les mécanismes aboutissant au déclin de populations animales comme celles du caribou forestier au Québec. L'identification des facteurs principaux en cause dans les phénomènes de dégradation et de perte d'habitat est au cœur de ces questionnements et s'avère bien souvent la clé d'actions de conservation efficaces (Schneider 2001, Coristine & Kerr 2011, Gonçalves-Souza et al. 2020). Tandis que la littérature traitant des facteurs anthropiques s'étoffe, les conséquences des changements climatiques sur les distributions passées, présentes et futures des espèces animales figureront certainement parmi les sujets phares des prochaines décennies en conservation (Thuiller 2007, Sirami et al. 2017). Dans ce contexte, les outils de prédiction, dont le rôle est fondamental dans l'orientation des projets de conservation, sont en perpétuel perfectionnement (Thuiller 2007, Zimmermann et al. 2010, Santini et al. 2021), à l'instar de la mise en évidence du biais de modélisation identifié par notre étude. À cet effet, les données de réanalyses jointes aux données de distribution

historiques sont des outils efficaces et prometteurs. Leur utilisation conjointe, ici novatrice, est fortement encouragée puisqu'elle facilite la prise de recul face aux distributions géographiques actuelles. Elle permet de générer des reconstitutions robustes qui s'appuient sur des données climatiques historiques d'une grande fiabilité et qui permettent d'analyser des territoires dont la couverture en stations météorologiques est particulièrement déficiente. De futures études pourront se saisir des informations générées ici pour améliorer la capacité prédictive des modèles de niche et ainsi faire des projections de meilleure qualité. Ces éléments donneront lieu à un meilleur éclairage dans la prise de décision concernant la conservation du caribou forestier, et d'autres espèces de grands mammifères, sur les moyen et long termes.

De nombreux éléments restent encore à explorer dans la relation complexe entre les changements climatiques et la distribution des espèces animales (Potter et al. 2013, Schleuning et al. 2020). Il est cependant certain que le temps dont nous disposons pour mettre en place des solutions de conservation permettant aux populations de grands mammifères de se restaurer est compté. Bien que leur mise en application se heurte souvent à des enjeux politiques et économiques (Hebblewhite 2017), de nombreuses propositions dans ce sens, basées sur les études scientifiques des dernières décennies, ont déjà été faites dans le cas spécifique du caribou forestier (Courtois et al. 2004, MFFP 2021, St-Laurent et al. 2022). Les études à venir qui formuleront des prévisions quant aux futures zones géographiques présentant des conditions climatiques propices à la présence du caribou forestier viendront participer à cet effort.

RÉFÉRENCES BIBLIOGRAPHIQUES

- Alliance Forêt Boréale (2019). *Caribou forestier : mythes et réalités*. Accessed September 20th, 2022. <https://allianceforetboreale.org/caribou-forestier--mythes-et-realites>
- Angilletta Jr, M. J., Cooper, B. S., Schuler, M. S., & Boyles, J. G. (2010). The evolution of thermal physiology in endotherms. *Frontiers in Bioscience-Elite*, 2(3), 861-881.
- Arlt, M. L., & Manseau, M. (2011). Historical changes in caribou distribution and land cover in and around Prince Albert National Park: land management implications. *Rangifer*, 17-31.
- Banfield, A. W. F. (1961). *A revision of the reindeer and caribou, genus Rangifer* (No. 66). Queen's Printer.
- Barber, Q. E., Parisien, M. A., Whitman, E., Stralberg, D., Johnson, C. J., St-Laurent, M. H., Delancey, E. R., Price, D. T., Arseneault, D., Wang, X., & Flannigan, M. D. (2018). Potential impacts of climate change on the habitat of boreal woodland caribou. *Ecosphere*, 9(10), e02472.
- Bartlett, L. J., Newbold, T., Purves, D. W., Tittensor, D. P., & Harfoot, M. B. (2016). Synergistic impacts of habitat loss and fragmentation on model ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, 283(1839), 20161027.
- Bernardo-Silva, J., Martins-Ferreira, C., Maneyro, R., & Freitas, T. D. (2012). Identification of priority areas for conservation of two endangered parapatric species of red-bellied toads using ecological niche models and hotspot analysis. *Natureza & Conservação*, 10(2), 207-213.
- Bieniek, P. A., Bhatt, U. S., Walsh, J. E., Lader, R., Griffith, B., Roach, J. K., & Thoman, R. L. (2018). Assessment of Alaska rain-on-snow events using dynamical downscaling. *Journal of Applied Meteorology and Climatology*, 57(8), 1847-1863.
- Boivin, N. L., Zeder, M. A., Fuller, D. Q., Crowther, A., Larson, G., Erlandson, J. M., Denham, T., & Petraglia, M. D. (2016). Ecological consequences of human niche construction: Examining long-term anthropogenic shaping of global species distributions. *Proceedings of the National Academy of Sciences*, 113(23), 6388-6396.

- Boyles, J. G., Seebacher, F., Smit, B., & McKechnie, A. E. (2011). Adaptive thermoregulation in endotherms may alter responses to climate change. *Integrative and Comparative Biology*, 51(5), 676-690.
- Brooks, D. R., & Hoberg, E. P. (2007). How will global climate change affect parasite–host assemblages? *Trends in Parasitology*, 23(12), 571-574.
- Brown, R. D., & Mote, P. W. (2009). The response of Northern Hemisphere snow cover to a changing climate. *Journal of Climate*, 22(8), 2124-2145.
- Callaghan, T. V., Björn, L. O., Chernov, Y., Chapin, T., Christensen, T. R., Huntley, B., Ims, R. A., Johansson, M., Jolly, D., Jonasson, S., Matveyeva, N., Panikov, N., Oechel, W., Shaver, G., Elster, J., Henttonen, H., Laine, K., Taulavuori, K., Taulavuori, E., & Zöckler, C. (2004). Biodiversity, distributions and adaptations of Arctic species in the context of environmental change. *AMBIO: A Journal of the Human Environment*, 33(7), 404-417.
- Chapin III, F. S., McGuire, A. D., Randerson, J., Pielke, R., Baldocchi, D., Hobbie, S. E., Roulet, Eugster, N. W., Kasischke, E., Rastetter E. B., Zimov, S. A. & Running, W. (2000). Arctic and boreal ecosystems of western North America as components of the climate system. *Global Change Biology*, 6(S1): 211-223.
- Colman, J. E., Pedersen, C., Hjermand, D. Ø., Holand, Ø., Moe, S. R., & Reimers, E. (2003). Do wild reindeer exhibit grazing compensation during insect harassment? *The Journal of Wildlife Management*, 11-19.
- Cordes, L. S., Blumstein, D. T., Armitage, K. B., CaraDonna, P. J., Childs, D. Z., Gerber, B. D., Martin, J. G. A., Oli, M. K., & Ozgul, A. (2020). Contrasting effects of climate change on seasonal survival of a hibernating mammal. *Proceedings of the National Academy of Sciences*, 117(30), 18119-18126.
- Coristine, L. E., & Kerr, J. T. (2011). Habitat loss, climate change, and emerging conservation challenges in Canada. *Canadian Journal of Zoology*, 89(5), 435-451.
- Courtois, R., Ouellet, J. P., Gingras, A., Dussault, C., Breton, L., & Maltais, J. (2003). Historical changes and current distribution of caribou, *Rangifer tarandus*, in Quebec. *The Canadian Field-Naturalist*, 117(3), 399-414.
- Courtois, R., Ouellet, J. P., Dussault, C., & Gingras, A. (2004). Forest management guidelines for forest-dwelling caribou in Québec. *The Forestry Chronicle*, 80(5), 598-607.
- Courtois, R., Ouellet, J. P., Breton, L., Gingras, A., & Dussault, C. (2007). Effects of forest disturbance on density, space use, and mortality of woodland caribou. *Ecoscience*, 14(4), 491-498.

- Crooks, K. R., Burdett, C. L., Theobald, D. M., King, S. R., Di Marco, M., Rondinini, C., & Boitani, L. (2017). Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. *Proceedings of the national Academy of Sciences*, *114*(29), 7635-7640.
- Cunningham, S. J., Gardner, J. L., & Martin, R. O. (2021). Opportunity costs and the response of birds and mammals to climate warming. *Frontiers in Ecology and the Environment*, *19*(5), 300-307.
- Davidson, A. D., Shoemaker, K. T., Weinstein, B., Costa, G. C., Brooks, T. M., Ceballos, G., Radeloff, V. C., Rondinini, C., & Graham, C. H. (2017). Geography of current and future global mammal extinction risk. *PLoS One*, *12*(11), e0186934.
- Davis, E. B., McGuire, J. L., & Orcutt, J. D. (2014). Ecological niche models of mammalian glacial refugia show consistent bias. *Ecography*, *37*(11), 1133-1138.
- Dawe, K. L., & Boutin, S. (2016). Climate change is the primary driver of white-tailed deer (*Odocoileus virginianus*) range expansion at the northern extent of its range; land use is secondary. *Ecology and Evolution*, *6*(18), 6435-6451.
- Deb, J. C., Forbes, G., & MacLean, D. A. (2020). Modelling the spatial distribution of selected North American woodland mammals under future climate scenarios. *Mammal Review*, *50*(4), 440-452.
- Díaz, S., Settele, J., Brondízio, E. S., Ngo, H. T., Agard, J., Arneth, A., Balvanera, P., Brauman, K. A., Butchart, S. H. M., Chan, K. M. A., Garibaldi, L. A., Ichii, K., Liu, J., Subramanian, S. M., Midgley, G. F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, S., Purvis, A., Razzaque, J., Reyers, B., Chowdhury, R. R., Shin, Y.-J., Visseren-Hamakers, I., Willis, K. J., & Zayas, C. N. (2019). Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science*, *366*(6471), eaax3100.
- Dormann, C. F., Schymanski, S. J., Cabral, J., Chuine, I., Graham, C., Hartig, F., Kearney, M., Morin, X., Römermann, C., Schröder, B., & Singer, A. (2012). Correlation and process in species distribution models: bridging a dichotomy. *Journal of Biogeography*, *39*(12), 2119-2131.
- Drever, C. R., Hutchison, C., Drever, M. C., Fortin, D., Johnson, C. A., & Wiersma, Y. F. (2019). Conservation through co-occurrence: Woodland caribou as a focal species for boreal biodiversity. *Biological Conservation*, *232*, 238-252.
- ECMWF. (July 7th, 2022)a. *ERA5. ECMWF (European Centre for Medium-Range Weather Forecasts)*. Accessed 8 Jul. 2022. <https://www.ecmwf.int/en/forecasts/datasets/reanalysis-datasets/era5>

- ECMWF. (July 1st, 2022). *CERA-20C*. ECMWF (European Centre for Medium-Range Weather Forecasts). Accessed 8 Jul. 2022. <https://www.ecmwf.int/en/forecasts/datasets/reanalysis-datasets/cera-20c>
- Elith, J., & Leathwick, J. R. (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, 40: 677-697.
- Elmhagen, B., Kindberg, J., Hellström, P., & Angerbjörn, A. (2015). A boreal invasion in response to climate change? Range shifts and community effects in the borderland between forest and tundra. *Ambio*, 44(1), 39-50.
- Environnement Canada (2011). Évaluation scientifique aux fins de la désignation de l'habitat essentiel de la population boréale du caribou des bois (*Rangifer tarandus caribou*) au Canada : Mise à jour 2011. 116 p. et annexes.
- Environnement et Changement climatique Canada (27 novembre 2020). Programme de rétablissement modifié du caribou des bois (*Rangifer tarandus caribou*), population boréale, au Canada [Proposition] 2019. Gouvernement du Canada. https://www3.mffp.gouv.qc.ca/faune/especes/menacees/fiche.asp?noEsp=53&_ga=2.205379029.431219693.1647537695-1554414406.1647361964&_gl=1*11qxr19*_ga*MTU1NDQxNDQwNi4xNjQ3MzYxOTY0*_ga_7KG0CGH2EY*MTY0NzUzNzY5NC4yLjAuMTY0NzUzNzY5NC4w
- Festa-Bianchet, M., Ray, J. C., Boutin, S., Côté, S. D., & Gunn, A. (2011). Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. *Canadian Journal of Zoology*, 89(5): 419-434.
- Flato, G. M., & Boer, G. J. (2001). Warming asymmetry in climate change simulations. *Geophysical Research Letters*, 28(1): 195-198.
- Fryxell, J. M., Avgar, T., Liu, B., Baker, J. A., Rodgers, A. R., Shuter, J., Thompson, I. D., Reid, D. E. B., Kittle, A. M., Mosser, A., Newmaster, S. G., Nudds, T. D., Street, G. M., Brown, G. S., & Patterson, B. (2020). Anthropogenic disturbance and population viability of woodland caribou in Ontario. *The Journal of Wildlife Management*, 84(4), 636-650.
- García Criado, M., Myers-Smith, I. H., Bjorkman, A. D., Lehmann, C. E., & Stevens, N. (2020). Woody plant encroachment intensifies under climate change across tundra and savanna biomes. *Global Ecology and Biogeography*, 29(5), 925-943.
- Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A. Z., & Schepaschenko, D. G. (2015). Boreal forest health and global change. *Science*, 349(6250), 819-822.

- Goldblum, D., & Rigg, L. S. (2010). The deciduous forest–boreal forest ecotone. *Geography Compass*, 4(7), 701-717.
- Gonçalves-Souza, D., Verburg, P. H., & Dobrovolski, R. (2020). Habitat loss, extinction predictability and conservation efforts in the terrestrial ecoregions. *Biological Conservation*, 246, 108579.
- Guralnick, R., & Pearman, P. B. (2010). Using species occurrence databases to determine niche dynamics of montane and lowland species since the Last Glacial Maximum. *Data Mining for Global Trends in Mountain Biodiversity*, 125-134.
- Hebblewhite, M. (2017). Billion dollar boreal woodland caribou and the biodiversity impacts of the global oil and gas industry. *Biological Conservation*, 206: 102-111
- Hogg, E. H. (1994). Climate and the southern limit of the western Canadian boreal forest. *Canadian Journal of Forest Research*, 24(9), 1835-1845.
- Holland, M. M., & Bitz, C. M. (2003). Polar amplification of climate change in coupled models. *Climate Dynamics*, 21(3-4): 221-232.
- Hornseth, M. L., & Rempel, R. S. (2016). Seasonal resource selection of woodland caribou (*Rangifer tarandus caribou*) across a gradient of anthropogenic disturbance. *Canadian Journal of Zoology*, 94(2), 79-93.
- Hoy, S. R., Vucetich, L. M., Peterson, R. O., & Vucetich, J. A. (2021). Winter tick burdens for moose are positively associated with warmer summers and higher predation rates. *Frontiers in Ecology and Evolution*, 9: 758374.
- Huey, R. B., Kearney, M. R., Krockenberger, A., Holtum, J. A., Jess, M., & Williams, S. E. (2012). Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1596), 1665-1679.
- Humphries, M. M., Umbanhowar, J., & McCann, K. S. (2004). Bioenergetic prediction of climate change impacts on northern mammals. *Integrative and Comparative Biology*, 44(2), 152-162.
- Hutchinson, G. (1957). Concluding remarks. Cold Springs Harbor Symposium on Quantitative Biology, 22: 415-427.
- IPCC. (2007). Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M. and Miller, H.L. (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 996 pp.

- IPCC. (2014). Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Barros, V. R., Field, C. B., Dokken, D. J., Mastrandrea, M. D., Mach, K. J., Bilir, T. E., Chatterjee, M., Ebi, K. L., Estrada, Y. O., Genova, R. C., Girma, B., Kissel, E. S., Levy, A. N., MacCracken, S., Mastrandrea, P. R. and White, L. L. (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 688 pp. ISBN 9781107058163.
- IPCC. (2019). Summary for Policymakers. In: Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems [Shukla, P.R., Skea, J., Calvo Buendia, E., Masson-Delmotte, V., Pörtner, H.- O., Roberts, D. C., Zhai, P., Slade, R., Connors, S., van Diemen, R., Ferrat, M., Haughey, E., Luz, S., Neogi, S., Pathak, M., Petzold, J., Portugal Pereira, J., Vyas, P., Huntley, E., Kissick, K., Belkacemi, M., Malley, J.(eds.)]. In press.
- Johnstone, J. F., Hollingsworth, T. N., Chapin III, F. S., & Mack, M. C. (2010). Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Global Change Biology*, 16(4): 1281-1295.
- Kafle, P., Peacock, S. J., Grond, S., Orsel, K., & Kutz, S. (2018). Temperature-dependent development and freezing survival of protostrongylid nematodes of Arctic ungulates: implications for transmission. *Parasites & Vectors*, 11(1), 1-12.
- Kasischke, E. S., Verbyla, D. L., Rupp, T. S., McGuire, A. D., Murphy, K. A., Jandt, R., Barnes, J. L., Hoy, E. E., Duffy, P. A., Calef, M., & Turetsky, M. R. (2010). Alaska's changing fire regime - implications for the vulnerability of its boreal forests. *Canadian Journal of Forest Research*, 40(7): 1313-1324.
- Krebs, C. J., Boonstra, R., Gilbert, B. S., Kenney, A. J., & Boutin, S. (2019). Impact of climate change on the small mammal community of the Yukon boreal forest. *Integrative Zoology*, 14(6), 528-541.
- Kutz, S. J., Jenkins, E. J., Veitch, A. M., Ducrocq, J., Polley, L., Elkin, B., & Lair, S. (2009). The Arctic as a model for anticipating, preventing, and mitigating climate change impacts on host–parasite interactions. *Veterinary Parasitology*, 163(3), 217-228.
- Kutz, S. J., Ducrocq, J., Verocai, G. G., Hoar, B. M., Colwell, D. D., Beckmen, K. B., Polley, L., Elkin, B. T., & Hoberg, E. P. (2012). Parasites in ungulates of Arctic North America and Greenland: a view of contemporary diversity, ecology, and impact in a world under change. *Advances in Parasitology*, 79, 99-252.
- Lachenbruch, A. H., & Marshall, B. V. (1986). Changing climate: geothermal evidence from permafrost in the Alaskan Arctic. *Science*, 234(4777): 689-696.

- Lafontaine, A., Drapeau, P., Fortin, D., Gauthier, S., Boulanger, Y., & St-Laurent, M. H. (2019). Exposure to historical burn rates shapes the response of boreal caribou to timber harvesting. *Ecosphere*, *10*(5), e02739.
- Laliberte, A. S., & Ripple, W. J. (2004). Range contractions of North American carnivores and ungulates. *BioScience*, *54*(2), 123-138.
- Lamb, C. T., Mowat, G., Reid, A., Smit, L., Proctor, M., McLellan, B. N., Nielsen, S. E. & Boutin, S. (2018). Effects of habitat quality and access management on the density of a recovering grizzly bear population. *Journal of Applied Ecology*, *55*(3), 1406-1417.
- Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Muriienne, J., & Grenouillet, G. (2020). Species better track climate warming in the oceans than on land. *Nature Ecology & Evolution*, *4*(8), 1044-1059.
- Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, *462*(7276), 1052-1055.
- Lochhead, K. D., Kleynhans, E. J., & Muhly, T. B. (2022). Linking woodland caribou abundance to forestry disturbance in southern British Columbia, Canada. *The Journal of Wildlife Management*, *86*(1), e22149.
- Love, O. P., Gilchrist, H. G., Descamps, S., Semeniuk, C. A., & Bêty, J. (2010). Pre-laying climatic cues can time reproduction to optimally match offspring hatching and ice conditions in an Arctic marine bird. *Oecologia*, *164*(1), 277-286.
- Lyons, S. K., Smith, F. A., & Brown, J. H. (2004). Of mice, mastodons and men: human-mediated extinctions on four continents. *Evolutionary Ecology Research*, *6*(3), 339-358.
- MacNearney, D., Nobert, B., & Finnegan, L. (2021). Woodland caribou (*Rangifer tarandus*) avoid wellsite activity during winter. *Global Ecology and Conservation*, *29*, e01737.
- Malakoutikhah, S., Fakheran, S., Hemami, M. R., Tarkesh, M., & Senn, J. (2020). Assessing future distribution, suitability of corridors and efficiency of protected areas to conserve vulnerable ungulates under climate change. *Diversity and Distributions*, *00*:1-14
- Mantyka-Pringle, C. S., Martin, T. G., & Rhodes, J. R. (2012). Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Global Change Biology*, *18*(4), 1239-1252.
- Masood, S., Van Zuiden, T. M., Rodgers, A. R., & Sharma, S. (2017). An uncertain future for woodland caribou (*Rangifer tarandus caribou*): the impact of climate change on winter distribution in Ontario. *Rangifer*, *37*(1), 11-30.
- Mattson, D. J., & Merrill, T. (2002). Extirpations of grizzly bears in the contiguous United States, 1850–2000. *Conservation Biology*, *16*(4), 1123-1136.

- McGuire, J. L., & Davis, E. B. (2013). Using the palaeontological record of *Microtus* to test species distribution models and reveal responses to climate change. *Journal of Biogeography*, 40(8), 1490-1500.
- Meredith, M. et al., 2019: Polar Regions. In: IPCC Special Report on the Ocean and Cryosphere in a Changing Climate 2 [Pörtner, H.-O., D. C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. 3 Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama and N. M. Weyer (eds.)], pp. 118.
- MFFP. (2021b). Revue de littérature sur les facteurs impliqués dans le déclin des populations de caribous forestiers au Québec et de caribous montagnards de la Gaspésie. Accessed September 20th, 2022. https://consultation.quebec.ca/uploads/decidim/attachment/file/122/RevueLitterature_CaribouVF.pdf
- Morrison, J. C., Sechrest, W., Dinerstein, E., Wilcove, D. S., & Lamoreux, J. F. (2007). Persistence of large mammal faunas as indicators of global human impacts. *Journal of Mammalogy*, 88(6), 1363-1380.
- Munguía, M., Townsend Peterson, A., & Sánchez-Cordero, V. (2008). Dispersal limitation and geographical distributions of mammal species. *Journal of Biogeography*, 35(10), 1879-1887.
- Murray, D. L., Peers, M. J., Majchrzak, Y. N., Wehtje, M., Ferreira, C., Pickles, R. S., Row, J. R., & Thornton, D. H. (2017). Continental divide: Predicting climate-mediated fragmentation and biodiversity loss in the boreal forest. *PLoS One*, 12(5), e0176706.
- Nagy-Reis, M., Dickie, M., Calvert, A. M., Hebblewhite, M., Hervieux, D., Seip, D. R., Gilbert, S. L., Venter, O., DeMars, C., Boutin, S. & Serrouya, R. (2021). Habitat loss accelerates for the endangered woodland caribou in western Canada. *Conservation Science and Practice*, 3(7), e437.
- Neilson, E. W., Castillo-Ayala, C., Beckers, J. F., Johnson, C. A., St-Laurent, M. H., Mansuy, N., Price, D., Kelly, A., & Parisien, M. A. (2022). The direct and habitat-mediated influence of climate on the biogeography of boreal caribou in Canada. *Climate Change Ecology*, 3, 100052.
- Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhousseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Laginha Pinto Correia, D., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.W., & Purvis, A. (2015) Global effects of land use on local terrestrial biodiversity. *Nature*, 520, 45–50.

- Newton, E. J., Patterson, B. R., Anderson, M. L., Rodgers, A. R., Vander Vennen, L. M., & Fryxell, J. M. (2017). Compensatory selection for roads over natural linear features by wolves in northern Ontario: Implications for caribou conservation. *PloS one*, *12*(11), e0186525.
- NOAA (May 11th, 2022). *NOAA/CIRES/DOE 20th Century Reanalysis (V3)*. *NOAA Physical Sciences Laboratory*. Accessed July 8th, 2022. https://www.psl.noaa.gov/data/gridded/data.20thC_ReanV3.html
- Northrup, J. M., Anderson Jr, C. R., & Wittemyer, G. (2015). Quantifying spatial habitat loss from hydrocarbon development through assessing habitat selection patterns of mule deer. *Global Change Biology*, *21*(11), 3961-3970.
- Pandey, R., & Papeş, M. (2018). Changes in future potential distributions of apex predator and mesopredator mammals in North America. *Regional Environmental Change*, *18*(4), 1223-1233.
- Pardini, R., Nichols, E., & Püttker, T. (2017). Biodiversity response to habitat loss and fragmentation. *Encyclopedia of the Anthropocene*, *3*, 229-239.
- Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*(6918): 37-42.
- Parmesan, C. (2007). Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology*, *13*(9): 1860-1872.
- Parmesan, C., Morecroft, M.D., Trisurat, Y., Adrian, R., Anshari, G.Z., Arneith, A., Gao, Q., Gonzalez, P., Harris, R., Price, J., Stevens, N., and Talukdarr, G.H. (2022). Terrestrial and Freshwater Ecosystems and Their Services. In: *Climate Change 2022: Impacts, Adaptation and Vulnerability*. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Pörtner, H.-O., Roberts, D.C., Tignor, M., Poloczanska, E.S., Mintenbeck, K., Alegria, A., Craig, M., Langsdorf, S., Löschke, S., Möller, V., Okem, A., Rama, B. (eds.)]. Cambridge University Press, Cambridge, UK and New York, NY, USA, pp. 197–377.
- Parry, M., Parry, M. L., Canziani, O., Palutikof, J., Van der Linden, P., & Hanson, C. (Eds.). (2007). *Climate change 2007-impacts, adaptation and vulnerability: Working group II contribution to the fourth assessment report of the IPCC (Vol. 4)*. Cambridge University Press.
- Peterson, A. T., Papeş, M., & Soberón, J. (2015). Mechanistic and correlative models of ecological niches. *European Journal of Ecology*, *1*(2): 28-38.
- Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., Raven, P. H., Roberts, C. M., & Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, *344*(6187), 1246752.

- Plass, G. N. (1956). The carbon dioxide theory of climatic change. *Tellus*, 8(2): 140-154
- Potter, K. A., Arthur Woods, H., & Pincebourde, S. (2013). Microclimatic challenges in global change biology. *Global Change Biology*, 19(10), 2932-2939.
- Proctor, M. F., McLellan, B. N., Strobeck, C., & Barclay, R. M. (2005). Genetic analysis reveals demographic fragmentation of grizzly bears yielding vulnerably small populations. *Proceedings of the Royal Society B: Biological Sciences*, 272(1579), 2409-2416.
- Pyke, C. R. (2004). Habitat loss confounds climate change impacts. *Frontiers in Ecology and the Environment*, 2(4), 178-182.
- Raponi, M., Beresford, D.V., Schaefer, J.A., Thompson, I.D., Wiebe, P.A., Rodgers, A.R. & Fryxell, J.M. (2018). Biting flies and activity of caribou in the boreal forest. *Journal of Wildlife Management*, 82: 833-839.
- Ray, J. C. (2010). Conservation planning with large carnivores and ungulates in Eastern North America: learning from the past to plan for the future. In *Landscape-scale Conservation Planning* (pp. 167-204). Springer, Dordrecht.
- Riquelme, C., Estay, S. A., López, R., Pastore, H., Soto-Gamboa, M., & Corti, P. (2018). Protected areas' effectiveness under climate change: a latitudinal distribution projection of an endangered mountain ungulate along the Andes Range. *PeerJ*, 6, e5222.
- Rinnan, D. S., & Lawler, J. (2019). Climate-niche factor analysis: a spatial approach to quantifying species vulnerability to climate change. *Ecography*, 42(9), 1494-1503.
- Robertson, M. P., Peter, C. I., Villet, M. H., & Ripley, B. S. (2003). Comparing models for predicting species' potential distributions: a case study using correlative and mechanistic predictive modelling techniques. *Ecological Modelling*, 164(2-3), 153-167.
- Rosenzweig, C., Karoly, D., Vicarelli, M., Neofotis, P., Wu, Q., Casassa, G., Menzel, A., Root, T. L., Estrella, N., Seguin, B., Tryjanowski, P., Liu, C., Rawlins, S. & Imeson, A. (2008). Attributing physical and biological impacts to anthropogenic climate change. *Nature*, 453(7193): 353-357.
- Santini, L., Benítez-López, A., Maiorano, L., Čengić, M., & Huijbregts, M. A. (2021). Assessing the reliability of species distribution projections in climate change research. *Diversity and Distributions*, 27(6), 1035-1050.
- Santomauro, D., Johnson, C. J., & Fondahl, G. (2012). Historical-ecological evaluation of the long-term distribution of woodland caribou and moose in central British Columbia. *Ecosphere*, 3(5), 1-19.

- Scanes, C. G. (2018). Human activity and habitat loss: destruction, fragmentation, and degradation. In *Animals and Human Society* (pp. 451-482). Academic Press.
- Schaefer, J. A. (2003). Long-term range recession and the persistence of caribou in the taiga. *Conservation Biology*, *17*(5), 1435-1439.
- Schleuning, M., Neuschulz, E. L., Albrecht, J., Bender, I. M., Bowler, D. E., Dehling, D. M., Fritz, S. A., Hof, C., Mueller, T., Nowak, L., Sorensen, M. C., Böhning-Gaese, K., & Kissling, W. D. (2020). Trait-based assessments of climate-change impacts on interacting species. *Trends in Ecology & Evolution*, *35*(4), 319-328.
- Schloss, C. A., Nuñez, T. A., & Lawler, J. J. (2012). Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proceedings of the National Academy of Sciences*, *109*(22), 8606-8611.
- Schneider, M. F. (2001). Habitat loss, fragmentation and predator impact: spatial implications for prey conservation. *Journal of Applied Ecology*, *38*(4), 720-735.
- Schwartz, M. W. (2012). Using niche models with climate projections to inform conservation management decisions. *Biological Conservation*, *155*, 149-156.
- Serrouya, R., Seip, D. R., Hervieux, D., McLellan, B. N., McNay, R. S., Steenweg, R., Heard, D. C., Hebblewhite, M., Gillingham, M., & Boutin, S. (2019). Saving endangered species using adaptive management. *Proceedings of the National Academy of Sciences*, *116*(13), 6181-6186.
- Settele, J., R. Scholes, R. Betts, S. Bunn, P. Leadley, D. Nepstad, J.T. Overpeck, and M.A. Taboada, 2014: Terrestrial and inland water systems. In: Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Field, C.B., V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea, and L.L. White (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 271-359.
- Sharma, S., Couturier, S., & Cote, S. D. (2009). Impacts of climate change on the seasonal distribution of migratory caribou. *Global change biology*, *15*(10), 2549-2562.
- Sirami, C., Caplat, P., Popy, S., Clamens, A., Arlettaz, R., Jiguet, F., Brotons, L., & Martin, J. L. (2017). Impacts of global change on species distributions: obstacles and solutions to integrate climate and land use. *Global Ecology and Biogeography*, *26*(4), 385-394.
- Soberón, J., & Peterson, A. T. (2005). Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics*, *2*, 1-10.

- St-Gelais, S., & Gilbert, A. (Novembre 30, 2021). Le caribou forestier : le cœur et la raison. Retrieved from https://boisaco.com/wp-content/uploads/2021/11/Le-caribou-forestier-le-coeur-et-la-raison_30-11-2021.pdf
- St-Laurent, M. H., Boulanger, Y., Cyr, D., Manka, F., Drapeau, P., & Gauthier, S. (2022). Lowering the rate of timber harvesting to mitigate impacts of climate change on boreal caribou habitat quality in eastern Canada. *Science of The Total Environment*, 156244.
- Steltzer, H., & Post, E. (2009). Seasons and life cycles. *Science*, 324(5929): 886-887.
- Stewart, I. T., Cayan, D. R., & Dettinger, M. D. (2004). Changes in snowmelt runoff timing in western North America under a “business as usual” climate change scenario. *Climatic Change*, 62(1-3): 217-232.
- Stewart, F. E., Nowak, J. J., Micheletti, T., McIntire, E. J., Schmiegelow, F. K., & Cumming, S. G. (2020). Boreal caribou can coexist with natural but not industrial disturbances. *The Journal of Wildlife Management*, 84(8), 1435-1444.
- Stone, R. S., Dutton, E. G., Harris, J. M., & Longenecker, D. (2002). Earlier spring snowmelt in northern Alaska as an indicator of climate change. *Journal of Geophysical Research: Atmospheres*, 107(D10), ACL-10.
- Stralberg, D., Wang, X., Parisien, M. A., Robinne, F. N., Sólymos, P., Mahon, C. L., Nielsen, S. E., & Bayne, E. M. (2018). Wildfire-mediated vegetation change in boreal forests of Alberta, Canada. *Ecosphere*, 9(3), e02156.
- Sultaire, S. M., Pauli, J. N., Martin, K. J., Meyer, M. W., Notaro, M., & Zuckerberg, B. (2016). Climate change surpasses land-use change in the contracting range boundary of a winter-adapted mammal. *Proceedings of the Royal Society B: Biological Sciences*, 283(1827), 20153104.
- Suzuki, N., & Parker, K. L. (2016). Potential conflict between future development of natural resources and high-value wildlife habitats in boreal landscapes. *Biodiversity and Conservation*, 25(14), 3043-3073.
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, O. L. & Williams, S. E. (2004). Extinction risk from climate change. *Nature*, 427(6970), 145-148.
- Thuiller, W. (2007). Climate change and the ecologist. *Nature*, 448(7153), 550-552.
- Tilman, D., Clark, M., Williams, D. R., Kimmel, K., Polasky, S., & Packer, C. (2017). Future threats to biodiversity and pathways to their prevention. *Nature*, 546(7656), 73-81.

- Tingley, M. W., Monahan, W. B., Beissinger, S. R., & Moritz, C. (2009). Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences*, *106*(supplement_2), 19637-19643.
- Trenberth, K. E. (2011). Changes in precipitation with climate change. *Climate Research*, *47*(1-2), 123-138.
- Urban, M. C., Zarnetske, P. L., & Skelly, D. K. (2013). Moving forward: dispersal and species interactions determine biotic responses to climate change. *Annals of the New York Academy of Sciences*, *1297*(1), 44-60.
- Venier, L. A., Thompson, I. D., Fleming, R., Malcolm, J., Aubin, I., Trofymow, J. A., Langor, D., Sturrock, R., Patry, C., Outerbridge, R. O., Holmes, S. B., Haeussler, S., De Grandpré, L., Chen, H. Y. H., Bayne, E., Arsenault, A. & Brandt, J. P. (2014). Effects of natural resource development on the terrestrial biodiversity of Canadian boreal forests. *Environmental Reviews*, *22*(4), 457-490.
- Vincent, L. A., Zhang, X., Brown, R. D., Feng, Y., Mekis, E., Milewska, E. J., Wan, H., & Wang, X. L. (2015). Observed trends in Canada's climate and influence of low-frequency variability modes. *Journal of Climate*, *28*(11), 4545-4560.
- Vors, L. S., Schaefer, J. A., Pond, B. A., Rodgers, A. R., & Patterson, B. R. (2007). Woodland caribou extirpation and anthropogenic landscape disturbance in Ontario. *The Journal of Wildlife Management*, *71*(4), 1249-1256.
- Vors, L. S., & Boyce, M. S. (2009). Global declines of caribou and reindeer. *Global Change Biology*, *15*(11), 2626-2633.
- Walther, G. R. (2010). Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1549), 2019-2024.
- Warszawski, L., Friend, A., Ostberg, S., Frieler, K., Lucht, W., Schaphoff, S., Beerling, D., Cadule, P., Ciais, P., Clark, D. B., Kahana, R., Ito, A., Keribin, R., Kleidon, A., Lomas, M., Nishina, K., Pavlick, R., Rademacher, T. T., Buechner, M., Piontek, F., Schewe, J., Serdeczny, O., and Schellnhuber, H. J. (2013). A multi-model analysis of risk of ecosystem shifts under climate change. *Environmental Research Letters*, *8*(4), 044018.
- Weber, M. G., & Flannigan, M. D. (1997). Canadian boreal forest ecosystem structure and function in a changing climate: impact on fire regimes. *Environmental Reviews*, *5*(3-4): 145-166.
- Weladji, R. B., Holand, Ø., & Almøy, T. (2003). Use of climatic data to assess the effect of insect harassment on the autumn weight of reindeer (*Rangifer tarandus*) calves. *Journal of Zoology*, *260*(1), 79-85.

- Wiens, J. A., Stralberg, D., Jongsomjit, D., Howell, C. A., & Snyder, M. A. (2009). Niches, models, and climate change: assessing the assumptions and uncertainties. *Proceedings of the National Academy of Sciences*, *106*(supplement_2), 19729-19736.
- Williams, J. W., Kharouba, H. M., Veloz, S., Vellend, M., McLachlan, J., Liu, Z., Otto-Bliesner, B., & He, F. (2013). The ice age ecologist: testing methods for reserve prioritization during the last global warming. *Global Ecology and Biogeography*, *22*(3), 289-301.
- Witter, L. A., Johnson, C. J., Croft, B., Gunn, A., & Poirier, L. M. (2012). Gauging climate change effects at local scales: weather-based indices to monitor insect harassment in caribou. *Ecological Applications*, *22*(6), 1838-1851.
- Wittmer, H. U., Sinclair, A. R., & McLellan, B. N. (2005). The role of predation in the decline and extirpation of woodland caribou. *Oecologia*, *144*(2): 257-267.
- Wittmer, H. U., McLellan, B. N., Serrouya, R., & Apps, C. D. (2007). Changes in landscape composition influence the decline of a threatened woodland caribou population. *Journal of Animal Ecology*, *76*(3): 568-579.
- Wright, D. H. (1987). Estimating human effects on global extinction. *International Journal of Biometeorology*, *31*(4), 293-299.
- Zhou, L., Tucker, C. J., Kaufmann, R. K., Slayback, D., Shabanov, N. V., & Myneni, R. B. (2001). Variations in northern vegetation activity inferred from satellite data of vegetation index during 1981 to 1999. *Journal of Geophysical Research: Atmospheres*, *106*(D17): 20069-20083.
- Zhu, G., Papeş, M., Giam, X., Cho, S. H., & Armsworth, P. R. (2021). Are protected areas well-sited to support species in the future in a major climate refuge and corridor in the United States?. *Biological Conservation*, *255*, 108982.
- Zimmermann, N. E., Edwards Jr, T. C., Graham, C. H., Pearman, P. B., & Svenning, J. C. (2010). New trends in species distribution modelling. *Ecography*, *33*(6), 985-989.

